



Disentangling the effects of region, forest-management intensity and plant diversity on litterfall quantity, quality and turnover in temperate forests

Wolfgang Wilcke · Vera Zimmer ·
Jürgen Bauhus · Ingo Schöning ·
Marion Schrumpf · Beate Michalzik · Jan Siemens

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Abstract

Purpose Simultaneous effects of more than one global change driver on ecosystem functioning have rarely been assessed.

Methods We disentangled the effects of region encompassing climatic and edaphic conditions, forest-management intensity and community plant diversity on litterfall quantity, quality and turnover in 27 temperate forests across an environmental gradient.

Results Region significantly influenced litterfall and organic layer mass and chemical quality and litter and element turnover. After accounting for the influence of region, increasing forest-management intensity (ForMI) significantly decreased litterfall mass, N, P and K concentrations and nutrient fluxes and slowed down litter and nutrient turnover. Because increasing ForMI

reflected the man-made contributions of coniferous trees, these results can partly be attributed to the lower litterfall at our study sites and slower litter turnover of coniferous than deciduous trees. After accounting for the influences of region and ForMI, increasing diversity of the vascular plant community on the study plots measured as species richness or Shannon index significantly increased C and decreased N, P and S concentrations in litterfall. Together with the significantly decreased N and P concentrations in the organic layer with increasing plant diversity, these results indicated an increased within-stand nutrient-use efficiency and a more complete soil nutrient use with increasing plant diversity.

Conclusions Our results demonstrate that increasing ForMI, which is associated with increasing conifer shares, leaves element stocks in the organic layer unchanged but slows down C turnover and thus increases temporary C storage in soil organic layers. Moreover, community vascular plant diversity helps close nutrient cycles.

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W. Wilcke (✉) · V. Zimmer
Institute of Geography and Geoecology, Karlsruhe
Institute of Technology (KIT), Reinhard-Baumeister-Platz
1, 76131 Karlsruhe, Germany
e-mail: wolfgang.wilcke@kit.edu

J. Bauhus
Albert Ludwigs University Freiburg, Freiburg, Germany

I. Schöning · M. Schrumpf
Max Planck Institute for Biogeochemistry, Jena, Germany

B. Michalzik
Institute of Geography, Friedrich Schiller University Jena,
Jena, Germany

B. Michalzik
German Centre for Integrative Biodiversity Research
(iDiv) Halle-Jena-Leipzig, Leipzig, Germany

J. Siemens
Institute of Soil Science and Soil Conservation, iFZ
Research Center for BioSystems, Land Use and Nutrition,
Justus Liebig University Giessen, Giessen, Germany

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Introduction

Litterfall and its turnover in the soil organic layer are important components of the C and nutrient cycles in forests (Krishna and Mohan 2017; Prescott and Vesterdal 2021; Vogt et al. 1986). The frequently measured fine litterfall consists of leaves/needles, twigs, flowers, fruits, seeds and other small dead organic materials dropping from the forest canopies to the soil. Fine litterfall is usually collected with several at least 0.25 m²-large traps. Fine litterfall accounts for about one third of the net primary production (Bray and Gorham 1964; Chave et al. 2010). The above-ground fine litterfall primarily accumulates on top of the mineral soil as soil organic layer, which can be differentiated into the Oi (fresh litter), Oe (shredded, hyphenated litter), and the Oa (amorphous organic matter) horizons (IUSS Working Group WRB 2022). The ratio between the organic matter mass and C and nutrient stocks in the soil organic layer including fine and medium roots and the annual litterfall mass and C and nutrient fluxes with litterfall, provides a rough estimate of the residence times of the organic matter and these elements in the organic layer and thus of both C retention and nutrient availability. This ratio can be referred to the fresh litter (Oi horizon) alone or to the whole organic layer (K_{Oi} and K_{OL} values with the unit “yrs”, respectively; Vogt et al. 1986). However, considering only aboveground litterfall and neglecting root litter input can result in an overestimation of the residence times of organic matter, C and nutrients in the organic layer (Vogt et al. 1986).

Mass, C and nutrient concentrations of litterfall and organic layers and the residence times of the organic matter, C and nutrients in the organic layer are driven by tree species, stand age and site conditions (Binkley 2021; Vogt et al. 1986). Joly et al. (2023) showed that macroclimate and litter properties are the most important drivers of litter decomposition. Soil properties together with the climate control nutrient availability (Krishna and Mohan 2017; Prescott and Vesterdal 2021; Vogt et al. 1986). In a comprehensive early review, Vogt et al. (1986) have shown that on a global scale litterfall correlates

negatively with latitude because of the strong influence of light availability. The N concentration in litterfall was positively correlated with the litterfall mass, while P concentrations did not correlate with litterfall mass. This suggests that the availability of N plays a particularly important role for litterfall production (Vogt et al. 1986). However, in the global meta-analysis of LeBauer and Treseder (2008), litterfall alone did not respond to increasing N availability while aboveground net primary production increased.

The centuries-long management of Central European forests has resulted in a higher share of conifers than would occur naturally (FAO 2011; McGrath et al. 2015; Sala et al. 2000). Coniferous forests are usually managed in shorter rotations. The more frequent tree harvests represent a management intensification (Schmitz et al. 2005). Coniferous forests are reported to produce less litter than deciduous forests (Vogt et al. 1986). Although Neumann et al. (2018) confirmed this for European forests on average (19.4 vs. 24.0 g m⁻² yr⁻¹ for coniferous vs. deciduous forests), the reverse was true for regions in the North and the South of Europe. Hansen et al. (2009) even reported that three coniferous and two deciduous tree species did not show significantly different litterfall if growing on similarly fertile soils in a common garden experiment in Denmark. Thus, the influence of conifers on litterfall seems to depend on site conditions including climate and soil fertility. The changed tree composition has implications for chemical litter properties including the concentrations of phenolic compounds and the lignin:N and C:nutrient ratios, which influence litter turnover (Aerts 1997; Hättenschwiler et al. 2005; Vogt et al. 1986). The increased conifer share has additionally impacted biogeochemical nutrient cycling compared to native deciduous forests because of e.g., changed throughfall quality, changed nutrient leaching from the organic layer (Augusto et al. 2002; De Schrijver et al. 2007) and a reduced base pump effect (Achilles et al. 2021a). Forest management can have effects on the C storage of forest soils (Mayer et al. 2020) and the composition of soil biota (Chauvat et al. 2011; Siira-Pietikäinen et al. 2001). Inagaki et al. (2004) have shown that tree age and species composition, which are the result of management in forests available for wood production, drives N mineralization. Thinning, which is a common management treatment particularly of age-class forests, temporally increases litterfall of individual

trees but reduces total litterfall and associated nutrient transport to the soil (Blanco et al. 2006; Doukalianou et al. 2022). Thinning also accelerates the turnover of the organic layer, because of increased soil temperatures (Kunhamu et al. 2009). Tree harvesting can compact the soils increasing erosion risks, particularly in wheel ruts. Harvesting can also cause organic matter loss and nutrient removal (Burger and Kelting 1999; Grigal 2000; Mayer et al. 2020). Clear-cutting, the most common forest harvest practice worldwide, drastically changes the microclimate potentially favoring mineralization and thus resulting in C losses (Marshall 2000; Mayer et al. 2020).

