



Leaf litter arthropods show little response to structural retention in a Central European forest

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Received: 1 February 2023 / Revised: 18 June 2023 / Accepted: 26 June 2023 / Published online: 5 July 2023
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Abstract

Decomposition of leaf litter is a central process of energy and nutrient cycling in forests, in which arthropods hold important roles. Thus, safeguarding the diversity of organisms including arthropods is increasingly being considered in contemporary forestry, not least to facilitate continued ecosystem functioning. Retention forestry tries to achieve biodiversity conservation by preservation of tree structural elements such as deadwood and tree microhabitats to provide more heterogeneous habitat. Leaf litter arthropods are, however, only indirectly connected with tree structure, which raises the question if and how the currently practised retention forestry influences the leaf litter arthropod community. As the leaf litter arthropod community includes a very diverse range of taxa that is challenging to identify morphologically, we sampled environmental DNA from leaf litter on 66 plots in the Black Forest in southern Germany that were distributed over gradients of forest and landscape features and differed in forest management intensity. We found that the richness of operational taxonomic units, a surrogate for species, was not related to forest structure but tended to increase with recent harvest intensity (which did not exceed a medium harvest intensity on our plots). Community composition was related to the share of coniferous trees present on a plot, and to a lesser extent to elevation and leaf litter coverage. Our results indicate that the leaf litter arthropod community is not responsive towards different degrees of forest structural changes introduced by management as long as the forest type is retained.

Keywords eDNA · Leaf litter · Retention forestry · Arthropods · Habitat heterogeneity · Harvest intensity

Communicated by Akihiro Nakamura.

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Introduction

Decomposition of leaf litter and woody debris holds a central position in the nutrient cycling of terrestrial ecosystems (Gessner et al. 2010; Reichle 1977). For many organisms above and belowground, the decomposition of organic material is an important energy input, which fuels a network of complex interactions (Hättenschwiler et al. 2005). Arthropods are central in this interaction network, for example as decomposers and predators (De Smedt et al. 2019; Hartshorn 2020). Complex networks such as the nutrient cycling network are the basis for the functioning of ecosystems and in order to maintain these functions, biodiversity conservation is being increasingly considered in forest management (Gustafsson et al. 2020; Storch et al. 2020). One integrative conservation approach is retention forestry, which aims to preserve structural elements such as deadwood and habitat trees (Bauhus et al. 2009) to provide and improve habitat continuity and connectivity for forest organisms (Gustafsson et al. 2012). According to the habitat-heterogeneity hypothesis (MacArthur and MacArthur 1961), the availability of more diverse habitat leads to a higher species diversity. Therefore, by adding and preserving different habitats than the ones available in a structurally impoverished commercial forest, the retention of structural heterogeneity can potentially promote greater species diversity in forests (*sensu* MacArthur and MacArthur 1961). For arthropods, positive responses of abundance and richness to structural elements have been observed for e.g. deadwood retention/addition (Herrera-Alvarez et al. 2020; Rappa et al. 2023; Seibold et al. 2016; Ulyshen and Hanula 2009) and multi-layered vegetation (Knuff et al. 2020; Rappa et al. 2022).

However, even with structural retention measures in place, many central European forests, including our study system in the Black Forest in southern Germany, have a disproportionately high share of coniferous dominated forest stands at low elevations (below 1000 m a.s.l.) where deciduous or mixed forest with European beech (*Fagus sylvatica* L.) is the potential natural vegetation (Röder et al. 2010; Storch et al. 2020). The plantations of economically valuable conifers like Norway spruce (*Picea abies* L.) often have an overall low tree species diversity, are poor in structure and lack natural disturbance processes (Felton et al. 2020; Paillet et al. 2009). Therefore, managed spruce forests typically do not provide heterogeneous habitat. These structurally poor Norway spruce dominated forests have been observed to have decreased abundance of predominantly herbivorous insect taxa (Knuff et al. 2020; Leidinger et al. 2021) and ground-dwelling beetles (Lange et al. 2014) in comparison to stands with higher shares of broadleaf tree species. In contrast, the diversity of leaf-litter ants increases with tree diversity (Skarbek et al. 2020) and the diversity of the invertebrate community reliant on coarse woody debris increases with mixed canopy type (Herrera-Alvarez et al. 2020). Furthermore, tree composition also directly determines the composition of the leaf litter and therefore the inhabiting arthropod community (Barberena-Arias and Aide 2003). Additionally, to forest type and tree composition, which influence the leaf litter community directly via leaf litter production, structural retention elements like lying deadwood are assumed to influence the leaf litter arthropod community indirectly. This indirect influence of structural retention elements is facilitated by their provision of microhabitats, high amounts of key nutrients in their surrounding (Ulyshen and Hanula 2009) or simply by allowing for leaf litter accumulation (Seibold et al. 2016). Considering the central role of leaf litter arthropods as detritivores in forests, it is important to investigate if the practiced structural retention measures are effective to preserve this community or if

conservation practices need to focus on environmental variables which directly influence the leaf litter.

