

Soil mineral nitrogen content is increased by soil mesofauna and nematodes – a meta-analysis

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Abstract

The world's soils maintain various ecosystem processes and functions, such as the provision of nitrogen, which is the basis for plant growth. Microorganisms are the key actors in nitrogen transformation processes, but soil fauna can also affect nitrogen cycling, e.g. through food-web interactions or by changing the soil habitat. Several individual studies report increases of soil nitrogen due to soil meso- or microfaunal effects. Recent meta-analyses have shown that nitrogen content and fertility of soils is substantially increased by earthworms. However, we still lack a quantitative synthesis of the influence of smaller soil fauna on soil nitrogen. We present a meta-analysis of effects of soil mesofauna (i.e. enchytraeidae, springtails, mites) and microfauna (i.e. nematodes) on ammonium (NH₄⁺), nitrate (NO₃⁻), and total mineral nitrogen (ammonium + nitrate, N_{min}). We furthermore investigated whether the faunal effects depend on functional characteristics (i.e. trophic groups or size classes) or faunal density; or were modulated by experimental conditions or soil characteristics. Our results show that soil meso- and microfauna generally increased NO₃⁻ and N_{min} concentrations, but did not affect NH₄⁺. Increases of soil nitrogen are found in presence of microbi-detritivores or faunal communities that span various trophic levels. Micro- and mesofauna improve nitrogen availability in the soil in short- to intermediate term of up to two months. Furthermore, the provision of organic material plays an important role, as micro- and mesofauna have a positive effect on soil nitrogen especially when organic material is added and incorporated into the soil. This has important implications for agricultural management with regards to handling of organic residues. No significant moderating influence of micro- and mesofaunal density, litter C:N ratio, soil organic-carbon content, initial amount of NH₄⁺, NO₃⁻ or N_{min}, or experimental temperature was found. However, data availability or replication across factor categories was low for some of these moderators, and we could not differentiate between size classes (i.e., micro- or mesofauna) for all moderators or investigate interactions among different moderators. Thus, our study reveals important knowledge gaps that should be addressed in future research. Overall, our results underline the role of micro- and mesofauna for soil nitrogen cycling.

Keywords Inorganic nitrogen | microfauna | mineralization | nitrogen cycle | soil fauna

1. Introduction

The world's soils provide the basis for terrestrial life as they maintain several ecosystem functions such as primary productivity, carbon sequestration, water storage and filtering, or the storage and recycling of nutrients. These functions are the outcome of natural processes, in

which soil organisms play a key role (Brussaard 2012). An essential function of soils is the provision of mineral nitrogen, which is a nutrient basis for plant growth and food production. By influencing nutrient cycles soil organisms provide a link between aboveground- and belowground processes, as increased nutrient availability results in higher plant biomass production (Gebremikael

et al. 2016). During decomposition, dead organic material is degraded from complex organic compounds to mineral nutrients.

Microorganisms are the key actors in nitrogen transformation processes, but around 30% of nitrogen mineralization can be assigned to soil faunal activity (Neher & Barbercheck 1998). The soil faunal contribution to nitrogen cycling can be direct, e.g. through the excretion of nitrogenous compounds (Lang & Russell 2022), or indirect, e.g. through food-web interactions or changes in the soil habitat for microbial communities. Earthworms modify the soil habitat and affect the microbial community composition (Medina-Sauza et al. 2019), thus increasing water infiltration, litter decomposition and nitrogen mineralization (Blouin et al. 2013). Enchytraeidae affect carbon and nitrogen cycling by changing the soil habitat for soil microorganisms, ingesting bacteria, fungi and protists, and decomposing organic material (Brussaard 2012, Porre et al. 2016, Pelosi & Roembke 2018). Bacterivore or fungivore species within the meso- and microfauna affect nitrogen cycling by their influence on the microbial community composition, biomass and activity (Verhoef & Brussaard 1990, Vedder et al. 1996, Xiao et al. 2010). Generally, microbial biomass is decreased in presence of microbiodetritivores (Trap et al. 2016), but microbial growth may also be stimulated (Ingham et al. 1985). Fungal biomass is found to increase or decrease due to invertebrate grazing, depending on faunal density and grazing intensity (Crowther et al. 2012). The influence of microbial-feeding soil fauna on the soil microbial biomass is reported to vary depending on species, soil texture, and carbon and nitrogen supply (Mamilov et al. 2001, Trap et al. 2016). For instance, species may have feeding preferences for specific (groups of) fungi (Maraun et al. 2003, Schneider et al. 2005). Faunal population size is correlated with pore size distribution (Hassink et al. 1993a, van Vliet et al. 2004), which may cause differences in grazing intensity and nitrogen mineralization rates depending on soil texture (Hassink et al. 1993b). Also, the provision of organic material may affect nitrogen mineralization, as higher microbial activities and densities as well as faster litter decay rates are reported when organic material is buried, as opposed to when it is left on the surface (Holland & Coleman 1987, Beare et al. 1992).

Nitrogen cycling may not only be affected by microbiodetritivore species, but predatory species can also affect the microbial community by preying on microbiodetritivore animals (i.e. trophic cascades) (Thakur & Geisen 2019). Moreover, non-trophic interactions such as the competition for resources may affect nitrogen cycling in complex communities through the regulation of faunal populations. For instance, Sulkava et al.

