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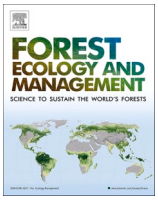

Drivers of litter dynamics across Spanish forests: An assessment using ICP-forests Level I monitoring data

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ABSTRACT

Litter stocks account for approximately 8.7 % of total carbon stocks in European forests, playing a crucial role in nutrient cycling, carbon storage, and forest ecosystem health. This study analyzes the climatic, environmental, and structural drivers of litter accumulation and quality in Spanish forests across four bioclimatic regions. Using data from 620 plots monitored through the ICP Forests Level I network over three measurement cycles (2014–2024), we evaluated spatial and temporal patterns of litter biomass and quality using Generalized Linear Mixed Models. Our results show the highest litter stocks in the Atlantic bioregion, especially in mixed conifer-broadleaf forests, (up to 11.21 ± 7.7Mg ha^{-1}), while significant declines were observed over the time span considered in Subalpine and Montane Conifer and Deciduous Broadleaf forests. The Mediterranean region also displayed high litter stocks but with marked declines. In contrast, the Alpine and Macaronesian bioregions showed no significant changes. Litter quality, assessed via C/N ratios, varied substantially among regions and forest types. The Mediterranean region displayed both the highest mean C/N values and the widest range, particularly in coniferous and mixed stands. Significant temporal declines in C/N were observed in the Mediterranean, Alpine, and Atlantic regions. Overall, litter dynamics were driven by a combination of factors, including mean tree age, climatic variables, forest types, bioregion and site conditions. The study provides statistical indications of a decline in both litter stocks and C/N ratio over the past 11 years, emphasizing the need to integrate spatial and ecological variables to better understand forest litter dynamic.

1. Introduction

Forests are one of the main carbon (C) sinks, storing between 40 % and 60 % of all terrestrial C and sequestering approximately 33 % of the C emitted by fossil fuels each year (Denman and Brasseur, 2007; Pan et al., 2024). However, this capacity is diminishing due to deforestation and ecosystem degradation, with total C stocks dropping from 668 to 662 gigatonnes between 1990 and 2020 (FAO, 2020). Forest C is stored in five main pools: above- and belowground biomass, deadwood, forest floor, and soil (Penman et al., 2003). Among these, litterfall is key for transferring organic C and nutrients into the soil, sustaining nutrient cycling and overall ecosystem health (Krishna and Mohan, 2017).

Composed of leaves, twigs, and other organic material, litter is a primary pathway for nutrient return and an indicator of forest productivity (Chave et al., 2010; Uri et al., 2022). Through decomposition, it contributes to humus formation, soil structure, moisture retention, and microbial activity (Berg and Laskowski, 2005; Cao et al., 2024). In European forests, litter represents about 8.7 % of total C stocks, with soils accounting for 53.9 % (Forests Europe, 2020). In addition to supporting nutrient cycling and C storage, litterfall plays a role in pollutant sequestration, capturing atmospheric elements such as mercury (Hg), sulfur dioxide (SO_2), ozone (O_3), and ammonia (NH_3) (Fowler et al., 1989; Méndez-López et al., 2023). This dual function underscores its role in sustaining ecosystem health.

Litter quantity and quality are shaped by ecological and environmental factors such as climate, soil fertility, and forest characteristics, influencing its composition, timing, and production (Neumann et al., 2018). Studies highlight regional variability: in subtropical forests, litterfall production is negatively correlated with maximum temperature during the wet season, positively influenced by wind speed, and varies significantly by forest type, highlighting the complex interplay between climatic and ecological factors (Liu et al., 2024); In temperate zones,

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litterfall is positively associated with stand age and site quality, but the magnitude of this effect depends on the age distribution of stands (Uri et al., 2022). In tropical South America, soil type emerges as a critical factor, with significantly lower litterfall observed on nutrient-poor white sand soils, underscoring the importance of edaphic conditions in shaping litter production in these ecosystems (Chave et al., 2010). Other drivers include stand density, disturbances, and pathogen outbreaks (Neumann et al., 2018; Seidl et al., 2014). Beyond litter inputs, litter stocks are also controlled by decomposition, which depends, among other constraints, on site conditions and litter trait (Canessa et al., 2021; Joly et al., 2023; Shaolin and Qiang, 2002a). As over 90 % of nitrogen and phosphorus used by plants is recycled through litter (Stuart Chapin et al., 2002), both its production and decomposition are critical to nutrient cycling. Decomposition rates are shaped by litter quality—often measured by the initial C/N ratio—and by factors such as soil biota, climate, and nutrient availability (Aerts and Chapin, 2000; Stuckenberg et al., 2025; Zhang et al., 2016).

In Europe, climate change poses one of the greatest challenges to forest ecosystems, with regional variability making its impacts hard to predict (Michel et al., 2023). This underscores the need for models that integrate seasonality, spatial variability, and forest characteristics to better understand litter dynamics under changing climatic conditions. For example, C sequestration in European temperate forests dropped by 12 % from the 2000s to 2010s, likely due to forest maturation (Pan et al., 2024). At the same time, prolonged droughts have triggered bark beetle outbreaks in Central Europe, compromising forest health and potentially shifting some areas from C sinks to C sources.

Assessing how litter stocks respond to climate is essential for understanding forest–climate interactions, especially in vulnerable areas like the Iberian Peninsula (Enríquez-de-Salamanca, 2025; Joly et al., 2023; Shaolin and Qiang, 2002b). This requires long-term, large-scale monitoring, such as the framework established by the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests), which allows comparisons between model predictions and empirical data (Michel et al., 2023; Neumann et al., 2018).

This study analyzes litter stock drivers in Spain using Generalized Linear Mixed Models (GLMM), examining environmental, climatic, and forest variables across forest types, bioregions, and time. Our goals are to: i) investigate temporal trends in litter stock and quality over the past 11 years, and ii) identify the environmental drivers related to litter stocks and quality across Spain. We hypothesize that litter stock and quality across Spanish forests is primarily driven by: (i) climatic variables, with higher temperatures and lower precipitation associated with reduced litter accumulation and altered litter C/N ratios and, (ii) forest structure and composition, with older stands and conifer-dominated forests showing higher litter accumulation.

2. Materials and methods

2.1. ICP Forests monitoring network: the systematic large-scale monitoring (Level I)

ICP Forests is a comprehensive long-term network dedicated to monitoring forests across Europe and other regions, with 42 countries participating. Founded in 1985, its aim is to gather, compile, and assess data on forest ecosystems, tracking changes in forest conditions and performance over time. The systematic large-scale monitoring Level I (ICP-Forest I) is based on 5628 observational plots, arranged on a transnational 16 × 16 km grid across European forests and beyond, to provide insights into geographic and temporal variations in forest condition (Ferretti et al., 2020; Kai Schwärzel et al., 2022). In Spain, the network comprises 620 plots, where a range of measurements (geomorphological and stand data such as defoliation) are conducted at regular time intervals. In this context, 'litter', in ecological terms, refers to two concepts: the layer of dead plant material accumulated on the soil surface or detached plant material originating from living plants (Krishna and Mohan, 2017). Three litter measurement cycles were completed across all 620 plots (Fig. 1). The first cycle was from 2014 to 2017, the second from 2018 to 2020, and the third from 2021 to 2024. Note that no measurements were conducted in 2015. The first and third cycles spans four years instead of three as it was not possible to complete the entire cycle of plots within the usual three-year period. Each year, an average of 206 plots are measured.

Fieldwork involved collecting litter using a square container with no base, measuring 50 × 50 cm, positioned 6 m from the center of each plot and oriented in the North (N), East (E), South (S), and West (W) directions. To ensure representative data, four collection points were taken from each plot. To avoid potential influences from previous sampling activities, these collection points are relocated within the plots each cycle, allowing measurements to be taken in fresh, undisturbed areas. At each sampling point, all fresh organic material, whether intact or partially decomposed and from which the plant origin could still be identified, was gathered.

In the laboratory, each litter sample was sieved through a 2 mm mesh, discarding material smaller than this size. The samples were then dried in an air oven at 70°C for 48 h before being weighed. Finally, the concentrations of C and nitrogen (N) were determined using dry combustion analysis with an automated analyzer (LECO model CN-2000). Having obtained these two concentrations, we determined the C/N ratio as a measure of litter quality. High litter C/N ratios were interpreted as indicators of slower decomposition and reduced nitrogen availability due to potential nitrogen immobilization (Cotrufo et al., 2005; González et al., 2022).

2.2. Characterization of ICP plots

We utilized the most up-to-date data from the Spanish National Forest Map to assign a forest type to each ICP plot (MITECO, 2022). However, this map contains over 70 different forest types, which could complicate interpretation. To facilitate the analysis and assess general trends, we aggregated these forest types into broader categories following the methodology outlined by Moreno-Fernández et al. (2024). The resulting categories are as follows: Subalpine and montane conifers (n = 102 plots), Mediterranean conifers (n = 148 plots), Deciduous broadleaves (n = 81 plots), Evergreen broadleaves (n = 126 plots), Macaronesian conifers (n = 9 plots), Macaronesian broadleaves (n = 2 plots), Open woodlands (n = 63 plots), and Mixed stands of conifers and broadleaves (n = 89 plots). This classification provides a more standardized and interpretable framework for data analysis, enabling clearer insights.

Furthermore, we used ERA5 climate reanalysis data, which provides hourly estimates of a large number of atmospheric, land, and oceanic climate variables at a spatial resolution of ~31 km globally (Hersbach et al., 2020), to climatically characterize each ICP plot. In particular, we focused on mean annual temperature and annual precipitation. Finally, geomorphological data (coordinates, elevation in m, slope in degrees and aspect as an eight-level factor) along with stand defoliation data (expressed as the portion of affected canopy (%) with respect to the whole crown and grouped in 5 % intervals and mean dominant stand age) were obtained from the ICP-Forest I dataset (http://www.icp-forests.net). The mean values for these variables are presented in Table 1.

2.3. Statistical analysis

Initially, Wilcoxon tests were used to analyze differences in litter stock and litter quality (C/N ratio) across the three sampling cycles and the different forest types. This non-parametric test was chosen to compare paired samples and identify significant differences between cycles.

