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Invasion from the canopy: altered litterfall and nutrient input in European temperate forests

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Abstract: Non-native tree species effects on litterfall production and element inputs remain difficult to generalize, particularly in mature, mixed-species forests under long-term conservation, where structural complexity and species interactions may override simple biomass-driven patterns. Over three consecutive years, we quantified total and leaf-litterfall biomass and associated inputs of major elements (C, N, P, K, Ca, Mg, Mn) across 14 stands differing in species composition and invasion status in Wielkopolska National Park (western Poland). We compared functionally relevant forest types dominated by: (i) invasive *Quercus rubra versus* native *Q. petraea*; (ii) invasive *Robinia pseudoacacia versus* native maples (*Acer platanoides* and *A. pseudoplatanus*); and (iii) *Pinus sylvestris* forests differing in understory composition (with native *A. pseudoplatanus*, invasive *Prunus serotina*, or both). These forest types represented habitat-level competition between native and non-native species.

Maximum differences in mean annual litterfall among individual plots reached 1821 kg ha^{-1} (25%), however, post-hoc comparisons revealed no consistent differences within forest-type groups. Linear mixed-effects models showed no effect of forest type on total litterfall biomass, whereas leaf-litterfall differed significantly among types, the highest in *Q. rubra* forests (4466±254 kg ha^{-1} year^{-1}) and the lowest in *P. sylvestris* forests with *P. serotina* understory (3266±186 kg ha^{-1} year^{-1}). Mean annual inputs of all tested elements differed significantly among forest types. While C input was tightly linked to leaf-litterfall biomass ($R^2=0.94$, $p<0.0001$), inputs of other elements showed weak or non-significant relationships with litterfall quantity. These results demonstrate that differences in leaf chemical composition among species outweigh differences in litterfall biomass in determining element inputs in mixed forests. Non-native tree species influenced ecosystem functioning not primarily by increasing litterfall quantity, but by altering the chemical quality of litter inputs. *Quercus rubra* contributed large quantities of chemically recalcitrant litter, whereas *R. pseudoacacia* and *P. serotina* supplied smaller amounts of element-rich litter capable of accelerating nutrient turnover. Consequently, the ecological effects of non-native tree species on forest element inputs cannot be inferred from litterfall quantity alone. Instead, species-specific litter chemistry and proportional canopy contributions play a dominant role, weakening simple biomass-element relationships and underscoring the need to integrate litter quality into assessments of non-native species impacts on forest biogeochemical cycling.

Keywords: litterfall, elements cycling, biological invasions, invasive species, tree species effect, carbon, nitrogen, calcium, potassium, magnesium, phosphorus

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Introduction

Litterfall represents a major flux of organic matter in forest ecosystems, providing the main source of carbon and other elements, driving soil processes and sustaining biogeochemical cycling (Neumann et al., 2018; Jevon et al., 2022). Its quantity may vary substantially among different forest types (Lonsdale, 1988; Liu et al., 2004). The most thoroughly investigated factors affecting the magnitude of litterfall production include, at the global scale, climatic variability and geographical zone, and, at the local scale, stand structure, age, and species composition, together with topography, habitat conditions, and disturbance events (Lonsdale, 1988; Pedersen & Bille-Hansen, 1999; Matala et al., 2008; Liu et al., 2019; Geng et al., 2022). Under comparable local conditions, however, stand species identity remains the key determinant of annual litterfall production and element return (Hansen et al., 2009; Mazza et al., 2021). Consequently, both the quantity and the quality of litterfall may vary considerably even among forest ecosystems developing under similar habitat conditions (Reich et al., 2005; Neumann et al., 2018). Litter quality refers not only to element concentrations but also to structural and biochemical leaf traits that regulate the rate of element release during decomposition, thereby shaping carbon and other element cycling efficiency (Cornwell et al., 2008; Berg & McClaugherty, 2020).

Accurately quantifying litterfall production at both global and local scales is essential for refining carbon budget estimates and understanding element dynamics within forest ecosystems (Matala et al., 2008). At the global level, litterfall-based carbon fluxes are typically derived from broad-scale models, which often by definition overlook local heterogeneity in species composition and stand structure (Chun-jiang et al., 2003; Liu et al., 2019). However, at local scales – especially in mixed or unmanaged forests – species interactions, canopy complementarity, and varying leaf traits produce substantial spatial and temporal variation in litter inputs and element fluxes (Huang et al., 2017; Wilcke et al., 2024). Therefore, ensuring adequate representativeness of studies in various ecosystems is crucial as it determines the outcome of the overall estimates. Moreover, evaluating these fluxes becomes even more important when non-native tree species are involved. Invasive trees often function as ecosystem engineers or habitat transformers (Jones et al., 1994; Richardson et al., 2000), modifying, among others, the quantity and the quality of litter entering the forest floor (Aerts et al., 2017; Desie et al., 2020, 2023). Their presence can disrupt established element cycling pathways and alter stoichiometric balances between carbon and other elements, which in turn, may entail further consequences for ecosystem functioning (Hawkes et al., 2005; Sardans et al., 2017). Moreover, their impact can be perceived as either negative or positive, which, in times of an anthropocentric view of forests, will not always be objective but is certainly context-dependent (Vilà et al., 2011; Castro-Díez et al., 2019). For example, Horodecki et al. (2019) concluded that, apart from the non-native origin of *Prunus serotina*, *Robinia pseudoacacia*, and *Quercus rubra*, and the potential ecological risks associated with their invasiveness, their presence in novel, soilless post-mining habitats may have locally beneficial effects. Depending on reclamation objectives, these species may accelerate soil formation and thereby enhance ecosystem productivity through rapid mineralization of nutrient-rich litter (*P. serotina* and *R. pseudoacacia*), or increase carbon sequestration in soils *via* enhanced litter humification (*R. pseudoacacia* and *Q. rubra*; Horodecki et al., 2019). However, the direction and magnitude of introduced changes brought by non-native species are generally species- and habitat-specific (Vilà et al., 2011; Jo et al., 2016), which further highlights the need to broaden the research scope in this field. Numerous studies indicate that the influence of non-native tree species is more pronounced in long-invaded stands where they have accumulated substantial biomass and exert strong control over ecosystem processes (Sofaer et al., 2018; Bradley et al., 2019; Bury & Dyderski, 2025). For instance, Jagodziński et al. (2024) found that increasing abundance of the invasive hybrid × *Sorbaronia fallax* nothosubsp. *mitschurinii* in mature pine forest decreased light availability and vascular plant richness, while simultaneously increasing certain element pools in upper soil layers. Similar patterns have been observed in long-established *Eucalyptus* and *Acacia* plantations in southern China, where the duration of alien tree presence and accumulated biomass were positively related to changes in litter-derived carbon stocks and soil microbial activity (Zhang et al., 2020; Xu et al., 2020).

Non-native tree species may act as a game-changer in terms of litterfall production and decomposition within invaded habitats. In this context, the increasing habitat suitability for non-native tree species in European forests (Puchałka et al., 2021, 2023) poses an important ecological challenge. Non-native tree species may accelerate or slow down element turnover depending on their litterfall production and quality, but evidence remains contradictory and highly species- and habitat-specific (Jo et al., 2016; Ahmad et al., 2021; Wohlgemuth et al., 2022). One of the most widespread invasive tree species in Europe, *Quercus rubra*, produces high amounts of litter, which decomposes relatively slowly, resulting in comparatively low element return to the ecosystem (Reich et al., 2005; Horodecki & Jagodziński, 2017; Stanek et al., 2020). This combination of high litterfall production and slow decomposition can influence nutrient cycling and ecosystem functioning, potentially affecting long-term stand dynamics (Bonifacio et al., 2015; Woziwoda et al., 2025).

Robinia pseudoacacia is another invasive tree species increasing its potential range in Europe due to its high ecological flexibility (Puchałka et al., 2021). Its ability to modify habitats through litterfall production works in a way disparate from *Q. rubra*. Thanks to its N-fixing symbioses, *R. pseudoacacia* may contribute disproportionately to nitrogen inputs, but its relatively low litterfall production and moderate to relatively slow decomposition process can limit the net effect on soil element pools (Castro-Díez et al., 2009; Cierjacks et al., 2013; Vítková et al., 2017; Nicolescu et al., 2020).

Prunus serotina in its second range appears mostly as an understory shrub species in poor forest habitats (Godefroid et al., 2005; Aerts et al., 2017; Engel et al., 2024). It produces element-rich litter which decomposes at high rates (e.g., Horodecki & Jagodziński, 2017). Rather spotty presence of its leaves within the forests fertilizes microhabitats locally, however, it may not improve soil and overall litter quality (Aerts et al., 2017), or soil microbial abundance (Urbanowski et al., 2021).

