Earthworms increase forest litter mass loss irrespective of deposited compounds – A field manipulation experiment in subtropical forests

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Abstract

Earthworms modulate the carbon and nitrogen cycling in terrestrial ecosystems, their effect may be affected by deposited compounds due to human activity such as industrial emissions. However, studies investigating how deposited compounds affect the role of earthworms in carbon cycling such as litter decomposition are lacking, although they are important for understanding the influence of deposited compounds on ecosystems and the bioremediation by applying earthworms. For this, we performed a 365-day in situ litterbag decomposition experiment in a deciduous (Quercus variabilis) and coniferous (Pinus massoniana) forest in southeast China. We manipulated nitrogen (N), sodium (Na) and polycyclic aromatic hydrocarbon (PAH) deposited compounds during litter decomposition with and without earthworms (Eisenia fetida). After one year, N, Na and PAH compounds all slowed down litter mass loss, with the effects of Na being the strongest. By contrast, E. fetida generally increased litter mass loss and their positive effects were uniformly maintained irrespective of the type of deposited compounds. Further, the pathways earthworms increasing litter mass loss varied among the types of deposited compounds and forests. As indicated by structural equation modeling, earthworms maintained their positive effects and mitigated the negative effects of deposited compounds by directly increasing litter mass loss and indirectly increasing soil pH and microbial biomass. Overall, the results indicate that the acceleration of earthworms on litter mass loss is not affected by deposited compounds, with the pathways of earthworms increasing litter mass loss varying among the types of deposited compounds and forests. This suggests that the effects of atmospheric deposited compounds and earthworms on terrestrial ecosystem processes need to be taken into account because earthworms may cancel out the detrimental influence of deposited compounds on litter decomposition.

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Keywords : Aboveground–belowground linkages, Carbon cycling, Brown food web, *Eisenia fetida* , Atmospheric depositions, Subtropic forests

1 Introduction

Human activities such as industrial emissions increase the inputting of atmospheric deposited compounds to natural ecosystems, these compounds affect major process of carbon cycling such as litter decomposition (Knorr et al., 2005). In terrestrial ecosystems, litter decomposition is accelerated by soil decomposers such as soil engineers, earthworms (Cortez, 1998). Although the effects of deposited compounds and earthworms on litter decomposition were studied separately, their interactive effect remains elusive (Zhang et al., 2018; Huang et al., 2020). However, this gap limits our understanding of the influence of deposited compounds on terrestrial ecosystems and the role of earthworms under the increasing input of deposited compounds. In addition, filling this gap is important for bioremediation, e.g., applying earthworms to forests contaminated by industrial emissions.

Earthworms as major soil detritivores form part of the soil macrofauna, they have been suggested to contribute to litter decomposition by directly fragmenting litter and indirectly influencing soil properties, and the structure and activities of both microbes and fauna (Schulmann and Tiunov, 1999; Kizilkaya et al., 2011; Sackett et al., 2013).*Eisenia fetida* was found abundant in compost heaps where it accelerates organic matter decomposition (Aira et al., 2006). However,*E. fetida* also lives in natural forests in southern Europe and eastern China, in particular close to urban areas (Huang et al., 2003). This epigeic species predominantly colonizes in the litter layer, and able to live in contaminated sites (Rodriguez-Campos et al., 2014). Whereas, how the effect of *E. fetida* on forest litter decomposition varied with different deposited compounds received little attention, this is a very essential work to explore the application method of using epigeic earthworms for the bioremediation of contaminated forest soils.

Atmospheric depositions are changing terrestrial ecosystems at global scales (Holland et al., 2005; Liu et al., 2011). In particular, human activities such as industrial emissions are leading to increase the input of different deposited compounds into forests soil, e.g., ammonium (N), sodium (metal ions Na) and polycyclic aromatic hydrocarbons (organic contaminant PAHs) (Wang et al., 2015; Li et al., 2016). In the forests near urban regions, artificial road salt in winter may also increase the Na content in soil (Tiwari & Rachlin, 2018). Although three deposited compounds are generally at relatively low rates in natural conditions, each of them has been shown to affect litter mass loss by influencing soil microbial, faunal decomposer and the habitat of these decomposers (Knorr et al., 2005; Qasemian et al., 2012; Kaspari et al., 2014). Especially, these deposited compounds at high concentrations may detrimentally affect litter mass loss (Liu et al., 2011; Zhang et al., 2016). In addition, the effects of the three deposited compounds during litter mass loss may be different based on their specific chemical properties. For example, N addition may promote soil acidification but affect effect of soil fauna little (Zhang et al., 2016; Lin et al., 2017); Na addition may meet the Na shortage of soil fauna but prohibit microbial activities in inland forests (Kaspari et al., 2014; Jia et al., 2015); PAHs are toxic to soil microbial and faunal decomposers (Cotrufo et al., 2014; Klamerus-Iwan et al., 2015). Although the effects of N, Na and PAHs on litter mass loss were well studied separately (Knorr et al., 2005; Qasemian et al., 2012; Kaspari et al., 2014), their effects on litter mass loss have not been investigated in concert with earthworms in forests. This, however, is important for understanding the interactive effects of deposited compounds and soil keystone species on nutrient cycling in terrestrial ecosystems.

Here, we explored how the effects of earthworms on litter mass loss interactive with atmospheric deposited compounds including N, Na and PAHs. We performed an in-situ litter decomposition experiment in deciduous (*Quercus variabilis*) and coniferous (*Pinus massoniana*) forests with and without addition of the earthworm*Eisenia fetida* in Eastern China. During one year, we measured litter mass loss, total carbon (C) and N loss, soil pH and soil microbial biomass. To better understand the pathways how the effect of earthworms on litter mass loss varies with different types of deposited compounds, we applied structural equation modelling. We hypothesized that (1) N, Na and PAHs addition all decrease litter mass loss; (2) the positive effect of earthworms on litter mass loss is significantly decreased by the addition of N, Na and PAHs, and (3) soil pH and microbial biomass as the modulators on litter mass loss are reduced by N, Na and PAHs addition, but enhanced by earthworm.

2 Materials and Methods

2.1 Study sites

The experiment was conducted at a subtropical forest in Zijin Mountain between April 2018 and May 2019 (32°4'N, 118deg51'E; Nanjing, Eastern China). The forest is mainly covered by *Quercus variabilis* and*Pinus massoniana* (Lin et al., 2017), and the herb layer is dominated by *Parthenocissus quinquefolia* or graminoids, mainly*Carex* spp. (Tian et al., 2018). Mean annual rainfall and air temperature of the subtropical monsoon climate is 1106 mm and 15.4 degC, respectively. The rainfall concentrated in summer (on average 163 mm per month between June and August) and low in winter (on average 50 mm per month between October to March). The bedrock is sandstone and shale, with a humus layer rich in organic matter and nutrients. For a more comprehensive understanding of the role of deposited compounds and earthworms in different forests, we selected a deciduous *Q. variabilis* forest and a coniferous *P. massoniana* forest for this study (This work was conducted in the two forests respectively and without the replicates of the deciduous or coniferous forest). The two forests were about 900 m away from each other and located at similar altitude (65 and 175 m, respectively). More details on site conditions are given in Table 1.