Subsequently, a GLMM was employed to model both litter stock and quality and assess the influence of various explanatory variables selected

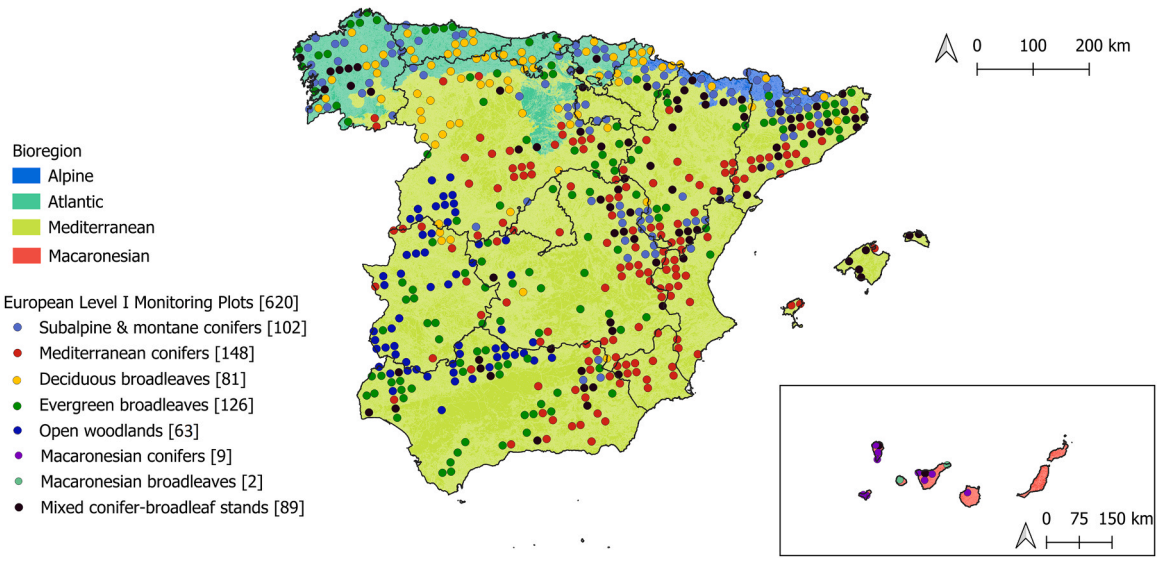

Fig. 1. Overview of the 620 plots in Spain from the ICP-Forests Level I Monitoring Data where litter has been measured across three consecutive cycles. The figure highlights the distribution of plots across different bioregions and forest types.

Table 1
Predictor variables used to estimate litter biomass across different forest types.

Predictor categories and variables	Unit	Min	Max	Mean ± sd
1) Climatic predictors				
Mean temperature	°C	5.53	20.47	14.01 ± 2.58
Total precipitation	mm	87.98	1869.47	753 ± 349.48
2) Spatial and geomorphological characteristics				
X coordinate (UTM ETRS89, zone 30 N)	m	354663	4116345	−3435049 ± 354663
Y coordinate (UTM ETRS89, zone 30 N)	m	2499537	4371678	4051916 ± 2499537
Elevation	m asl	396.89	1725	776.62 ± 396.89
Slope	°	1	10	3.36 ± 1.96
Aspect[a]	-	-	-	-
3) Stand predictors				
Defoliation	%	5.79	76.74	22.76 ± 8.92
Mean age	years	10	150	62.11 ± 49.86

[a] Categorical variables with eight classes.

for their ecological relevance and statistical significance. Climatic variables, including mean annual temperature and total precipitation, were included to capture environmental influences. Stand-related variables such as defoliation (as a proxy for forest health and disturbance) and stand age (as a proxy for forest maturity) were also considered. Additionally, aspect (included as it can influence microclimatic conditions such as soil temperature and moisture), monitoring time (included as a categorical variable to account for temporal variation through three completed cycles), and forest type (to reflect differences in species composition and stand structure) were also included as fixed effects. To account for site-specific variability in litter dynamics, we included an additional random effect of the plot (σ_i).

A full model (Eq.1) was fitted using the glmmTMB function from the glmmTMB R package v1.1.10 (Brooks et al., 2017), which estimates parameters via maximum likelihood using the Template Model Builder (TMB) framework. A Gamma distribution of errors with a log link function was specified to account for the skewness in the response variable.

The full model specification was as follows:

$$\log(y_i) = \beta_0 + \beta_1 Forest\ types_i + \beta_2 Age_i + \beta_3 Aspect_i + \beta_4 Defoliation_i + \beta_5 Precipitation + \beta_6 Temperature_i + \beta_7 Time + \sigma_i \quad (1)$$

The response variable y_i represents the average litter stock per plot (or the C/N ratio in the case of the second model), calculated as the mean of four subsample measurements taken within each plot. The parameter β_0 represents the intercept of the model. Climatic variables (mean temperature and total precipitation). Stand-related predictors, such as defoliation and stand age were also included. Aspect, time and the different forest types were considered as categorical variables. β_n represents the parameter coefficient for the n^{th} fixed effect. σ_i represents the plot random effects.

To identify a parsimonious and ecologically meaningful model set, we used the dredge function from the MuMIn package (Barton, 2016) to evaluate all possible combinations of fixed effects while retaining the random structure. Only models within 4 AICc units ($\Delta AICc \leq 4$) of the best-ranked model were retained (Burnham and Anderson, 2002). Model-averaged parameter estimates were then calculated using Akaike weights across this candidate set, providing estimates of coefficients, standard errors, and *p-values* via the model.avg function.

This same analytical approach was applied to model litter quality (C/N ratio), using the same set of explanatory variables and full model (Eq.1).

All statistical analyses and graphical outputs were conducted using R software (R Core Team, 2019).

Before interpreting the results, comprehensive diagnostic checks were conducted to ensure the robustness of the model. Collinearity among predictors was assessed using the performance package (D. Lüdecke et al., 2021), with all Variance Inflation Factor (VIF) values remaining below the threshold of 3, indicating low correlation. Spatial autocorrelation was examined using the DHARMa package (Hartig, 2024) and evaluated using Moran's I test, which showed no significant spatial patterns. Furthermore, all model assumptions were rigorously evaluated using DHARMa diagnostics, confirming that the model was well-specified and suitable for inference.

Differences in mean annual temperature and mean annual total precipitation among monitoring cycles were tested using one-way analysis of variance (ANOVA) to determine whether group means differed significantly. When significant differences were detected, Tukey's Honest Significant Difference (HSD) post hoc test was applied to

identify which specific pairs of monitoring cycles showed significant contrasts.

3. Results

3.1. Litter biomass dynamics

Litter accumulation is first analyzed at global level in Spain, providing an overview of its dynamics without differentiating between forest types or bioregions (Fig. 2). The results show a gradual decline in litter accumulation across the monitoring cycles. The first cycle (2014–2017) recorded the highest average value (6.51 Mg ha^{-1}), followed by cycle 2 (2018–2020) with 6.23 Mg ha^{-1}, and cycle 3 (2021–2024) with the lowest accumulation (5.45 Mg ha^{-1}). According to the Wilcoxon's test, no significant differences were found between cycles 1 and 2, whereas the reductions observed between cycle 1 and cycle 3, as well as between cycle 2 and cycle 3, were statistically significant (*p-value* < 0.001 in both cases).

When grouping the data into four Spanish bioregions (Mediterranean, Atlantic, Alpine, and Macaronesian) across different forest types, litter stock values varied considerably across forest types, bioregions, and cycles (Fig. 3).

The Atlantic bioregion, on average, recorded the highest litter stocks, particularly in mixed conifer-broadleaf stands and subalpine and montane conifers during the first cycle, with values reaching 11.21 $\pm$ 7.7 and 9.51 $\pm$ 4.91 Mg ha^{-1} respectively. In this bioregion, while mixed conifer–broadleaf stands and evergreen broadleaf forests showed no significant differences between cycles, both subalpine and montane conifers and deciduous broadleaf forests exhibited a significant decline in litter stocks between the first and third cycles, with *p-values* of < 0.03 and < 0.001, respectively.

In the Mediterranean region, litter stocks were generally lower than in the Atlantic bioregion. Among forest types, Subalpine and montane conifers showed the highest litter stock values, reaching 7.78 $\pm$ 4.98 Mg ha^{-1}, with significant declines observed between the first and third cycles (*p-value* < 0.01), and the second and third (*p-value* < 0.04). By the third cycle, litter values had decreased to 6.40 $\pm$ 6.90 Mg ha^{-1}. Similarly, Mediterranean conifers and evergreen broadleaf stands also displayed a similar downward trend, with significant reductions between the first and third cycles (*p-value* $= 0.01$ and 0.03, respectively), and between the second and third cycles (*p-value* $= 0.04$, and 0.05, respectively). In contrast, deciduous broadleaf forests, mixed conifer-broadleaf stands and open woodlands showed consistent litter stocks across all cycles. Open woodlands, in particular, exhibited the lowest litter stock, with values around 2.37 $\pm$ 1.76 Mg ha^{-1}.

In the Alpine bioregion, litter stock values were generally lower than those in the Mediterranean and Atlantic regions, and no significant differences observed between cycles within either forest type. Subalpine and montane conifers had the highest average litter values within this region, reaching 6.87 $\pm$ 4.68 Mg ha^{-1}. On the other hand, mixed conifer-broadleaf stands displayed the lowest average litter stocks, at 3.95 $\pm$ 1.23 Mg ha^{-1} across all three cycles.

In the Macaronesian bioregion, conifer stands exhibited a non-significant decrease in litter stock values, declining from 7.74 $\pm$ 1.37 Mg ha^{-1} to 4.68 $\pm$ 2.69 Mg ha^{-1} (*p-value* $= 0.06$). Broadleaf and mixed conifer-broadleaf stands also showed a decreasing trend in litter stocks across the cycles, although these changes were not statistically significant. However, it is important to note that the number of plots in this bioregion is limited, which may affect the robustness and representativeness of the results.