Such contrasting functional strategies can lead to profound shifts in element dynamics, litter residence time, and ultimately in the balance of carbon and element cycling at the stand scale. Direct evaluation of these strategies by comparison with the effects of native tree species, that non-native species compete with, is of high importance to understand their overall influence on invaded ecosystems. Despite extensive research on non-native trees, most studies have emphasized litter decomposition and soil properties, while quantitative data on annual litterfall and element inputs remain scarce. Moreover, even recent meta-analyses indicate strong knowledge gaps (Wohlgemuth et al., 2022), particularly for *P. serotina*, *Q. rubra*, and *R. pseudoacacia*, which are among the most widespread alien tree species in Europe (Wagner et al., 2017). This study represents one of only the few attempts to study Central European temperate forests, that involves diverse forest types with the presence of native and invasive species. Due to the substantial time and lab effort needed, such a comprehensive approach is rarely observed. In this study, we combined three-year litterfall collection with species- and component-level sorting and seasonal elemental analyses to quantify litter and element inputs across multiple forest types. By focusing on *P. serotina*, *Q. rubra*, and *R. pseudoacacia* occurring in different stand compositions, we provide a rare, integrative assessment of how invasive tree species influence annual litterfall fluxes and the supply of key elements to the forest floor compared to native-dominated forests. Based on species-specific functional traits and known differences in litter quality, we hypothesized that alien tree species modify element inputs to forests where they co-occur with native species. We further expected that this effect is driven by two non-exclusive mechanisms: (i) increased litterfall production (*Q. rubra*), and (ii) differences in litter quality relative to native competitors (*P. serotina*, *R. pseudoacacia*).

Methods

Study area

The study was conducted in Wielkopolska National Park (WNP; western Poland; 52°16’N, 16°48’E). Before the park’s establishment in 1957, numerous non-native tree species were introduced, mainly for economic purposes (Żukowski, 1995; Purcel, 2009). *Robinia pseudoacacia* and *Quercus rubra* are relatively common in WNP forests, occurring either as monocultures or admixtures. Moreover, historical forest management practices transformed the original mixed and broadleaved forest ecosystems into Scots pine (*Pinus sylvestris*) monocultures, where *Prunus serotina* is now a frequent component of the understory (Purcel, 2009). The climate of WNP is temperate, with a mean annual precipitation of 521 mm and a mean annual temperature of 8.4 °C (based on 1951–2010 data).

Data collection

To assess litterfall production, we selected 14 plots from a set of 168 permanent experimental plots in WNP (Dyderski & Jagodziński, 2021). Their area ranged from 0.095 to 0.325 ha, depending on forest structure, composition, and homogeneity. Study plots represent seven categories of forest types (Table 1), defined according to the composition of dominant tree and understory species, including either invasive tree species or their native competitors. We compared forest types in functionally relevant pairs or groups dominated by: (i) invasive (*Quercus rubra*; further *QuRu*) and native oaks (*Q. petraea*; further *QuPe*); (ii) invasive black locust (*Robinia pseudoacacia*; further *RoPs*) and native maples (*Acer platanoides* and *A. pseudoplatanus*; further *AcPl+AcPs*); and (iii) Scots pine forests (*Pinus sylvestris*; further *PiSy*) differing in understory compositions: sycamore maple (*PiSy+AcPs*), black cherry (further *PiSy+PrSe* (*Prunus serotina*)), or both (*PiSy+AcPs+PrSe*). These plots were selected purposively, to capture habitat-level competition between forests dominated by invasive species and their native counterparts, focusing on forest types most commonly represented across the

Table 1. The main characteristics of study plots with studied species contributions to total stand basal area and overall leaf-litterfall. Basic soil characteristics after Dyderski & Jagodziński (2020). Abbreviations: Forest type – tree species composition; *RoPs – Robinia pseudoacacia, AcPl – Acer platanoides*; *AcPs – A. pseudoplatanus*; *PiSy – Pinus sylvestris*; *PrSe – Prunus serotina*; *QuRu – Quercus rubra*; *QuPe – Q. petraea*; LAI – leaf area index; BA – stand basal area; L-L – leaf-litterfall. Note that litter traps could occasionally capture leaves from trees outside plot boundaries due to canopy overhang or wind transport; this potential bias is discussed in the Study limitations

Plot	Forest type	Area (ha)	LAI ($m^2\ m^{-2}$)	BA ($m^2\ ha^{-1}$)	Soil C:N	Soil pH	Soil type	% in	Species proportion (%)							
									AcPl	*AcPs*	*PiSy*	*PrSe*	*QuPe*	*QuRu*	*RoPs*	other
1	*RoPs*	0.132	4.86	47.86	15.5	4.35	haplic luvisols	BA	13.78	3.77	2.02	0.00	0.00	0.00	73.49	6.93
								L-L	49.89	3.71	5.61	0.01	1.09	0.04	26.76	12.88
2		0.15	4.96	38.24	11.3	5.19	haplic luvisols	BA	11.09	11.97	0.00	0.00	0.00	0.00	71.42	5.52
								L-L	36.9	18.63	0.86	0.01	0.52	0.03	31.70	11.36
3	*AcPl + AcPs*	0.1728	4.64	27.77	17.3	4.63	haplic luvisols	BA	36.4	29.16	22.13	0.00	0.00	0.00	4.39	7.92
								L-L	56.94	19.75	7.15	0.00	4.89	0.19	4.39	6.68
4		0.17	5.05	38.58	18.3	3.99	haplic luvisols	BA	4.46	33.75	45.49	0.00	0.00	0.00	0.00	16.29
								L-L	15.98	61.23	5.38	0.03	5.22	0.17	2.77	9.23
5	*PiSy + AcPs*	0.17	5.33	33.25	27.2	3.93	brunic arenosols	BA	0.00	23.38	76.62	0.00	0.00	0.00	0.00	0.00
								L-L	0.09	25.92	65.58	0.02	0.02	7.27	0.00	1.09
6		0.095	4.29	39.61	27.2	4.15	luvisols	BA	0.00	8.77	90.82	0.41	0.00	0.00	0.00	0.00
								L-L	0.16	40.18	55.97	1.39	0.13	1.22	0.00	0.94
7	*PiSy + AcPs + PrSe*	0.17	4.03	33.22	19.5	4.2	brunic arenosols	BA	0.00	6.73	75.89	2.90	0.68	0.00	0.00	13.79
								L-L	0.00	26.92	56.57	5.75	0.23	0.12	0.00	10.40
8		0.1518	4.61	38.25	30.0	4.05	brunic arenosols	BA	0.00	7.24	84.6	1.61	0.00	0.00	0.00	6.55
								L-L	0.00	24.29	59.95	7.88	0.07	0.08	0.00	7.73
9	*PiSy + PrSe*	0.1925	3.18	29.41	26.3	4.22	brunic arenosols	BA	0.00	0.40	98.87	0.37	0.37	0.00	0.00	0.00
								L-L	0.03	7.64	50.81	17.85	3.13	16.85	0.00	3.69
10		0.15	4.66	32.46	31.7	3.83	brunic arenosols	BA	0.00	2.62	89.29	7.33	0.00	0.00	0.00	0.76
								L-L	0.00	3.54	65.68	27.38	0.03	1.19	0.01	2.17
11	*QuRu*	0.26	4.92	38.19	22.5	4.01	cambic brunic arenosols	BA	0.00	0.00	0.00	0.00	9.63	67.84	0.00	22.53
								L-L	0.02	0.00	1.96	0.07	36.97	37.0	0.00	23.97
12		0.1215	4.19	27.74	24.6	4.42	brunic arenosols	BA	0.00	0.00	0.00	0.00	4.37	95.63	0.00	0.00
								L-L	0.00	0.22	5.20	0.01	4.68	89.63	0.00	0.26
13	*QuPe*	0.325	4.97	34.74	19.8	4.08	cambic brunic arenosols	BA	0.00	0.00	21.75	0.00	74.16	1.61	0.00	2.48
								L-L	0.00	1.19	15.61	0.01	72.28	0.56	0.00	10.34
14		0.132	4.16	24.57	23.3	4.56	brunic arenosols	BA	0.00	0.00	3.93	0.12	88.26	0.00	0.00	7.70
								L-L	0.06	0.04	1.53	0.12	92.45	5.72	0.01	0.09

full set of 168 permanent plots. Within each forest type category, two representative plots were chosen based on species composition, age, and stand homogeneity. This design ensured coverage of the dominant ecological contexts in which the studied species co-occur, while maintaining a feasible sampling effort. As a result, the study prioritizes ecological relevance over strict statistical representativeness. The spatial distribution of study plots is presented in Fig. 1.

To capture spatial variation in litter input, in September 2019, we installed six litter traps within each of the experimental plots (84 litter traps in total). Traps were placed by selecting an initial position for first of them, and then walking a short distance in different directions, maintaining approximate spacing between traps. We aimed to distribute traps evenly across the plot to obtain representative litter-fall samples. Litter traps were made from wooden boards and agro-nonwoven fabric, each with an inner surface area of 0.36 m². Litterfall was collected six times per year, over three consecutive years (October 2019 – September 2022), to capture both seasonal leaf fall and additional phenological or weather-driven events. All litter traps were emptied at the end of each month from September to December to capture the full dynamics of autumnal leaf-litterfall while minimizing material loss due to decomposition. To account for litterfall outside the main leaf fall season – such as flowers, cones, seeds, and leaves dislodged by strong winds – two additional collections were performed annually at the end of April and August. These spring and late-summer harvests allowed the inclusion of phenological components (e.g., flowering and fruiting structures) and occasional premature leaf shedding.