2.2 Experimental set up

In each forest we identified an area of 30 m x 20 m for establishing the experiment. Two factors, type of deposited compounds (control, N, Na, PAHs) and earthworms (with and without), were investigated. In each forest, each treatment (deposited compounds x earthworms) was replicated four times resulting 32 experimental units comprising of individual mesocosms, which were installed from February to April 2018 (for details see Fig. S1). For installation we first dug up an area of 0.5 m x 0.5 m to a depth of 0.2 m, i.e., a volume of about 50 L. From the excavated litter and soil material we hand-sorted earthworms. Then, we placed a 1 m x 1 m nylon bag into the pit (0.16 mm mesh size) and filled back the excavated soil and litter to fit the natural layering, doing that herb seedlings were removed. The nylon bags were then closed by zipper at the top and were covered with leaf litter. The pits were located away from main roots of trees. Individual mesocosms were established as fast as possible (< 30 min) to minimize effects of sunshine and drying. The mixing of soil broke the initial hotspots in soil surface, e.g., the worms' burrows and the rhizosphere of fine roots; and the nylon bags blocked the exchange of macrofauna, parts of mesofauna, run-off and nutrients. Thus, the plots may slow down the rates of litter mass loss but overall the differences in micro-environment between plots were reduced. The distance between mesocosms was 3 – 5 m, and mesocosms were located at least 20 m away from the border of the forest to avoid edge effects.

After finalizing the establishment of the mesocosms in April 2018, we placed 10 litterbags (20 cm x 10 cm) on the soil surface within each mesocosm (Fig. S1d). Litterbags were either filled with litter of*Q. variabilis* or *P. massoniana* , which were collected from December 2017 to January 2018 and dried at 40 degC for one month (for litter traits see Table 1). To disentangle effects of different fauna groups, two mesh sizes were used, fine mesh of 0.2 mm and coarse mesh of 5 mm. The fine and coarse mesh litterbags were used to evaluate the net contributions of microbe- and fauna-driven mass loss and were filled with 4 and 8 g litter (dry mass), respectively (Yin et al., 2022). The higher amount in the large mesh size litterbags was used as we assumed the litter to be decomposed faster due to access by macrofauna. The period of litter decomposition was 365 days from April 2018 to April 2019.

To manipulate deposited compounds, we added 500 mL aqueous solutions of NH_4NO_3, NaCl and PAH to the N, Na and PAH treatment every 35 days. Control mesocosms received 500 mL distilled water. The aqueous solutions of NH_4NO_3were added following Lin et al. (2017) and were equivalent to the mean annual deposited amount of N in the region of Nanjing (47 kg N ha^{-1} y^{-1}). NaCl was added at a Na mass percentage of 0.5 % and was equivalent to a rate of 39.36 g Na m^{-2} y^{-1}. The Na addition followed Jia et al. (2015) simulating future Na accumulation due to the input of Na by human activities e.g., via road salt (Li et al., 2016; Tiwari & Rachlin, 2018). We assumed this concentrations to detrimentally affect litter decomposition due reducing microbial activity (Ji et al., 2020). For PAHs, we included fluoranthene (Flu), pyrene (Pyr), chrysene (Chr), benzo[a]pyrene (BaP) and phenanthrene (Phe). The five PAHs accounted for 54% of the mass of sixteen prioritized PAHs in the soil of the urban region of Nanjing and Zijin Mountain (Wang et al., 2015). The PAHs added to a total of 128 mg per microcosm per year, which is equivalent to 1.813 μg g^{-1} dry soil y^{-1} and thus doubled the total amount of soil PAHs in study sites (Wang et al., 2015).

For investigating the actual effect of earthworms in field, treatments with earthworms received a total of 60 individuals of *E. fetida*per mesocosm in deciduous and 20 individuals in coniferous forest resembling the density in these forests as investigated in 2018 (Table S2). *E. fetida* dominated 55.47% and 66.91% earthworm abundance in deciduous and coniferous forest as we investigated. Earthworms were picked by hand from the mesocosms, counted and placed back during May to August 2019 to validate the treatment. From April 2018 to April 2019, litterbags and soil samples were taken at 70, 140, 210, 280, 365 days resulting in a total of 640 litterbags (2 forests × 4 deposited compounds treatments × 2 earthworm treatment × 2 mesh sizes × 4 replicates × 5 sampling dates) and 640 soil samples (0 – 5 cm depth under litterbags). At the 140-day sampling, one nylon bag in deciduous forest was found broken and excluded from the analysis.

2.3 Litter mass loss, C and N loss

The litter taken out of the litterbags was cleaned from debris using distilled water and dried at 60 °C for 72 h. Total C and N of litter were measured from the samples taken after 70, 210 and 365 days using an elemental analyzer (Elemental Vario Micro, Germany). From these data changes in litter mass, and amount of C and N was calculated and expressed as percentages of initial.

2.4 Soil pH and microbial biomass

Fresh soil samples were sieved through 1 mm and used to determine soil moisture and soil microbial biomass; after 7 days of air drying, dry soil samples were used to determine soil pH. Soil pH was measured in a 1 : 2.5 soil and water solution using a pH meter (Mettler Toledo, Switzerland, Dick et al., 2000). Soil microbial biomass was determined by substrate-induced respiration (SIR) following Bailey et al. (2002) and Lin et al. (2017). In brief, fresh soil samples equivalent to 1 g dry weight were adjusted to 60 % of the water holding capacity. Then, 1 mL of glucose solution was added to soil to achieve 10 mg glucose g^{-1} dry weight of soil. Samples were then incubated at 25 °C, and CO_2 was determined using an infrared gas analyzer after one hour. SIR was expressed as CO_2 per g soil per hour (ppm g^{-1} dry soil h^{-1}).

2.5 Statistical analyses

All analyses were performed using R version 4.0.5 (https://www.r-project.org/). We analyzed litter mass loss using linear mixed effects models (LMMs). Data of the deciduous and coniferous forests were analyzed separately. In each LMM, type of deposited compounds (control, N, Na, PAHs), earthworms (with and without), mesh size (fine and coarse) and time (five sampling dates) were treated as fixed factors. Mesh size was nested in mesocosms and included as random factor to account for non-independence of litterbags within mesocosms and repeated sampling. To evaluate the effects of type of deposited compounds, earthworms and mesh size, we used planned contrasts between the control and the respective treatment. Data were log(x + 1) transformed to meet normality if needed. Due to the response variables being log transformed, contrasts are analogous to log response ratios (Piovia-Scott et al., 2019). We used 'nlme' to fit mixed-effect models and 'emmeans' for planned contrast. The changes in litter mass loss, C and N loss were shown as percentages and were calculated as$|m_t - m_c| \times 100\%$, with m_t andm_c are the mass loss percentages of the treatment and control, respectively. In another word, the percentages shown in the results are true mass percentages to total litter mass (not the ratio of treatment to control, or the ratio of the difference in treatment and control to control). To evaluate effects of the addition of *E. fetida* , we modelled abundance and biomass of earthworms at the end of the experiment using generalized linear models with quasi-Poisson distribution to account for model over- or under-dispersion.