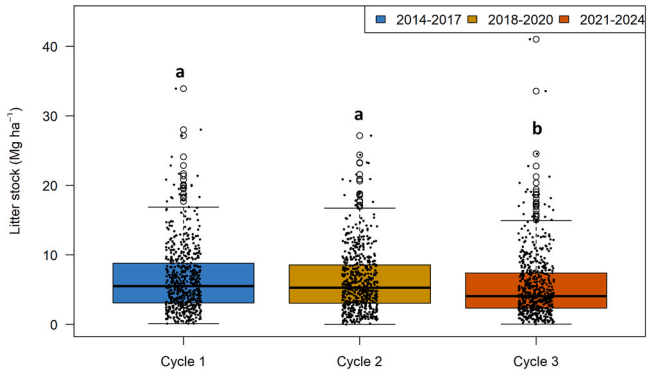

Fig. 2. Litter stock values over three cycles at the national level. Significant differences among the cycles were determined using Wilcoxon test. The letters indicate statistically significant differences between cycles.

3.2. Litter quality dynamics

At the national scale in Spain, the litter nutrient C/N ratio was highest during the first cycle, with a mean value of 53.2 $\pm$ 22.3. The corresponding mean C and N percentages were 48.5 % and 1.04 %, respectively. A statistically significant decrease was observed in subsequent cycles, with the C/N ratio falling to 48.5 $\pm$ 17.5 in cycle 2 (2018–2020; *p-value* < 0.001), accompanied by mean C and N percentages of 46.4 % and 1.06 %, respectively. This downward trend continued in cycle 3 (2021–2024), where the C/N ratio further decreased to 44.4 $\pm$ 20.7 in cycle 3 (2021–2024; *p-value* < 0.001), with corresponding mean C and N percentages of 46.5 % and 1.21 %, respectively Fig. 4.

In addition, we estimated differences in the litter nutrient C/N ratio across various forest types within different bioregions. As shown in Fig. 5, the C/N ratio varied significantly among the forest types studied. Generally, conifer forest types exhibited higher C/N ratios compared to broadleaf forests.

When examining the same group of forest types across the four bioclimatic regions, the Mediterranean region is that which exhibits both higher mean values and a broader range of C/N ratios. This is particularly notable in Subalpine and Montane Conifers (mean = 58.2 $\pm$ 21.1), Deciduous Broadleaves (mean = 37.4 $\pm$ 18.8), and Mixed Conifer–Broadleaf stands (mean = 50.9 $\pm$ 19.5). In contrast, the Alpine and Atlantic bioregions show more moderate averages for these forest types, reflecting less variability than those observed in the Mediterranean region.

Furthermore, the Macaronesian region, particularly coniferous forest, exhibits the highest C/N ratios observed across all regions, with values of 88.1 $\pm$ 41.1, 69.0 $\pm$ 22.5, and 49.1 $\pm$ 21.2 for the first, second, and third cycles, respectively. Although these differences are not statistically significant, the relatively small number of plots (n = 9) for this forest type should be considered when interpreting the results.

In the Atlantic bioregion, significant reductions in the litter C/N ratio between the second and third cycles were observed in Subalpine and Montane Conifer forests (*p-value* < 0.01), Deciduous Broadleaf forests (*p-value* $= 0.05$), and Evergreen Broadleaf forests (*p-value* $= 0.01$). The C/N ratios in these forest types varied widely, ranging from approximately 20 to 100. Additionally, the Mixed Conifer–Broadleaf forest type, which had a small sample size (n = 9), exhibited a decrease in the C/N ratio from the first to the third cycle though this change was not statistically significant (*p-value* $= 0.09$).

In the Mediterranean bioregion, the C/N ratio significantly declined between the first and third cycles in several forest types, including Subalpine and Montane Conifers, Mediterranean Conifers, Open Woodlands, and Mixed Conifer–Broadleaf stands (*p-value* < 0.001, *p-value* < 0.001, *p-value* < 0.001, and *p-value* < 0.001, respectively). Here, C/N ratios displayed a broader range, from values below 15 to above 180 depending on the forest type, with Conifers reaching the highest average values.

In the Alpine bioregion, significant reductions in the litter C/N ratio were observed in Subalpine and Montane Conifer forests between the

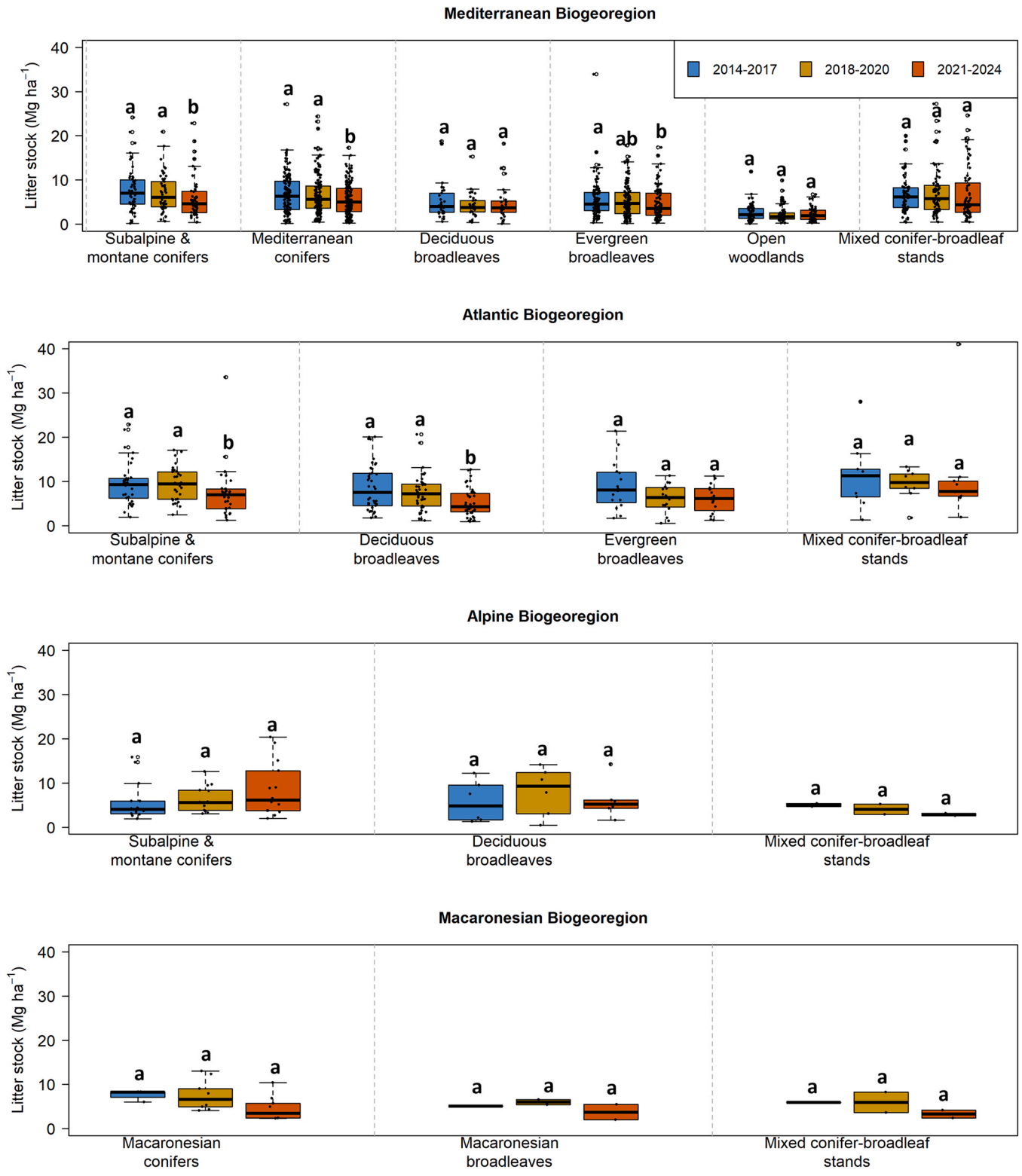

Fig. 3. Litter stock values over three cycles in four bioregions: Mediterranean, Atlantic, Alpine, and Macaronesian, across various forest types, presented separately for each bioregion. Significant differences among the cycles for each forest type and bioregion were determined using Wicoxon test. The letters indicate statistically significant differences between cycles.

first and third cycles (*p-value* < 0.01), as well as between the second and third cycles (*p-value* $= 0.02$).

In contrast, forest types within the Macaronesian bioregion showed no statistically significant differences in C/N ratios between cycles.

3.3. Model performance

3.3.1. Litter biomass dynamics in the Iberian Peninsula

Litter stock was driven by mean tree age, climatic variables (mean annual temperature and total annual precipitation), monitoring time,

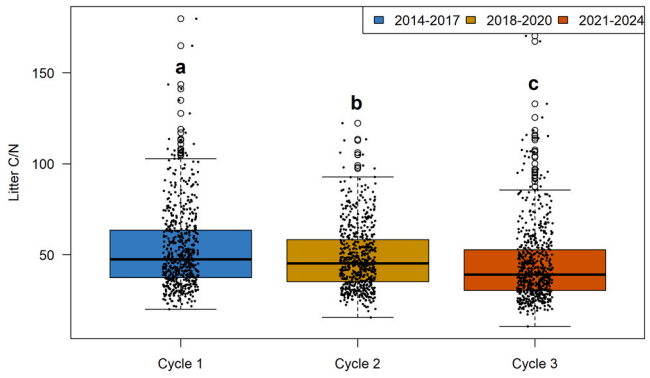

Fig. 4. Comparison of carbon-to-nitrogen (C/N) ratio over three cycles at the national level. Significant differences among the cycles were determined using Wilcoxon test. The letters indicate statistically significant differences between cycles.

forest types, and location. The sum of Akaike weights indicated that monitoring time, forest types, and total precipitation were the most important variables (weight = 0.79), consistently present in all top models. In contrast, mean tree age and mean annual temperature showed lower importance (weights of 0.11 and 0.10, respectively), appearing in fewer candidate models (Table 2).

In our study, annual litter across bioregions ranges from 5.64 ± 4.40–7.95 ± 5.10 Mg ha^{-1} . While litter varies among different forest types in Spain specifically, deciduous broadleaves, evergreen broadleaves, and open woodlands were associated with a significant negative effect on litter accumulation, with *p-values* < 0.001, < 0.001, and < 0.001, respectively. The strongest negative effect was observed for open woodlands (Estimate $= -0.9863$, *p-value* < 0.001), suggesting that this forest formation type contributes less to litter biomass compared to the baseline. Climatic variables, particularly total precipitation, showed a strong positive association with litter biomass (*p-values* < 0.001), emphasizing the role of precipitation in enhancing litter production. Mean temperature also had a significant effect (Estimate $= 0.029$, *p-value* $= 0.03$), indicating a moderate positive influence of temperature on litter biomass.