All collected samples were oven-dried at 65 °C for at least 72 h to a constant weight. Once dried, material from each trap was carefully sorted in the laboratory into the following fractions: leaves, fruits/

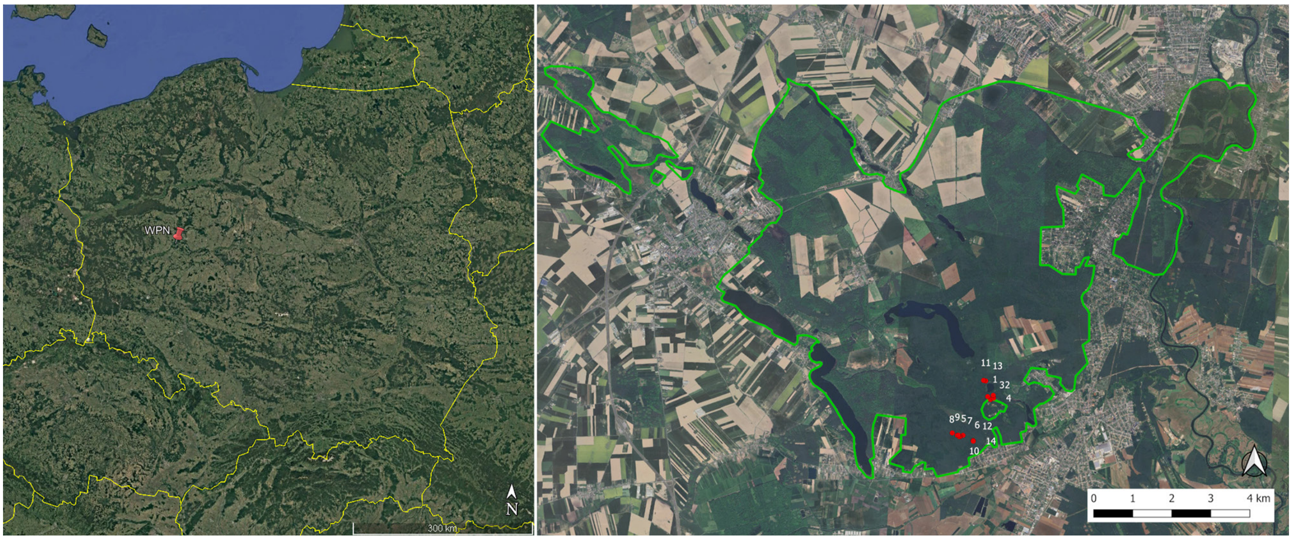

Fig. 1. Location of the study area and experimental plots within Wielkopolska National Park

seeds, twigs, bark, and flowers. Non-identifiable material was classified as “remnants”. Leaf material was further separated by species based on recognizable morphological traits, allowing species-level attribution for all studied tree species. Leaf blade fragments that could not be reliably identified to species level were grouped as “other”, representing leaves of tree species not individually distinguished in the analysis. Dry mass was recorded for each component using a precision scale (with an accuracy of 0.01 g).

To calculate stand basal area, we measured the diameter at breast height (DBH; including bark) of all living individuals ≥5 cm DBH within each plot. For all individuals with DBH <5 cm, a standard DBH of 2.5 cm was assumed (see Dyderski & Jagodziński, 2019, 2021). Leaf area index (LAI) was quantified using the LAI-2200 plant canopy analyzer (Li-Cor Inc., Lincoln, NE, USA). We performed eight series of 10 readings at 0.5 m above the ground, following Machado and Reich (1999). Measurements were taken in early August to capture peak canopy foliage development.

Chemical analyses

For chemical analyses, we merged species-specific samples from each plot within one collection period. For that purpose, we chose 12 autumnal collections over three years (2019–2022). Prior to mineralization leaf material was re-dried for 72 h at 65 °C in a forced-air circulation oven and weighed. The samples were carefully cleaned with a soft brush to remove adhering dust and other particles, and subsequently ground to a fine powder using a mixer mill (MM 200, Retsch, Haan, Germany). Total nitrogen (N) and carbon (C) content (% of dry weight) was determined in ground samples by dry combustion using an Elemental Combustion System CHNS/O Analyzer 2400 Series II (PerkinElmer, USA). Calibration and analytical quality control were performed using certified organic standards, i.e., acetanilide, sorghum flour standard (OAS), and BCR 482 lichen (*Pseudevernia furfuracea*). For multi-element analysis, subsamples were mineralized in closed vessels with ultrapure 67–69% HNO_3 using a microwave digestion system (Multiwave 3000, Anton Paar, GmbH, Austria). Concentrations of calcium (Ca), potassium (K), magnesium (Mg), phosphorus (P), and manganese (Mn) were determined by inductively coupled plasma time-of-flight mass spectrometry (ICP-TOF-MS) using a Spectrometer OptiMass 9500 (GBC, Australia). Analytical accuracy and digestion efficiency were controlled using certified reference materials NIST 1515 Apple Leaves (National Institute of Standards and Technology, USA) and NCS DC 73349 Bush branches and leaves (China National Analysis Centre for Iron and Steel). Obtained values were within the acceptable range of certified concentrations. Results were expressed on a dry weight basis.

Statistical analyses

Descriptive statistics of between-plot variability of litterfall are presented in Table 2.

We used linear models to explore relationships between key structural variables and litterfall production. Specifically, we tested the regression of total and leaf-litterfall (kg ha^{-1} $year^{-1}$) on (i) total stand basal area (BA; m^2 ha^{-1}), (ii) the percentage share of *P. sylvestris* in BA, and (iii) the leaf area index (LAI; m^2 m^{-2}). BA was included as a proxy for overall stand productivity and biomass accumulation potential. LAI reflects canopy development and is directly linked to leaf area production and, by extension, litterfall quantity. We also included the proportion of *P. sylvestris* because conifers generally produce lower

Table 2. Three-year mean total and leaf-litterfall in the experimental plots (kg ha^{-1}) and the proportion of components in total litterfall (%). Abbreviations: Forest type – tree species composition; *RoPs – Robinia pseudoacacia, AcPl – Acer platanoides*; *AcPs – A. pseudoplatanus*; *PiSy – Pinus sylvestris*; *PrSe – Prunus serotina*; *QuRu – Quercus rubra*; *QuPe – Q. petraea*

Plot	Forest type	Litterfall (kg ha^{-1}; ±SE)	Leaves (kg ha^{-1}; ±SE)	Leaves (%)	Twigs (%)	Bark (%)	Fruits/seeds (%)	Flowers (%)	Remnants (%)
1	*RoPs*	5608 (708)	3629 (360)	64.72	11.39	3.14	14.70	1.01	5.05
2		6337 (681)	4042 (312)	63.77	9.98	1.15	17.61	1.05	6.43
3	*AcPl+AcPs*	6906 (988)	4283 (480)	62.02	15.46	3.47	11.95	1.24	5.87
4		6830 (586)	4395 (393)	64.35	9.24	2.92	15.73	0.74	7.03
5	*PiSy+AcPs*	7102 (961)	4234 (238)	59.62	23.23	10.64	1.49	0.16	4.86
6		5753 (586)	3597 (238)	62.52	20.05	10.13	1.72	0.28	5.30
7	*PiSy+AcPs+PrSe*	5894 (749)	3858 (272)	65.46	15.35	10.05	2.11	0.74	6.29
8		5471 (398)	3687 (336)	67.39	14.86	9.53	1.68	0.48	6.06
9	*PiSy+PrSe*	5428 (800)	3230 (223)	59.50	19.66	11.52	3.09	0.45	5.76
10		5666 (611)	3336 (240)	58.87	19.25	11.84	4.07	0.43	5.53
11	*QuRu*	7249 (320)	4562 (120)	62.93	15.66	4.52	9.51	0.44	6.94
12		6038 (311)	4380 (134)	72.54	11.25	3.32	6.50	0.41	5.98
13	*QuPe*	6245 (602)	4089 (200)	65.48	17.47	4.45	7.59	0.21	4.80
14		6200 (782)	4051 (237)	65.33	16.64	6.56	4.34	0.56	6.56

quantities of leaf litter compared to broadleaved species, due to differences in leaf morphology and longevity (Liu et al., 2004; Berg & McClaugherty, 2020).