Structural equation models (SEMs) were used to inspect pathways linking earthworms and deposited compounds to litter mass loss (see Fig. 4 and Fig. S4; Tian et al., 2018, Yin et al., 2022). To compare the effects of different types of deposited compounds and earthworms on litter mass loss, we merged six models for each forest as one including the three types of deposited compounds and two mesh sizes. In each model, deposited compounds and earthworms were included as categorical variables (with and without) and the other variables as numeric; values of all variables were scaled to 0 - 1 before modeling. Direct effects of Na on litter mass loss were built-in models of the coniferous forest according to the modification indices in R; direct effects of earthworms on SIR were removed to improve fitting (Shipley, 2009; Yin et al., 2022).

3 Results

3.1 Changes in the abundance of earthworms

The addition of *E. fetida* resulted in significantly increased abundance and biomass of total earthworms including original existing*E. fetida* in both deciduous and coniferous forests ($P < 0.001$, Table S1). Specifically, the addition of *E. fetida*increased the abundance of total earthworms by factors of 4.66 and 2.93 in mesocosms of deciduous and coniferous forests, respectively (Table S2).

3.2 Changes in litter mass loss, C and N loss

Deposited compounds uniformly reduced litter mass loss in both deciduous and coniferous forests, with the effects being independent of mesh size (Table 2, Figs 1, 2). The effects were strongest for Na, which decreased mass loss by 9.13% and 5.60% in deciduous and coniferous forests, respectively. Similar to mass loss, deposited compounds also reduced litter C and N loss (Table S3). Again, the effects were strongest for Na, which reduced litter C loss by 7.15% and litter N loss by 7.63% in the deciduous and coniferous forests, respectively (Figs 3). Addition of N and PAHs reduced litter mass, C and N loss but less than Na, e.g., N and PAHs reduced litter mass loss by 4.82%, 7.68% in deciduous forest and 3.42%, 1.46% in coniferous forest, respectively (Figs 1, 2, 3).

Earthworms generally accelerated litter mass loss in both deciduous and coniferous forests, with the effect being independent of deposited compounds (Table 2, Figs 1, 4). The positive effect of earthworms on the loss of litter mass and litter C was similar but varied between forests. In the deciduous forest, earthworms significantly accelerated litter mass loss and C loss in coarse (6.66% and 6.20%) but not in fine bags (Figs 1, 4, 5, S2). In the coniferous forest, earthworms significantly accelerated the litter mass loss and C loss in both coarse and fine bags, but the effect was less strong than in the deciduous forest (2.02% and 2.80%; Table S3, Figs 1, 4, 5, S2).

3.3 Pathways affecting litter mass loss

The pathways of positive earthworm effects on fauna- and microbe-driven mass loss varied with the types of deposited compounds (N, Na, PAHs) and forests (deciduous, coniferous; Figs 6, S4, Table S4). Earthworms directly increased fauna-driven mass loss in the deciduous forest, but increased microbe-driven mass loss in the coniferous forest. Further, in the deciduous forest, earthworms increased litter mass loss driven by fauna and microbes' decomposition by promoting soil pH in the Na addition treatment and by promoting soil microbial biomass in the PAH treatment.

The negative effects of deposited compounds on litter mass loss were mainly due to reduced soil pH in both the deciduous and coniferous forests (Fig. 6). Further, the addition of PAHs reduced fauna-driven litter mass loss via reducing soil microbial biomass in both the deciduous and coniferous forests. By contrast, in the coniferous forest Na addition directly decreased both litter mass loss driven by fauna and microbes without changing soil pH and microbial biomass.

4 Discussion

Human activities increase the input of atmospheric deposited compounds into natural ecosystems, the deposited compounds including inorganic and nonmetal ions, metal ions and organic contaminants (Li et al., 2016). These compounds may have different influence on nutrient cycling of natural ecosystems based on the difference of their chemical properties. Soil engineers, earthworms play a key role in nutrient cycling of terrestrial ecosystems (Blouin et al., 2013). However, the lacking of studies about the interactive effect of deposited compounds and earthworms on nutrient cycling limits our understanding of the mechanism of deposited compounds affecting terrestrial C and N cycling, and also limits the bioremediation such as apply earthworms to forests contaminated by atmospheric deposited compounds. This study investigated how the effects of earthworms are affected by different types of deposited compounds during major nutrient cycling in forests such as litter decomposition. Unexpectedly, earthworms uniformly increased litter mass loss irrespective of different deposited compounds. Notably, the pathways earthworms affect litter mass loss varied among different types of deposited compounds due to different pathways of these compounds affecting litter mass loss.

4.1 Effects of earthworms on litter mass loss irrespective of deposited compounds

As hypothesized, N, Na and PAHs all decreased litter mass loss. Effects of deposited compounds on litter mass loss have been shown to vary with their concentrations, with detrimental effects typically increasing at higher concentrations (Knorr et al., 2005; Ji et al., 2020). Our N and PAHs treatments doubled the deposited amount of N and PAHs at our study sites and the negative effects were in line with previous studies, but were relatively small. Fast cycling and losses of N via leaching (Kreutzer et al., 2009; Wang et al., 2021) might have been responsible for the weak N effect. Although increased by a factor of two, the concentration of PAHs in this study (1.813 µg g^{-1} dry soil) may have little toxic effects on soil decomposers according to previous studies (Rodriguez-Campos et al., 2014; Zhang et al., 2016). Further, earthworms and lignin-degrading fungi, known to stimulate the degradation of PAHs (Haritash & Kaushik, 2009; Rodriguez-Campos et al., 2014), may have contributed to the weak effects of PAHs on litter mass loss. Compared to N and PAHs, Na addition more strongly reduced litter mass loss, potentially due to the rather high concentrations of Na added (0.5% NaCl solution, 3.28 g Na^{+} m^{-2} $month^{-1}$) (Kaspari et al., 2009, 2014; Jia et al., 2015). In the region of Nanjing, the input of Na of predominantly natural (marine) origin into terrestrial ecosystems is only 40.79 µg $m^{-2}month^{-1}$ (Li et al., 2016). The results support earlier findings that in contrast to small Na input, high amounts of Na inhibit both faunal and microbial activity, and thereby decreases litter mass loss (Jia et al., 2015). Overall, the results suggest that the effect of deposited compounds on litter mass loss depends on the type of compounds with the effects of low concentrations of deposited compounds affecting litter mass loss in subtropical forest ecosystems only moderately.

Notably, the positive effect of earthworms on litter mass loss was not significantly modified by deposited compounds, this is opposed to our second hypothesis. The species characteristics such as epigeic group and highly contamination tolerance may contribute to the stable role of*E. fetida* on litter mass loss under different deposited compounds. Effects of earthworms on litter mass loss have been shown to vary among ecological groups of earthworms, with the effects of epigeic species may be bigger than others (Suarez et al., 2006). Correspondingly the epigeic species *E. fetida* increased litter mass loss, which is in line with previous studies (Heungens, 1969; Rajapaksha et al., 2013). Previous studies found *E. fetida* to be able to live in highly contaminated soil (Geissen et al., 2008) suggesting that *E. fetida* is rather insensitive to soil contaminations and may even contribute to the decontamination of soils (Rodriguez-Campos et al., 2014). Thus *E. fetida* increased litter mass loss regardless of deposited compounds although the compounds such as PAHs are toxic and high concentrations of Na inhibit animal activity (Peng et al., 2008; Jia et al., 2015).