(1996) found a strong correlation of nitrogen contents with enchytraeid biomass but not with microarthropod biomass. However, microarthropods still affected nitrogen mineralization as they reduced enchytraeid populations via competitive interactions.

Interestingly, models of nitrogen cycling usually do not acknowledge the role of soil fauna (Osler & Sommerkorn 2007, Salo et al. 2016). A first step towards the improvement of modeling approaches by integration of soil fauna requires a quantification of soil faunal effects as well as an understanding of influencing factors. Recent meta-analyses found increases of the nitrogen content and fertility of soils due to earthworm activity (Groenigen et al. 2019, Xue et al. 2022, Lang et al. 2023) and increased nitrogen mineralization in presence of bacterivorous soil fauna (Trap et al. 2016). However, we still lack a comprehensive quantitative synthesis of the influence of soil meso- and microfaunal groups on soil nitrogen that incorporates the controlling influence of further biotic or abiotic factors.

Here, we present a meta-analysis of effects of soil mesofauna (i.e. enchytraeidae, springtails, mites) and microfauna (i.e. nematodes) on soil mineral nitrogen in the form of ammonium (NH_4^+) and nitrate (NO_3^-), as well as total mineral nitrogen (the sum of NH_4^+ and NO_3^- pools in the soil; hereafter: N_{min}). Our main objective was to estimate the impact of meso- and microfaunal activity on these nitrogen compounds. Furthermore, we investigated whether faunal effects depend on functional characteristics (i.e. trophic groups or size classes) or faunal density; or were modulated by experimental conditions or soil characteristics.

2. Methods

2.1 Data search and selection

To identify suitable publications for a meta-analysis of soil micro- and mesofaunal effects on NH_4^+ , NO_3^- or N_{min} , we conducted a systematic literature search in compliance with the Preferred Reporting Items for Systematic Reviews and Meta-analysis PRISMA framework (Fig. S1, Moher et al. 2009). We used the Web of Science search engine (Core collection, from 1980 to March 2021) to search for literature using the keywords: (microarthropod* NEAR/2 soil OR collembola* OR springtail OR mite* OR nematod* NEAR/2 soil OR enchytraeid* OR potworm*) AND ('N minerali\$ation' OR 'nitrogen minerali\$ation' OR 'mineral N' OR 'mineral nitrogen' OR nitrification OR nitrogen NEAR/2 soil OR ammoni* NEAR/2 soil OR nitrate NEAR/2 soil

OR ‘inorganic nitrogen’ OR ‘inorganic N’). The search returned 453 articles, and six further studies were included by searching bibliographies of reviews and articles (Fig. S1). The articles were screened for their suitability for the meta-analysis based on the following selection criteria: (1) studies investigated faunal effects on at least one of the following soil nitrogen compounds: NH_4^+ , NO_3^- or N_{min} ; (2) measurements of nitrogen were reported for faunal and control (without fauna) treatments with the same experimental setup; (3) nitrogen compounds were measured in soil samples using standard chemical methods (excluding measurements of nitrogen leaching and litterbag experiments); (4) experiments did not contain plants (excluding the influence of plants on soil nitrogen); (5) mineral soils were used (excluding organic soils, e.g. peat or turf).

2.2 Data extraction and preparation

To create a database, we collected pairwise comparisons (observations) of nitrogen (NH_4^+ , NO_3^- , N_{min}) measurements for fauna and control treatments from the selected articles. For each observation, mean values, standard deviations (*SD*) or standard errors (*SE*), and the number of replicates (*n*) for control and faunal treatments were obtained from text and tables or extracted from figures using the image-digitization software ImageJ (Rasband 1997). When publications reported mean values of soil ammonium and nitrate but not of mineral nitrogen, N_{min} was calculated by summing NH_4^+ and NO_3^- . Standard errors were transformed into *SD* values for the analysis. For publications that did not report *SD* or *SE*, *SD* values were imputed by using the average coefficient of variation across all observations separately for each respective taxonomic group and nitrogen compound for control and fauna treatments. When no *SD* values were available for a specific combination of taxonomic group and nitrogen compound, the average coefficient of variation across all observations within the respective nitrogen compound was used. Additional data was provided by the authors of two publications.

As the impact of soil fauna on soil nitrogen may be potentially influenced by controlling factors (hereafter: moderators), we extracted additional information on experimental setup (laboratory or controlled field experiment, location, experimental duration, experimental temperature, addition of organic material, C:N ratio of organic material), soils (texture, soil organic carbon content (SOC), soil C:N ratio, initial content of N-compounds) and organisms (taxonomic major group, species, size class, trophic group, abundance) for each observation (Tab. S1). Soil fauna were categorized