Mixtures of tree species increase productivity across tropical and temperate plantations relative to monocultures (Forrester and Bauhus 2016; Piotta 2008). Cardinale et al. (2012) reviewed 20 years of biodiversity-ecosystem functioning research confirming that tree species richness increases wood production in forests. Furthermore, increasing plant species richness enhances aboveground C sequestration in forests, accelerates nutrient mineralization, and increases organic matter storage, although the results concerning the long-term (> 10 yr) C storage were mixed (Cardinale et al. 2012). In line with these results, tree species richness showed weak positive relationships with the decomposition rate of cellulose and the C stock in the topsoil in 209 European forest stands (Dawud et al. 2017; Joly et al. 2017). Similarly, tree diversity was positively related with C and N accumulation in the soils of Canada's National Forest Inventory (Chen et al. 2023). Alberti et al. (2017) also confirmed that mixing tree species in a temperate forest may accelerate organic matter turnover and nutrient cycling. However in their study, this resulted in lower soil C stocks relative to monocultures. In another study in a temperate Australian forest, Forrester et al. (2013) reported that the C stocks might increase in spite of an accelerated litter turnover in mixed relative to monoculture forests. In a forest biodiversity experiment in Panama, Potvin et al. (2011) observed, in contrast, a decrease of the decomposition rate of coarse woody debris and soil respiration in 3- to 6-species mixtures relative to monocultures and suggested increased C storage with increasing species richness. The contrasting results illustrate that we do not yet fully understand the relationship between plant or tree richness in forests and C turnover and storage.

In the forest biodiversity experiment in Panama, three-species mixtures increased mean Ca concentrations in branches and stems and increased N, P, K, Ca and Mg storage in aboveground biomass compared to monocultures suggesting complementary resource uptake (Oelmann et al. 2010). In contrast, Xu et al. (2020) did not detect significant species richness effects on soil moisture, pH, N and P concentrations, respiration, litter decomposition rate and microbial communities in their global meta-analysis of 95 biodiversity-ecosystem functioning studies. Moreover, Schwarz et al. (2014) found that an increasing species richness improved the N retention from atmospheric deposition in the forest canopy. Schwarz et al. (2016) reported reduced N leaching from mull-type organic layers with increasing plant diversity. Thus, the assumption that species-rich plant assemblages improve community nutrient-use efficiency through complementary nutrient use, which was found in grassland experiments (Tilman et al. 1996; Weisser et al. 2017) and agriculturally used grasslands (Kleinebecker et al. 2014), may also hold true for forests (Scherer-Lorenzen et al. 2005). For forests, Vitousek (1982) proposed to use the inverse of the nutrient concentration in bulk fine litterfall of entire forest stands as easily accessible indicator of within-stand nutrient-use efficiency, because of the widespread measurement of bulk fine litterfall and its chemical properties.

Our overall objective was to disentangle the influences of region (reflecting climatic and edaphic site conditions), forest-management intensity and community vascular plant diversity on litterfall, organic layer mass, residence times of the organic layer, nutrient concentrations in litterfall and organic layer, nutrient fluxes with litterfall and residence times of nutrients in the organic layer. Our study included 27 temperate forests spanning a gradient in environmental conditions, forest-management intensity and associated community vascular plant diversity in Germany. We consider the study forests as representative for a large part of Central Europe. Specifically, we tested the hypotheses that (i) region has an effect on nearly all target variables, (ii) increasing forest-management intensity results in decreasing litter production because of increasing shares of conifers but nevertheless increasing organic layer masses, because of reduced litter turnover and thus longer C residence times in the organic layer, and (iii) after accounting

for the effects of region and forest-management intensity, increasing community vascular plant diversity helps close nutrient cycling by increasing the within-stand nutrient-use efficiency, i.e., the bulk fine litterfall produced per unit nutrient in the litter and by more comprehensively exploiting the nutrient pool in the organic layer.

Material and methods

Study area

Our study was conducted on the 27 very intensively studied forest plots of the Biodiversity Exploratories (<https://www.biodiversity-exploratories.de>) in three regions in Germany, i.e., Schorfheide-Chorin, Hainich-Dün and Schwäbische Alb (from northeast to southwest Germany; Fischer et al. 2010). The three research regions differing in climate, geological parent materials and soil cover are representative for large parts of Central Europe (Fig. S1, Table S1). The studied forests are age-class, i.e., forests consisting of one or more even-aged development stages which are harvested at 80–120 year intervals by clear cut or shelterwood logging, or near-natural stands. Most of them are regularly managed with a different intensity except for some stands that had been protected for at least 60 yr. Between 2008 and 2012, the mean diameter at breast height of the study plots was determined to range from 13 to 85 cm (Schwarz et al. 2014). The study plots had a size of 100 m × 100 m. The tree species composition was dominated by European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* (L.) H. Karst.) or Scots pine (*Pinus sylvestris* L.) (Table S2). The tree species compositions of the studied forests are representative for large parts of the respective study region (Fischer et al. 2010). We considered a forest stand as coniferous trees- or deciduous trees-dominated if coniferous or deciduous trees included > 50% of the stems with a diameter at breast height > 10 cm.

Field sampling

We collected organic layer samples in 14 replicates per plot with a 15 cm × 15 cm metal frame, determined the thickness of the three organic horizons Oi, Oe, and Oa, dried the samples at 60 °C and weighed

the quantitatively collected horizon samples to determine the bulk density of each organic horizon. We used averaged data of the soil sampling campaigns in May 2014 and 2017. An exception were the element concentrations in the organic layer at Hainich-Dün and Schwäbische Alb, which were determined in the samples of the sampling campaign in May 2011. In temperate forests, the thickness of the Oi horizon usually varies in the course of the year. Because we sampled the organic layer in May the element stocks in the Oi horizon and their residence times refer to an intermediate Oi mass.

To collect litterfall, we used five traps per plot. Each trap had a collecting area of 0.25 m² and consisted of a wooden frame and a polyethylene net. The litterfall was collected biweekly, although this was not always possible because of logistic problems or access restrictions to the plots. Litterfall was collected from the end of October 2013 to the beginning of October 2016 covering three years.