The leaf litter arthropod community includes a very diverse array of taxa, many of which are challenging to identify morphologically, especially in the mesofauna (Dopheide et al. 2019; Yang et al. 2014). Also, due to historically lower sampling effort in the soil and leaf litter compared to other substrates (e.g. deadwood), a sizeable proportion of leaf litter arthropods is not yet formally described. Thus, metabarcoding is increasingly being used to identify arthropods from the leaf litter (Zinger et al. 2019), either by directly barcoding specimens or by barcoding the DNA traces they leave in the environment (environmental DNA, from now on referred to as eDNA). Metabarcoding is a high-throughput multitaxon identification method, based on sequencing of distinct DNA regions called barcodes (Taberlet et al. 2012). Other than traditional DNA barcoding, which targets single specimens (Valentini et al. 2009), metabarcoding can be used to simultaneously identify the bulk of taxa from mixed samples like insect trap collections and environmental DNA samples. Although the species pool captured with eDNA may slightly deviate from classical collection methods (Dopheide et al. 2019; Young and Hebert 2022) the observed richness and diversity patterns are highly congruent (Yang et al. 2014; Young and Hebert 2022), which makes eDNA metabarcoding a suitable method to investigate responses of the arthropod community to changes in the environment.

Here we used eDNA of leaf litter to investigate leaf litter arthropod communities on 66 plots with differing tree composition and management intensity. We expected an increase in arthropod richness with increasing habitat heterogeneity provided by structural retention elements such as standing and lying deadwood (Herrera-Alvarez et al. 2020; Seibold et al. 2016; Ulyshen and Hanula 2009) related to higher resource and habitat heterogeneity. Additionally, we expected a higher richness of arthropods in broadleaf forests than in coniferous forests (Knuff et al. 2020; Lange et al. 2014). Finally, we expected the community composition of the leaf litter arthropods to vary with forest type and amount of structural retention.

Materials and methods

Study area

This study was conducted in the framework of the ‘Conservation of forest biodiversity in multiple-use landscapes of Central Europe’ (ConFoBi) project (Storch et al. 2020). The ConFoBi project aims towards a comprehensive analysis of the potential of retention forestry to support different components of biodiversity in the southern Black Forest (Baden-Württemberg, Germany), as a model for temperate multiple-use forests in central Europe (Storch et al. 2020). The study area is a continuous cover forest ranging over 5000 km² with 75% forest cover. Since 2010, forestry is practiced under the guidelines of a state-wide retention program that aims to harmonise practical implementation of conservation law and economic use. In 2017, 135 1 ha plots in state-owned, managed forests were selected, which have been excluded from management for the project duration (except for the removal of bark beetle infested trees). Plot selection was originally based on two gradients: (1) the number of snags detected in aerial images, ranging from zero to more than 20 snags per ha; (2) the forest cover of the surrounding landscape (circular, 2500 ha), comprising a gradi-

ent from low (3.0%) to high (92.2%) landscape-level forest cover. The minimum distance between neighbouring plot centres is 750 m. The plots are distributed at elevations between 400 and 1300 m a.s.l., and vary in slope from 1 to 34°. Plots do not contain permanent bodies of water and are not crossed by forest roads. The study area is dominated by coniferous forests with planted Norway spruce (*Picea abies L.*) and silver fir (*Abies alba Mill*) being the primary tree species on the majority of the plots and European beech (*Fagus sylvatica L.*) being the most common deciduous species. Other tree species tend to occur only with few individuals leading to an overall low tree richness in the study area.

Sample collection and processing

Field sampling was done in the last week of August and first two weeks of September 2021 on 66 (of the 135) plots that were selected to represent the widest possible gradient of share of conifers (calculated based on the number of coniferous trees from forest inventory data of all trees inside the plots with DBH > 7 cm), canopy closure (percentage of light not reaching 3 m above ground level, derived from UAV data, Frey et al. 2020) and volume of coarse lying deadwood (calculated from length and diameter of deadwood sampled along a V-transect during a full forest inventory in 2017). The chosen plots included strictly protected forest with no management and forest with different levels of retention forestry management. These retention forestry plots varied from structurally rich forest plots to monocultures, of which the later apply only the single tree harvest concept of the retention framework.

Three leaf litter samples were collected at each plot centre and 20 m NE and SW from plot centres. For each sample, we collected leaf litter from a 30×30 cm area that was sifted (1 cm mesh size) into a bucket to remove coarse debris. Sifted litter was thoroughly mixed. We then filled a 50 ml centrifuge tube with the sifting to the 50 ml mark and discarded what remained. The tubes were immediately filled with 100% Ethanol until all of the litter was immersed and sealed with parafilm (Carl Roth GmbH+Co. KG, Karlsruhe, Germany). We kept samples in a cool box until transferring them to a -20 °C freezer at the end of each day. To avoid cross contamination, different buckets and sieves were used for each plot and were always sterilized overnight in 2% chlorine-based bleach after use. The samples were processed for eDNA metabarcoding by AIM – Advanced Identification Methods GmbH (Leipzig, Germany). DNA extraction was done with 5 ml lysis volume and a 313 bp cytochrome c oxidase I (COI) fragment (Leray et al. 2013) was PCR amplified for sequencing on an Illumina MiSeq System (2×300 bp). The sequences were processed in the AIMs bioinformatic pipeline (as described in Hausmann et al. 2020). In brief, paired-end merging was performed using usearch v11.0.667 and primers were trimmed with cutadapt 1.18 with Python 2.7.15. Sequences were quality filtered with vsearch 2.9.1 to have a minimum length of 300 and a maximum of one expected error. Additionally, data was dereplicated by keeping only unique (COI), non-singleton sequences, to remove unspecific sequences and sequencing errors. Vsearch 2.9.1 was then used for clustering into operational taxonomic units (OTUs) with 98% similarity and chimera detection. The final set of sequences was blasted against the commonly used reference databases BOLD and NCBI.