into size classes as mesofauna (i.e. enchytraeidae, springtails, mites) and microfauna (i.e. nematodes). As mesofaunal density was usually reported in individuals per area and nematode density in individuals per soil weight, the influence of soil faunal density was investigated separately for microfauna and mesofauna. Classification of trophic groups was conducted based on author statements. Enchytraeidae as secondary decomposers that also graze on microorganisms (Engell et al. 2021) were included in microbi-detritivores. Faunal assemblages that contained diverse trophic groups, e.g. microbi-detritivores and predators, were denoted as ‘mixed trophic groups’. Soil textures were categorized as clays (sandy clay, silty clay, clay), loams (sandy loam, loam, silt, silt loam, silty clay loam, sandy clay loam, clay loam) and sands (sand, loamy sand). The categorization was based on the description in the original studies or estimated from the particle size distribution using a soil texture calculator (USDA 2019). Experimental duration was categorized as short (up to 31 days), intermediate (> 31 days to < 70 days) and long (≥ 70 days). In total, we collected 428 observations from 21 publications (Tab. 1, data available at the BonaRes repository: <https://doi.org/10.20387/bonares-0z00-ac96>), with 136 observations for NH_4^+ , 157 observations for NO_3^- and 135 observations for N_{min} (see Tab. S2 for the species covered). Standard deviation values were imputed for 36% of faunal and control treatments for NH_4^+ , for 50% of the faunal treatments and 14% of the control treatments for NO_3^- , and for 63% of faunal and control treatments for N_{min} . The moderators included in our meta-analysis with their ranges (continuous variables) or subgroups (categorical variables) are shown in table S1.

2.3 Statistical analyses

To estimate the magnitude and direction of the soil faunal effect on soil nitrogen, we analyzed the dataset using the software R 4.1.2 (R Core Team 2021) in the following manner. We used the natural logarithm of the response ratio as effect size, $\ln R = \ln(E/C)$, where *E* and *C* are the mean contents of NH_4^+ , NO_3^- or N_{min} in the faunal and control treatments, respectively (Hedges et al. 1999). A positive effect size denotes a higher nitrogen content in the faunal treatment, and a negative effect size a lower nitrogen content in the presence of soil fauna. Before calculation of the response ratio, we added 0.001 to the mean values of all observations to avoid invalid values in the calculation of the effect size, as some measurements of nitrogen compounds were zero. In the main text, the results are reported as percentage change ($\% \text{ change} = (\exp(\ln R) - 1) * 100$) to ease interpretation.

Table 1. Studies included in the meta-analysis. n = number of effect sizes calculated; TG = Trophic groups, abbreviated as MD = Microbi-detritivores; M = Mixed trophic groups present; O = Omnivore; P = Predator

Reference	n	Continent	Size group	Taxonomic group	Taxon	TG	Reported N compound
Adejuyigbe et al. 2006	6	Africa	Mesofauna	Mesofauna	Mixed mesofauna	M	NH ₄ ⁺ , NO ₃ ⁻ , N _{min}
Anderson et al. 1983	16	North America	Microfauna	Nematoda	<i>Mesodiplogaster lheritieri</i> (Maupas, 1919) Goodey, 1963	MD	NH ₄ ⁺
Bouwman et al. 1994	15	Europe	Microfauna	Nematoda	<i>Rhabditis</i> sp. Dujardin, 1845, <i>Acrobeloides buetschlii</i> (de Man, 1884)	MD	NH ₄ ⁺ , NO ₃ ⁻ , N _{min}
Brussaard et al. 1995	4	Europe	Microfauna	Nematoda	<i>Acrobeloides buetschlii</i> (de Man, 1884)	MD	N _{min}
Brussaard et al. 1995	4	Europe	Mesofauna	Acari	<i>Alliphis halleri</i> (G. & R. Canestrini, 1881)	P	N _{min}
Brussaard et al. 1995	4	Europe	Micro- and mesofauna	Nematoda + acari	<i>Acrobeloides buetschlii</i> (de Man, 1884), <i>Alliphis halleri</i> (G. & R. Canestrini, 1881)	M	N _{min}
Djigal et al. 2004	12	Africa	Microfauna	Nematoda	<i>Zeldia punctata</i> (Thorne, 1925)	MD	NH ₄ ⁺ , NO ₃ ⁻ , N _{min}
Gebremikael et al. 2014	15	Europe	Microfauna	Nematoda	Mixed nematoda	M	NH ₄ ⁺ , NO ₃ ⁻ , N _{min}
Griffiths 1986	12	Europe	Microfauna	Nematoda	<i>Rhabditis</i> sp. Dujardin, 1845	MD	NH ₄ ⁺ , NO ₃ ⁻ , N _{min}
Haimi & Siira-Pietkainen 2003	6	Europe	Mesofauna	Enchytraeidae	<i>Cognettia sphagnetorum</i> (Vejdovský, 1878)	MD	NH ₄ ⁺
Holajjer et al. 2016	60	Asia	Microfauna	Nematoda	<i>Cephalobus persegnis</i> Bastian, 1865	MD	NH ₄ ⁺ , NO ₃ ⁻ , N _{min}
Ingham et al. 1985	15	North America	Microfauna	Nematoda	<i>Aphelenchus avenae</i> Bastian, 1865	MD	NH ₄ ⁺ , NO ₃ ⁻ , N _{min}
Kaneda & Kaneko 2008	9	Asia	Mesofauna	Collembola	<i>Folsomia candida</i> Willem, 1902	O	NH ₄ ⁺ , NO ₃ ⁻ , N _{min}
Kaneda & Kaneko 2011	12	Asia	Mesofauna	Collembola	<i>Folsomia candida</i> Willem, 1902	O	NH ₄ ⁺ , NO ₃ ⁻ , N _{min}
Mebes & Filser 1998	56	Europe	Mesofauna	Collembola	<i>Parisotoma notabilis</i> (Schäffer, 1896), <i>Onychiurus armatus</i> group (Gisin), <i>Folsomia quadrioculata</i> (Tullberg, 1871), <i>Lepidocyrtus cyaneus</i> Tullberg, 1871, <i>Heteromurus nitidus</i> (Templeton, 1835)	MD, O	NO ₃ ⁻
Porre et al. 2016	18	Europe	Mesofauna	Acari	<i>Rhizoglyphus robini</i> Claparède, 1869, <i>Acarus siro</i> Linnaeus, 1758, <i>Stratiolaelaps scimitus</i> (Berlese, 1892)	MD, M, P	NH ₄ ⁺ , NO ₃ ⁻ , N _{min}
Porre et al. 2016	6	Europe	Mesofauna	Enchytraeidae	<i>Enchytraeus albidus</i> (Henle, 1837)	MD	NH ₄ ⁺ , NO ₃ ⁻ , N _{min}