The richness of all vascular plants of the whole community was annually determined in each forest stand in a 20 m × 20 m subplot including all non-woody species (herb layer), shrubs (woody species with a height < 5 m), understory trees (woody species with a height from 5 to 10 m) and canopy trees (woody species with a height > 10 m). The surface area covered by each species was separately estimated for the four vegetation layers. The annual data was combined from two surveys in April and in June–August to make sure that all species, irrespective of their growing time, were recognized. We used averaged data of the years 2010–2015. There were no data from 2012.

We used the Forest Management Intensity Index (ForMI), which is based on inventory data from 2008 to 2012 regarding the living trees, stumps and dead wood. The ForMI is the sum of three component indicators taking into account the proportion of potential total standing tree volume that was harvested in the past approximately 40 years, which was the assumed turnover time of stumps as indicated by stumps, where a cut of a chain saw was visible, the share of tree species in the standing volume that are not part of the natural forest community, and the proportion of the total amount of dead wood with signs of saw cuts indicating that it was generated through harvesting or thinning. Each indicator received a value between 0 (no sign of management) and 1 (intensive

management) and the three components were then added up to yield the ForMI, which can assume a value between 0 and 3 (Kahl and Bauhus 2014).

Chemical analyses

For chemical analysis, organic horizon and bulk litterfall samples were ground with a ball mill. We determined total C, N and S concentrations by element analysis via thermal combustion at 1020 °C, catalytic reduction of N and detection by thermal conductivity after chromatographic separation of CO₂, N₂ and SO₂. To determine Ca, K, Mg and P concentrations, we digested aliquots of the ground litterfall and organic horizon samples with 8 mL concentrated HNO₃ and 2 mL H₂O₂ in a microwave oven. The element concentrations in the digests were quantified with Atomic Absorption Spectrometry or Inductively-coupled Plasma-Optical Emission Spectroscopy. To control for background contamination, we included blank digests, the results of which were subtracted if we detected measurable concentrations of the target element. To check the accuracy of our measurements, we used a certified reference material (NIST 1515, apple tree leaves). Our measurements deviated by < 5% from the certified element concentrations.

Calculations and statistical evaluation

Mean nutrient concentrations in bulk annual litterfall and in the whole organic layer were mass-weighted based on the litterfall of each sampling interval and the mass of the three organic horizons O_i, O_e and O_a, respectively. We calculated the ratio of mass or the stock of C or nutrient in the O_i horizon or whole organic layer to the annual flux of mass, C or nutrient by litterfall (K_{O_i} and K_{OL} values, respectively) following Vogt et al. (1986). The K_{O_i} and K_{OL} values represent the mean residence times [yrs] of organic matter or an element in the O_i horizon or the whole organic layer. As an indicator of the within-stand nutrient-use efficiency, we used the inverse of the nutrient concentrations in bulk litterfall [i.e., g litterfall mass per mg nutrient] following Vitousek (1982).

For each forest plot, the Shannon index of the vegetation community (i.e., all vascular plant species on the plot including all four vegetation layers) was calculated according to Eq. 1:

$$\text{Shannon index} = - \sum_{i=1}^S p_i \ln(p_i) \quad (1)$$

where S denotes the total number of plant species present, i identifies an individual species, and p_i is the contribution of species i to the total cover of the four vegetation layers.

We used one-way ANOVA followed by Tukey's Honest Significant Difference post-hoc test to compare mean properties of the three Exploratories. Data handling and analysis were performed in R version 4.1.1 (R Development Core Team 2021).

We hierarchically analyzed the effects of (i) region (Biodiversity Exploratory, i.e., Schwäbische Alb, Hainich-Dün and Schorfheide-Chorin), (ii) ForMI, and either the (iiia) Shannon index or the (iiib) plant species richness (in separate models) with linear mixed models using the function *lmer()* of the package *lme4* (Bates et al. 2015). The homogeneity of variances was tested with Levene's test and the normal distribution of residuals by visual inspection. In some cases, we had to transform the data to meet these prerequisites and such transformations are noted in the results tables. We repeated the same analyses for a reduced data set only including the deciduous trees-dominated stands ($n=18$) to assess the influence of the conifers on our results.

Results

Schorfheide-Chorin had the significantly highest mean organic layer mass and the longest mean residence time of the organic layer (K_{OL}), while the mean organic layer masses and K_{OL} values at Schwäbische Alb and Hainich-Dün were not different from each other (Table 1). Hainich-Dün had the significantly highest mean K and S concentrations in litterfall and K and Mg concentrations in the organic layer. Schorfheide-Chorin had the significantly lowest Ca and S concentrations in litterfall and C, K and S concentrations in the organic layer. Schorfheide-Chorin had the significantly highest C/S ratio in the litterfall and mean within-stand nutrient-use efficiencies of Ca and S, while Schwäbische Alb had the highest N/P ratio in litterfall and within-stand nutrient-use efficiency of K (Table S3). Schorfheide-Chorin had the highest mean stocks of all elements in the organic layer

Table 1 Means \pm standard errors of the nine study sites at each of the three Biodiversity Exploratories (Schwäbische Alb, Hainich-Dün and Schorfheide-Chorin) of the annual litterfall (mean of three years; 2013–2016), the organic layer mass (mean of two determinations in 2014 and 2017), the residence times of the Oi horizon (K_{Oi}) and the whole organic layer (K_{OL} – both residence times calculated as mean Oi/whole organic layer mass of the determinations in 2014 and 2017 divided by mean annual litterfall of three years), the C, N, P, K, Ca, Mg and S concentrations in annual litterfall (mean of three years; 2013–2016) and in the whole organic layer (from 2011 at Hainich-Dün and Schwäbische Alb and mean of 2014 and 2017 at Schorfheide-Chorin; all concentrations mass-weighted)