Data cleaning

Sub-samples were sequenced separately and subsequently pooled, yielding one list of OTUs per plot. Plot-level pooling of sub-samples was done to create comprehensive OTU lists, since sub-samples had little overlap in identified taxa. To reduce the impact of unspecific and replicate identifications, all OTUs which did not correspond to arthropods and were not identified at least to family level were discarded from the dataset and replicate species identifications were merged. Leaf litter does not only contain DNA traces from those species functionally associated with it, but acts as a sink accumulating DNA from other arthropods in the surrounding area. We therefore focused only on taxonomic orders and families which are confirmed to commonly be found in leaf litter according to the relevant literature (e.g. Dunger 2008; Freude et al. 2009; Greenberg and McGrane 1996; Hartshorn 2020; Karg 1994; Ulyshen et al. 2011; Westheide and Rieger 2013; Zaiatz et al. 2017). While we potentially lost some leaf litter relevant OTUs during this filtering step, the removal of unspecific OTUs from other forest strata allows more accurate examination of the relationships between the leaf litter community and environmental variables. Full tables of the included and excluded taxa are available in Supplementary Data 1. To evaluate the influence of constraining the data to leaf litter-associated taxa, all subsequent analyses were also calculated with the unfiltered data (Supplementary Data 2 and 3). As DNA is deposited very locally in the environment and distribution is limited in terrestrial systems, eDNA metabarcoding is susceptible to false negatives (Ficetola et al. 2015; Valentin et al. 2021). We accounted for this by calculating jackknife1 estimators and comparing species accumulation curves, to assess sampling completeness. Based on the results we decided to include only OTUs which were detected on at least two study plots in the analysis.

Environmental variables

A suite of environmental variables was chosen to characterize the study plots. Average elevation (m a.s.l.) was derived from digital terrain modelling by the State Agency of spatial information and rural development of Baden-Württemberg (Landesamt für Geoinformation und Landentwicklung, lgl-bw.de, 2005). Cumulative basal area of all living trees >7 cm DBH and percentage of coniferous tree species were calculated from data gathered during full forest inventories in 2017. Average light availability was calculated using 18 hemispherical photographs taken on each plot using the device Solariscope SOL300 in the height of the apparent herb layer vegetation (Ing.-Büro Behling, Wedemark). The species richness of the herb layer on the study plots was calculated from data collected at the same 18 points on the study plots as the Solariscope pictures were taken. All vascular plants up to a height of 150 cm were identified and only non-woody species were included in the richness of herbs. The average leaf litter coverage was estimated as the percentage of coverage of the three 30×30 cm sampling locations prior to the collection of the leaf litter. The three leaf litter coverage values for each study plot were averaged. The Stand Structural Complexity Index (SSCI) for each plot was taken from Frey et al. (2020). The SSCI is calculated from mean fractal dimension and effective number of layers derived from terrestrial laser scanning data at the northwest southeast and centre of the plot and is used as a measure of spatial complexity in 3D space (Ehbrecht et al. 2017; Frey et al. 2020). We use SSCI to comprehensively quantify forest structure across vegetation layers, which can provide heterogeneous

resources and influence plot microclimate (Ehbrecht et al. 2021). Lying and standing deadwood volumes were calculated from the 2017 forest inventory with deadwood sampling conducted along V-transects on each plot, measuring all deadwood structures > 7 cm DBH and minimum height of 1.3 m at the upper slope. These variables were chosen because of their relation to structural retention approaches. Additionally, harvest activities can create local forest canopy gaps and disturb the ground, which may both have cascading effects on overall species richness and community composition. To account for the influence of harvesting, we include the harvest intensity index (I_{harv}, sensu Kahl and Bauhus 2014) as an environmental variable. We calculated the harvest intensity index as the ratio of harvested volume to the sum of harvested and standing volume. As the decaying of stumps can vary strongly based on local conditions in e.g. moisture or temperature we only included stumps with saw cuts of decay stage 1, 2 and 3 (stumps of decay stage 1: freshly dead, 2: partial barks loss but >50% remaining and 3: <50% bark remaining, Renvall 1995) of the commonly used decay stages from 1 (least decayed) to 6 (almost completely decayed) by Renvall 1995, to only consider harvest activities of recent years. Finally, the percentage of forest cover within 5 km² (500 ha/5sqkm moving window on Landsat land cover data by Landesanstalt für Umwelt Baden-Württemberg LUBW 2010) was included to account for forest connectivity and habitat availability on a landscape scale. An overview of the minimum, maximum and average values of the tested and considered variables is available in Supplementary Data 4. Other variables that had originally been considered but were finally not used due to potential collinearity (i.e. pairwise Kendall correlation > 0.6) were leaf litter depth (0.62 correlation with leaf litter coverage) and soil moisture in September 2019 (German Meteorological Service Climate Data Center: Monthly grids of soil moisture under grass and sandy loam, version 0.x, 11.03.2022; 0.78 correlation with elevation).