Temporal dynamics, represented by the three monitoring cycles, had a significant impact on litter stocks. The second and third cycles showed a reduction in litter biomass relative to the first cycle, with estimates of -0.098 (*p-values* < 0.001) and -0.218 (*p-values* < 0.001), respectively, indicating a decrease in litter biomass during these periods compared to first cycle.

Mean forest age was negatively associated with litter biomass (*p-value* < 0.001), indicating that older stands might have reduced litter accumulation (Table 2, Fig. 6).

3.3.2. *Litter quality dynamics in the Iberian Peninsula*

Following model selection, only the highest-ranked model among 128 candidates satisfied the $\Delta AICc \leq 4$ criterion ($\Delta AICc = 0$), indicating strong empirical support relative to alternative models; consequently, only this model was retained for inference. The final GLMM, fitted with a

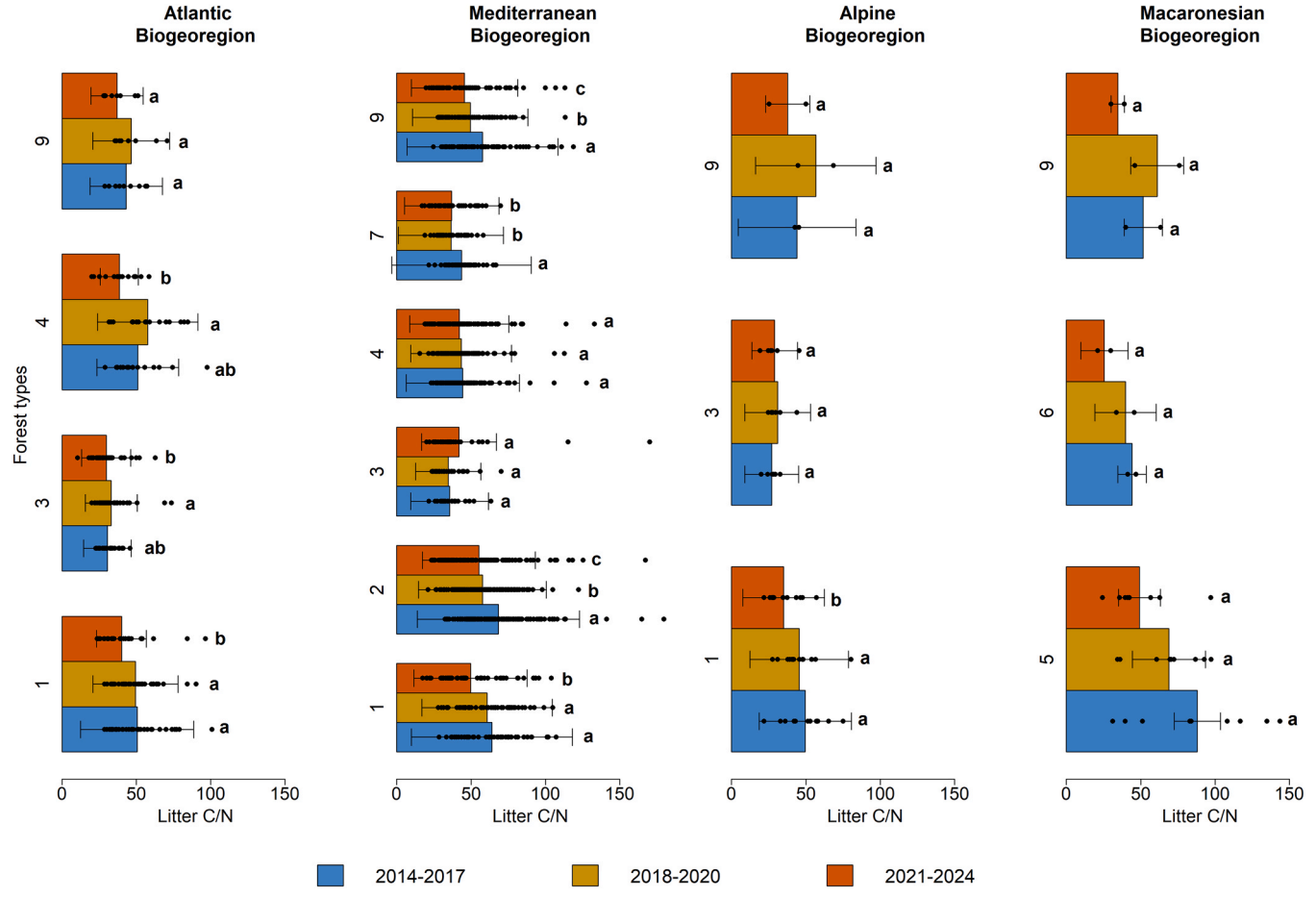

Fig. 5. Comparison of litter C/N (carbon-to-nitrogen) ratios across different forest types for four bioregions: Mediterranean, Macaronesian, Atlantic, and Alpine. The forest types are: 1 - *Subalpine and montane conifers*, 2 - *Mediterranean conifers*, 3 - *Deciduous broadleaves*, 4 - *Evergreen broadleaves*, 5 - *Macaronesian conifers*, 6 - *Macaronesian broadleaves*, 7 - *Open woodlands*, and 9 - *Mixed conifer-broadleaf stands*. Error bars represent the standard deviation. Significant differences among the cycles for each forest type and bioregion were determined using Wicoxon test. The letters indicate statistically significant differences between cycles.

Table 2
Variables included in the top three models (1 if included, 0 otherwise) of litter stock, with corresponding corrected Akaike Information Criterion (AICc) values, model weights, and averaged model performance.

		AICc top models			Average model	
Variable		1	2	3	Estimate (log-scale)	Pr(>|z|)
Intercept		1	1	1	-	***
Time	Cycle 2, Cycle 3	1	1	1	−0.0988 (cycle2)−0.2185 (cyclo3)	*** ***
Forest type	2, 3, 4, 5, 6, 7, 9	1	1	1	−0.0219 (2), −0.3256 (3), −0.2463 (4),+ 0.3168 (5), + 0.1516 (6), −0.9863 (7), + 0.0342 (9)	*** (3, 4, 7)n.s. (2,5,6,9)
Defoliation	-	0	0	0	-	-
Mean age	-	0	1	1	−0.0018	***
Aspect	-	0	0	0	-	-
Precipitation	-	1	1	1	+ 0.000516	***
Temperature	-	0	0	1	+ 0.02863	*
AICc		9189.1	9193.1	9193.2		
Weight		0.79	0.11	0.10		
R^2 cond.		0.66	0.70	0.70	0.69	
R^2 marg.		0.19	0.21	0.20	0.2	

The forest types are: 1 - Subalpine and montane conifers, 2 - Mediterranean conifers, 3 - Deciduous broadleaves, 4 - Evergreen broadleaves, 5 - Macaronesian conifers, 6 - Macaronesian broadleaves, 7 - Open woodlands, and 9 - Mixed conifer-broadleaf stands. Cycle 2: 2018–2020; Cycle 3: 2021–2024. Significance codes: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, $p < 0.1$, n.s. $p \geq 0.1$. Cond.: conditional.Marg.:marginal.

Gamma error distribution and log link function, included monitoring time, forest types, and mean annual temperature as fixed effects, while a random intercept for plot was incorporated to account for site-specific heterogeneity in litter quality dynamics.

The model was based on 1838 observations across 620 plots, with the following performance statistics: AICc = 15002, conditional $R^2 = 0.573$, and marginal $R^2 = 0.299$.

Analysis showed significant temporal shifts in litter quality. Relative to the baseline period (2014–2017), the litter C/N ratio declined significantly during 2018–2020 (Estimate = −0.069, *p-value* < 0.001) and further during 2021–2024 (Estimate = −0.177, *p-value* < 0.001), indicating a decrease in litter C/N ratio over time (Fig. 6, b). Forest type was also a significant predictor of litter quality; specifically, broadleaves forest types exhibited the strongest negative effect on C/N ratio, suggesting higher nitrogen content compared to the reference forest type (subalpine & Montane Conifers), Fig. 6, b.

Temperature had a significant and positive effect on C/N ratio (Estimate = 0.029, *p-value* < 0.001), indicating that warmer conditions are associated with higher C/N ratio.

4. Discussion

This study highlights the complex interactions between environmental variables and forest characteristics on litter biomass and quality dynamics across Spain, spanning different bioregions and timeframes. The significant effects of forest type indicate that litter dynamics are not only a function of local climate conditions but are also strongly influenced by forest characteristics such as species composition and stand structure.

4.1. Bioregion, spatial effects and forest types

4.1.1. Litter biomass

The observed differences between bioregions align with previous studies highlighting the influence of climate and forest composition on litter biomass dynamics versus latitude (Berg et al., 1999; E, Andivia et al., 2018; Liu et al., 2004). The Atlantic bioregion generally exhibited higher litter stock values compared to the Mediterranean, Alpine and Macaronesian regions, a pattern that reflects the diverse climatic conditions, forest compositions, and spatial characteristics inherent to each region.

In Atlantic regions, mixed conifer-broadleaf stands, followed by Subalpine and montane conifer forests, exhibited the highest litter stock values, particularly during the earlier cycles. This suggests that these forest types, characterized by dense canopy cover, tend to accumulate more litter probably due to the combination of favourable climatic conditions and forest composition, with these areas being dominated by more productive forest types, such as *Pinus radiata* D.Don, *Pinus pinaster* Ait., and *Eucalyptus* spp. (Aguirre et al., 2022). This result aligns with a study conducted in the United States, which found that conifer-dominated stands generally had the highest mean estimated litter stocks across the country (Domke et al., 2016). By contrast, open woodland stands, particularly in the Mediterranean region, recorded the lowest litter stocks, which in turn result from lower forest productivity and growth rates (Gea-Izquierdo et al., 2009). This likely reflects the more sparse vegetation and open canopy structure, which limits both litterfall and litter accumulation (Blanco et al., 2009).