Reference	n	Continent	Size group	Taxonomic group	Taxon	TG	Reported N compound
Porre et al. 2016	18	Europe	Mesofauna	Enchytraeidae + acari	<i>Enchytraeus albidus</i> (Henle, 1837), <i>Rhizoglyphus robini</i> Claparède, 1869, <i>Acarus siro</i> Linnaeus, 1758, <i>Stratiolaelaps scimitus</i> (Berlese, 1892)	MD, M	NH ₄ ⁺ , NO ₃ ⁻ , N _{min}
Postma-Blaauw et al. 2005	12	Europe	Microfauna	Nematoda	<i>Bursilla monhystera</i> (Bütschli 1873), <i>Acrobeloides nanus</i> (de Man, 1880), <i>Plectus parvus</i> Bastian, 1865	MD	N _{min}
Ronn et al. 2001	10	NA	Microfauna	Nematoda	Mixed nematoda	M	N _{min}
Porre et al. 2016	18	Europe	Mesofauna	Enchytraeidae + acari	<i>Enchytraeus albidus</i> (Henle, 1837), <i>Rhizoglyphus robini</i> Claparède, 1869, <i>Acarus siro</i> Linnaeus, 1758, <i>Stratiolaelaps scimitus</i> (Berlese, 1892)	MD, M	NH ₄ ⁺ , NO ₃ ⁻ , N _{min}
Postma-Blaauw et al. 2005	12	Europe	Microfauna	Nematoda	<i>Bursilla monhystera</i> (Bütschli 1873), <i>Acrobeloides nanus</i> (de Man, 1880), <i>Plectus parvus</i> Bastian, 1865	MD	N _{min}
Ronn et al. 2001	10	NA	Microfauna	Nematoda	Mixed nematoda	M	N _{min}
Thakur et al. 2014	12	Europe	Mesofauna	Acari	<i>Rhizoglyphus echinopus</i> (Fumouze & Robin, 1868), <i>Acarus siro</i> Linnaeus, 1758, <i>Hypoaspis miles</i> (Berlese, 1892)	MD, M	NH ₄ ⁺ , NO ₃ ⁻ , N _{min}
Thakur et al. 2014	6	Europe	Mesofauna	Enchytraeidae	<i>Enchytraeus albidus</i> (Henle, 1837)	MD	NH ₄ ⁺ , NO ₃ ⁻ , N _{min}
Thakur et al. 2014	18	Europe	Mesofauna	Enchytraeidae + acari	<i>Enchytraeus albidus</i> (Henle, 1837), <i>Rhizoglyphus echinopus</i> (Fumouze & Robin, 1868), <i>Acarus siro</i> Linnaeus, 1758, <i>Hypoaspis miles</i> (Berlese, 1892)	MD, M	NH ₄ ⁺ , NO ₃ ⁻ , N _{min}
van Vliet et al. 2004	48	North America	Mesofauna	Enchytraeidae	<i>Enchytraeus minutus</i> Nielsen & Christensen, 1961	MD	NH ₄ ⁺ , NO ₃ ⁻ , N _{min}
Woods et al. 1982	13	North America	Microfauna	Nematoda	<i>Mesodiplogaster lheritieri</i> (Maupas, 1919) Goodey, 1963, <i>Acrobeloides</i> sp. Cobb, 1924	MD	NH ₄ ⁺
Xiao et al. 2010	15	Asia	Microfauna	Nematoda	Mixed nematoda	M	NH ₄ ⁺ , NO ₃ ⁻ , N _{min}
Zhu et al. 2018	6	Asia	Microfauna	Nematoda	<i>Rhabditis intermedia</i> de Man, 1880, <i>Protorhabditis oxyuroides</i> Sudhaus, 1974	MD	NH ₄ ⁺ , NO ₃ ⁻ , N _{min}

All studies contributed to the meta-analysis with multiple observations, due to publications reporting results for several taxonomic groups or species, at multiple time points, or for a different experimental setup (e.g. usage of organic material). Additionally, some faunal treatments were compared to the same non-faunal control. To account for the dependencies among effect sizes, we used robust variance estimation. This method can handle statistically dependent effect sizes but, in contrast to multivariate meta-analysis, does not require information of the precise dependence structure (Tanner-Smith et al. 2016). Instead, a working model is used to approximate the dependence structure. The analysis was conducted following these steps: 1) The *escalc* function in the package *metafor* (version 2.5-86, Viechtbauer 2010) was used to calculate effect sizes; 2) the function *impute_covariance_matrix* in the *clubSandwich* package (version 0.5.2, Pustejovsky 2020) was used to impute a variance-covariance matrix. As publications did not report sampling covariances, we assumed a correlation of $r = 0.5$ between dependent