Statistical analysis

The relationship between OTU richness and environmental variables was analysed using a generalized linear model (GLM) with a negative binomial distribution. The multiple model included the variables elevation, basal area of living trees, percentage of coniferous trees, average light, species richness of the herb layer, leaf litter coverage, SSCI, volume of lying deadwood, volume of standing deadwood, harvest intensity index and the forest cover within 5 km² as fixed effects and the richness of leaf litter arthropod OTUs with more than two detections as response variable. Additionally, OTU richness of all arthropod species detected was tested using a negative binomial GLM with the same environmental variables (Supplementary Data 2). Interacting effects were not tested.

All fixed effects were scaled (mean=0, SD=1) and if necessary log transformed (lying deadwood volume) or square-root transformed (basal area, standing deadwood volume, average light, harvest intensity index) to increase normality and homogeneity. We tested for spatial autocorrelation by calculating Moran's I with the DHARMA (Hartig 2016) package, permuting model residuals with the latitude and longitude of the plots.

As richness and community composition may respond differently to environmental variables, we also analysed community composition. The read data of the OTUs was transformed into a presence-absence matrix, as true abundances are difficult to infer with eDNA metabarcoding, e.g. due to uneven primer fit or DNA quality and amount. To assess the influence of environmental variables on community composition, we used non-metric mul-

tidimensional scaling (NMDS, Jaccard dissimilarity, Dimensions=3, Iterations=100). With permutational multivariate analysis of variance (PERMANOVA, Permutations=10,000, type II sums of squares) we tested for the relationship between composition and the same environmental variables that were assessed in the richness analyses, all in a single multiple model. We also performed a post-hoc correlation test (Permutations=10,000) between the scores of the first two NMDS axes and the environmental variables. The NMDS and PERMANOVA were also calculated for the unfiltered arthropod OTU dataset (Supplementary Data 3). For better visualisation, we categorized the study plots into broadleaf plots (percentage coniferous < 0.33), coniferous plots (percentage coniferous > 0.66) and mixed plots (percentage coniferous 0.34–0.66). We did not conduct analyses for individual arthropod orders, as it would have been beyond the scope of the study. All statistical analyses were performed with R version 4.1.1, using the vegan package (Oksanen et al. 2020) for all multivariate procedures, ggplot2 (Wickham 2016), psych (Revelle 2013), viridis (Garnier et al. 2021), tidyverse (Wickham et al. 2019) and glmmTMB (Brooks et al. 2017).

Results

In total, 13.9 million paired-end reads (27.86 million singles) were obtained from the 198 (66 plots x 3 samples) leaf litter samples. After quality filtering, 8.9 million sequences were retained of which 6.2 million were unique. Following dereplication, 473,193 unique, non-singleton sequences were clustered, resulting in 27,306 OTUs. Of these, 17,722 OTUs remained after de novo chimera detection, with 12,655 finding matches in the databases. Of these matches 2280 were assigned to arthropods, 1354 passing the quality filtering for >97% similarity, leaving 1280 OTUs after removal of duplicate species (Table 1). Of these remaining OTUs 332 were classified as leaf litter taxa (Table 1; Fig. 1).

The species accumulation curves and jackknife1 estimators showed that sampling efficiency for the total leaf litter OTUs was at 64% (332 OTUs detected of estimated jackknife1 = 514 ± 50 SE; Fig. 2). If only OTUs that were detected on a minimum of two or three plots are considered, 100% of the expected species, based on the jackknife1 estimator, were sampled.

Leaf litter arthropod OTU richness increased with increasing harvest intensity index (estimate = 0.195 ± 0.090 SE, $p = 0.031$, Table 2). However, visualization of the data and model prediction indicated that this statistical relationship may be driven by a single plot with the highest harvesting intensity (Fig. 3). Upon removal of this plot from the dataset the effect of harvesting intensity was no longer significant (estimate = 0.140 ± 0.089 SE, $p = 0.114$). No other environmental variable was related to OTU richness. There was no indication of spatial autocorrelation (Moran's I, $p = 0.263$). Statistical results for the unfiltered arthropod richness data were similar with, no environmental variable showing a significant relationship (Supplementary Data 2).