Mediterranean regions with drier, warmer climates exhibited lower litter production, suggesting that harsher environmental conditions, combined with the prevalence of open woodland and Mediterranean conifer forests, contribute to reduced litter inputs (Aguirre et al., 2022; Moreno-Fernández et al., 2018). This spatial variation highlights the critical role of regional climatic and geographic factors in shaping litter dynamics across the Iberian Peninsula. Furthermore, the inclusion of a random effect to account for site-level variability significantly improved the performance of both models (litter stock and litter quality). In the litter quality model, approximately 27.4 % of the explained variance was attributable to differences intra-sites. In the litter stock model, site-level variation accounted for 46.9 % of the total explained variance. These results underscore the importance of incorporating random effects in capturing spatial heterogeneity in litter dynamics.

4.1.2. Litter C/N ratio

In this study in the Mediterranean bioregion, Subalpine and Montane conifer forests, as well as Mediterranean conifer forests, display higher C/N values compared to the other forest types analyzed, suggesting slower litter decomposition, which likely contributes to nitrogen immobilization in these systems when mean C/N values are > 40, according to Moore et al. (2006). In contrast, Subalpine and Montane conifer forests in the Atlantic and Alpine bioregions, which show lower C/N values (Fig. 5), the release of C would be favoured, indicating more rapid decomposition rates and a more active nitrogen cycle (Moore, Prescott.,2011). However, other authors have suggested that this critical index varies widely depending on a wide variety of factors (Stohlgren, 2011), for example in conifers, critical C/N ratios ranging from 109 to 19 have been found (Berg, 1986; Edmonds, 1980).

In addition to the C/N ratio, the chemical composition of the litter also influences its decomposition rate. Several studies have

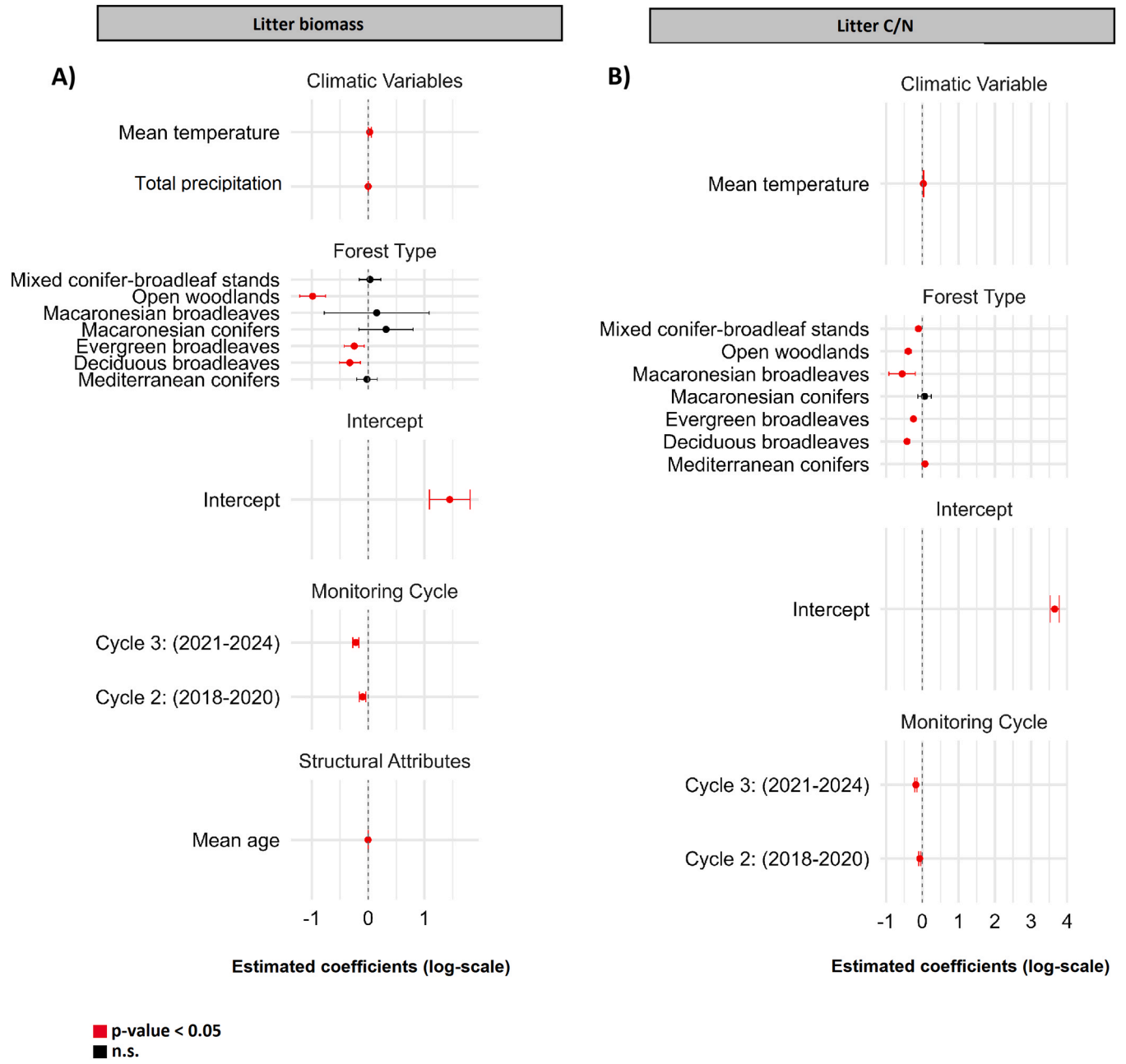

Fig. 6. Estimated coefficients (log-scale) and significance of variables for the average model of litter stocks (A) and the best model for litter C/N ratio (B).

demonstrated the critical role of water-soluble substances, lignin content and the lignin/N ratio in plant litter decomposition (Keerthika et al., 2024; Taylor et al., 1989; Zhang et al., 2023). In general, high-quality litter is associated with a higher concentration of soluble compounds and initial nutrients concentration, lower lignin content, and a low lignin/N ratio, these being characteristics which are more typical of litter from broadleaf species (Bonanomi et al., 2023; Gholz et al., 2000; Moro and Domingo, 2000; Rawat et al., 2020). This trend is reflected in the higher mean C/N values observed in coniferous forests in the Mediterranean bioregion (Fig. 5).

Several studies (Ahirwal et al., 2021; Joly et al., 2023; Neumann et al., 2018) have highlighted the fact that the decomposition process is also influenced by climate factors such as temperature and humidity. The higher litter decomposition rates in the rainy season reflect the favourable effect of precipitation on decomposition of the litter of different species. Low soil moisture and low temperature in the winter season, however, decrease the activity of decomposer organisms, resulting in a slower rate of decomposition (Ge et al., 2022; Tripathi and Singh, 1992; Zhou et al., 2018). For instance, moderate temperatures and humidity, often present in the Atlantic bioregion, would favour the biological activity of the soil and therefore would promote nitrogen mineralization, thereby lowering the C/N ratio and facilitating nitrogen availability, as can be observed in Fig. 5. Furthermore, forest productivity is higher in the Atlantic bioregion than in warmer areas such as the Mediterranean (Moreno-Fernández et al., 2018), which could potentially imply larger aboveground biomass (Verkerk et al., 2019) in Atlantic forests and larger litter inputs from the litterfall (Blanco et al., 2009).

The Mediterranean bioregion is highly heterogeneous, encompassing forests that grow under diverse climatic conditions. These range from savanna-like forests in arid regions to high mountain forests with lower water deficits (Moreno-Fernández et al., 2020). This variability leads to

differences in litter decomposition and accumulation rates. In addition, specific factors within the Mediterranean bioregion—such as lower precipitation, highly variable microclimatic conditions, litter composition, forest type, or management practices may be contributing to the higher C/N ratios observed in some forest types (e.g., Subalpine and Montane conifers and Mediterranean conifers in Fig. 5), which suggests slower decomposition and nitrogen immobilization despite the climatic conditions (Krishna and Mohan, 2017). This fact in Mediterranean ecosystems could also be due to the ease with which the soil surface dries during the only periods when water availability and temperatures are sufficient to allow for higher decomposition rates (spring and fall) (Berg et al., 1993).

In addition to the points mentioned above, to explain the variability in the C/N ratio it is also necessary to consider, apart from the climate and litter quality, the interactions between litter type and site conditions, as some studies have suggested that decomposer communities may be specialized in a specific type of litter characteristic of a given ecosystem (Hunt et al., 1988; Shigyo et al., 2024).

4.2. Climatic, and biotic drivers. Litter stock and quality

At regional level, precipitation and temperature are key climatic factors influencing ecological processes. Variations in litterfall are often closely linked to these climate variables, with factors like temperature, precipitation, and climate-related aspects such as latitude or altitude playing a significant role in explaining litterfall patterns (Ahirwal et al., 2021; Liu et al., 2004). In our study, precipitation showed a significant positive effect on litter accumulation, with a higher relative importance than temperature, highlighting its dominant role in controlling litter stock. This finding aligns with the well-established role of moisture in enhancing litterfall, as increased rainfall promotes canopy growth and, consequently, litter production (Bou et al., 2015; Toledo et al., 2011). Conversely, temperature more strongly influenced litter quality. Specifically, we observed an increase in litter C/N ratio with rising temperatures.

However, when examining changes over time, we observed a progressive decrease in the litter C/N ratio from cycle 1 to cycle 3, driven by a 4.2 % reduction in C concentration and an increase in 16.7 % N concentration from the first to third cycle. This temporal trend suggests an overall improvement in litter quality and may reflect shifting nutrient dynamics or environmental conditions beyond temperature alone, such as atmospheric N deposition or changes in forest productivity. Beyond climatic influences, leaf N content in Spanish forests is also modulated by species composition and site-specific factors such as soil fertility (Sardans and Peñuelas, 2013). Consequently, the spatial variability observed in litter C/N likely reflects complex interactions between climate, vegetation composition, and edaphic factors.