	Organic layer		Litterfall										Organic layer											
	Litterfall kg m ⁻² yr ⁻¹	K_{Oi} kg m ⁻² yrs	K_{OL}	C	N	P	K	Ca	Mg	S	C	N	P	K	Ca	Mg	S	C	N	P	K	Ca	Mg	S
Schwäbische Alb	0.54 ± 0.03	2.9 $\pm 0.56b$	11 $\pm 1.5b$	474 ± 2.4	12 ± 0.41	0.72 ± 0.08	2.3 $\pm 0.09b$	12 $\pm 0.78a$	0.78 ± 0.07	0.77 $\pm 0.02ab$	410 $\pm 13a$	13 ± 0.69	0.88 ± 0.08	3.4 $\pm 0.49b$	16 $\pm 1.5a$	1.7 $\pm 0.15ab$	1.5 $\pm 0.07a$	410 $\pm 13a$	13 ± 0.69	0.88 ± 0.08	3.4 $\pm 0.49b$	16 $\pm 1.5a$	1.7 $\pm 0.15ab$	1.5 $\pm 0.07a$
Hainich-Dün	0.61 ± 0.05	3.1 $\pm 0.40b$	5.2 $\pm 0.73b$	471 ± 2.9	12 ± 0.35	0.85 ± 0.06	3.5 $\pm 0.29a$	12 $\pm 0.55a$	1.1 ± 0.06	0.81 $\pm 0.04a$	379 $\pm 12a$	12 ± 0.5	0.83 ± 0.04	6.8 $\pm 0.49a$	15 $\pm 1.1a$	2.9 $\pm 0.65a$	1.4 $\pm 0.04a$	379 $\pm 12a$	12 ± 0.5	0.83 ± 0.04	6.8 $\pm 0.49a$	15 $\pm 1.1a$	2.9 $\pm 0.65a$	1.4 $\pm 0.04a$
Schorfheide-Chorin	0.55 ± 0.01	15.5 $\pm 0.18a$	28 $\pm 3.2a$	479 ± 3.2	11 ± 0.78	0.94 ± 0.10	3.3 $\pm 0.41ab$	6.7 $\pm 0.56b$	0.89 ± 0.10	0.67 $\pm 0.05b$	216 $\pm 0.79b$	8.7 ± 0.28	0.77 ± 0.06	0.95 $\pm 0.09c$	4.3 $\pm 0.53b$	0.75b ± 0.10	0.85 $\pm 0.04b$	216 $\pm 0.79b$	8.7 ± 0.28	0.77 ± 0.06	0.95 $\pm 0.09c$	4.3 $\pm 0.53b$	0.75b ± 0.10	0.85 $\pm 0.04b$

Lower case letters indicate significant differences according to Tukey's Honest Significant Difference post-hoc test. Lacking letters indicate no significant differences

except for Ca and K, while Hainich-Dün had the highest mean K stock in the organic layer (Table S3). Schorfheide-Chorin had the significantly longest residence times of all elements except for Ca and K in the whole organic layer (K_{OL}), while the K_{OL} values of all elements were not significantly different between Hainich-Dün and Schwäbische Alb (Table S3).

In our hierarchical linear mixed model, region (i.e., Schwäbische Alb, Hainich-Dün and Schorfheide-Chorin) encompassing climatic and edaphic conditions had a marginally significant effect on litterfall and a significant effect on soil organic layer mass and residence time of the total organic layer (K_{OL} , Table 2). Region had an at least marginally significant effect on all element concentrations in litterfall except that of P and on all element fluxes with litterfall except that of C (Table 2). Moreover, region had a significant effect on all element concentrations except that of P and all element stocks in the organic layer except that of Ca. Region did not influence the K_{Oi} value of any element but significantly influenced the K_{OL} value of all elements except K (Table S4).

After accounting for region, the forest-management intensity (measured as ForMI) was significantly negatively related with litterfall (Fig. 1a) and significantly positively with the K_{OL} value (Fig. 1d). Moreover, ForMI had a marginally significant positive effect on the organic layer mass and K_{Oi} value (Fig. 1b, c). Because ForMI includes a measure of the share of tree species that are not part of the natural forest community, which are mostly coniferous trees, the coniferous trees-dominated stands usually showed a higher ForMI ($1.9 \pm$ standard error 0.12, $n = 9$) than the deciduous stands (0.78 ± 0.14 , $n = 18$). When we omitted the three coniferous trees-dominated stands at each of the three Biodiversity Exploratories and recalculated our linear mixed models, the effects of ForMI on litterfall ($p < 0.001$) and on the K_{Oi} value ($p = 0.078$) were still (marginally) significant, while the effects of ForMI on the organic layer mass and the K_{OL} value disappeared. Considering all 27 forest stands, ForMI was significantly positively related with the C concentration and C/N and C/S ratios in litterfall but negatively with N, P and K concentrations in litterfall (Tables 2 and S4). When we analyzed the data set without the coniferous trees-dominated stands, only the negative relationship between ForMI and K concentration in litterfall remained. As a consequence, increasing ForMI at least marginally

Table 2 Effects of region, forest-management intensity (ForMI), Shannon index and species richness in hierarchical linear mixed models on litterfall, organic layer mass, residence time of the Oi horizon (K_{Oi}), residence time of the whole organic layer (K_{OL}), C and nutrient concentrations in and fluxes with litterfall

The effects of Shannon index and species richness were tested in separate models. SS is the sum of squares. In the models including the Shannon index, the N concentrations in litterfall were square root-transformed and the P concentrations in litterfall and P and K fluxes with litterfall were log-transformed. In the models including species richness, most data sets were log-transformed except Ca and N concentrations (square root) and fluxes of Mg (no transformation), N (reverse plus 10) and P (power of 2). Significant p values are in bold and marginally significant ones ($p < 0.1$) in italics. The direction of the influence (if directed) is shown with an arrow

		Region	ForMI	Shannon index	Species richness
	df	2	2	2	2
Litterfall	SS	2770	15800	0.214	4.22
	p	<i>0.088</i>	< 0.001 ↓	0.523	0.810
Organic layer mass	SS	76200	3740	838	986
	p	< 0.001	<i>0.069</i> ↑	0.376	0.336
K_{Oi}	SS	3220	3840	0.030	0.013
	p	0.227	<i>0.065</i> ↑	0.865	0.799
K_{OL}	SS	2580	286	9.1	13.3
	p	< 0.001	0.005 ↑	0.426	0.509
Element concentrations in litterfall					
C	SS	278	526	244	242
	p	<i>0.073</i>	0.003 ↑	0.033 ↑	0.034 ↑
N	SS	0.187	0.425	0.203	0.129
	p	<i>0.089</i>	0.002 ↓	0.024 ↓	<i>0.079</i> ↓
P	SS	0.161	0.300	0.391	0.220
	p	0.250	0.028 ↓	0.014 ↓	<i>0.074</i> ↓
K	SS	7.46	8.10	0.397	0.007
	p	0.003	< 0.001 ↓	0.373	0.697
Ca	SS	174	2.45	2.66	0.697
	p	< 0.001	0.428	0.410	0.453
Mg	SS	0.346	0.087	0.140	0.094
	p	<i>0.051</i>	0.202	0.110	0.264
S	SS	0.103	0.020	0.051	0.041
	p	0.019	0.193	0.041 ↓	0.172
Element fluxes with litterfall					
C	SS	541E+3	304E+4	79E+3	589E+8
	p	0.138	< 0.001 ↓	0.434	0.902
N	SS	712.0	5285.4	96.4	0.00
	p	0.008	< 0.001 ↓	0.211	0.181
P	SS	0.285	1.57	0.241	1.79
	p	<i>0.062</i>	< 0.001 ↓	0.031 ↓	<i>0.090</i> ↓
K	SS	1.20	2.61	0.009	0.003
	p	< 0.001	< 0.001 ↓	0.645	0.793
Ca	SS	6390	2850	249	66E+11
	p	< 0.001	< 0.001 ↓	0.157	0.349
Mg	SS	20.6	27.3	1.73	0.799
	p	0.001	< 0.001 ↓	0.219	0.408
S	SS	6630	15300	0.423	0.581
	p	< 0.001	< 0.001 ↓	0.167	0.102

significantly increased within-stand nutrient-use efficiencies of N, P, K and S (Table S4), when all forest stands were considered but only of K when the coniferous trees-dominated stands were omitted. Moreover, increasing ForMI resulted in a decrease of

all considered element fluxes with litterfall no matter if all 27 or only the 18 deciduous trees-dominated stands were considered (Table 2). Although ForMI did not influence any element concentration or stock in the organic layer irrespective of the consideration