Litterfall mass was further analyzed using linear mixed-effects models (LMMs), separately for all litterfall components. We initially tested mixed-effects models with forest type as a fixed factor and plot and year as random effects. Including a random intercept for plot generally increased AICc, reduced the marginal R^2, and absorbed much of the variance explained by the fixed effect, resulting in weaker statistical support for forest type – most notably for total litterfall. This outcome was expected given the study design, as plots were selected purposefully to represent specific forest types, and the variance attributable to plots largely overlapped with that explained by forest type. Adding random slopes for plot within forest types did not improve model fit. In contrast, a simpler model with a random intercept for year consistently produced generally lower AICc, higher marginal R^2, and more stable estimates of the fixed effect. Therefore, we adopted this parsimonious model structure (forest type as fixed effect, year as random effect) for all subsequent analyses. All response variables were log-transformed to normalize residuals and stabilize variance. Then, to evaluate model support, we compared all model variants, including forest type as a fixed effect, using Akaike's Information Criterion, corrected for small sample size (AICc). We selected the model with the lowest AICc as the final model. To illustrate how strongly the data supported the inclusion of forest type as a fixed effect, we additionally reported the AICc of a null (intercept-only) model that retained the same random-effects structure (AICc). This comparison allowed us to quantify the improvement in model fit attributable to forest type and thus validate the final model structure. To visualize differences among forest types, we plotted marginal means with standard errors (SE), estimated from the LMMs and back-transformed to the original scale. Pairwise comparisons between forest types were conducted using estimated marginal means (EMMs), with Tukey-adjusted p-values.

To assess the role of leaf chemistry in litter element inputs, we examined mean elemental concentrations in freshly fallen leaves across sampling periods (Table S2). These values were used to estimate element inputs by multiplying species-specific leaf litter mass collected in each autumnal period with corresponding elemental concentrations. For non-identifiable parts of leaf-blades (classified as "other"), element concentrations were unknown. To avoid underestimating overall element inputs, we used weighted mean elemental concentrations calculated separately for each plot. These were based on the species-level concentrations, weighted by their proportional contribution to leaf-litterfall within that plot.

We examined correlations between mean annual leaf-litterfall mass and elemental inputs to evaluate the extent to which differences in element fluxes scaled with litterfall production *versus* reflecting variability in leaf elemental composition among the studied tree species.

We also applied linear mixed-effects models to evaluate differences in element inputs among forest types. Similarly to the models based on litterfall mass, we log-transformed element input values, and we used the same random effects structure (year as a random intercept). Pairwise comparisons among forest types were conducted using EMMs with Tukey correction.

Finally, to explore multivariate patterns in litter inputs, we conducted principal component analysis (PCA) based on standardized leaf-litterfall and element input values (N, P, K, Ca, Mg, Mn) calculated as mean annual values for each sample plot (n=14).

Due to strong collinearity between leaf-litterfall and C input ($R^2=0.94$), C input was excluded from the PCA to avoid redundancy and improve interpretability of stoichiometric patterns. Variables were centered and scaled to unit variance prior to analysis to ensure comparability among elements with different scales.

All analyses and visualizations were conducted using JMP® Pro 18 (SAS Institute Inc., Cary, NC, USA).

Results

Mean annual litterfall

The total mean annual litterfall differed between the investigated plots by 1821 kg ha^{-1}, ranging from 5428 kg ha^{-1} (±800) in *PiSy+PrSe* up to 7249 kg ha^{-1} (±320) in *QuRu* (see Table 2). Leaves constituted the largest proportion of total tree litterfall in all plots, accounting for 59% to 73% (Table 2). Twigs represented the second largest fraction in 11 plots (9–23%), followed by bark in six (1–12%), and fruits/seeds in four plots (1–18%). Flowers contributed only marginally (0–1%), while non-identifiable remnants accounted for 5–7% of the total litterfall.

Total litterfall was not related to stand basal area ($p=0.71$, $R^2=0.01$), nor was leaf-litterfall ($p=0.67$, $R^2=0.02$). The relationship between total litterfall mass and the share of *PiSy* in stand basal area was statistically insignificant ($p=0.14$, $R^2=0.17$), whereas leaf-litterfall showed a significant negative dependence ($p=0.0131$, $R^2=0.41$). The linear relationship between LAI and leaf-litterfall was slightly below the threshold of statistical significance ($p=0.0550$, $R^2=0.27$).

The performed analyses did not reveal any statistically significant differences in total litterfall and remnants masses between forest types (Table 3, Table S1). The forest type explained 17.4% of the variability in total litterfall and 15.4% in remnants masses. The combination of fixed and random effects (study year) increased explained variance to 72.9% and 50.9%, respectively. In contrast, we found significant differences between forest types in the mean annual input of fruits/seeds, bark, leaves, flowers, and twigs to the forest floor (Table 3, Table S1). The forest type explained 86.7%, 64.9%, 42.9%, 25.5%, and 16.9% of their variability, respectively, while together with year of investigation, these explanations increased to 93.4%, 77.7%, 57.7%, 55.7%, and 80.8%, respectively.

We found the highest leaf-litterfall in *QuRu* forests (marginal means ±SE 4466±254 kg ha^{-1} year^{-1}; Fig. 2A), and the lowest in *PiSy+PrSe* (3266±186 kg ha^{-1} year^{-1}). Although the leaf-litterfall differed significantly between forest types ($p=0.0004$), pairwise comparisons between particular types revealed no statistically significant differences. Nonetheless, the observed differences were biologically meaningful: leaf-litterfall under *PiSy+AcPs* (3888±221 kg ha^{-1} year^{-1}) was 19% higher than under *PiSy+PrSe*, and 4% higher than under *PiSy+AcPs+PrSe*. Similarly, *AcPl+AcPs* (4296±245 kg ha^{-1} year^{-1}) produced 13% more leaf litter than *RoPs* (3800±206 kg ha^{-1} year^{-1}), while *QuRu* exceeded *QuPe* (4058±231 kg ha^{-1} year^{-1}) by 10%.

Mean annual element inputs

Mean elemental concentrations in freshly fallen leaves varied noticeably depending on the sampling period (Table S2). The highest relative difference in C concentration reached 13.2% and was observed in

Table 3. Summary of linear mixed-effects models describing differences in particular components of litterfall mass (log-transformed), among studied forest types (fixed effects). Study year was considered as random effect (RE). Abbreviations: SE – standard error; SD – standard deviation; RE – random effect; *RoPs – Robinia pseudoacacia, AcPl – Acer platanoides; AcPs – A. pseudoplatanus; PiSy – Pinus sylvestris; PrSe – Prunus serotina; QuRu – Quercus rubra; QuPe – Q. petraea*

Variable				Predictor	Estimate	SE	DFDen	t	Pr>|t|
litterfall				Intercept (*RoPs*)	8.6801	0.1021	2.8	84.99	<0.0001
AICc	−43.101	$AICc_0$	−41.215	*AcPl+AcPs*	0.1413	0.0605	33	2.34	0.0257
R^2_m	0.174	R^2_c	0.729	*PiSy+AcPs*	0.0692	0.0605	33	1.14	0.26
F Ratio	3.543	Prob>F	0.08	*PiSy+AcPs+PrSe*	−0.0464	0.0605	33	−0.77	0.45
Year RE SD	0.1606	Residual RE SD	0.1048	*PiSy+PrSe*	−0.0751	0.0605	33	−1.24	0.22
Total RE SD	0.1918	Year RE p-Value	0.33	*QuPe*	0.0435	0.0605	33	0.72	0.48
				QuRu	0.1149	0.0605	33	1.90	0.07
leaves				Intercept (*RoPs*)	8.2431	0.0566	7.5	145.73	<0.0001
AICc	−47.578	$AICc_0$	−37.576	*AcPl+AcPs*	0.1226	0.0610	33	2.01	0.0527
R^2_m	0.429	R^2_c	0.577	*PiSy+AcPs*	0.0227	0.0610	33	0.37	0.71
F Ratio	5.636	Prob>F	0.0004	*PiSy+AcPs+PrSe*	−0.0142	0.0610	33	−0.23	0.82
Year RE SD	0.0634	Residual RE SD	0.1057	*PiSy+PrSe*	−0.1514	0.0610	33	−2.48	0.0183
Total RE SD	0.1232	Year RE p-Value	0.40	*QuPe*	0.0655	0.0610	33	1.07	0.29
				QuRu	0.1614	0.0610	33	2.65	0.0124