Forest age emerged as a significant predictor of litter biomass, with higher litter accumulation observed during the early maturity phase, where rapid growth and high leaf production lead to increased litter input. Subsequently, litter biomass declined notably as forests continue to age, probably due to factors such as reduced tree density from natural mortality and decreased leaf activity. This pattern aligns with general forest dynamics, where litter production is highest in young to mid-aged stands, then stabilizes during maturity, and eventually decreases in older stands (Huang et al., 2011; Liu et al., 2024). In parallel, recent research has shown that forest age is also a key driver of litter quality variation, contributing substantially to the overall variation in *Fagus sylvatica* L. leaf litter quality traits observed across European forests. Together, these findings underscore the dual role of forest age in shaping both the quantity and quality of litter inputs, with important implications for nutrient cycling, decomposition rates, and broader ecosystem functioning throughout forest development (Trap et al., 2013).

However, it is important to note that the forest age variable used in this study refers only to the age class of dominant trees in each plot, which may not fully represent the structural complexity or age heterogeneity of the stand. A more detailed dataset capturing the full age distribution of trees within each plot could provide a more detailed understanding of the relationship between stand age and litter dynamics. Additionally, the analysis includes species with very different life spans and rotations—some capable of living up to 400 years, while others have a lifespan closer to 80—potentially influencing age-related litter patterns in ways not captured by the current classification. Furthermore, this study does not account for within-plot tree mortality or the specific management practices that may affect stand development, both of which could alter litter input over time. These limitations should be considered when interpreting the observed effects of forest age on litter production.

Canopy defoliation, represented as a percentage of biotic and abiotic damage, reflects the extent of tree-crown foliage loss and serves as an important indicator of tree and forest health (Ferretti et al., 2021), potentially affected by a number of anthropogenic and natural factors (Michel et al., 2023). Although this predictor was not included in the average final model, it was considered in the full model (Eq.1) and remains an ecologically relevant variable. Defoliation reduces the amount of litter produced, probably due to reduced leaf production and canopy cover. This is consistent with the understanding that defoliation caused by biotic and abiotic stressors (such as pests, diseases, drought, or snow) impairs the photosynthetic capacity, overall health, and productivity of a tree (Ferretti et al., 2021; Pajtík et al., 2022).

The results obtained have important implications for forest management, particularly regarding the quantification and balance of C in forest ecosystems. Litter accumulation represents an important fraction of the C stored in these systems, making its detailed monitoring essential for assessing C storage trends and understanding C fluxes across different forest types. However, to achieve a comprehensive estimation of C pools, it is also necessary to account for other tree components, such as roots, stems, and branches.

In this context, forest management strategies aimed at climate change adaptation—especially relevant in Mediterranean forests, where summer drought is a key limiting factor—often promote stand density reduction (Cabon et al., 2018). While this practice enhances resilience to extreme climatic events, it may also reduce litter production per hectare, thereby diminishing the forest's C sink capacity. Therefore, evaluating and analyzing trends in litter dynamics, as conducted in this study, is crucial for properly assessing the effectiveness of adaptive forest management strategies.

4.3. Time component

The time component, composed of three completed cycles (spanning from 2014 to 2024), significantly influences litter biomass and quality. Both the second and third cycles show a substantial negative effect on litter biomass and quality compared to cycle 1.

The observed moderate decline in litter biomass during cycle 2, followed by a more pronounced reduction in cycle 3, indicates a downward trend in litter input relative to the baseline period. This pattern aligns with significant reductions in precipitation detected in the Mediterranean bioregion between cycles 2 and 3 ($p\text{-value} < 0.001$), and in the Atlantic bioregion between cycles 1 and 2 ($p\text{-value} < 0.001$), with no significant changes in other bioregions. These findings are consistent with broader climatic trends in Spain, where both reduced precipitation and rising temperatures have been reported in recent years (Arellano et al., 2025; Vicente-Serrano et al., 2017). Climatic variables, particularly precipitation and temperature, are key drivers of canopy productivity and litterfall rates. Multiple studies demonstrate that reduced precipitation can limit canopy productivity and decrease litterfall, especially in water-limited forests (Breda et al., 2006; Gazol et al., 2018).

Referent to litter quality, the litter C/N ratio declined significantly from cycle 1 to cycle 3, indicating a progressive decrease over time. This reduction in the C/N ratio reflects an improvement in litter quality, as

lower C/N ratios are associated with higher N concentrations in the remaining litter biomass (Sardans and Peñuelas, 2013). The observed decline in litter stock suggests reduced carbon inputs to the forest floor, which may further increase the relative N content in the litter. This aligns with the decreases in mean C percentage and increases in mean N percentage observed across the cycles.

The results underscore the importance of temporal dynamics in litter biomass and quality, captured by the time component of the model. The findings also highlight the crucial role of forest monitoring in tracking temporal patterns in litter production and quality, which can help inform decisions related to nutrient cycling, C storage, and ecosystem health.

An important consideration is that additional years of observation would be necessary to confirm the trends identified, and a more intensive sampling effort could help to reduce uncertainty and better capture the variability in litter dynamics over time. Moreover, the number of plots per forest type is imbalanced, which may influence the robustness, representativeness and generalizability of the results. While formations such as Mediterranean conifers (n = 148), subalpine and montane conifers (n = 102), and evergreen broadleaves (n = 126) are well represented, other formations are underrepresented in terms of plot number. Notably, the Macaronesian forest types are poorly represented, with only 9 plots for Macaronesian conifers and just 2 plots for Macaronesian broadleaves. This limited representation affects the robustness of the results obtained for these specific ecosystems. Therefore, interpretations for these formations should be undertaken with caution, and future research should prioritize expanding sampling efforts in underrepresented forest types to strengthen the reliability of the results.

5. Conclusions

The study provides statistical evidence of a decline in litter stocks and litter C/N ratio over the past 11 years (2014–2024) although additional years of observation would be necessary to confirm the identified trend. Spatial variation in litter stocks and quality across bioregions reflects not only the impact of forest composition but also the broader geographic and climatic conditions unique to each region. These results underscore the necessity to integrate spatial and ecological variables in order to comprehensively understand the complexity of the litter dynamic in forest ecosystems.

The Atlantic bioregion consistently exhibited the highest litter stocks, especially in mixed conifer-broadleaf forests, while the Mediterranean region presented lower values and significant declines over time. Subalpine and montane conifers, along with deciduous broadleaf forests, exhibited notable reductions in litter stocks between the first and third cycles. In contrast, lower overall litter stocks were recorded in the Alpine bioregion, along with an absence of significant temporal changes.

Regional and forest-type differences in litter C/N ratios reveal distinct ecological patterns. Coniferous-dominated stands tended to maintain higher C/N ratios compared to broadleaf forests, with particularly elevated values in the Mediterranean region. The observed reduction in C/N ratios over time indicates increasing litter nutrient availability. This downward trend was especially pronounced in several forest types within the Mediterranean, Alpine, and Atlantic bioregions, pointing to region-specific shifts in litter decomposition dynamics and nutrient cycling.

From a forest management perspective, the findings of this study highlight the importance of monitoring litter accumulation, as it represents an important fraction of the C stored in forest ecosystems. However, for an accurate assessment of the C balance, it is essential to consider all tree components: roots, stems, branches, and litter. Incorporating these components into C accounting enables a more precise understanding of forest C dynamics and helps identify potential imbalances that may compromise the forest's role as a C sink.

Understanding these temporal patterns is vital to interpret long-term changes in ecosystem productivity and resilience. Further research is needed to disentangle the specific environmental, biotic, and anthropogenic factors driving these patterns, as well as their implications for forest dynamics and ecosystem services.

CRediT authorship contribution statement

Daniel Moreno-Fernández: Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Isabel González:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Patricia Adame:** Writing – review & editing, Validation, Methodology, Conceptualization. **Iciar Alberdi:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Conceptualization. **Przemysław A. Jankowski:** Methodology, Formal analysis, Data curation. **Nerea Oliveira:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Isabel Cañellas:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition, Conceptualization. **Alicia Fuertes:** Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

References

Aerts, R., Chapin, F.S., 2000. The Mineral Nutrition of Wild Plants Revisited: A Re-evaluation of Processes and Patterns, in: Advances in Ecological Research. pp. 1–67. https://doi.org/10.1016/S0065-2504(08)60016-1.

Aguirre, A., Moreno-Fernández, D., Alberdi, I., Hernández, L., Adame, P., Cañellas, I., Montes, F., 2022. Mapping forest site quality at national level. For. Ecol. Manag. 508. https://doi.org/10.1016/j.foreco.2022.120043.

Ahirwal, J., Saha, P., Nath, A., Nath, A.J., Deb, S., Sahoo, U.K., 2021. Forests litter dynamics and environmental patterns in the Indian himalayan region. For. Ecol. Manag. 499, 119612. https://doi.org/10.1016/j.foreco.2021.119612.

Andivia, E., Bou, J., Fernandez, M., Caritat, A., Alejano, R., Vilar, L., Vázquez-Piqué, J., 2018. Assessing the relative role of climate on litterfall in Mediterranean cork oak forests. iForest -. Biogeosciences For 786–793. https://doi.org/10.3832/ifor2825-011.

Barton, K., 2016. Package 'MuMIn.' CRAN Repos https//cran. r-project. org/web/packages/MuMIn/MuMIn. pdf.

Arellano, B., Zheng, Q., Roca, J., 2025. Analysis of Climate Change Effects on Precipitation and Temperature Trends in Spain. Land 14. https://doi.org/10.3390/land14010085.

Berg, B., 1986. Nutrient release from litter and humus in coniferous forest soils-a mini review. Scand. J. For. Res. 1, 359–369. https://doi.org/10.1080/02827588609382428.

Berg, B., Laskowski, R., 2005. Litter decomposition: a guide to carbon and nutrient turnover. Adv. Ecol. Res. 38, 38001. https://doi.org/10.1016/S0065-2504(05), 9.