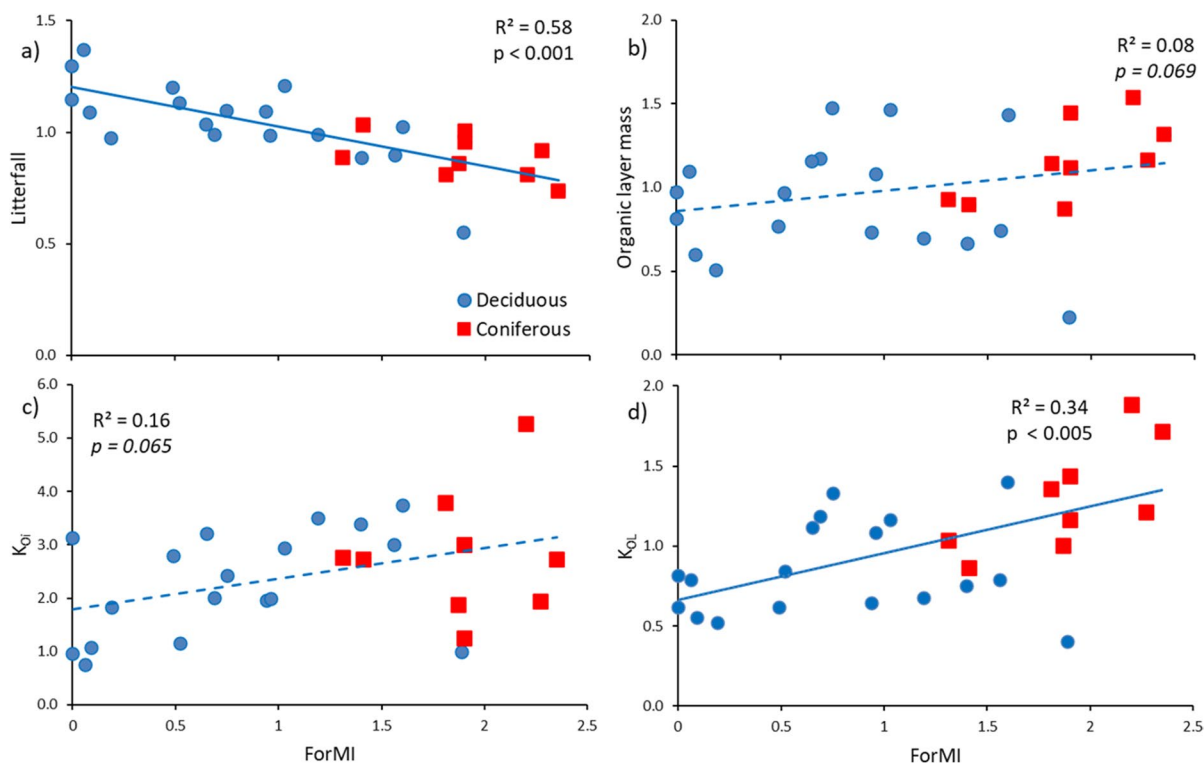


Fig. 1 Relationship between the Forest Management Index (ForMI) and **a)** litterfall, **b)** organic layer mass, **c)** the residence time of the Oi horizon (K_{Oi} in years), and **d)** the residence time of the whole organic layer (K_{OL}). Blue dots are deciduous trees (beech)-dominated forests, red squares are coniferous trees (Norway spruce or Scots pine)-dominated forests. The litterfall, organic layer mass and K_{OL} value were divided by the mean of the respective Exploratory (i.e.,

Schwäbische Alb, Hainich-Dün, Schorfheide-Chorin) to eliminate the influence of region which was at least marginally significant and are therefore unitless. The p values are taken from the results of the hierarchical linear mixed model; p values in italics indicate marginal significance ($p < 0.1$) and regression lines are dashed if the relationship is only marginally significant

of all sites or of only the deciduous trees-dominated stands, increasing ForMI increased the K_{Oi} and K_{OL} values of all elements at least marginally significantly except the K_{OL} value of Ca (Table S4). When the coniferous trees-dominated stands were omitted, only a marginally significant positive effect of ForMI on the K_{Oi} value of Ca remained.

After accounting for both the influence of region and ForMI, community vascular plant diversity measured as Shannon index was significantly positively related with the C concentration in litterfall (Fig. 2a) and negatively with N, P and S concentrations (Fig. 2b-d). Species richness influenced the C and nutrient concentrations in litterfall similarly, except that it only had a marginally significant effect on the N and P concentrations and did not influence

the S concentration (Table 2). As a consequence, the within-stand nutrient-use efficiency of N, P, Mg and S increased at least marginally significantly with increasing plant diversity (Table S4). The Shannon index was not fully independent of the presence of coniferous trees as indicated by a weak but significant positive correlation with ForMI ($r = 0.58$, $p = 0.002$, $n = 27$). Therefore, we again recalculated our models after omitting the nine coniferous trees-dominated stands. Without the coniferous trees-dominated stands, of the above described relationships only a marginally significant negative effect of species richness on P concentrations in litterfall persisted. However, there was a new significant positive effect of the Shannon index and a marginally significant one of the species richness on the Ca concentration in litterfall