The composition of leaf litter arthropods among plots was mainly related to the share of coniferous trees (PERMANOVA, $R^2 = 0.035$, $p < 0.001$, Table 3). This relationship (Fig. 4)

Table 1 Summary of taxonomic distribution of all arthropod OTUs and for leaf litter specific OTUs

	OTUs	Class	Order	Family	Genus	Species
Arthropod OTUs	1280	6	29	238	658	724
Leaf Litter OTUs	332	6	25	55	184	234

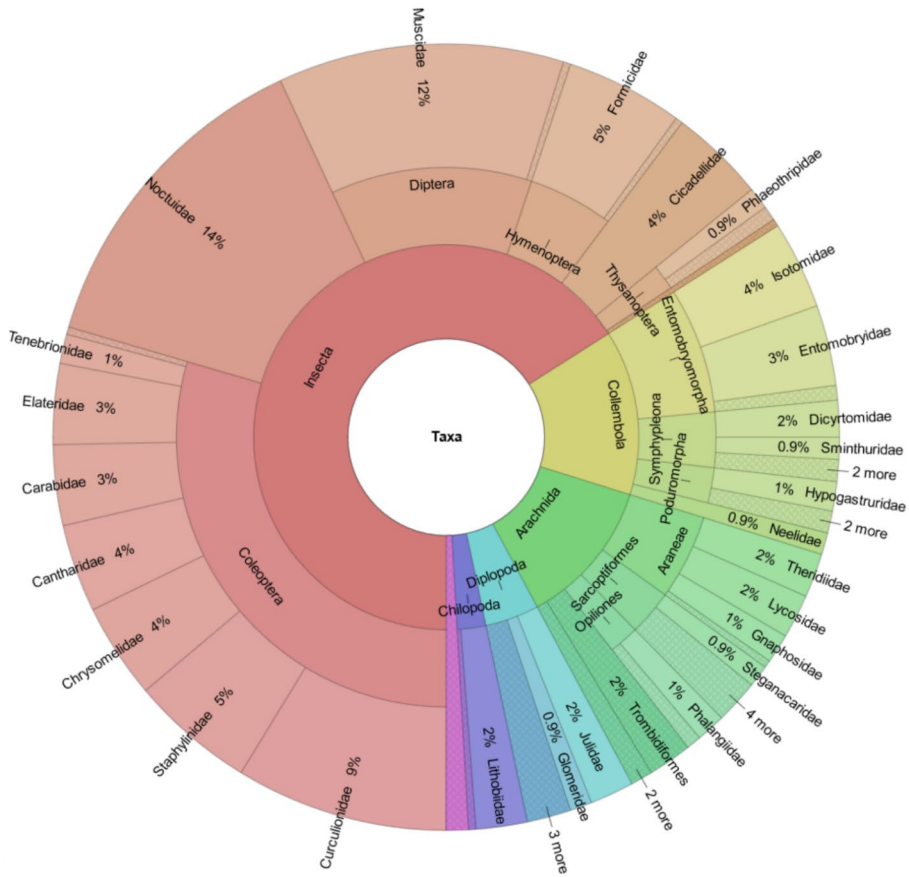


Fig. 1 Overview of taxonomic distribution of leaf litter specific arthropod OTUs detected. From the inside to the outside within the three circular sections the shares of detected taxonomic classes, orders and families in the whole leaf litter arthropod dataset are shown. 66% of the OTUs were insects, 14% Collembola, 12% Arachnida, 5% Diplopoda, 2% Chilopoda and 1% Isopoda. These higher-level taxa were made up by 55 families and 184 genera

was also apparent in the post hoc correlation of the first two NMDS axes (envfit, $R^2=0.353$, $p<0.001$). Additionally, community composition changed with elevation (PERMANOVA, $R^2=0.024$, $p=0.021$, Table 3) and with the amount of leaf litter coverage (PERMANOVA, $R^2=0.025$, $p=0.018$, Table 3). Furthermore, the species richness of herbs showed a tendency to influence the community composition but was not significant (PERMANOVA, $R^2=0.021$, $p=0.065$, Table 3). Taken together, about 18.3% of the variation observed in the community composition was explained by the PERMANOVA.

Fig. 2 Species accumulation curve for all leaf litter arthropod OTUs detected (black) and for leaf litter arthropod OTUs detected at least two (green) or three times (blue). The shaded polygons mark the 95% confidence interval of the species accumulation curve. The horizontal dashed lines indicate the expected number of OTUs based on the jackknife1 estimator (\pm SE)

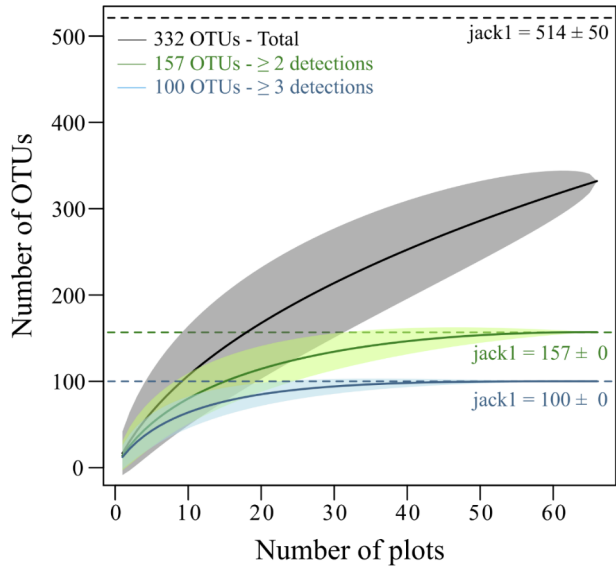


Table 2 Summary statistics of the negative binomial GLM for the OTU richness of leaf litter arthropods detected on a minimum of two plots and the selected environmental variables