Berg, B., Berg, M.P., Bottner, P., Box, E., Breymeyer, A., de Anta, R.C., Couteaux, M., Escudero, A., Gallardo, A., Kratz, W., Madeira, M., Mälkönen, E., McClaugherty, C., Meentemeyer, V., Muñoz, F., Piussi, P., Remacle, J., de Santo, A.V., 1993. Litter mass loss rates in pine forests of Europe and eastern United States: some relationships with

climate and litter quality. Biogeochemistry 20, 127–159. https://doi.org/10.1007/BF00000785.
Berg, B., Albrektson, A., Berg, M.P., Cortina, J., Johansson, M.-B., Gallardo, A., Madeira, M., Pausas, J., Kratz, W., Vallejo, R., McClaugherty, C., 1999. Amounts of litter fall in some pine forests in a european transect, in particular Scots pine. Ann. For. Sci. 56, 625–639. https://doi.org/10.1051/forest:19990801.
Blanco, J.A., Imbert, J.B., Castillo, F.J., 2009. Thinning affects nutrient resorption and nutrient-use efficiency in two pinus sylvestris stands in the pyrenees. Ecol. Appl. 19, 682–698. https://doi.org/10.1890/1051-0761-19.3.682.
Bonanomi, G., Motti, R., De Marco, A., Idbella, M., 2023. Temperature sensitivity and decomposition rate of 101 leaf litter types from Mediterranean ecosystems. Sci. Total Environ. 894, 165026. https://doi.org/10.1016/j.scitotenv.2023.165026.
Bou, J., Caritat, A., Vilar, L., 2015. Litterfall and growth dynamics relationship with the meteorological variability in three forests in the montseny natural park. Folia For. Pol. Ser. A 57, 145–159. https://doi.org/10.1515/ffp-2015-0015.
Breda, N., Roland, H., Granier, A., Dreyer, E., 2006. Temperate forest trees and stands. Ann. For. Sci. 63, 625–644.
Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9, 378–400. https://doi.org/10.32614/rj-2017-066.
Burnham, K., Anderson, D., 2002. Multimodel inference: a practical Information-Theoretic approach. Sociol. Methods Res.
Cabon, A., Mouillot, F., Lempereur, M., Ourcival, J.M., Simioni, G., Limousin, J.M., 2018. Thinning increases tree growth by delaying drought-induced growth cessation in a Mediterranean evergreen oak coppice. For. Ecol. Manag. 409, 333–342. https://doi.org/10.1016/j.foreco.2017.11.030.
Canessa, R., van den Brink, L., Saldaña, A., Rios, R.S., Hättenschwiler, S., Mueller, C.W., Prater, I., Tielbörger, K., Bader, M.Y., 2021. Relative effects of climate and litter traits on decomposition change with time, climate and trait variability. J. Ecol. 109, 447–458. https://doi.org/10.1111/1365-2745.13516.
Cao, T., Zhang, Q., Chen, Y., Li, Q., Fang, Y., Luo, Y., Duan, C., chen, Q., Song, X., Tian, X., 2024. Enlarging interface reverses the dominance of fungi over bacteria in litter decomposition. Soil Biol. Biochem 198, 109543. https://doi.org/10.1016/j.soilbio.2024.109543.
Chave, J., Navarrete, D., Almeida, S., Álvarez, E., Aragão, L.E.O.C., Bonal, D., Châtelet, P., Silva-Espejo, J.E., Goret, J.Y., Von Hildebrand, P., Jiménez, E., Patiño, S., Peñuela, M.C., Phillips, O.L., Stevenson, P., Malhi, Y., 2010. Regional and seasonal patterns of litterfall in tropical South America. Biogeosciences 7, 43–55. https://doi.org/10.5194/bg-7-43-2010.
Cotrufo, M.F., De Angelis, P., Polle, A., 2005. Leaf litter production and decomposition in a poplar short-rotation coppice exposed to free air CO2 enrichment (POPFACE). Glob. Chang. Biol. 11, 971–982. https://doi.org/10.1111/j.1365-2486.2005.00958.x.
Denman, K., Brasseur, G., 2007. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Couplings Between Changes in the Climate System and Biogeochemistry. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA New York. https://doi.org/10.1021/acs.bioconjchem.6b00417.
Domke, G.M., Perry, C.H., Walters, B.F., Woodall, C.W., Russell, M.B., Smith, J.E., 2016. Estimating litter carbon stocks on forest land in the United States, 469–478 Sci. Total Environ. 557–558. https://doi.org/10.1016/j.scitotenv.2016.03.090.
Edmonds, 1980. Litter decomposition and nutrient release in Douglas-fir, red alder, Western hemlock and pacific silver fir ecosystems in Western Washington. Can. J. For. Res. 10, 327–337.
Enríquez-de-Salamanca, Á., 2025. Expected impacts on Mediterranean forest species under climate change. Climate 13, 1–23. https://doi.org/10.3390/cli13020041.
FAO, 2020. Global Forest Resources Assessment 2020 – Key findings. https://doi.org/https://doi.org/10.4060/ca8753en The.
Ferretti, M., Fischer, R., Mues, V., Granke, O., Lorenz, M., Seidling, W., Nicolas, M., 2020. ICP Part II: Basic Design Principles for the ICP Forest Monitoring Networks. Version 2020-2, Manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air polution on forests.
Ferretti, M., Bacaro, G., Brunialti, G., Calderisi, M., Croisé, L., Frati, L., Nicolas, M., 2021. Tree canopy defoliation can reveal growth decline in mid-latitude temperate forests. Ecol. Indic. 127. https://doi.org/10.1016/j.ecolind.2021.107749.
Forests Europe, 2020. State of Europe's Forests 2020. Ministerial Conference on the Protection of Forests in Europe - FOREST EUROPE Liaison Unit Bratislava. State Eur. For.
Fowler, D., J., N.C, Unsworth M.H.., 1989. Deposition of atmospheric pollutants on forestsPhil. Trans. R. Soc. Lond. B324247–265. Philos. Trans. R. Soc. London. B, Biol. Sci. 324.1223, 247–265. https://doi.org/http://doi.org/10.1098/rstb.1989.0047.
Gazol, A., Camarero, J.J., Vicente-Serrano, S.M., Sánchez-Salguero, R., Gutiérrez, E., de Luis, M., Sangüesa-Barreda, G., Novak, K., Rozas, V., Tíscar, P.A., Linares, J.C., Martín-Hernández, N., Martínez del Castillo, E., Ribas, M., García-González, I., Silla, F., Camisón, A., Génova, M., Olano, J.M., Longares, L.A., Hevia, A., Tomás-Burguera, M., Galván, J.D., 2018. Forest resilience to drought varies across biomes. Glob. Chang. Biol. 24, 2143–2158. https://doi.org/10.1111/gcb.14082.
Ge, X., Wang, C., Wang, L., Zhou, B., Cao, Y., Xiao, W., Li, M.H., 2022. Drought changes litter quantity and quality, and soil microbial activities to affect soil nutrients in moso bamboo forest. Sci. Total Environ. 838, 156351. https://doi.org/10.1016/j.scitotenv.2022.156351.
Gea-Izquierdo, G., Martín-Benito, D., Cherubini, P., Cañellas, I., 2009. Climate-growth variability in quercus ilex L. West iberian open woodlands of different stand density, 802 Ann. For. Sci. 66, 802. https://doi.org/10.1051/forest/2009080.
Gholz, H.L., Wedin, D.A., Smitherman, S.M., Harmon, M.E., Parton, W.J., 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Glob. Chang Biol. 6, 751–765. https://doi.org/10.1046/j.1365-2486.2000.00349.x.
González, I., Sixto, H., Rodríguez-Soalleiro, R., Cañellas, I., Fuertes, A., Oliveira, N., 2022. How can leaf-litter from different species growing in short rotation coppice contribute to the soil nutrient pool? For. Ecol. Manag. 520. https://doi.org/10.1016/j.foreco.2022.120405.
Hartig, F., 2024. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.
Hersbach, H., Bell, B., Berrisford, P., Hirahara, S., Horányi, A., Muñoz-Sabater, J., Nicolas, J., Peubey, C., Radu, R., Schepers, D., Simmons, A., Soci, C., Abdalla, S., Abellan, X., Balsamo, G., Bechtold, P., Biavati, G., Bidlot, J., Bonavita, M., De Chiara, G., Dahlgren, P., Dee, D., Diamantakis, M., Dragani, R., Flemming, J., Forbes, R., Fuentes, M., Geer, A., Haimberger, L., Healy, S., Hogan, R.J., Hólm, E., Janisková, M., Keeley, S., Laloyaux, P., Lopez, P., Lupu, C., Radnoti, G., de Rosnay, P., Rozum, I., Vamborg, F., Villaume, S., Thépaut, J.N., 2020. The ERA5 global reanalysis. Q. J. R. Meteorol. Soc. 146, 1999–2049. https://doi.org/10.1002/qj.3803.
Huang, Y.H., Li, Y.L., Xiao, Y., Wenigmann, K.O., Zhou, G.Y., Zhang, D.Q., Wenigmann, M., Tang, X.L., Liu, J.X., 2011. Controls of litter quality on the carbon sink in soils through partitioning the products of decomposing litter in a forest succession series in south China. For. Ecol. Manag. 261, 1170–1177. https://doi.org/10.1016/j.foreco.2010.12.030.
Hunt, H.W., Ingham, E.R., Coleman, D.C., Elliott, E.T., Reid, C.P.P., 1988. Nitrogen Limitation of Production and Decomposition in Prairie, Mountain Meadow, and Pine Forest Published by: Wiley Stable URL: http://www.jstor.org/stable/1941256 REFERENCES Linked references are available on JSTOR for this article: You may need to. Ecology 69, 1009–1016.
Joly, F.X., Scherer-Lorenzen, M., Hättenschwiler, S., 2023. Resolving the intricate role of climate in litter decomposition. Nat. Ecol. Evol. 7, 214–223. https://doi.org/10.1038/s41559-022-01948-z.
Kai Schwärzel, Seidling, W., Hansen, K., Strich, S., Lorenz, M., 2022. ICP Part I: Objectives, Strategy and Implementation of ICP Forests. Version 2022-2. UNECE ICP For. Program. Co- ordinating Cent. Man. methods criteria Harmon. sampling, assessment, Monit. Anal. Eff. air polution For. 2, 20.
Keerthika, A., Parthiban, K.T., Chavan, S.B., Shukla, A.K., Gupta, D.K., Venkatesh, V., 2024. Leaf litter decomposition in different tree species of multifunctional agroforestry: decay constant and initial litter chemistry. Environ. Dev. Sustain 27, 17005–17027. https://doi.org/10.1007/s10668-024-04536-2.
Krishna, M.P., Mohan, M., 2017. Litter decomposition in forest ecosystems: a review. Energy Ecol. Environ. 2, 236–249. https://doi.org/10.1007/s40974-017-0064-9.
Liu, C., Westman, C.J., Berg, B., Kutsch, W., Wang, G.Z., Man, R., Ilvesniemi, H., 2004. Variation in litterfall-climate relationships between coniferous and broadleaf forests in eurasia. Glob. Ecol. Biogeogr. 13, 105–114. https://doi.org/10.1111/j.1466-882X.2004.00072.x.
Liu, X., Feng, Y., Zhao, X., Cui, Z., Liu, P., Chen, X., Zhang, Q., Liu, J., 2024. Climatic drivers of litterfall production and its components in two subtropical forests in south China: a 14-year observation. Agric. For. Meteor. 344, 109798. https://doi.org/10.1016/j.agrformet.2023.109798.
Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., Makowski, D., 2021. Performance: an r package for assessment, comparison and testing of statistical models, 6, 3139. https://doi.org/10.21105/joss.03139.
Méndez-López, M., Parente-Sendín, A., Calvo-Portela, N., Gómez-Armesto, A., Eimil-Fraga, C., Alonso-Vega, F., Arias-Estévez, M., Nóvoa-Muñoz, J.C., 2023. Mercury in a birch forest in SW Europe: deposition flux by litterfall and pools in aboveground tree biomass and soils. Sci. Total Environ. 856. https://doi.org/10.1016/j.scitotenv.2022.158937.
Michel, A., Kirchner, T., Prescher, Anne-Katrin Schwärzel, K., 2023. Forest Condition in Europe Europe - The 2023 Assessment, Thünen Institut.
MITECO, 2022. Mapa Forestal de España (MFE) de máxima actualidad [WWW Document]. ⟨URL https://www.miteco.gob.es/es/cartografia-y-sig/ide/descargas/biodiversidad/mfe.aspx⟩ (accessed 2.22.24).
Moore, Trofymow, Prescott, Titus, 2011. Nature and nurture in the dynamics of C, n and p during litter decomposition in Canadian forests. Ecosyst 9, 46–62. https://doi.org/10.1007/s10021-004-0026-x.
Moore, Trofymow, Prescott, Fyles, Titus, 2006. Patterns of carbon, nitrogen and phosphorus dynamics in decomposing foliar litter in Canadian forests. Ecosystems 9, 46–62. https://doi.org/10.1007/s10021-004-0026-x.
Moreno-Fernández, D., Álvarez-González, J.G., Rodríguez-Soalleiro, R., Pasalodos-Tato, M., Cañellas, I., Montes, F., Díaz-Varela, E., Sánchez-González, M., Crecente-Campo, F., Álvarez-Álvarez, P., Barrio-Anta, M., Pérez-Cruzado, C., 2018. National-scale assessment of forest site productivity in Spain. For. Ecol. Manag. 417, 197–207. https://doi.org/10.1016/j.foreco.2018.03.016.
Moreno-Fernández, D., Cañellas, I., Rubio-Cuadrado, Á., Alberdi, I., 2020. National scale variability in forest stand variables among regions of provenances in Spain. Ann. For. Sci. 77. https://doi.org/10.1007/s13595-020-00943-3.
Moreno-Fernández, D., Cañellas, I., Hernández, L., Adame, P., Alberdi, I., 2024. Nested plot designs used in forest inventory do not accurately capture tree species richness in southwestern european forests. Ann. For. Sci. 81. https://doi.org/10.1186/s13595-024-01237-8.
Moro, M.J., Domingo, F., 2000. Litter decomposition in four woody species in a Mediterranean climate: weight loss, n and p dynamics. Ann. Bot. 86, 1065–1071. https://doi.org/10.1006/anbo.2000.1269.
Neumann, M., Ukonmaanaho, L., Johnson, J., Benham, S., Vesterdal, L., Novotný, R., Verstraeten, A., Lundin, L., Thimonier, A., Michopoulos, P., Hasenauer, H., 2018.