In deciduous and coniferous forests, earthworms' positive effects on litter mass loss were both not affected by different types of deposited compounds. Considering the pathways earthworms stimulated litter mass loss varied between the deciduous and coniferous forest (also the different soil conditions), suggesting earthworms get rid of negative effects of deposited compounds on litter mass loss via multiple ways. However, we lacked replication of forest types and only studied a single deciduous (*Q. variabilis*) and a single coniferous (*P. massoniana*) forest, and the effects of earthworms cannot be compared in a straightforward way as we added a larger number of earthworms to the deciduous than the coniferous forest and it has been shown that the effect of earthworms on litter mass loss increases with earthworm abundance in forests (Gonzalez et al., 2003; Szlavecz et al., 2011; Huang et al., 2020).

4.2 Pathways linking the effect of deposited compounds and earthworms to litter mass loss

Partly supported the third hypothesis, our SEM indicated that N, Na and PAH all indirectly inhibited litter mass loss in the deciduous forest by acidifying the soil, but they little affected soil microbial biomass in particular in fine litterbags suggesting that deposited compounds changed the activity rather than biomass of microorganisms. N and PAHs also indirectly inhibited fauna-driven litter mass loss by acidifying the soil. Zhang et al. (2016) reported that N addition does not affect fauna-driven mass loss, supporting our results that acidification due to N addition (Lin et al., 2017) was responsible for the detrimental effects of N (and PAHs) on fauna-driven litter mass loss, potentially due to deteriorating habitat properties of detritivores. Notably, PAHs also indirectly inhibited fauna-driven litter mass loss by reducing microbial biomass in both forests. Since PAHs may accumulate in soil organisms (Jonker & van der Heijden, 2007; Muijs & Jonker, 2009), the negative effects of PAHs aggravate with time indicating that in the long-term their detrimental effects may exceed those of N and Na depositions. The lack of effects of Na on fauna-driven litter mass loss may have been due to detrimental effects of high concentrations of Na being cancelled out by Na functioning as essential element for soil animals (Kaspari et al., 2014). Results of our SEM further indicated that in the coniferous forest Na directly inhibited litter mass loss suggesting that it also affects animal and microbial activity. Overall, our SEM suggest deposited compounds acidified the soil and thereby inhibited the activity of soil detritivores and microorganisms, but the pathways of the detrimental effects of these compounds on litter mass loss varied among the types of deposited compounds studied. In the long-term detrimental effects of PAHs are likely to exceed the negative effects of N and Na due to their accumulation in litter and decomposer organisms.

Earthworms increased litter mass loss by directly affecting fauna- and microbe-driven litter mass loss, and indirectly affecting soil pH and soil microbial biomass, supporting the third hypothesis. The pathways earthworms promoted litter mass loss differed between forests, and corresponded to the different responses of earthworms to deposited compounds. Earthworms directly promoted fauna-driven litter mass loss in the deciduous forest, but promoted microbe-driven litter mass loss in the coniferous forest. Since earthworms prefer to feed on high quality litter (Rajapaksha et al., 2013) and earthworm abundance and litter mass loss correlate positively (Huang et al., 2020), earthworm abundance and litter quality may have contributed to the different effects of earthworms on litter mass loss in the deciduous and coniferous forest. Further, the mitigation of the negative effect of Na on litter mass loss in the deciduous forest by earthworms likely was due to earthworms reducing the negative effect of Na on soil pH. Earlier studies also found earthworms to alter soil pH (Sackett et al., 2013), but our results indicate that this may depend on the type of deposited compounds. By contrast, the mitigation of the negative effect of the addition of N on litter mass loss (and soil pH) in the coniferous forest by earthworms according to our SEM was due to earthworms directly increasing litter mass loss. Further, the negative effect of PAHs on fauna-driven litter mass loss was mitigated by earthworms via beneficially affecting pH and microbial biomass, but also directly by increasing litter mass loss.

5 Conclusion

This study provided novel and detailed insight into how atmospheric deposited compounds and earthworms affect the nutrient cycling in interactive ways. Importantly, using SEM we identified mechanisms and pathways responsible for these interactions. Our results suggest that the positive effects of earthworms on litter mass loss are not modified by different types of deposited compounds, and the mechanisms vary between the types of deposited compounds. Although not replicated, the results further suggest that the mechanisms responsible for earthworms maintain uniform and positive effects on litter mass loss under different types of deposited compounds vary with forest type. The results highlight the importance of studying the effects of deposited compounds and earthworms on terrestrial nutrient cycling in concert as earthworms may persist in their beneficial roles and mitigate the influence of detrimental deposited compounds.

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Conflict of Interest

The authors declare that they have no conflict of interest.

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Tables

Table 1

Site conditions and litter traits of the deciduous and coniferous forests studied; means +- SD. Letters indicate significant differences; t-test ($p < 0.05$, $n = 5$). Values of soil C, soil N and soil C/N ratio were taken from Tian et al. (2018).

Site conditions	**Deciduous**	**Coniferous**
Latitude (°N)	32.0555	32.0635
Longitude (°E)	118.8736	118.8727
Elevation (m a.s.l.)	65	175
Slope (°)	5	15
Soil pH	5.30 ± 0.19a	5.62 ± 0.48a
Soil moisture (%)	24.25 ± 1.86a	21.48 ± 0.40b
Soil C (g kg^{-1})	20.30a	15.40b
Soil N (g kg^{-1})	1.30a	1.10a
Soil C: N	15.52a	14.39a
Litter traits	*Quercus variabilis*	*Pinus massoniana*
Lignin (%)	31.20 ± 1.08b	40.60 ± 0.77a
Total C (%)	49.50 ± 0.83b	51.30 ± 1.26a
Total N (%)	1.27 ± 0.07a	0.85 ± 0.08b
Lignin: N	33.31 ± 1.77b	60.53 ± 5.77a
C: N	24.63 ± 2.68b	48.47 ± 6.86a

Table 2

F- and P-values of linear mixed effect models on the effects of deposited compounds (N, Na, PAHs), earthworms (with, without), mesh size (fine, coarse), time (70, 140, 210, 280, 365 days) and their interactions on litter mass loss in deciduous and conifer forests.