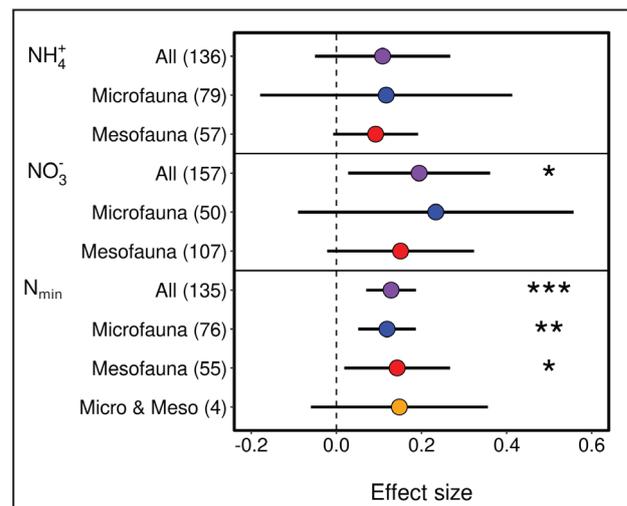


Figure 1. Overall effect of the presence of soil (micro- and/or meso) fauna ('All', purple), as well as differentiated by size classes (blue: microfauna, red: mesofauna, orange: micro- and mesofauna) on soil mineral nitrogen compounds. Shown are the mean effect sizes (logarithm of the response ratio), 95% confidence intervals, and the number of observations (within parentheses). Asterisks indicate levels of significance (* $P = 0.05$, ** $P = 0.01$, *** $P < 0.001$).

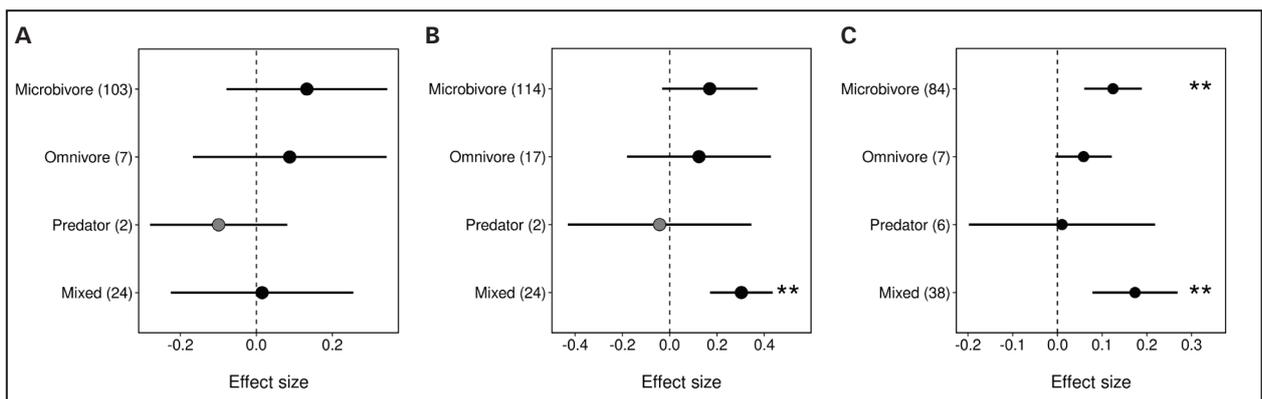


Figure 2. Effects of micro- and mesofaunal presence on (A) NH₄⁺, (B) NO₃⁻ and (C) N_{min} differentiated by trophic groups. Shown are the mean effect sizes (logarithm of the response ratio), 95% confidence intervals, and the number of observations (within parentheses). Effect size means represented as grey points indicate lack of observations (less than three). Microbivore denotes microbi-detritivores. Asterisks indicate levels of significance (* $P = 0.05$, ** $P = 0.01$, *** $P < 0.001$).

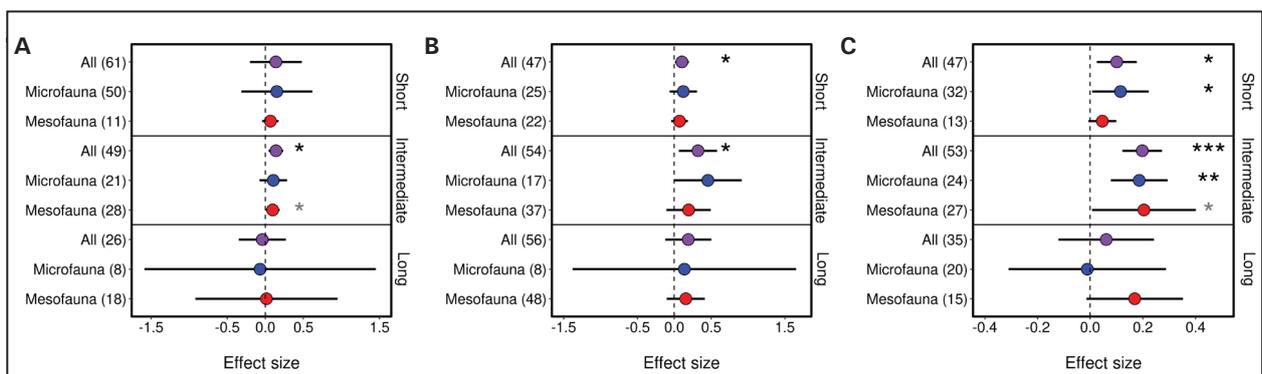


Figure 3. Influence of the experimental duration (short: up to 31 days; intermediate: > 31 days < 70 days; long: ≥ 70 days) on the effect of overall soil fauna ('All', purple), and the two size classes separately (blue: microfauna, red: mesofauna) on (A) NH₄⁺, (B) NO₃⁻ and (C) N_{min}. Shown are the mean effect sizes (logarithm of the response ratio), 95% confidence intervals, and the number of observations (within parentheses). Significance levels are indicated by asterisks (* $P = 0.05$, ** $P = 0.01$, *** $P < 0.001$), results that are not considered significant due to low degrees of freedom (see methods for explanation) are shown with grey asterisks.