Environmental variable	Estimate	Std. Error	z-value	p-value
Average elevation	-0.046	0.079	-0.59	0.556
Average leaf litter coverage	-0.047	0.097	-0.49	0.626
Average light (sqrt)	0.011	0.103	0.10	0.917
Basal area (sqrt)	0.055	0.092	0.60	0.548
Forest cover 5 km ²	0.059	0.068	0.85	0.394
Harvesting intensity (sqrt)	0.195	0.090	2.16	0.031
Herb richness	0.109	0.074	1.47	0.142
Lying deadwood (log)	-0.111	0.087	-1.28	0.201
Percentage coniferous	-0.097	0.083	-1.16	0.246
SSCI	0.060	0.078	0.76	0.445
Standing deadwood (sqrt)	-0.048	0.103	-0.46	0.644

The correct rows are marked in bold

Discussion

In this study we used eDNA metabarcoding to sample leaf litter arthropod assemblages on 66 study plots in the southern part of the temperate central European Black Forest. We found that the composition of the arthropod assemblages is influenced by the share of coniferous trees on a research plot, but also that species richness is only weakly associated with environmental and management variables.

Fig. 3 The richness of OTUs of leaf litter arthropods detected on a minimum of two plots increased with the harvest intensity index. Shown is the prediction of a negative binomial GLM (solid line) with 95% CI (dashed lines). The plot with the highest harvest intensity index value is marked as a red triangle

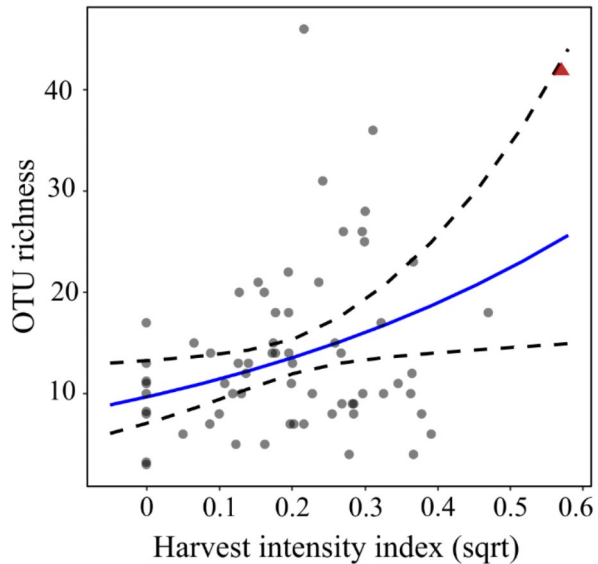


Table 3 Summary of the results from PERMANOVA (based on Jaccard dissimilarity) testing the influence of environmental variables on the composition of leaf litter arthropod OTUs that were detected on a minimum of two plots

Environmental variable	R ²	F	p-value
Average elevation	0.024	1.640	0.021
Average leaf litter coverage	0.025	1.684	0.016
Average light (sqrt)	0.008	0.517	0.973
Basal area (sqrt)	0.006	0.441	0.989
Forest cover 5 km ²	0.019	1.265	0.173
Harvesting intensity (sqrt)	0.009	0.583	0.945
Herb Richness	0.021	1.457	0.065
Lying deadwood (log)	0.013	0.854	0.681
Percentage coniferous	0.035	2.397	<0.001
SSCI	0.011	0.779	0.775
Standing deadwood (sqrt)	0.012	0.835	0.707

The correct rows are marked in bold

OTU richness and structural retention

Increasing forest structural heterogeneity, for example by adding or retaining deadwood, has been observed to increase the abundance of litter-dwelling arthropods (Ulyshen and Hanula 2009) and also arthropods in general (Rappa et al. 2023; Seibold et al. 2016). These observations are in accord with the habitat-heterogeneity hypothesis, which predicts species diversity to increase with increasing habitat heterogeneity (MacArthur and MacArthur 1961).

Contrary to our expectation of a similar positive influence of forest structure on leaf litter arthropods, the species richness of leaf litter arthropods did not increase with higher structural complexity or deadwood amounts that are targeted by retention measures. However, there was a trend towards a weakly positive influence of harvest intensity on species richness. Several ecological mechanisms may explain a higher arthropod richness on plots that had received higher biomass removal and thus more disturbance in the past. The removal of