Factor	**Deciduous**	**Deciduous**	**Deciduous**	**Coniferous**	**Coniferous**	**Coniferous**
	df	F	P	df	F	P
(Intercept)	*1,184*	40344.93	**<0.001**	*1,192*	30229.79	**<0.001**
Deposited compounds (D)	*3,23*	4.53	**0.012**	*3,24*	1.17	0.342
Earthworms (E)	*1,23*	5.28	**0.031**	*1,24*	7.28	**0.013**
Mesh size (M)	*1,23*	34.29	**<0.001**	*1,24*	5.81	**0.024**
Time (T)	*4,184*	273.86	**<0.001**	*4,192*	341.1	**<0.001**
D x E	*3,23*	0.89	0.460	*3,24*	1.55	0.227
D x M	*3,23*	1.37	0.276	*3,24*	1.71	0.192

Factor	Deciduous	Deciduous	Deciduous	Coniferous	Coniferous	Coniferous
E x M	*1,23*	9.41	**0.005**	*1,24*	0.49	0.492
D x T	*12,184*	1.09	0.369	*12,192*	2.48	**0.005**
E x T	*4,184*	0.46	0.766	*4,192*	0.40	0.806
M x T	*4,184*	9.74	**<0.001**	*4,192*	29.83	**<0.001**
D x E x M	*3,23*	0.64	0.597	*3,24*	1.32	0.292
D x E x T	*12,184*	0.62	0.819	*12,192*	0.74	0.712
D x M x T	*12,184*	1.17	0.306	*12,192*	0.62	0.824
E x M x T	*4,184*	1.32	0.262	*4,192*	0.37	0.829
D x E x M x T	*12,184*	0.47	0.929	*12,192*	0.90	0.552

Appendix

Tables

Table S1

Changes in the abundance and biomass of total earthworms and of*Eisenia fetida* due to deposited compounds (D) and earthworms (E) in mesocosms of deciduous and coniferous forests; Chi^2- and P-values based on generalized linear models.

		Deciduous	Deciduous	Coniferous	Coniferous	Coniferous
	Df	Chi^2	P	Chi^2	P	P
Total abundance						
Deposited compounds (D)	3	3.18	0.364	11.96	**0.008**	**0.008**
Earthworms (E)	1	19.83	**<0.001**	14.14	**<0.001**	**<0.001**
D × E	3	0.86	0.835	1.43	0.698	0.698
Total biomass	**Total biomass**					
Deposited compounds (D)	3	5.59	0.134	20.27	**<0.001**	**<0.001**
Earthworms (E)	1	27.04	**<0.001**	19.99	**<0.001**	**<0.001**
D × E	3	0.14	0.987	2.42	0.490	0.490
Eisenia **abundance**	*Eisenia* **abundance**					
Deposited compounds (D)	3	1.11	0.775	4.26	0.234	0.234
Earthworms (E)	1	18.02	**<0.001**	17.81	**<0.001**	**<0.001**
D × E	3	1.65	0.648	5.44	0.142	0.142
Eisenia **biomass**	*Eisenia* **biomass**					
Deposited compounds (D)	3	2.98	0.394	4.14	0.246	0.246
Earthworms (E)	1	17.67	**<0.001**	15.59	**<0.001**	**<0.001**
D × E	3	0.69	0.875	4.07	0.254	0.254

Table S2

Total abundance and biomass of earthworms in mesocosms of the Deciduous (D) and coniferous (C) forest with and without addition of *E. fetida* (E); means ± SD, n = 5 for initial values and n = 4 for other values.

	Initial	Control	N
Abundance (number per mesocosm)	**Abundance** (number per mesocosm)	**Abundance** (number per mesocosm)	**A**
D	60.60 ± 9.71	3.67 ± 6.35	3.7
D+E		10.00 ± 4.69	15
C	19.60 ± 8.08	0.50 ± 0.58	1.7

	Initial	**Control**	**N**
C+E		3.75 ± 3.20	4.0
Biomass (g per mesocosm)	**Biomass** (g per mesocosm)	**Biomass** (g per mesocosm)	**Bi**
D	1.69 ± 0.41	0.04 ± 0.06	0.0
D+E		0.50 ± 0.37	0.9
C	0.81 ± 0.25	0.01 ± 0.01	0.0
C+E		0.08 ± 0.05	0.1

Table S3

F- and P-values of linear mixed-effect models on the effects of deposited compounds (N, Na, PAHs), earthworms (with, without), mesh size (small, large) and time (70, 140, 210, 280, 365 days) on changes in litter C and N in deciduous and coniferous forests.

Factor	**Deciduous**	**Deciduous**	**Deciduous**	**Deciduous**	**Deciduous**	**Coniferous**	**Conife**
		C loss	C loss	N loss	N loss		C loss
	df	F	P	F	P	df	F
(Intercept)	*1,92*	91514.6	**<0.001**	962.47	**<0.001**	*1,96*	36201.2
Deposited compounds (D)	*3,23*	2.48	0.086	3.41	**0.034**	*3,24*	1.23
Earthworms (E)	*1,23*	9.65	**0.005**	0.00	0.945	*1,24*	4.60
Mesh size (M)	*1,23*	0.17	0.685	28.35	**<0.001**	*1,24*	75.82
Time (T)	*2,92*	1274.58	**<0.001**	75.33	**<0.001**	*2,96*	744.49
D x E	*3,23*	0.25	0.863	4.27	**0.015**	*3,24*	0.61
D x M	*3,23*	0.62	0.610	0.34	0.794	*3,24*	0.13
E x M	*1,23*	4.54	**0.044**	0.12	0.728	*1,24*	0.44
D x T	*6,92*	3.48	**0.004**	0.67	0.675	*6,96*	1.15
E x T	*2,92*	1.69	0.191	0.03	0.967	*2,96*	0.06
M x T	*2,92*	3.11	**0.049**	0.82	0.442	*2,96*	51.36
D x E x M	*3,23*	0.38	0.766	2.29	0.106	*3,24*	0.24
D x E x T	*6,92*	0.85	0.535	3.49	**0.004**	*6,96*	0.57
D x M x T	*6,92*	1.32	0.256	1.17	0.330	*6,96*	0.23
E x M x T	*2,92*	4.03	**0.021**	3.60	**0.031**	*2,96*	0.04
D x E x M x T	*6,92*	0.41	0.869	1.47	0.198	*6,96*	0.29

Table S4

Fit values of structural equation modeling on the effect of deposited compounds (N, nitrogen; Na, sodium; PAHs, polycyclic aromatic hydrocarbons) and earthworms (micro, without; fauna, with) in deciduous (D) and coniferous forest (C). P indicates the p-value of models, X^2/df indicates the ratio of chi-square and degrees of freedom, GFI indicates the goodness of fit, RMSEA indicates the root mean square error of approximation, $P_{\text{-RMSEA}}$ indicates the p-value of RMSEA, R^2_Loss, R^2_SIR and R^2_pH indicates the estimate of variances of mass loss, soil microbial biomass and soil pH, respectively.