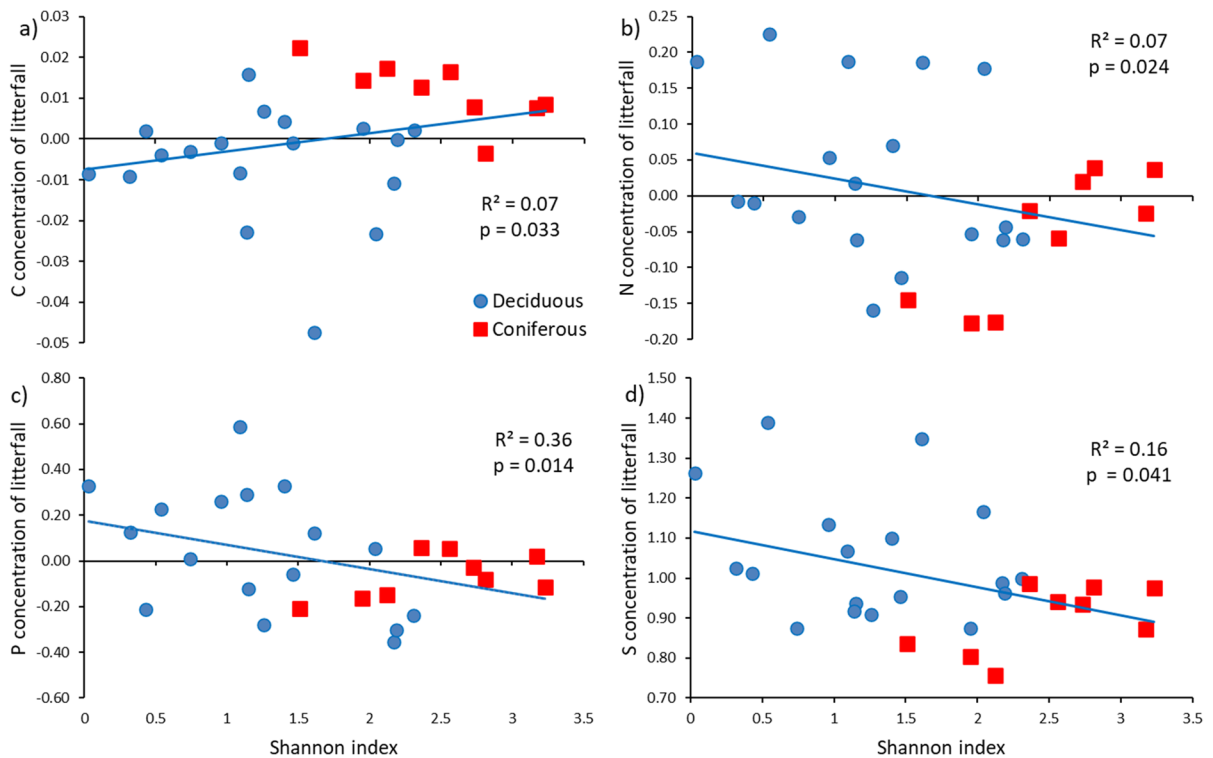


Fig. 2 Relationship between the Shannon index of all vascular plants on the study plots and the **a**) C, **b**) N, **c**) P and **d**) S concentrations in litterfall. The C, N and S concentrations in litterfall were divided by the mean of the respective Exploratory (i.e., Schwäbische Alb, Hainich-Dün, Schorfheide-Chorin) to eliminate the influence of region, which was at least marginally significant and are therefore unitless (Table 2). From the C and N concentrations, additionally the significant influence of forest-management intensity (ForMI) was mathematically removed by subtracting the expected concentration modeled

by a regression of the element concentrations normalized to the Exploratories on ForMI. From the P concentration (in mg g^{-1}), the significant influence of the ForMI was mathematically removed from the original data by subtracting the expected concentration modeled by a regression of the element concentration on ForMI, because the effect of the region was not significant. Blue dots are deciduous trees (beech)-dominated forests, red squares are coniferous trees (Norway spruce or Scots pine)-dominated forests. The p values are taken from the results of the hierarchical linear mixed model (Table 2)

and corresponding significant negative ones on the Ca-use efficiency.

The Shannon index and species richness were significantly and marginally significantly negatively related with the P flux with litterfall, respectively, and the Shannon index was significantly positively related with the K_{O_i} value of K (Tables 2 and S4). The species richness was marginally significantly positively related with the K_{O_i} value and the Shannon index and the species richness were significantly and marginally significantly positively related with the K_{O_L} value of Mg (Table S4). Moreover, the Shannon Index was marginally significantly and significantly negatively related with the N and P concentrations in the organic layer, respectively (Fig. 3, Table S4). Species richness was marginally

significantly negatively related with the P concentration in the organic layer (Table S4). The Shannon index was marginally significantly positively related with the C/P and N/P ratios in the organic layer. Without the coniferous trees-dominated stands, there was a marginally significant negative effect of the Shannon index on the S concentration in the organic layer and a marginally significant positive one on the C/N ratio of the organic layer. Without the coniferous trees-dominated stands, species richness had a significant negative effect on the S concentration of the organic layer (Fig. S2), significant positive effects on the C/N, C/P and C/S ratios in the organic layer and marginally significant positive effects on the N/P ratio in the organic layer (Fig. S3) and the K_{O_i} value of K.

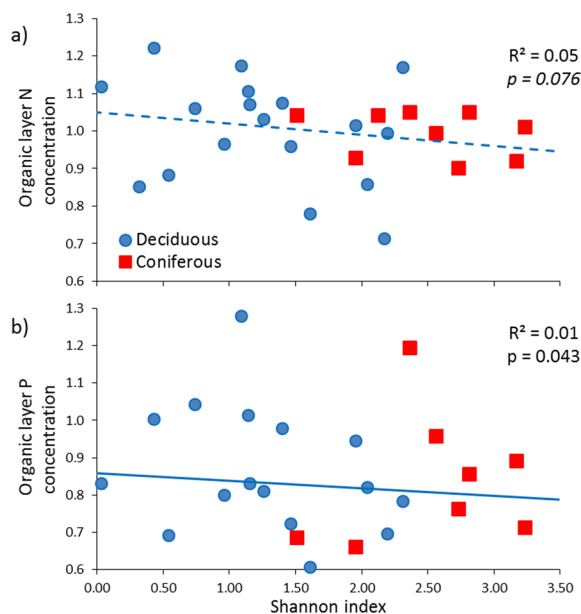


Fig. 3 Relationship between the Shannon index and the **a)** N and **b)** P concentrations (in mg g^{-1}) in the whole organic layer. Blue dots are deciduous trees (beech)-dominated forests, red squares are coniferous trees (Norway spruce or Scots pine)-dominated forests. The N concentrations were divided by the mean of the respective Exploratory (i.e., Schwäbische Alb, Hainich-Dün, Schorfheide-Chorin) to eliminate the influence of region, because the influence of the region was significant and are therefore unitless. The p value is taken from the results of the hierarchical linear mixed model (Table S4); p values in italics indicate marginal significance ($p < 0.1$) and the regression line is dashed if the relationship is only marginally significant