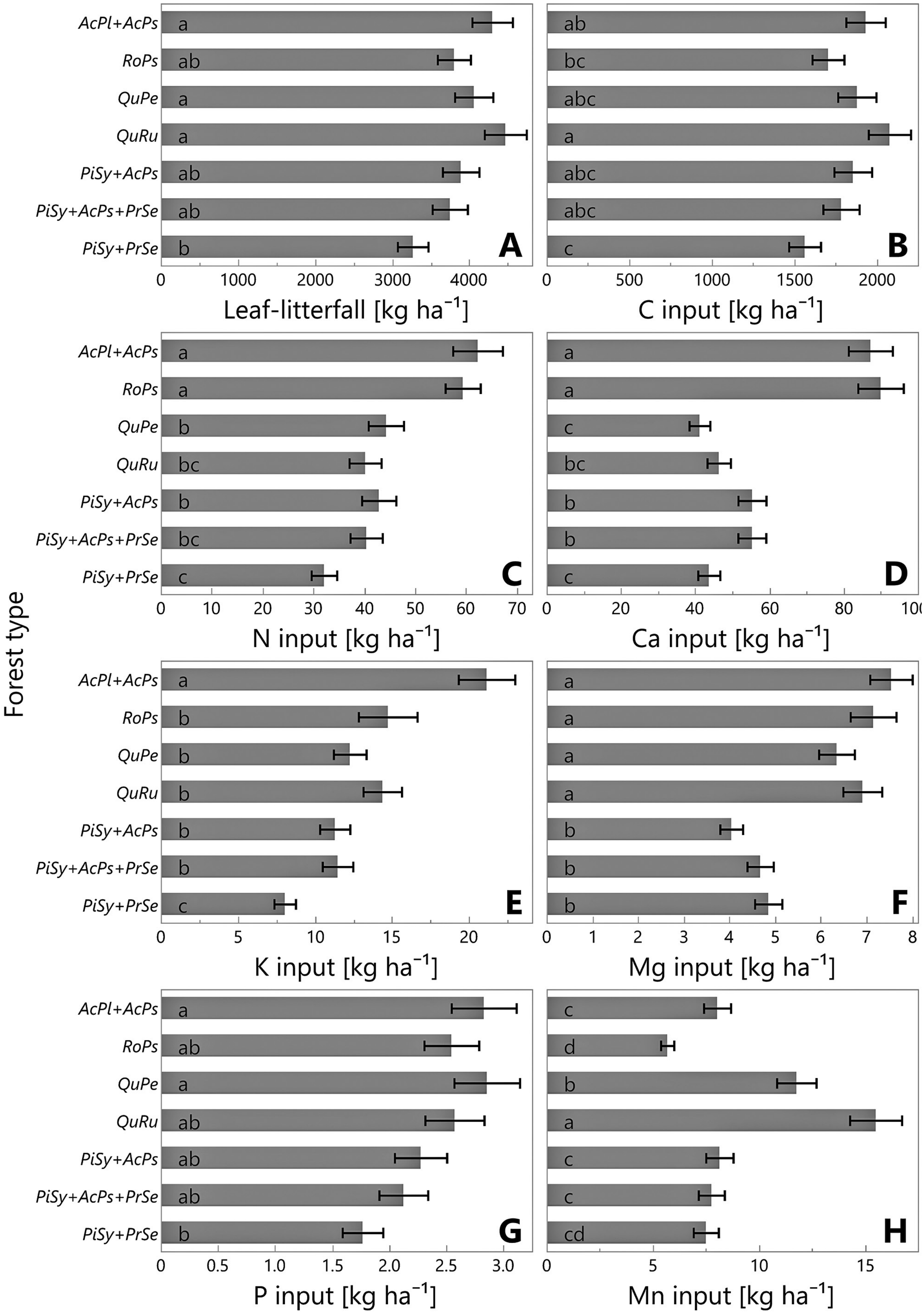

Fig. 2. Marginal mean (+SE) inputs of leaf-litterfall mass and elements for studied forest types, estimated using linear mixed-effect models (Table 3; Table 4). Abbreviations: *RoPs – Robinia pseudoacacia, AcPl – Acer platanoides; AcPs – A. pseudoplatanus; PiSy – Pinus sylvestris; PrSe – Prunus serotina; QuRu – Quercus rubra; QuPe – Q. petraea*

AcPs leaves. In other species, differences were lower: 9.4% in *RoPs,* 8.2% in *PrSe,* 7.7% in *QuRu,* 7.4% in *PiSy,* 7.0% in *AcPl,* and 5.3% in *QuPe*. In contrast, the range of differences in the concentrations of other measured elements was considerably higher across the collection periods (Table S2).

Table 4. Summary of linear mixed-effects models describing differences in inputs of elements (log-transformed), among studied forest types (fixed effects). Study year was considered as random effect (RE). Abbreviations: SE – standard error; SD – standard deviation; RE – random effect; *RoPs – Robinia pseudoacacia, AcPl – Acer platanoides*; *AcPs – A. pseudoplatanus*; *PiSy – Pinus sylvestris*; *PrSe – Prunus serotina*; *QuRu – Quercus rubra*; *QuPe – Q. petraea*

Variable				Predictor	Estimate	SE	DFDen	t	Prob>|t|
C				Intercept (*RoPs*)	7.4418	0.057	7.6	130.67	<0.0001
AICc	−46.763	$AICc_0$	−41.299	*AcPl+AcPs*	0.1251	0.0616	33	2.03	0.0504
R^2_m	0.371	R^2_c	0.533	*PiSy+AcPs*	0.0844	0.0616	33	1.37	0.18
F Ratio	4.413	Prob>F	0.0022	*PiSy+AcPs+PrSe*	0.0451	0.0616	33	0.73	0.47
Year RE SD	0.0635	Residual RE SD	0.1067	*PiSy+PrSe*	−0.0869	0.0616	33	−1.41	0.17
Total RE SD	0.1242	Year RE p-Value	0.41	*QuPe*	0.0976	0.0616	33	1.58	0.12
				QuRu	0.1974	0.0616	33	3.20	0.0030
N				Intercept (*RoPs*)	4.1001	0.0583	23.2	70.37	<0.0001
AICc	−30.214	$AICc_0$	6.912	*AcPl+AcPs*	0.0475	0.0785	33	0.61	0.55
R^2_m	0.735	R^2_c	0.751	*PiSy+AcPs*	−0.3196	0.0785	33	−4.07	0.0003
F Ratio	16.823	Prob>F	<0.0001	*PiSy+AcPs+PrSe*	−0.3776	0.0785	33	−4.81	<0.0001
Year RE SD	0.0309	Residual RE SD	0.1359	*PiSy+PrSe*	−0.6017	0.0785	33	−7.67	<0.0001
Total RE SD	0.1393	Year RE p-Value	0.68	*QuPe*	−0.2878	0.0785	33	−3.67	0.0009
				QuRu	−0.3827	0.0785	33	−4.88	<0.0001
Ca				Intercept (*RoPs*)	4.5101	0.0681	5.9	66.20	<0.0001
AICc	−37.469	$AICc_0$	29.480	*AcPl+AcPs*	−0.0307	0.0681	33	−0.45	0.66
R^2_m	0.839	R^2_c	0.891	*PiSy+AcPs*	−0.4794	0.0681	33	−7.04	<0.0001
F Ratio	42.459	Prob>F	<0.0001	*PiSy+AcPs+PrSe*	−0.4801	0.0681	33	−7.05	<0.0001
Year RE SD	0.0835	Residual RE SD	0.118	*PiSy+PrSe*	−0.7111	0.0681	33	−10.44	<0.0001
Total RE SD	0.1445	Year RE p-Value	0.38	*QuPe*	−0.7689	0.0681	33	−11.29	<0.0001
				QuRu	−0.6529	0.0681	33	−9.58	<0.0001
K				Intercept (*RoPs*)	2.755	0.1294	3.1	21.30	0.0002
AICc	−13.713	$AICc_0$	28.926	*AcPl+AcPs*	0.3419	0.0868	33	3.94	0.0004
R^2_m	0.593	R^2_c	0.838	*PiSy+AcPs*	−0.2471	0.0868	33	−2.85	0.0075
F Ratio	20.213	Prob>F	<0.0001	*PiSy+AcPs+PrSe*	−0.2325	0.0868	33	−2.68	0.0114
Total RE SD	0.248	Residual RE SD	0.1503	*PiSy+PrSe*	−0.5538	0.0868	33	−6.38	<0.0001
Residual RE SD	0.133	Year RE p-Value	0.34	*QuPe*	−0.1708	0.0868	33	−1.97	0.06
				QuRu	−0.0228	0.0868	33	−0.26	0.7941
Mg				Intercept (*RoPs*)	2.0972	0.0701	4.4	29.94	<0.0001
AICc	−44.606	$AICc_0$	1.579	*AcPl+AcPs*	0.0469	0.0617	33	0.76	0.45
R^2_m	0.704	R^2_c	0.828	*PiSy+AcPs*	−0.4801	0.0617	33	−7.79	<0.0001
F Ratio	22.66	Prob>F	<0.0001	*PiSy+AcPs+PrSe*	−0.362	0.0617	33	−5.87	<0.0001
Year RE SD	0.095	Residual RE SD	0.1068	*PiSy+PrSe*	−0.3311	0.0617	33	−5.37	<0.0001
Total RE SD	0.1429	Year RE p-Value	0.36	*QuPe*	−0.1035	0.0617	33	−1.68	0.10
				QuRu	−0.0294	0.0617	33	−0.48	0.64
P				Intercept (*RoPs*)	1.2648	0.0942	7.3	13.43	<0.0001
AICc	−5.446	$AICc_0$	−6.902	*AcPl+AcPs*	0.077	0.1006	33	0.77	0.45
R^2_m	0.270	R^2_c	0.466	*PiSy+AcPs*	−0.079	0.1006	33	−0.79	0.44
F Ratio	2.801	Prob>F	0.0258	*PiSy+AcPs+PrSe*	−0.1262	0.1006	33	−1.25	0.22
Year RE SD	0.1069	Residual RE SD	0.1743	*PiSy+PrSe*	−0.2477	0.1006	33	−2.46	0.0192
Total RE SD	0.2044	Year RE p-Value	0.40	*QuPe*	0.084	0.1006	33	0.83	0.41
				QuRu	0.0078	0.1006	33	0.08	0.94
Mn				Intercept (*RoPs*)	1.899	0.0548	33.4	34.65	<0.0001
AICc	−32.142	$AICc_0$	21.292	*AcPl+AcPs*	0.3018	0.0791	33	3.82	0.0006
R^2_m	0.832	R^2_c	0.825	*PiSy+AcPs*	0.3137	0.0791	33	3.97	0.0004
F Ratio	28.412	Prob>F	<0.0001	*PiSy+AcPs+PrSe*	0.2712	0.0791	33	3.43	0.0016
Year RE SD	0	Residual RE SD	0.137	*PiSy+PrSe*	0.241	0.0791	33	3.05	0.0045
Total RE SD	0.137	Year RE p-Value	0.72	*QuPe*	0.6479	0.0791	33	8.19	<0.0001
				QuRu	0.9047	0.0791	33	11.44	<0.0001