Quantifying carbon and nutrient input from litterfall in european forests using field observations and modeling. Glob. Biogeochem. Cycles 32, 784–798. https://doi.org/10.1029/2017GB005825.
Pajtík, J., Sitková, Z., Marčiš, P., Bošeľa, M., Pavlenda, P., Konôpka, B., 2022. Radial increment and defoliation of pinus sylvestris (L.) on sandy soils relate to summer temperatures and ground water level. Cent. Eur. For. J. 68, 78–90. https://doi.org/10.2478/forj-2022-0002.
Pan, Y., Birdsey, R.A., Phillips, O.L., Houghton, R.A., Fang, J., Kauppi, P.E., Keith, H., Kurz, W.A., Ito, A., Lewis, S.L., Nabuurs, G.J., Shvidenko, A., Hashimoto, S., Lerink, B., Schepaschenko, D., Castanho, A., Murdiyarso, D., 2024. The enduring world forest carbon sink. Nature 631, 563–569. https://doi.org/10.1038/s41586-024-07602-x.
Penman, J., Gytarsky, M., Hiraishi, T., Krug, T., Kruger, D., Pipatti, R., Wagner, F., 2003. Good practice guidance for land use, land-use change and forestry.
R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing.
Rawat, M., Arunachalam, K., Arunachalam, A., Alatalo, J.M., Pandey, R., 2020. Predicting litter decomposition rate for temperate forest tree species by the relative contribution of Green leaf and litter traits in the Indian Himalayas region. Ecol. Indic. 119, 106827. https://doi.org/10.1016/j.ecolind.2020.106827.
Sardans, J., Peñuelas, J., 2013. Tree growth changes with climate and forest type are associated with relative allocation of nutrients, especially phosphorus, to leaves and wood. Glob. Ecol. Biogeogr. 22, 494–507. https://doi.org/10.1111/geb.12015.
Seidl, R., Schelhaas, M.J., Rammer, W., Verkerk, P.J., 2014. Increasing forest disturbances in Europe and their impact on carbon storage. Nat. Clim. Chang 4, 806–810. https://doi.org/10.1038/nclimate2318.
Shaolin, P., Qiang, L., 2002b. The dynamics of forest litter and its responses to global warming. Acta Ecol. Sin. 22, 1534–1544.
Shaolin, P., Qiang, L., 2002a. The dynamics of forest litter and its responses to global warming. Acta Ecol. Sin. 22, 1534–1544.
Shigyo, N., Umeki, K., Hirao, T., 2024. Soil microbial identity explains home-field advantage for litter decomposition. N. Phytol. 243, 2146–2156. https://doi.org/10.1111/nph.19769.
Stohlgren, T.J., 2011. Litter dynamics in two sierran mixed conifer forests. Ii. nutrient release in decomposing leaf litter. Can. J. For. Res. 18, 1136–1144. https://doi.org/10.1139/x88-175.
Stuart Chapin, F., Matson, P.A., Vitousek, P.M., 2002. Principles of terrestrial ecosystem ecology. Principles of Terrestrial Ecosystem Ecology. Springe, New York. https://doi.org/10.1007/978-1-4419-9504-9.
Stuckenberg, T., Lu, J.Z., Scheu, S., 2025. C, n and p dynamics during litter decomposition in pure and mixed beech – conifer stands: effects of litter species, site conditions and native vs non-native conifer species. For. Ecol. Manag. 594, 122929. https://doi.org/10.1016/j.foreco.2025.122929.
Taylor, B., Parkinson, D., Parsons, W., 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. Ecology 70, 97–104.
Toledo, M., Poorter, L., Peña-Claros, M., Alarcón, A., Balcázar, J., Leaño, C., Licona, J.C., Llanque, O., Vroomans, V., Zuidema, P., Bongers, F., 2011. Climate is a stronger driver of tree and forest growth rates than soil and disturbance. J. Ecol. 99, 254–264. https://doi.org/10.1111/j.1365-2745.2010.01741.x.
Trap, J., Hättenschwiler, S., Gattin, I., Aubert, M., 2013. Forest ageing: an unexpected driver of beech leaf litter quality variability in european forests with strong consequences on soil processes. For. Ecol. Manag. 302, 338–345. https://doi.org/10.1016/j.foreco.2013.03.011.
Tripathi, S.K., Singh, K.P., 1992. Nutrient immobilization and release patterns during plant decomposition in a dry tropical bamboo savanna, India. Biol. Fertil. Soils 14, 191–199. https://doi.org/10.1007/BF00346060.
Uri, V., Kukumägi, M., Aosaar, J., Varik, M., Becker, H., Aun, K., Nikopensius, M., Uri, M., Buht, M., Sepaste, A., Padari, A., Asi, E., Sims, A., Karoles, K., 2022. Litterfall dynamics in Scots pine (Pinus sylvestris), Norway spruce (Picea abies) and birch (Betula) stands in Estonia. For. Ecol. Manag. 520. https://doi.org/10.1016/j.foreco.2022.120417.
Verkerk, P.J., Fitzgerald, J.B., Datta, P., Dees, M., Hengeveld, G.M., Lindner, M., Zudin, S., 2019. Spatial distribution of the potential forest biomass availability in Europe. For. Ecosyst. 6, 1–11. https://doi.org/10.1186/s40663-019-0163-5.
Vicente-Serrano, S.M., Rodríguez-Camino, E., Domínguez-Castro, F., El Kenawy, A., Azorín-Molina, C., 2017. An updated review on recent trends in observational surface atmospheric variables and their extremes over Spain. Cuad. Investig. Geogr. 43, 209–232. https://doi.org/10.18172/cig.3134.
Zhang, X., Liu, Z., Liu, X., Liang, X., 2016. Relationship between soil humus dissimilation, soil biological and chemical properties, and leaf litter characteristics in pure forests. Emir. J. Food Agric. 28, 616–624. https://doi.org/10.9755/ejfa.2016-04-355.
Zhang, Y., Xiong, S., You, C., Liu, S., Wang, L., Zhang, L., Li, H., Tan, B., Liu, Y., Xu, Z., 2023. Nitrogen addition promotes foliar litterfall and element return in a subtropical forest, southwestern China. J. For. Res. 34, 939–948. https://doi.org/10.1007/s11676-022-01543-9.
Zhou, S., Huang, C., Xiang, Y., Tie, L., Han, B., Scheu, S., 2018. Effects of reduced precipitation on litter decomposition in an evergreen broad-leaved forest in Western China. For. Ecol. Manag. 430, 219–227. https://doi.org/10.1016/j.foreco.2018.08.022.