observations; 3) the *rma.mv* function in *metafor* was used to fit multilevel meta-analytic models with a random intercept term where 'ID' (i.e., a unique value for each observation) was nested within 'Reference' (i.e., a unique value for each study); 4) the functions *coef_test* and *conf_int* in the *clubSandwich* package were used with the CR2 variance estimator to compute robust tests, provide standard errors using a sandwich estimator, and confidence intervals with a small-sample correction based on a Satterthwaite approximation. We thus accounted for the misspecification of the variance-covariance matrix in the first step; 5) we compared our results to analyses with a low ($r = 0.1$) or a high ($r = 0.9$) covariance to test the robustness of our analysis (i.e., sensitivity analysis).

Effect sizes were considered significant when their 95% confidence intervals did not overlap with zero. If Satterthwaite degrees of freedom were below four (e.g. caused by skewed or imbalanced covariates), we followed the recommendation to use a threshold of $p < 0.01$, as the p-value associated with the test is likely to under-estimate the type I error (Tanner-Smith et al. 2016).

Information on moderator variables was not available for all observations in the dataset. Therefore, we fitted separate models for each moderator using data subsets that contain the corresponding moderator data. Due to lack of data, we could not assess the significance of interactions among different moderators.

3. Results

3.1 Impact of soil fauna on soil nitrogen

Overall, the presence of all soil meso- and microfauna increased NO_3^- (+ 21%) and N_{min} (+ 17%) contents, whereas NH_4^+ content was not significantly affected (Fig. 1, Tab. S3). The differentiation by size classes shows that mesofauna (+ 15%) and nematodes (+ 13%) significantly increased N_{min} (Fig. 1, Tab. S3). We did not find a significant effect of individual taxonomic groups within the mesofauna (Tab. S4). The impact on soil nitrogen differs between trophic groups (Fig. 2, Tab. S5), with microbi-detritivores significantly

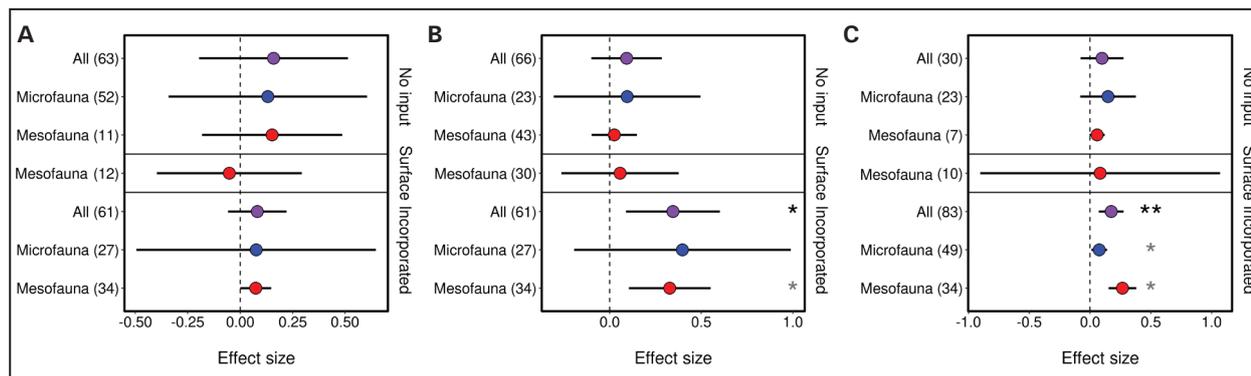


Figure 4. Influence of soil organic material as well site of input (left on surface or incorporated in soil profile) on the effect of overall soil fauna (*All*, purple), and the two faunal size classes separately (blue: microfauna, red: mesofauna) on (A) NH_4^+ , (B) NO_3^- and (C) N_{min} . Shown are the mean effect sizes (logarithm of the response ratio), 95% confidence intervals, and the number of observations (within parentheses). Significance levels are indicated by asterisks (* $P = 0.05$, ** $P = 0.01$, *** $P < 0.001$), results that are not considered significant due to low degrees of freedom (see methods for explanation) are shown with grey asterisks.