Among all sample plots, we found statistically significant positive correlations between mean annual leaf-litterfall and C ($R^2=0.94$, $p<0.0001$), K ($R^2=0.45$, $p=0.0088$), Mg ($R^2=0.36$, $p=0.0231$), P ($R^2=0.62$, $p=0.0008$), as well as Mn fluxes to the forest floor ($R^2=0.38$, $p=0.0182$). Relationships for N and Ca were weaker and statistically insignificant ($R^2=0.22$, $p=0.09$ and $R^2=0.04$, $p=0.47$, respectively; see Fig. S1).

We found statistically significant differences in the mean annual inputs of all tested elements between forest types. The fixed effect of forest type explained 83.9% of the variation in Ca input, 83.2% in Mn, 73.5% in N, 70.4% in Mg, 59.3% in K, 37.1% in C, and 27.0% in P, respectively (Table 4). Including random effects (study year) increased the explained variance to 89.1% for Ca, 75.1% for N, 82.8% for Mg, 83.8% for K, 53.3% for C, and 46.6% for P. For Mn, year accounted for no additional variance, resulting in a conditional R^2_c that was effectively identical to – but numerically slightly lower than – the marginal R^2_m due to the near-zero random-effect variance.

The highest mean annual C input to the forest floor was recorded in *QuRu* (2077±128 kg ha^{-1}), while the lowest occurred in *PiSy+PrSe* forests (1563±96 kg ha^{-1}; Fig. 2B). Although the overall effect of forest type was statistically significant ($p=0.0022$), Tukey's post-hoc tests did not reveal significant pairwise differences. Nevertheless, biologically meaningful contrasts were observed: *QuRu* had 198 kg ha^{-1} (10.5%) higher annual C input than *QuPe*, *AcPl+AcPs* exceeded *RoPs* by 227 kg ha^{-1} year^{-1} (13.3%), and *PiSy+AcPs* showed 292 kg ha^{-1} year^{-1} (18.7%) more than *PiSy+PrSe*, with intermediate values for *PiSy+AcPs+PrSe*. The highest annual N input was found in *AcPl+AcPs* (62±5 kg ha^{-1}; Fig. 2C), which was 5% higher than in *RoPs* forests (59±3 kg ha^{-1}). Among oaks, the difference reached 10.2% (*QuPe*: 44±3 kg ha^{-1} year^{-1} > *QuRu*: 40±3 kg ha^{-1} year^{-1}). Despite these biologically relevant trends, pairwise statistical comparisons did not yield significant differences within the aforementioned forests. The lowest annual N input was observed in *PiSy+PrSe* forests (32±3 kg ha^{-1}). Compared to this, input was 25% higher in *PiSy+AcPs+PrSe*, and 33.6% higher in *PiSy+AcPs*. The differences in N input between the two outermost pine forests were statistically significant. A similar pattern was observed for

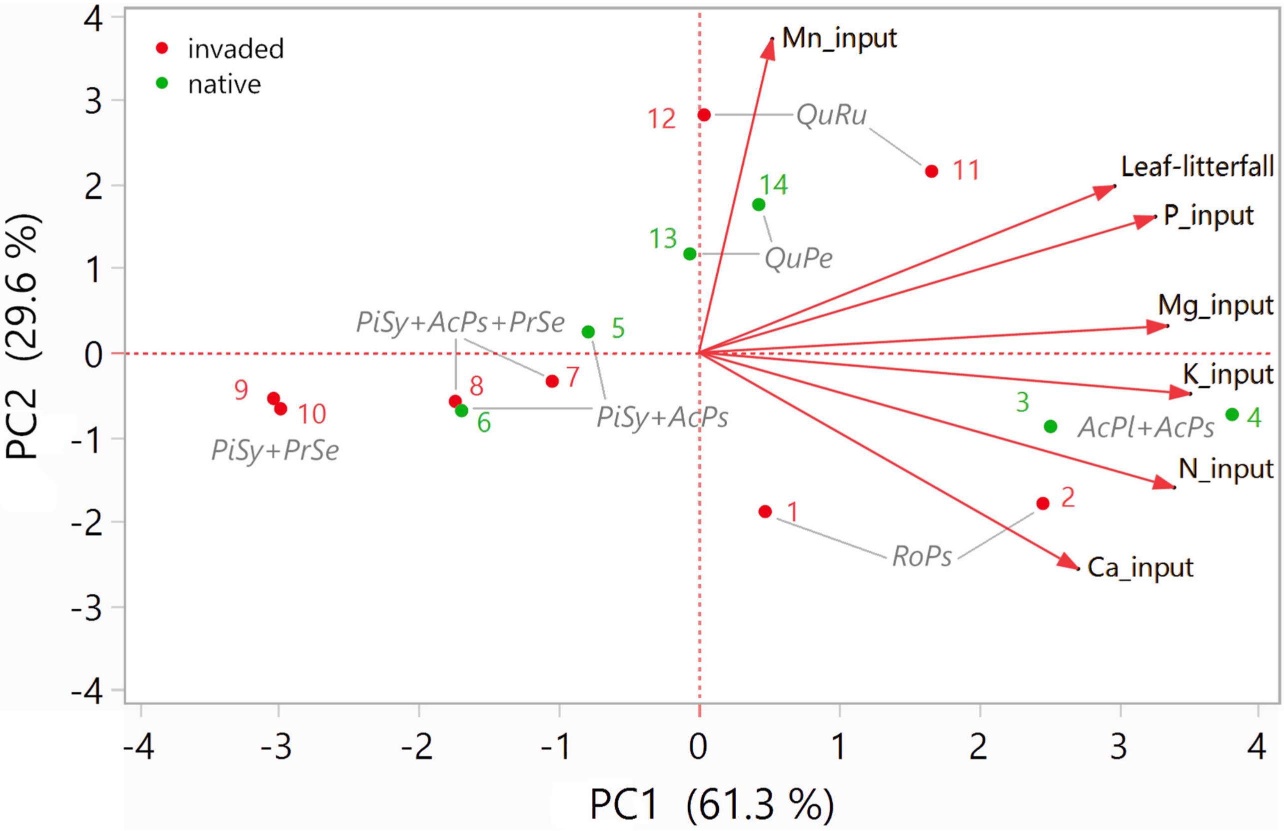

Fig. 3. Principal Components Analysis of mean annual leaf-litterfall and elements inputs (N, Ca, K, Mg, P, Mn) across 14 study plots (kg ha^{-1}). All variables were standardized prior to analysis. Arrows indicate the direction and strength of variable loadings. Numbers represent individual plots grouped by forest type: 1–2 – *Robinia pseudoacacia* (*RoPs*); 3–4 – *Acer platanoides* and *A. pseudoplatanus* (*AcPl+AcPs*); 5–6 – *Pinus sylvestris* with *A. pseudoplatanus* undergrowth (*PiSy+AcPs*); 7–8 – *P. sylvestris* with *A. pseudoplatanus* and *Prunus serotina* undergrowth (*PiSy+AcPs+PrSe*); 9–10 – *P. sylvestris* with *P. serotina* undergrowth (*PiSy+PrSe*); 11–12 – *Quercus rubra* (*QuRu*); 13–14 – *Q. petraea* (*QuPe*)