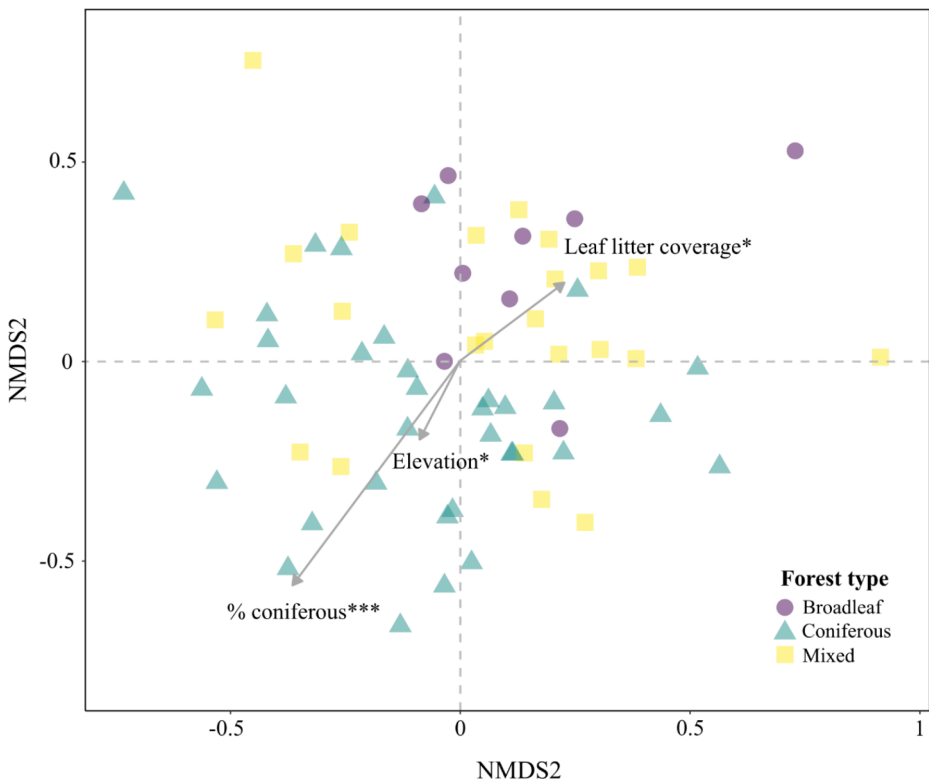


Fig. 4 NMDS ordination of leaf litter arthropod OTU composition (based on Jaccard dissimilarity) detected on a minimum of two plots (stress=0.22). The leaf litter arthropod community most strongly differed between broadleaf and coniferous-dominated plots. The clustering of the broadleaf-dominated plots aligned approximately with high leaf litter coverage in the post hoc correlation of the ordination axes with environmental variables. The OTU composition of plots with higher shares of conifers aligned with increasing elevation. The mixed forest plots were distributed between the coniferous and broadleaf-dominated plots. All environmental variables shown in this figure are significant in the PERMANOVA (p-value thresholds *= <0.05 , ***= <0.001)

single trees creates canopy gaps leading to areas with more direct light reaching the ground, which subsequently results in decreased moisture and increased understory vegetation cover (Tinya and Ódor 2016). Such altered conditions in the gap areas provide different habitat and microclimate than forest with closed canopy, and can increase the species richness and diversity of soil meso- and macrofauna (Huang et al. 2020; Perry et al. 2018). This increase would be expected to be most pronounced at an intermediate occurrence level of canopy gaps, according to the intermediate disturbance hypothesis (Dial and Roughgarden 1998). Additionally, recent harvest activity also leaves fresh deadwood, which provides resources for species specialized on early decay stages (Bouget 2005). However, the direct light measurements on the study plots did not show an influence on the OTU richness of leaf litter arthropods. Also, no correlation of average light with harvest intensity could be found, which would be expected if harvest intensity represents a higher occurrence of canopy gaps. This indicates, that potentially several environmental influences created by harvesting combined influence the leaf litter arthropod richness, rather than canopy gaps alone. This could

indicate that only a combination of ecological mechanisms represented by the harvest intensity index influences the OTU richness of leaf litter arthropods. Moreover, it could also indicate that the harvest intensity index, because it is calculated based on individually removed trees, represents effects on a smaller scale than the overall light measure on a study plot. While we caution against generalisation due to the statistical influence of a single plot with high harvesting intensity in comparison to most other plots, the relationship between harvest intensity and leaf litter arthropod species richness could potentially indicate that soil and litter fauna may benefit from moderate harvesting. However, as even the highest recent harvest intensity on our plots is only in the range of an intermediate disturbance (highest ratio of harvested volume to living volume=0.33), it is possible that our results only apply to the first half of the intermediate disturbance principle and that species richness will decrease if disturbance becomes too high (*sensu* Dial and Roughgarden 1998). Additionally, it should be noted that when tested with the unfiltered arthropod data, OTU richness and harvest intensity were not related, which indicates that other arthropod groups may respond differently to harvesting than leaf litter arthropods. To verify the influence of harvesting intensity on leaf litter arthropod richness and arthropod richness in general, further testing using plots representing a wider gradient of harvesting intensity or experiments where harvesting is manipulated would be necessary.

Nevertheless, the leaf litter arthropod species richness in our data was largely independent of the environment. Similar results have been found by Pollierer et al. (2021), in another German forest (Swabian Alp) with comparable tree composition, where forest type and management strongly influenced leaf litter without effects on arthropod biomass. Likewise, a study comparing litter produced by only deciduous trees in a German forest observed abundance, richness and composition of oribatid mites to be unaffected by species and identity of leaf litter (Bluhm et al. 2019). Further examples in forests of different climate type are available (e.g. Ghana, Belshaw and Bolton 1993), which indicate that the potential resistance of leaf litter arthropods is not restricted to temperate forests. This resistance of leaf litter arthropods to disturbance introduced by forest management may be explained by the leaf litter community benefiting from the presence of structural elements like deadwood (Seibold et al. 2016; Ulyshen and Hanula 2009) but not being directly reliant on them. Additionally, by long term annual input of consistent leaf litter type the available leaf litter composition and consequential soil chemistry provides continuity to this habitat, which may delay the effects of changes for example in the tree composition (Scheu et al. 2003). As most leaf litter arthropods do not seem to be specialised on litter of particular tree species (Donoso et al. 2010; Skarbek et al. 2020) and do not seem to benefit from tree diversity but rather the functional identity of leaf litter (Eissfeller et al. 2013; Raymond-Léonard et al. 2018; Sánchez-Galindo et al. 2021), change of tree composition may generally affect leaf litter arthropod species richness little as long as the forest type is not changed drastically. Consequently, the low tree species diversity in the Black Forest might not influence the overall leaf litter arthropod richness as long as the annual litter production is continuous.