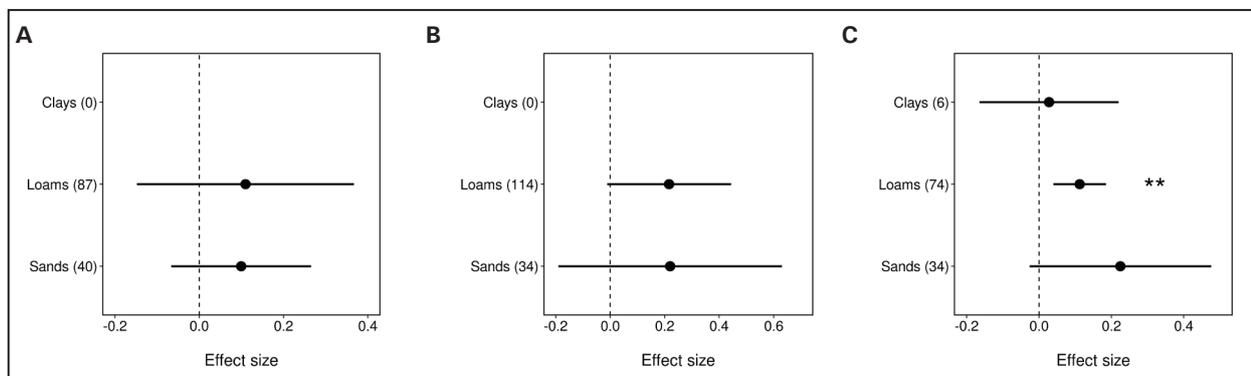


Figure 5. Effects of overall micro- and mesofaunal presence on (A) NH_4^+ , (B) NO_3^- and (C) N_{min} differentiated by soil textures. Shown are the mean effect sizes (logarithm of the response ratio), 95% confidence intervals, and the number of observations (within parentheses). Asterisks indicate levels of significance (* $P = 0.05$, ** $P = 0.01$, *** $P < 0.001$).

increasing N_{\min} (+ 13%) and faunal assemblages containing diverse trophic groups increasing NO_3^- (+ 35%) and N_{\min} (+ 19%). No significant influence of soil faunal density on NH_4^+ , NO_3^- or N_{\min} was found for microfauna (NH_4^+ : $p = 0.766$; NO_3^- : 0.14; N_{\min} : 0.364) or mesofauna (NH_4^+ : $p = 0.106$; NO_3^- : 0.493; N_{\min} : 0.431).

3.2 Influence of experimental and soil related moderators

Our results show that the presence of soil fauna significantly increased NH_4^+ (+ 15%) in experiments of intermediate duration, NO_3^- in experiments of short (+ 11%) and intermediate (+ 38%) duration, and N_{\min} in experiments of short (+ 11%) and intermediate (+ 22%) duration (Fig. 3, Tab. S6). The differentiation by size classes shows that microfauna significantly increases N_{\min} in experiments of short (+ 12%) and intermediate (+ 20%) duration (Fig. 3, Tab. S6). No significant faunal effects were found in studies lasting longer than 70 days.

We found a significant moderating influence of the addition and site (within the soil profile or on the soil surface) of organic material with soil fauna increasing NO_3^- (+ 41%) and N_{\min} (+ 19%) when organic material was incorporated into the soil (Fig. 4, Tab. S7). No significant faunal effects was found when organic material was absent or added on the soil surface. Soil fauna significantly increased N_{\min} in loamy soils (+ 12%, Fig. 5, Tab. S8). No significant moderating effect of the litter C:N ratio (NH_4^+ : $p = 0.588$; NO_3^- : $p = 0.467$; N_{\min} : $p = 0.677$), experimental temperature (NH_4^+ : $p = 0.807$; NO_3^- : $p = 0.846$; N_{\min} : $p = 0.995$), SOC (NH_4^+ : $p = 0.344$; NO_3^- : $p = 0.408$; N_{\min} : $p = 0.023$, d.f. = 2.36) or the initial amount of NH_4^+ ($p = 0.973$), NO_3^- ($p = 0.318$) or N_{\min} ($p = 0.179$) was found. Please note that we could not differentiate between size classes for all moderators in our analysis due to the low number of observations and a lack of replication within the size classes.

3.3 Sensitivity analysis

In our analysis, we used robust variance estimation with a variance-covariance matrix that assumed a correlation of $r = 0.5$ between dependent outcomes. In addition, we conducted the analysis assuming a correlation of $r = 0.1$ or $r = 0.9$ to check the robustness of our results. The analysis shows that, taking the degrees of freedom into account, our results are robust as they are consistent across varying correlations (Tab. S9).

4. Discussion

The present study provides quantitative evidence for a significant increase of mineral soil nitrogen in presence of soil micro- and mesofauna, thus underlining the importance of soil fauna for nitrogen cycling. We found that soil micro- and mesofauna in complex communities that encompass diverse trophic levels (i.e. mixed trophic groups) increase soil nitrogen contents. This is in line with the meta-analysis by de Graaff et al. (2015) who found an influence of faunal diversity on decomposition, and studies that suggest that soil nitrogen contents are increased when faunal assemblages contain diverse functional or trophic groups (Thakur et al. 2014, Eisenhauer et al. 2018). However, although a number of studies used more nature-resembling communities, often only a single taxonomic group was investigated, e.g. a nematode community that spans various trophic levels or a faunal assemblage of microbi-detrivore with predatory mites. Only few observations were available for faunal assemblages that contain micro- and mesofauna together. Hence, further research is needed to assess the effect of natural communities encompassing not only diverse trophic levels but also diverse size classes.

With regards to single trophic groups, especially microbi-detrivores are found to increase soil nitrogen contents. This may be caused by faunal-induced changes in the microbial community composition and activity (Xiao et al. 2010, Trap et al. 2016), especially of nitrifying microorganisms in the presence of microbi-detrivores (Griffiths 1989). However, observations for omnivores and predators are scarce, and the informative value of experiments using predators but no prey is questionable.