Ca (Fig. 2D). The highest annual Ca inputs were noted in *RoPs* (90±6 kg ha^{-1}), and *AcPl+AcPs* forests (87±6 kg ha^{-1}). Differences between oak forests reached 12.6% (*QuRu*: 46±3 kg ha^{-1} year^{-1} > *QuPe*: 41±3 kg ha^{-1} year^{-1}). The highest difference (26.7%) was noted between pine forests (*PiSy+AcPs* and *PiSy+AcPs+PrSe*: 55±4 kg ha^{-1} year^{-1} > *PiSy+PrSe*: 44±3 kg ha^{-1} year^{-1}). In the pairwise tests of Ca input, the statistically significant differences were again noted only for the outermost pine forests. For K, forest type had a statistically significant overall effect (Table 4), with mean annual input varying from 8.04±0.70 kg ha^{-1} in *PiSy+PrSe* to 21.13±1.83 kg ha^{-1} in *AcPl+AcPs* – a 162.9% increase (Fig. 2E). The Tukey's test confirmed statistically significant pairwise differences between *AcPl+AcPs* and *RoPs* (14.72±1.90 kg ha^{-1} year^{-1}), and between *PiSy+PrSe* and other pine forests (42.6% more in *PiSy+AcPs+PrSe* and 40.4% more in *PiSy+AcPs*). However, taxonomic contrasts between oak forests were also evident: 17.2% more K was input annually in *QuRu* compared to *QuPe* forests (14.37±1.25 *vs*. 12.25±1.06 kg ha^{-1}). Mean annual Mg input ranged from 4.04±0.25 kg ha^{-1} in *PiSy+AcPs* forests to 7.53±0.46 kg ha^{-1} in *AcPl+AcPs* (Fig. 2F). Pairwise differences were not statistically significant, but taxonomic contrasts were evident: for instance, Mg annual input in *PiSy+PrSe* (4.85±0.30 kg ha^{-1}) was 20.1% higher than in *PiSy+AcPs*. Mean annual P input ranged from 1.77±0.18 kg ha^{-1} in *PiSy+PrSe* to 2.85±0.29 kg ha^{-1} in *QuPe* (Fig. 2G). Again, no significant pairwise differences were found, but several biologically meaningful gaps occurred: 11.0% between *QuRu* (2.57±0.26 kg ha^{-1} year^{-1}) and *QuPe*; 11.2% between *RoPs* (2.54±0.24 kg ha^{-1} year^{-1}) and *AcPl+AcPs* (2.83±0.28 kg ha^{-1} year^{-1}); and 28.8% between *PiSy+PrSe* and *PiSy+AcPs* (2.27±0.23 kg ha^{-1} year^{-1}). The highest Mn annual input was found in *QuRu* forests (15.51±1.23 kg ha^{-1}), which was 3.74 kg ha^{-1} higher than in *QuPe* (Fig. 2H). The lowest annual input was observed in *RoPs* (5.68±0.31 kg ha^{-1}). The strongest relative contrast occurred between *RoPs* and *AcPl+AcPs* (8.03±0.64 kg ha^{-1} year^{-1}), reaching 41.4%. For both the aforementioned pairs of forest types, the differences noted were statistically significant. Mn input was most uniform (and statistically similar) across pine forests, with a range of only 8.5%: *PiSy+AcPs* (8.14±0.64 kg ha^{-1} year^{-1}) > *PiSy+AcPs+PrSe* (7.76±0.61 kg ha^{-1} year^{-1}) > *PiSy+PrSe* (7.50±0.59 kg ha^{-1} year^{-1}).

Relationships between element inputs and leaf-litterfall

Principal Component Analysis revealed clear separation among forest types based on annual leaf-litterfall and inputs of N, P, K, Ca, Mg, and Mn (Fig. 3, Fig. S2). The first two components explained 90.8% of the total variance (PC1: 61.3%, PC2: 29.6%), while the third component accounted for additional 4.6%.

The first principal component (PC1) was primarily associated with strong positive loadings of leaf-litterfall, Mg, K, P, and N inputs, while PC2 was mostly driven by variation in Mn inputs. Ca contributed moderately to both axes.

Study plots of various forest types were arranged along the PC1 gradient from *PiSy+PrSe* forests – characterized by the lowest leaf-litterfall mass and element fluxes – towards *AcPl+AcPs* forests, one *RoPs* plot (no. 2), and one *QuRu* plot (no. 11), which exhibited the highest overall leaf-litterfall and Mg and K inputs, along with relatively high N and P inputs. The PC2 axis further differentiated forest types: *QuRu* and *QuPe* were positioned in the upper part of the PCA space, reflecting higher Mn inputs, while *RoPs* and *AcPl+AcPs* clustered in the lower part of PC2, corresponding to relatively higher Ca inputs. The PC2–PC3 biplot (Fig. S2) further highlighted compositional differences among litter types, particularly in relation to Ca and Mn relative to other nutrients. Although this ordination provided additional resolution of secondary gradients, it did not alter the main pattern observed in the PC1–PC2 space.

Discussion

Differences in litterfall mass among forest types

The total mean annual litterfall found during our three-year experiment ranged from 42% to 56% of the maximal litterfall noticed in European forests by Neumann et al. (2018). When compared to the Central European average (4330 kg ha^{-1} year^{-1}), our values were 25% to 67% higher. Such differences are not unexpected, as litterfall production varies widely among various forests due to multiple interacting factors, including species composition and environmental conditions (e.g., Lonsdale, 1988; Liu et al., 2004). Even under relatively similar habitat conditions, differences in species composition alone can drive substantial variation in litterfall production. Moreover, litterfall production is shaped by a wide range of interacting factors, including environmentally induced variation in leaf traits. For example, even relatively small temperature fluctuations may alter leaf dimensions (Hodzic et al., 2025), potentially influencing litter quantity and related ecosystem processes. In our experimental design, where climatic conditions were uniform, the differences in litterfall production (shaped only by local factors) between experimental plots reached 33.6% for total and 41.2% for leaf-litterfall. Similar patterns were reported in studies comparing forests of different species located within the same study area. For example, Astel et al. (2009) found a 30% difference in total litterfall between pure pine and mixed birch-pine stands in the protected area of Słowiński National Park (N Poland). Hansen et al. (2009) reported 18% to 31% differences in total litterfall between various conifer stands within the same locations in Denmark.

The relatively small differences reported in our study could be explained by similar habitat conditions, the even age of all forests, and especially by the lack of management practices, which affected the stock density and crown complementarity. Thinning operations, common in managed forests, reduce canopy closure and then litterfall production in the following years (Pedersen & Bille-Hansen, 1999). Conservation practices, in turn, promote canopy and overall forest complementarity (Barrufol et al., 2013; Zheng et al., 2019). Empirical comparisons indicate that old-growth, multi-species, and structurally complex forests, as well as natural and semi-natural forests, typically exhibit higher and more spatially and temporally heterogeneous litterfall production than intensively managed monocultures or even-aged stands (e.g., Yang et al., 2005; Barlow et al., 2007; Huang et al., 2017). Moreover, the share of woody litterfall (branches, twigs, bark) in total litterfall in such forests is relatively high and may vary considerably between years (Staelens et al., 2011). The mature age of all investigated forest types (around 100 years) likely accentuated this pattern (Lebret et al., 2001; Berg & Laskowski, 2005; Berg & McClaugherty, 2020). In our study, leaves accounted for 64% of total litterfall and woody fractions (twigs and bark) for over 22% (Table 2), closely matching the values reported by Staelens et al. (2011) for 60-year-old unmanaged mixed forests in Belgium (67% leaves, 23% twigs and branches). Astel et al. (2009) found a higher contribution of branches and bark (30%) in a 140-year-old pine forest, similar to the woody fractions in our pine-dominated forests. Lebret et al. (2001) reported woody fractions of 12.5% and 16.2% in 83- and 147-year-old European beech-dominated forests, which correspond to the values observed in our deciduous-dominated forests (i.e., 17.1±1.6%; Table 2). Importantly, these patterns are highly sensitive to environmental conditions and forest characteristics, and may therefore be consistent with, or markedly different from trends reported in other studies (see e.g., Hansen et al., 2009; An et al., 2017; Ott & Watmough, 2021).

In general, direct comparison of our results with literature data is inherently difficult, as studies conducted under comparable conditions are largely lacking. Most available data originate from monocultures, whereas results from mixed forests are strongly shaped by local stand structure, species composition, and site-specific conditions, which limits their direct comparability with our experimental design. In this context, the complex experimental design involving long-protected mixed forests may also explain the absence of a clear relationship between litterfall biomass and stand-level structural metrics observed in our study. Although we did not find any statistically significant correlation between total or leaf-litterfall and BA, structural differences among experimental plots were substantial, with BA varying by up to 94.8% (Table 1). Previous studies indicate that strong relationships between BA and litterfall are mainly reported from monocultures and/or intensively managed stands (e.g., Berg et al., 1999), whereas in unmanaged or structurally complex forests such relationships are weak or inconsistent and overridden by species identity and canopy traits (see Huang et al., 2017). This pattern likely reflects substantial interspecific differences in crown architecture, biomass allocation patterns, leaf traits, and growth strategies, which decouple litterfall production from stand-level structural metrics (Staelens et al., 2011; Pretzsch, 2014; Forrester et al., 2017; Dyderski & Jagodziński, 2019; Paź-Dyderska et al., 2020). Consequently, species with similar contributions to BA may differ markedly in their contribution to annual leaf-litterfall, indicating that structural dominance does not directly translate into foliage production efficiency (Matala et al., 2008). The absence of strong correlations was therefore expected, as the studied forests differed markedly in species composition (Table 1) and were deliberately selected to assess the effects of various non-native tree species on litterfall and element inputs across contrasting forest types. The presence of alien tree species likely further modulated these relationships within the investigated ecosystems. For example, *R. pseudoacacia* tended to produce relatively less leaf litter compared to its contribution to BA, whereas *P. serotina* contributed proportionally more (Table 1). This pattern of disproportionate contribution was particularly evident in pine-dominated forests, where a high share of *P. sylvestris* in BA translated into a relatively low share of needle litter in total foliar litterfall. Thus, the observed negative correlation between the share of *P. sylvestris* in total BA and leaf-litterfall was also consistent with expectations, as in temperate forests coniferous species generally produce lower amounts of foliar litter than broadleaved species (Liu et al., 2004; Jevon et al., 2022). The relatively high light transmittance of pine-dominated canopies (Dyderski & Jagodziński, 2019) promoted substantial understory development (Jagodziński et al., 2018), which, however, did not compensate for lower leaf-litterfall production compared to the investigated broadleaved forests.