Discussion

Influence of region

The significantly highest organic layer mass and stocks of C and most nutrients in the organic layer, the longest residence times of the organic layer, C and most nutrients, i.e., K_{OL} values, the significantly lowest concentrations of several nutrients in litterfall and in the organic layer and resulting highest C/S ratios in litterfall and within-stand nutrient-use efficiencies at Schorfheide-Chorin among the three regions (Tables 1 and S3) can be attributed to the coarser soil texture, more acidic pH of the dominating soils, and the lower soil fertility than at the other two Exploratories (Table S1; Alt et al. 2011; Fischer et al. 2010). A coarse texture, high acidity and low

nutrient availability are known to decrease litter turnover and biological mixing of the litter into the mineral soil (Krishna and Mohan 2017; Prescott and Vesterdal 2021). Among all three regions, Schorfheide-Chorin had the highest mean stocks of most elements in the organic layer, because the slow turnover of the organic layer overcompensated the low element concentrations (Table S3). The significantly highest mean concentrations of some nutrients in litterfall and the organic layer, the lowest C/S ratios in litterfall and thus partly the lowest within-stand nutrient-use efficiencies together with the highest K stock in the organic layer indicated the highest nutrient availability of all three regions at Hainich-Dün, despite similar organic layer masses and K_{OL} values at Schwäbische Alb and Hainich-Dün (Tables 1 and S3). Schwäbische Alb showed the significantly highest N/P ratio in litterfall and the highest within-stand K-use efficiency (Table S3), indicating a low P and K availability. Because the ranges of the soil pH, which is the major driver of base cation availability, were similar at Hainich Dün (3.3–6.4) and Schwäbische Alb (3.9–6.5), while they were lowest at Schorfheide Chorin (3.2–4.3; Alt et al. 2011; Solly et al. 2013), we attribute these differences to the different parent materials at Hainich-Dün and Schwäbische Alb. The soils of Hainich-Dün mostly developed from thick loess deposits with initially moderate calcite concentrations, while those of the Schwäbische Alb mainly developed from the residual material left over after dissolution of the limestone (Fischer et al. 2010). We suggest that at Schwäbische Alb the abundant exchangeable Ca reduced the exchangeable K concentration in the organic layer and mineral soil. The high Ca availability also favors the precipitation of P as little soluble Ca phosphates limiting the P availability.

The finding that in our hierarchical linear mixed model region had significant effects on most of our measured target variables fully supports our first hypothesis and underlines the paramount importance of site conditions including (micro-)climate and soil properties for litter production, quality and turnover (Krishna and Mohan 2017; Prescott and Vesterdal 2021; Vogt et al. 1986). As a consequence, the study of forest-management intensity and biodiversity effects on litter production, quality and turnover requires the prior consideration of the strong influence of site conditions, e.g., in hierarchical ANOVA models, in which region is fitted before forest-management intensity and biodiversity.

Influence of forest-management intensity

The finding that litterfall decreased and the K_{OL} value of the organic layer increased significantly with increasing ForMI (Fig. 1) supports our second hypothesis that increasing forest-management intensity results in decreasing litter production because of increasing shares of conifers but nevertheless increasing organic layer masses, because of reduced litter turnover and thus longer C residence times in the organic layer. The marginally significant positive effects of ForMI on organic layer mass and K_{Oi} value further substantiate this claim. Figure 1 illustrates that the coniferous forests (dominated by Norway spruce at Schwäbische Alb and Hainich-Dün and by Scots pine at Schorfheide-Chorin) played an important role in explaining the observed (marginally) significant relationships. This is in line with reports of higher litterfall in deciduous than coniferous tree stands (Neumann et al. 2018; Vogt et al. 1986) and the observation that beech-dominated stands have thinner and more bioactive organic layers with a faster turnover and thus shorter residence times than conifer stands (Achilles et al. 2021b; Albers et al. 2004). Although the assumption of lower litterfall in coniferous than deciduous forests cannot be generalized (Hansen et al. 2009; Neumann et al. 2018), it was true for our study sites, where the beech-dominated stands showed the highest litterfall ($0.60 \pm 0.04 \text{ kg m}^{-2}$, $n=18$) followed by the pine-dominated stands (0.55 ± 0.01 , $n=3$) and the spruce-dominated stands (0.48 ± 0.02 , $n=6$). The fact that ForMI still influenced litterfall negatively and the K_{Oi} value positively after the coniferous sites had been removed from the analysis suggested that increasing forest-management intensity reduced litterfall and increased the residence time of the Oi horizon irrespective of tree species. One possible explanation for this finding might be a more pronounced thinning with increasing ForMI that reduces the Leaf Area Index and thus litterfall (Blanco et al. 2006; Doukalianou et al. 2022). The increasing removal of biomass and nutrients with increasing ForMI at the same time might have deteriorated the chemical litter quality and consequently reduced the turnover of the Oi horizon (Krishna and Mohan 2017; Prescott and Vesterdal 2021) in spite of the likely increasing soil temperature that should favor organic matter turnover (Kunhamu et al. 2009). In contrast, the mass of the organic layer and its total residence time was different

between deciduous trees- ($7.5 \pm 1.4 \text{ kg m}^{-2}$) and coniferous trees-dominated stands (spruce: 5.3 ± 0.9 ; pine: 18 ± 2.5). The organic layer mass was only related with ForMI, when the strong significant effect of region was eliminated (Table 2, Fig. 1d).

After the mathematical removal of the influence of region by dividing all values through the regional means, the slope of the regression line of litterfall on ForMI was -0.18 (Fig. 1a). Simultaneously, the slope of the regression line of the K_{OL} value on ForMI was 0.29 indicating a stronger increase of the organic layer mass than reduction of litterfall. We suggest that the reason for longer residence times of the organic layer with increasing ForMI is a deteriorated chemical litter quality and a loss of soil quality, e.g., by the loss of nutrients or soil compaction associated with harvesting and thus reduced biological activity (Burger and Kelting 1999; Grigal 2000; Inagaki et al. 2004; Mayer et al. 2020). Because the mean C concentration in the organic layer ($335 \pm 17.4 \text{ g kg}^{-1}$) was only approximately 30% lower than in litterfall (475 ± 1.65), the longer residence times of C in the organic layer overcompensated the smaller C input via litterfall resulting in a marginally significant increase of the K_{OL} value of C with increasing ForMI (Table S4). As a consequence, the intermediate-term C storage in the organic layer at the scale of years to a few decades increased with increasing ForMI at our study sites.