It should be noted, that our results may change based on the scale on which the management and environmental variables are resolved (*sensu* Jackson and Fahrig 2015). Evidence for the scale-dependency of leaf litter arthropod species richness and diversity is mixed, with a prevalence of small scale (e.g. Seibold et al. 2016) but also larger scale relations reported (e.g. Skarbek et al. 2020). In our study, the plot scale was chosen to investigate if responses of the leaf litter arthropod community can be observed at scales that are appli-

cable in forest management. This is also why the three different samples taken per plot were homogenised to a single composite sample. An investigation at a finer scale requiring more samples to cover the whole plot area may nevertheless show responses of the leaf litter community to variables, which have been without a statistical effect in our study. Similarly, as eDNA metabarcoding does not provide abundance data, it is also possible that leaf litter richness does not respond to the tested variables in our system, while abundance would show a response (e.g. Binkenstein et al. 2018; Müller et al. 2017).

Leaf litter arthropod composition and coniferous tree share

The composition of the leaf litter arthropod OTUs differed based on the forest type, with the strongest separation between broadleaf-dominated plots and coniferous-dominated plots. The plots with approximately evenly mixed forest ordinated between the broadleaf and coniferous plots in the NMDS. This difference in community composition depending on the percentage of coniferous trees was expected, as conifers and broadleaved trees, and the resources they provide to other organisms i.e. the leaf litter community, are fundamentally different (Díaz et al. 2016). Most arthropod species cannot utilize both tree types, for example because of the resin content of coniferous wood and litter (Brändle and Brandl 2006; Bussler et al. 2011). Consequently, a small share of coniferous trees in a plot can already change the composition of the arthropod assemblage. Additionally, needles of spruce, which is the most prevalent conifer in the Black Forest, form thicker organic layers than leaves from beech and other broadleaved trees, as the decomposition process is slowed by the acidification of the soil and because spruce needles are less favourable resources for microorganisms (Albers 2004; Scheu et al. 2003). The density characteristics and moisture therefore differ between litter consisting of needles or broadleaves (Scheu et al. 2003), which is supported in our data by the leaf litter coverage being approximately opposite to the percentage of coniferous trees in the ordination. Consequently, the arthropod communities in leaf litter with varying contributions from conifers can be expected to be composed differently based on the species' ability to utilize the specific local conditions created by the leaf litter type. In Central Europe a higher share of conifers is under natural conditions associated with higher elevation, which supports the separation based on the dominant tree type in our data. Influence of elevation on soil microarthropods have, however, also been observed in tropical montane rainforests (Marian et al. 2018), indicating that associated environmental variables such as temperature and moisture also have an effect on their own (Binkenstein et al. 2018), additionally to the coniferous share.

Conclusion

Like many temperate European forests, the Black Forest has a long history of management and is in its present state not comparable with its potential natural forest type. The overall small variation in the forest structure, with only few exceptions in protected areas, and unavailability of control areas with old growth forest makes it difficult to disentangle how leaf litter arthropods respond to retention measures. We found that the community composition of leaf litter arthropods differs based on the share of coniferous trees on plots, but that species richness is overall largely not influenced by environmental and management vari-

ables. These results may indicate that leaf litter arthropods are not responsive towards different degrees of forest structural changes introduced by management as long as the forest type is retained. However, to confirm this finding, a subsequent analysis might test associations between leaf litter organisms and variation in environmental on smaller scales to account for neighbourhood associations and microclimatic effects and include finer-scale variation in soil which might drive leaf litter arthropod richness and composition.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10531-023-02677-w>.

Acknowledgements This study was funded by the German Research Foundation within the Research Training Group ConFoBi (grant number GRK 2123/2). We thank the ConFoBi group for providing infrastructure and are most grateful to Forst Baden-Württemberg (ForstBW) for enabling and facilitating field work. We thank AIM methods and especially Jérôme Morinière for valuable insights and suggestions at various stages of this study. Two anonymous reviewers provided helpful comments to an earlier version of the manuscript.

Author contributions L.S.R., M.S. and G.S. conceptualized the study. L.S.R. conducted the fieldwork and sample processing. L.S.R., S.K. and M.S. analyzed the data. S.K., N.R. and J.F. provided data. L.S.R. wrote the main manuscript text and prepared figures. All authors revised previous drafts.

Funding Open Access funding enabled and organized by Projekt DEAL. This study was funded by the German Research Foundation within the Research Training Group ConFoBi (grant number GRK 2123/2).

Data Availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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