Differences in element inputs among forest types

The direction and magnitude of non-native tree species effects on ecosystem functioning are strongly species- and habitat-specific (Daehler, 2003; Vilà et al., 2011; Ahmad et al., 2021), and tend to increase with the abundance and persistence of the invader (Bury & Dyderski, 2025). In the context of litterfall production, non-native tree species may alter not only biomass inputs but also litter chemical quality and temporal dynamics. For example, non-native species have been shown to produce element-rich litter that accelerates element turnover and modifies element cycling pathways (Incerti et al., 2018; Jaafar et al., 2023). In temperate deciduous forests, invasion by *P. serotina* can additionally influence element cycling through changes in foliar traits of co-occurring tree species (Aerts et al., 2017). Consequently, long-term presence of non-native trees may ultimately lead to substantial changes in humus forms and soil organic layer properties (Gentili et al., 2019; Desie et al., 2023).

These examples indicate that changes in ecosystem functioning are not solely driven by litterfall biomass but also by inter- and intraspecific differences in elemental concentrations of leaf blades and other litter components, as well as their temporal variability. This temporal variability likely reflects both nutrient retranslocation during leaf senescence (Niinemets & Tamm, 2005) and interannual variation in weather conditions influencing leaf development and morphology (Yanai et al., 2012). Our results are consistent with this pattern. Leaf-litterfall itself showed comparatively low between-forest type variability, as demonstrated by the mixed-effects models, whereas element inputs exhibited much higher relative variability (excluding C and P, where this variability was slightly lower). Although C input was strongly correlated with leaf-litterfall biomass ($R^2=0.94$; Fig. S1), the mean C concentration in leaf blades varied only modestly among the investigated tree species (11.4%; Table S2). In contrast, mean concentrations of other elements differed substantially between species, ranging from 113% for P to 821.9% for Mn. The coefficients of variation calculated for elemental inputs further support this interpretation. While C input showed low variability (CV=9.7%), reflecting relatively stable C concentrations in leaf litter, the variability of other elements increased markedly, reaching 16.9% for P, over 23% for N and Mg, and exceeding 30% for K, Ca, and Mn. This pronounced inter-element and interspecific variability indicates that differences in leaf chemistry outweigh differences in litterfall biomass, thereby weakening biomass-input relationships for most elements. These patterns likely reflect species-specific nutrient-use strategies (Vitousek, 1982), differences in nutrient retranslocation efficiency (Niinemets & Tamm, 2005), and the contrasting mobility of elements in plant tissues, with mobile elements such as N, P, and K showing greater variability than more structurally bound elements like Ca or Mn (Lambers et al., 2008).

It is well established that *Q. rubra* contributes relatively large amounts of litter annually to invaded ecosystems (e.g., Reich et al., 2005), a pattern that was also evident in our results. However, the relatively low chemical quality of its litter (Hobbie et al., 2006; Staelens et al., 2011) slows decomposition rates (Bonifacio et al., 2015; Horodecki & Jagodziński, 2017), often resulting in the accumulation of a thick litter layer on the forest floor (Dobrylovská, 2001; Jagodziński et al., 2018). This may further translate into altered belowground functioning, including shifts in soil microbial communities relative to native tree species (Stanek & Stefanowicz, 2019). In contrast, *R. pseudoacacia*, when present in substantial amounts, enriches the forest floor with elements – particularly N (e.g., Rahmonov, 2009; Lazzaro et al., 2018). Despite its relatively low litterfall production (see Results; González et al., 2020), and possibly due to allelopathic effects on other plant species (Cierjacks et al., 2013), this species may be associated with comparatively low litter mass accumulation on the forest floor (Horodecki et al., 2025 *under review*), even though the decomposition rate of its own foliar litter is relatively low (Castro-Díez et al., 2012; Horodecki et al., 2019). *P. serotina*, in turn, contributes relatively small quantities of litter that are nonetheless rich in elements, which – similarly to *R. pseudoacacia* – can accelerate the decomposition of mixed-species litter (Aerts et al., 2017). The long-term presence of this species may therefore lead to a reduction in litter mass accumulated on the forest floor (Horodecki et al., 2025 *under review*).

Principal component analysis clearly separated forest types based on litterfall mass and element inputs, with *P. sylvestris*-dominated forests clustering at the low end of litter productivity and *Acer* spp.-dominated or *Q. rubra* forests at the high end. The positioning of *Quercus* plots along the Mn–Ca gradient indicates intrinsic chemical differences in their litter. This ordination highlights that forest types differ not only in litterfall quantity but also in the quality and stoichiometry of returned elements, with potential consequences for soil fertility and ecosystem functioning.

Study limitations

Several limitations of this study should be acknowledged. First, although litter traps were installed in a haphazard manner to achieve a broadly even distribution within each plot, they may have received material originating from outside plot boundaries, particularly where tree crowns extended beyond plot limits. Consequently, species absent from the recorded BA within a plot could still contribute to litterfall. This, however, is in line with natural processes. Second, a small fraction of leaf litter could not be reliably assigned to species and required the use of averaged elemental concentrations, which may have slightly reduced interspecific contrasts in element inputs. This reduction is, however, slight because of the small percentage of unidentifiable leaves and the content of elements in "other" reflects the proportional share of identifiable leaves within each plot (see Statistical analyses). Third, the relatively small number of plots (n=14), resulting from the high labor intensity of litter sorting and chemical analyses, limited statistical power and reduced the likelihood of detecting conventional levels of significance. Therefore, following American Statistical Association recommendations (Wasserstein & Lazar, 2016), we focused primarily on effect sizes rather than p-values alone.

Additional methodological constraints include potential overestimation of canopy density derived from LAI-2200 measurements, which also capture silhouettes of stem and branches. However, as LAI plays only a background role in our analyses, we accepted this limitation and used the measured values instead of modeled estimates.

Despite these limitations, the combination of species-level litter sorting, detailed chemical analyses, and multi-year sampling provides a robust basis for assessing litter-mediated element inputs in invaded, mature, mixed temperate forests.

Conclusions and practical implications

Our results demonstrate that in mature, mixed temperate forests, litterfall production and associated element inputs are governed primarily by forest type and tree species identity, while stand structural attributes, such as BA, play a subordinate and often inconsistent role under unmanaged conditions. Non-native tree species influence ecosystem functioning not only by contributing additional litter biomass, but more importantly by altering the chemical quality of litter inputs. Elemental inputs were only weakly related to leaf-litterfall biomass (excluding C), reflecting high interspecific variability in leaf chemistry. Consequently, differences in litter quality outweighed differences in litter quantity for most elements, weakening biomass-input relationships and complicating comparisons across forest types. The direction and magnitude of these effects were strongly species- and habitat-specific, confirming that non-native tree species cannot be treated as a functionally uniform group. From a practical perspective, these findings highlight that assessments of C and element budgets based solely on litter mass may substantially misrepresent ecosystem processes in mixed and invasion-prone forests. Forest management and conservation strategies should therefore explicitly account for species-specific litter traits and residence time of alien trees, as long-established invaders may disproportionately reshape element cycling and soil processes, even without dominating forest structure.

Authors' Contributions

Conceptualization: A.M.J., P.H. and M.K.D.; Methodology: A.M.J. and P.H.; Validation: A.M.J. and P.H.; Formal analysis: P.H.; Investigation: P.H.; M.K.D.; Resources: P.H.; M.K.D. and A.M.J.; Data curation: P.H.; M.K.D.; Writing – original draft preparation: P.H.; Writing – review and editing: M.K.D., A.M.J. and P.H.; Visualization: P.H.; Supervision: A.M.J.; Project administration: P.H..; Funding acquisition: P.H.

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Conflicts of Interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

Ethics approval

The study was conducted in Wielkopolska National Park under permission nos. 23/2019, 5/2021, and 6(a-c)/2022/n.

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