	P	X^2/df	GFI	RMSEA	$P_{\text{-RMSEA}}$	R^2_Loss	R^2_SIR	R^2_pH
D_N_fauna	0.112	2.530	0.979	0.143	0.145	0.036	0.025	0.036
D_N_micro	0.834	0.044	1.000	0.000	0.849	0.036	0.071	0.043
C_N_fauna	0.151	2.060	0.983	0.115	0.191	0.040	0.081	0.026
C_N_micro	0.368	0.810	0.993	0.000	0.414	0.038	0.057	0.037
D_Na_fauna	0.939	0.006	1.000	0.000	0.945	0.028	0.037	0.032

	P	X^2/df	GFI	RMSEA	P_{RMSEA}	R^2_Loss	R^2_SIR	R^2_pH
D_Na_micro	0.926	0.009	1.000	0.000	0.933	0.029	0.064	0.033
C_Na_fauna	0.613	0.256	0.998	0.000	0.647	0.053	0.075	0.025
C_Na_micro	0.854	0.034	1.000	0.000	0.868	0.034	0.072	0.029
D_PAHs_fauna	0.803	0.062	1.000	0.000	0.820	0.033	0.039	0.026
D_PAHs_micro	0.115	2.479	0.994	0.140	0.149	0.039	0.056	0.018
C_PAHs_fauna	0.882	0.022	1.000	0.000	0.893	0.020	0.039	0.026
C_PAHs_micro	0.170	1.880	0.986	0.105	0.212	0.031	0.043	0.026

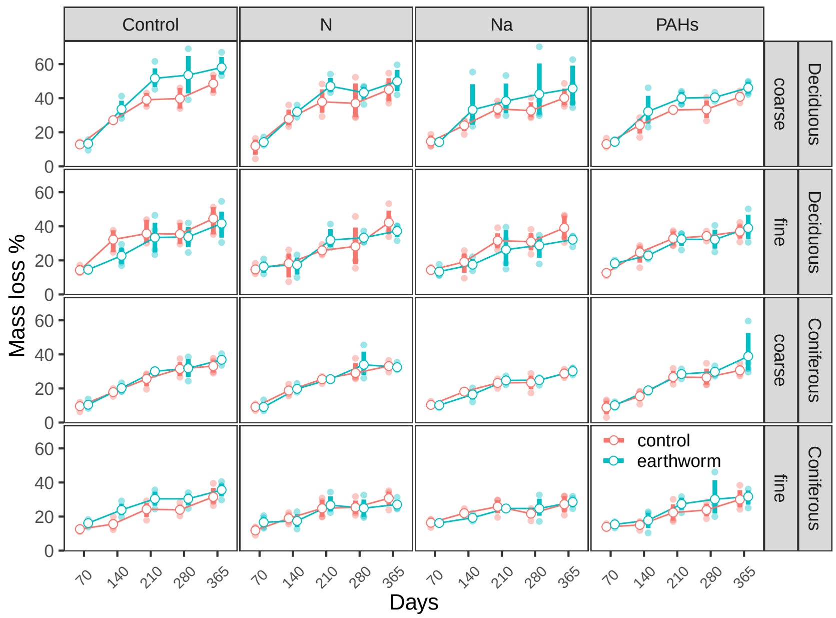


Figure 1 Changes in litter mass loss with time (70, 140, 210, 280, 365 days) as affected by different types of deposited compounds (Control, N, Na, PAHs) and earthworms (with, without) in coarse and fine mesh size litterbags in deciduous and coniferous forests; means ± SE, n = 4. For the changes in litter total C and N loss see Figure S2 and S3, respectively.

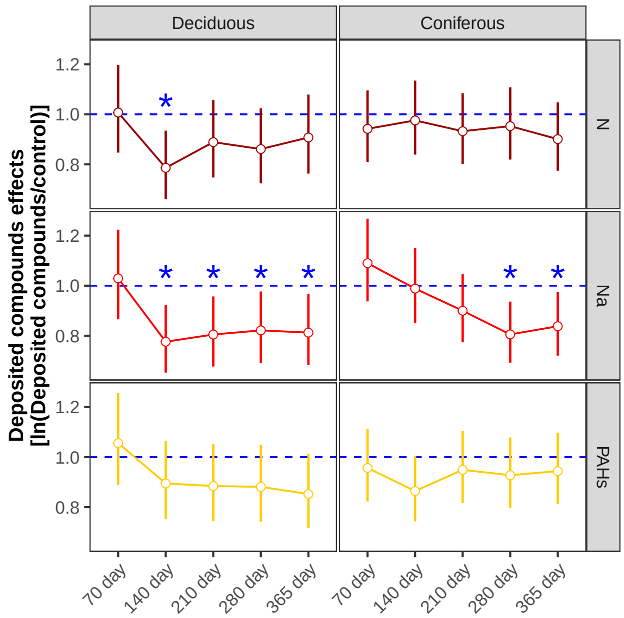


Figure 2 Changes in log response ratios [ln(deposited compounds/control)] of litter mass loss with time (70, 140, 210, 280, 365 days) as affected by different types of deposited compounds (N, Na, PAHs) in the deciduous (left) and coniferous forests (right); means with 95% confidence intervals; effect sizes were averaged across mesh size (coarse and fine) and earthworm treatment (with and without), n = 16.

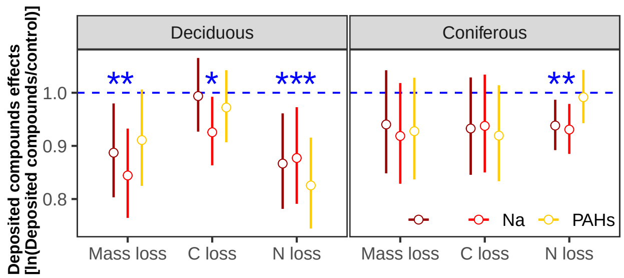


Figure 3 Effects of different types of deposited compounds (N, Na, PAHs) on litter mass loss, C loss and N loss in deciduous and coniferous forests; log response ratios [ln(deposited compounds/control)] equivalent to effect sizes ± 95% confidence intervals; effect sizes were averaged across mesh size (coarse and fine), earthworm treatment (with and without) and sampling dates (70, 140, 210, 280, 365 days), n = 80 for mass loss and n = 48 for C and N loss.

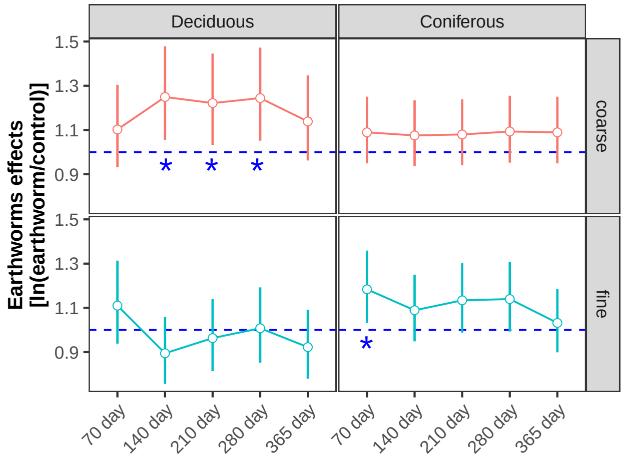


Figure 4 Changes in log response ratios [ln(earthworm/control)] of litter mass loss with time (70, 140, 210, 280, 365 days) as affected by earthworms (with, without) and mesh (coarse, fine) in the deciduous (left) and conifer forests (right); means with 95% confidence intervals; effect sizes were averaged across deposited compounds treatments (control, N, Na and PAHs), n = 16.