In contrast to studies that report a significant influence of microarthropod density on soil nitrogen (Kaneda & Kaneko 2008), faunal density was no significant moderator in our analysis. However, microbial community composition and activity, especially with regards to specific microorganisms involved in the processes of nitrogen mineralization, may be affected by soil fauna independently of faunal grazing intensity. It is also important to notice that we could not analyze the impact of faunal density for the various trophic groups separately due to lack of data. Therefore, this non-significant result cannot necessarily be interpreted as a lack of density effects for certain trophic groups, such as microbi-detrivores.

In our analysis we found evidence for a temporal aspect of soil faunal effects on soil nitrogen, as soil fauna affected soil nitrogen in the short (1 month) or intermediate (2 months) term, but not in the long term

(> 2 months). This is in line with other studies that found effects of soil fauna on soil nitrogen to disappear after some weeks (Bouwman et al. 1994, Brussaard et al. 1995) and may be caused by changes in microbial activity and community composition over time. Interactive effects with other factors may also play a role but could not be analyzed. For instance resource quality and litter placement (on the soil surface or buried) were found to affect nitrogen dynamics. In support of studies that report higher microbial activities and faster decomposition when organic material is buried (Holland & Coleman 1987, Beare et al. 1992), we found that the placement of organic material is important for faunal effects on nitrogen mineralization. Soil fauna significantly increased soil nitrogen contents when organic material was incorporated into the soil, but not when it was applied on the surface. This could be caused by the organic material being better accessible for microorganisms within the soil profile. For agricultural management, this has important implications regarding the handling of organic residues as farmers may profit stronger from soil faunal effects when organic material is incorporated into the soil. As observations for surface-applied organic material were generally scarce and only available for mesofauna, we call for future research to investigate the influence of the placement of organic material on nematode effects on soil nitrogen.

We furthermore aimed to investigate whether effects of soil fauna on soil nitrogen contents differ between soil textures, as faunal population sizes and grazing intensity may depend on pore size distribution (Hassink et al. 1993a, Hassink et al. 1993 b, van Vliet et al. 2004). Data availability largely varies across the three soil texture and faunal size classes, with the majority of experiments reporting observations for loamy soils and only few reporting observations for sands and clays. Most observations in loamy soils are for microfauna, whereas only few investigated the influence of mesofauna. Observations for sandy soils are only available for mesofauna, and observations for clay soils are only available for microfauna. We therefore could not differentiate by size classes in our analysis and call for further research, especially on the influence of soil mesofauna on soil nitrogen in loamy and clay soils, and of soil microfauna in sands and clays.

4. Conclusions and outlook

The present study provides quantitative evidence for a significant increase of soil mineral nitrogen in presence of soil micro- and mesofauna. This effect

is mainly caused by microbi-detritivores, and is also found in more complex communities with diverse trophic levels. Micro- and mesofauna improve nitrogen availability in the soil in short to intermediate terms. With regard to the management of organic residues, micro- and mesofauna especially have a positive effect on soil nitrogen contents when organic material is incorporated into the soil. In addition, our study reveals important knowledge gaps that should be addressed in future research. Most importantly, we lack research on effects of natural soil faunal communities and on the influence of faunal density for single trophic groups that showed a strong influence on soil nitrogen contents (i.e., microbi-detritivores). Further research is also needed for the investigation of interactive influences as well as the influence of micro- and mesofauna together. Nonetheless, our study generally underlines the importance of soil micro- and mesofaunal groups for nitrogen cycling.

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7. Author contributions

All authors contributed to the conception and design of the study. BL collected the data and reviewed the literature. Data analysis was performed by BL and BBC. All authors interpreted the results. The first draft of the manuscript was written by BL and all authors provided their comments and edited subsequent versions of the manuscript. All authors read and approved the final manuscript.

8. Additional information

Fig. S1: PRISMA flow diagram for the systematic literature search. n refers to the number of research articles.

Tab. S1: Overview on data availability with ranges for continuous variables or covered subgroups for categorical variables.

Tab. S2: Overview on the taxa included in the analysis with the number of observations for the different nitrogen compounds.

Tab. S3: Detailed results for the effect of overall soil fauna, and meso- and microfauna separately on NH_4^+ , NO_3^- and N_{min} .

Tab. S4: Detailed results for the effect of various mesofaunal taxonomic groups on NH_4^+ , NO_3^- and N_{min} .

Tab. S5: Detailed results for the effect of trophic groups on NH_4^+ , NO_3^- and N_{min} .

Tab. S6: Detailed results for the effect of all fauna, meso- and microfauna on NH_4^+ , NO_3^- and N_{min} for the various time categories.

Tab. S7: Detailed results for the effect of all fauna, meso- and microfauna on NH_4^+ , NO_3^- and N_{min} differentiated by the type of organic matter input.

Tab. S8: Detailed results for the faunal effect on NH_4^+ , NO_3^- and N_{min} differentiated by soil textures.

Tab. S9: Results for the sensitivity analysis with a variance-covariance matrix that assumed a correlation of $r = 0.5$ (main analysis), $r = 0.9$ or $r = 0.1$ between dependent outcomes.

Dataset: available at the BonaRes repository: <https://doi.org/10.20387/bonares-0z00-ac96>.

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