The significant increase in the C concentration and C/N and C/S ratios in litterfall with increasing ForMI and the corresponding significant decrease of many nutrient concentrations in litterfall and all nutrient fluxes with litterfall (Table 2) reflect both, a higher share of the nutrient-poorer coniferous trees and the higher biomass extraction associated with continuous nutrient losses that accumulate to decrease soil fertility (Burger and Kelting 1999; Schmitz et al. 2005; Vogt et al. 1986). The associated increase in the within-stand use efficiencies of several nutrients (Table S4) therefore is attributable to the higher share of the inherently more nutrient-efficient coniferous trees but might possibly also indicate an adaptation to the decreasing nutrient availability in response to increasing ForMI. The latter is supported by the finding that increasing ForMI still significantly decreased all nutrient fluxes with litterfall and increased the K-use efficiency and the K_{Oi} value of Ca when the coniferous tree-dominated stands were omitted.

Influence of plant diversity

The positive relationship of the Shannon index and partly also plant species richness with the C concentration and the negative ones with several nutrient concentrations in litterfall (Fig. 2, Table 2) went along with an increasing share of conifers. Because in our study the coniferous trees-dominated stands showed a higher diversity of the vascular plant community than the deciduous trees-dominated stands, we were unable to separate the effects of plant diversity and share of conifers. However, P concentrations in litterfall still decreased with increasing plant diversity if the coniferous trees-dominated stand were omitted. In the Jena Experiment, a grassland biodiversity experiment, it was observed that the C/N and C/P ratios in aboveground biomass increased with increasing species richness in most years (Weisser et al. 2017). Milcu et al. (2014) suggested that the increasing C:N ratio with increasing species richness in the Jena experiment was attributable to an increasing N-use efficiency. Similarly, Kleinebecker et al. (2014) reported that the community N-use efficiency of agriculturally used grasslands at the same three Biodiversity Exploratories as studied here increased with increasing species richness because of complementary nutrient use. In line with these findings for N and P, the decreasing P concentration in litterfall with increasing plant diversity irrespective of the inclusion or omission of coniferous trees-dominated stands might indicate an increasing P-use efficiency with increasing plant diversity.

The positive relationship between plant diversity and the Ca concentrations in litterfall of the deciduous trees-dominated stands can be explained by the positive correlation of the pH (in 0.01 M CaCl₂) of the A horizon with the Shannon index ($r=0.58$, $p=0.012$, $n=18$) and species richness ($r=0.60$, $p=0.08$, $n=18$), which was not significant if all 27 forest stands were included. In contrast, topsoil pH did not correlate with the P concentration in litterfall irrespective of the inclusion or omission of coniferous trees-dominated stands so that pH did not play a significant role in explaining the increasing P-use efficiency with increasing plant diversity.

The positive effects of the diversity of the vascular plant community (either as Shannon index or as species richness) on the K_{O_i} and K_{O_L} values of K, Ca

and Mg (Table S4) indicated that the cycling of base cations was slowed down with increasing plant diversity. Because the coniferous trees-dominated stands showed a higher plant diversity than the deciduous trees-dominated stands, the slowdown of the base cation cycle with increasing plant diversity is likely attributable to the inherently lower nutrient needs of coniferous than deciduous trees.

The decreasing N and P concentrations in the organic layer with increasing plant diversity (Fig. 3) might be explained via the N and P flux budgets of the organic layer, i.e., higher community plant uptake of N and P from the organic layer with increasing plant diversity as observed in grassland biodiversity experiments (Oelmann et al. 2011; Tilman et al. 1996; Weisser et al. 2017) and agriculturally used grassland (Kleinebecker et al. 2014) and/or higher N and P leaching with increasing plant diversity. The latter is unlikely, because Schwarz et al. (2016) reported for a subset of the same sites only including beech-dominated stands that increasing plant diversity reduced N leaching through the organic layers, while Apostolakis et al. (2022) did not observe a relationship between plant species richness and phosphate leaching risk. However, when the coniferous trees-dominated stands were omitted, there was no longer a significant relationship between the Shannon index or species richness and the N and P concentrations in the organic layer so that the relationships shown in Fig. 3 might again be attributable to the inherently higher N- and P-use efficiencies of coniferous than deciduous trees and the resulting return of N- and P-poorer litterfall to the soil. Nevertheless, the negative effect of the Shannon index on the S concentration in the organic layer and the positive effects of the Shannon index and/or the species richness on the C/N, C/P and C/S ratios in the organic layer (Fig. S3) and (marginally) on some K_{O_i} values (Table S4) still indicated that increasing plant diversity helps close nutrient cycling supporting our third hypothesis. A more closed nutrient cycling with increasing plant diversity has up to now mostly been known from grasslands (Karanika et al. 2007; Tilman et al. 1996; Weisser et al. 2017; Oelmann et al. 2021) and hardly been reported for forests (Schwarz et al. 2014, 2016). The positive correlation of species richness with the N/P ratio in the data set without coniferous tree-dominated stand suggests an increasing P limitation with increasing plant diversity.

Conclusions

Our results demonstrate that in line with our first hypothesis, the regionally varying site conditions including climate and soil properties influenced the mass and residence times of the organic layer and the chemical composition of litterfall and the organic layer.

Increasing forest management intensity measured as ForMI decreased litterfall, increased organic layer mass and decreased litter turnover and thus increased the temporary C storage in organic layers in line with our second hypothesis. This finding was influenced by the fact that in our study increasing ForMI was related with an increasing contribution of conifers. Conifers (Norway spruce and Scots pine) produced less litterfall at our study sites with a lower chemical quality and thus slower turnover. However, even when only deciduous forests were considered, increased forest-management intensity still decreased litterfall, K flux with litterfall and the residence times of the Oi horizon and of Ca in the Oi horizon.

Because in our study the share of conifers was positively correlated with plant diversity, it was not possible to differentiate effects of the higher nutrient-use efficiency of the conifers from those of plant diversity in the whole data set. However, the significant negative correlation of plant diversity with the S concentration in the organic layer, the positive one with C/nutrient ratios and residence time of K in the Oi horizon in a subset without the coniferous trees-dominated sites, indicated that increasing plant species richness helped close the nutrient cycles in support of our third hypothesis. Thus, in differently managed temperate forests, there is a positive effect of biodiversity on nutrient cycling after region and forest-management intensity are accounted for in a hierarchical linear mixed model in line with the many studies on grassland that had already demonstrated such a relationship.

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Author contributions Beate Michalzik, Jan Siemens and Wolfgang Wilcke designed the study making use of the existing plot design of the Biodiversity Exploratories. Jürgen Bausch, Beate Michalzik, Ingo Schöning, Jan Siemens, Marion Schrupf and Wolfgang Wilcke contributed to the data collection. Vera Zimmer realized the statistical evaluation. The first draft of the manuscript was written by Wolfgang Wilcke and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The data is available in the Biodiversity Exploratories Information System (BEXIS; <https://www.bexis.uni-jena.de/ddm/PublicSearch>, id no. of the used data sets: 16466, 20045, 20056, 23886, 27246) and will become public after an embargo period.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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