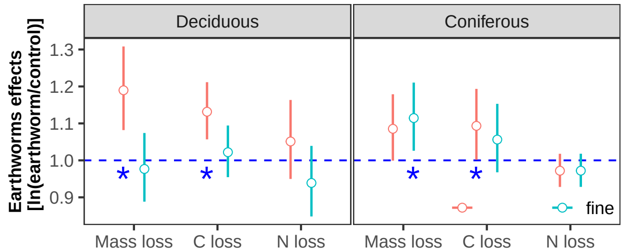
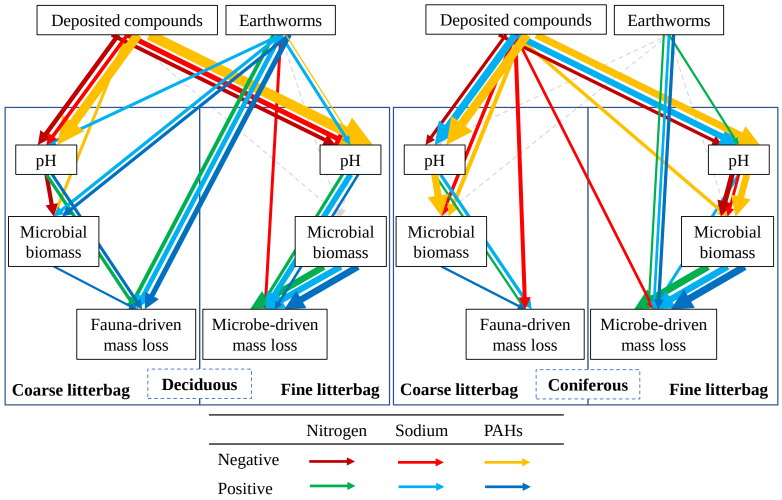


Figure 5 Changes in log response ratios [ln(earthworm/control)] of litter mass loss, C loss and N loss as affected by mesh (meso- and macrofauna) and earthworms (with, without) in the deciduous (left) and coniferous forests(right); means with 95% confidence intervals; effect sizes were averaged across deposited compounds treatment (control, N, Na and PAHs) and sampling dates (70, 140, 210, 280, 365 days), n = 80 for mass loss and n = 48 for C and N loss.



Deposited compounds
Earthworms
pH
Microbial biomass
Fauna-driven mass loss
Microbe-driven mass loss
Coarse litterbag
Deciduous
Fine litterbag
Deposited compounds
Earthworms
pH
Microbial biomass
Fauna-driven mass loss
Microbe-driven mass loss
Coarse litterbag
Coniferous
Fine litterbag
Nitrogen
Sodium
PAHs
Negative
Positive

Figure 6 Structural Equation Models (SEMs) on the effect of earthworms and deposited compounds (Na, N, PAHs; combined) on mass loss of litter in deciduous (left) and coniferous forests (right) via changes in soil pH and microbial biomass (for models on individual deposited compounds see Fig. S4 and Table S4). Solid arrows represent marginally significant or significant relationships ($P \leq 0.1$), dashed grey arrows represent non-significant relationships ($P > 0.1$). Dark red, red and yellow arrows represent negative effects of N, Na or PAHs, green, light blue and dark blue arrows represent positive effects. Arrow width is proportional to standardized path coefficients. Non-standardized path coefficients associated with solid arrows are not shown (see Fig. S4, Table S4); n = 80 (2 deposited compounds treatments × 2 earthworm treatments × 4 replicates × 5 sampling times); pH and microbial biomass refer to pH and microbial biomass in soil underneath the litterbags. The fauna-driven litter mass loss refers to the difference in litter mass loss between coarse and fine litterbags; microbial-driven mass loss refers to the litter mass loss in fine litterbags.

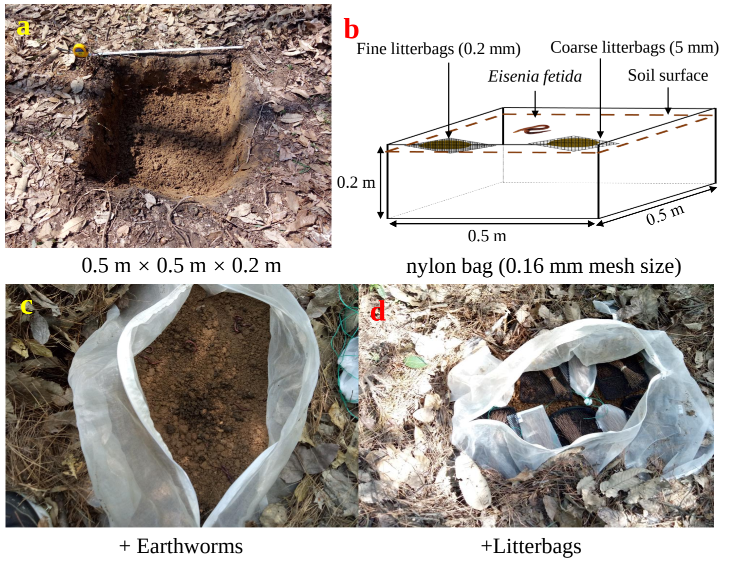


Fig. S1 Set-up of the mesocosms; (a) excavation of soil pit of 0.5 m × 0.5 m × 0.2 m; (b) the diagram of nylon bag (mesocosms) with earthworms, coarse and fine litter bags; (c) addition of *Eisenia fetida* individuals to the mesocosms; (d) placement of litterbags into the mesocosms.

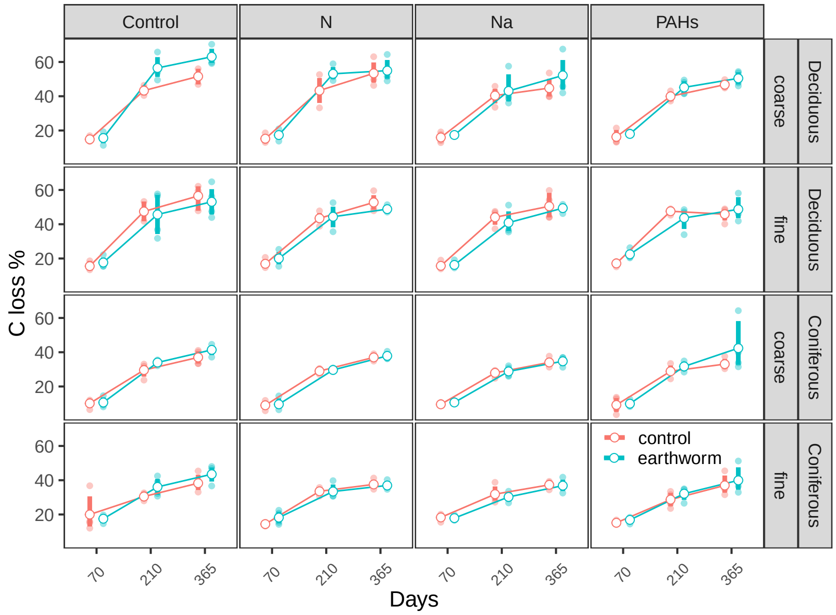


Fig. S2 Litter total C loss as affected by type of deposited compounds (Control, N, Na, PAHs) and addition of earthworms (with, green; without, red) in litterbags with coarse and fine mesh size in deciduous and coniferous forests; means ± SE; n = 4.

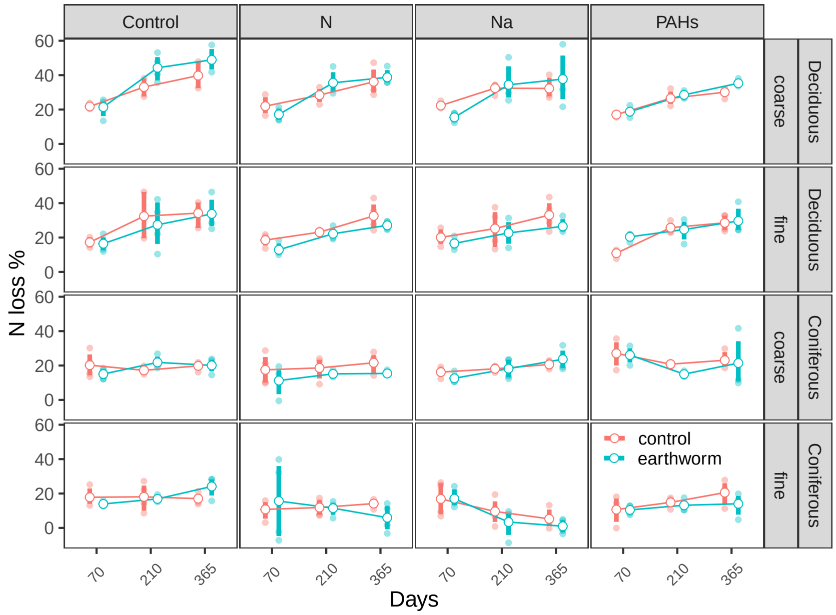


Fig. S3 Litter total N loss as affected by type of deposited compounds (Control, N, Na, PAHs) and addition of earthworms (with, green; without, red) in litterbags with coarse and fine mesh size in deciduous and coniferous forests; means ± SE; n = 4.

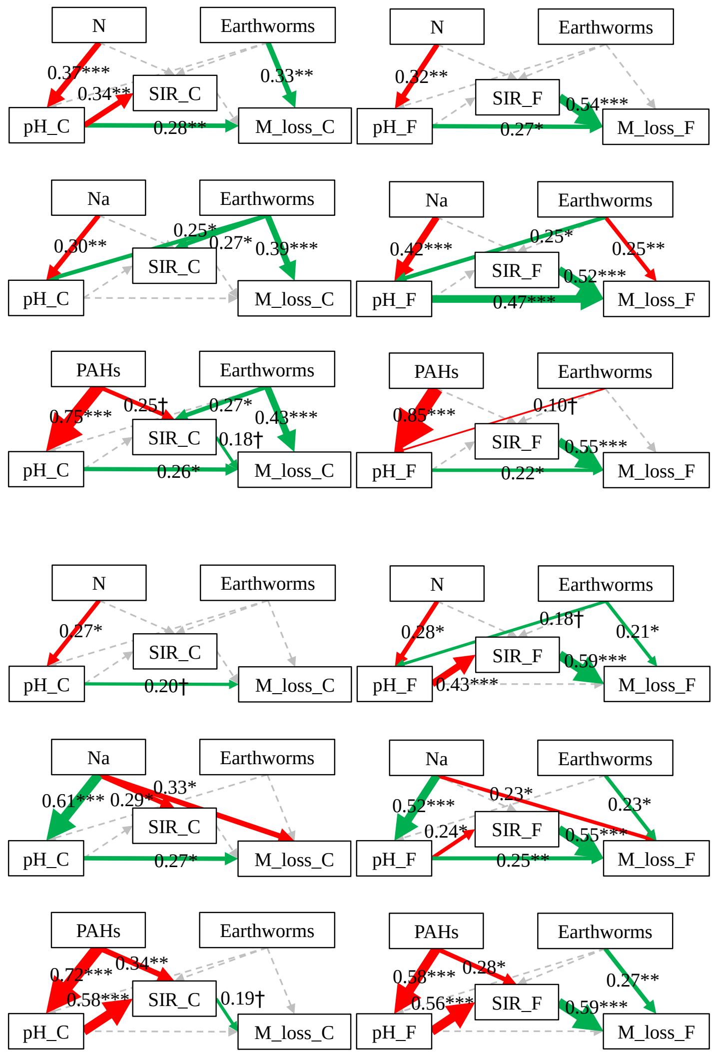

N
Earthworms
0.37***
0.34**
SIR_C
0.33**
pH_C
0.28**
M_loss_C
N
Earthworms
0.32**
SIR_F
0.54***
pH_F
0.27*
M_loss_F
Na
Earthworms
0.25*
0.30**
0.27*
0.39***
SIR_C
pH_C
M_loss_C
Na
Earthworms
0.25*
0.42***
0.25**
SIR_F
0.52***
pH_F
0.47***
M_loss_F
PAHs
Earthworms
0.75***
0.25†
0.27*
0.43***
SIR_C
0.18†
pH_C
0.26*
M_loss_C
PAHs
Earthworms
0.85***
0.10†
SIR_F
0.55***
pH_F
0.22*
M_loss_F
N
Earthworms
0.27*
SIR_C
pH_C
0.20†
M_loss_C
N
Earthworms
0.18†
0.28*
0.21*
SIR_F
0.59***
pH_F
0.43***
M_loss_F
Na
Earthworms
0.33*
0.61***
0.29*
SIR_C
pH_C
0.27*
M_loss_C
Na
Earthworms
0.23*
0.52***
0.23*
0.24*
SIR_F
0.55***
pH_F
0.25**
M_loss_F
PAHs
Earthworms
0.34**
0.72***
0.58***
SIR_C
0.19†
pH_C
M_loss_C
PAHs
Earthworms
0.28*
0.58***
0.27**
0.56***
SIR_F
0.59***
pH_F
M_loss_F

Fig. S4 Structural equation models on the effects of earthworm and types of deposited compounds (N, Na, PAHs) on fauna-driven (large mesh size litterbags) and microbial-driven decomposition (small mesh size litterbags) in deciduous (upper six graphs) and coniferous forest (lower six graphs). Arrows represent causal pathways. Solid arrows represent marginally significant relationships ($P \leq 0.1$), dashed grey arrows represent non-significant relationships ($P > 0.1$). Red arrows refer to negative effects, green arrows to positive effects. Arrow width represents the standardized path coefficients. Non-standardized path coefficients associated with each solid arrow are shown (†)P≤0.1, (*)P ≤ 0.05, (**)P ≤ 0.01, (***)P ≤ 0.001; n = 80 (2 deposited compounds treatments × 2 earthworm treatments × 4 replicates × 5 sampling times). SIR_C, microbial biomass in soil underneath coarse litterbags, pH_C, soil pH underneath coarse litterbags, SIR_F, microbial biomass in soil underneath fine litterbags, pH_F, soil pH underneath fine litterbags, M_loss_C, fauna-driven litter decomposition (i.e., the difference in mass loss between coarse and fine litterbags), M_loss_F, microbe-driven litter mass loss (fine litterbags).