Early stage litterfall decomposition dynamics in Pinus halepensis and Pinus brutia stands: Disentangling the effect of climate, species identity and management practices

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Abstract

Background and aims

Understanding the main drivers of decomposition, a fundamental ecosystem process, is crucial for predicting carbon dynamics in Mediterranean pine forests in the context of climate change. Litter decomposition is highly influenced by micro-environmental conditions, litter chemistry and forest management practices.

Methods

A multi-plot decomposition experiment was conducted in *Pinus brutia* and *Pinus halepensis*dominated forests at three regions in Greece. In each plot, different forest management practices have been implemented over the last decades (overstory thinning, understory removal and lack of management). The mass loss of pine needles and standardized material (cellulose papers, wood sticks) was systematically measured along with micro-environmental conditions. Nonlinear mixed-effect models were used to explore the influence of species, stand structure, and micro-climatic and soil conditions on the early decomposition rates.

Results

Needle litter in *P. halepensis* dominated stands decomposed approximately twice as fast as litter in *P. brutia* stands; however, these species-specific differences were probably masked by micro-environmental variation and therefore could not be attributed to differences in litter chemistry. The analysis of the decomposition rates of cellulose papers revealed an across-region positive effect of pH that interacts with variation in microclimate (air temperature and soil water content) and stand structure (total basal area and leaf area index). For wood sticks, pH was the single across-plot predictor of decomposition.

Conclusion

The process of early-stage decomposition across regions could be primarily controlled by variation in soil conditions and their microbial communities, with microclimate and stand structure operating at a smaller (plot-level) scale.

1. Introduction

Forests account for the largest terrestrial carbon (C) pool on the planet, playing a key role in removing anthropogenic CO_2 emissions from the atmosphere and storing them in their soil and biomass. At the global scale, approximately 1500 Pg C are stored at the top one meter of soil (FAO 2022) and ~320 Gt C in the aboveground plant biomass (Bar-On et al. 2018), while soil respiration releases approximately 87-95 Pg C yr^{-1} (Hashimoto et al. 2015). Shifting rainfall patterns, drought events and increased air and soil temperatures are modifying carbon and nitrogen balance, by affecting microclimatic conditions, litter chemistry and the decomposers' community. In the context of climate change, where Mediterranean ecosystems are considered highly vulnerable (IPCC 2023), a clear understanding of litter decomposition is thus needed for designing efficient forest adaptation practices.

Mediterranean ecosystems, such as low elevation pine forests, are characterized by remarkable dry-to-wet cycles that affect decomposition rates (Gallardo and Merino 1993; Fioretto et al. 2001, 2003; Kazakou et al. 2006; Jarvis et al. 2007; Arslan et al. 2010; Dimitrakopoulos et al. 2010; Incerti et al. 2011, 2018; de la Riva et al. 2019). During the wet season, microbial degradation is substantially enhanced by the incoming precipitation and other non-rainfall water sources such as fog or dew (Gliksman et al. 2018a). In dry season, photodegradation is strongly driven by the high radiation fluxes and the prevailing high temperatures (Grünzweig and Gliksman 2021). In general, the decomposition rates in Mediterranean ecosystems are considered optimal within a temperature range of 20-35^{o}C and a litter moisture range between 40-90% (Incerti et al. 2011). At the same time, recent studies highlight the role of microbial community biomass in regulating decomposition process, with mixed-species litter effects ranging from synergistic (where higher species richness accelerates decay to antagonistic effects that slow down decomposition rates (Gartner and Cardon 2004; Hättenschwiler et al. 2005; Ball et al. 2008; Dimitrakopoulos 2010; Sheffer et al. 2015; Zhao et al. 2022). Studies that systematically control the effect of all the above abiotic and biotic factors on the process of decomposition are highly relevant in the context of climate change, and its potential response to global change.

Forest management practices, such as canopy gap creation and understory removal, influence decomposition through different mechanisms. For example, canopy gaps, occurring either naturally or through stand thinning can accelerate litter decay through photodegradation (Gliksman et al. 2018b; Wang et al. 2021; 2022). Stand thinning can also enhance soil fertility and nutrients circulation (Lado-Monserrat et al. 2016), but reduce litterfall production and thus the forest floor biomass intake (Blanco et al. 2006; Doukalianou et al. 2022), affect water availability (Bueis et al. 2018), rain interception and soil microclimatic conditions (Whitford and Duval 2019; Grünzweig and Gliksman 2021), and shape the composition of understory vegetation (Navarro et al. 2013). Findings from studies of forest management practices' influence on litter decomposition dynamics are accumulating (Purahong et al. 2014; Jabiol and Chauvet 2015; Santonja et al. 2017; Lagomarsino et al. 2020; Matos et al. 2022), with their results suggesting that specific silvicultural treatments can mitigate fluctuations in regional temperature and humidity conditions (Bravo-Oviedo et al. 2017). In the context of adaptive forest management, the potential effect of different forest management practices on decomposition is highly relevant (Latterini et al. 2023).

Around the Mediterranean basin, *Pinus brutia* and *Pinus halepensis* forests cover approximately 7 million ha and play a major ecological and economic role (Chambel et al. 2013; Mauri et al. 2016). Decomposition studies in these forests have focused on their post-fire decomposition dynamics (Radea and Arianoutsou 2000; Sazeides et al. 2021a), the effect of different precipitation regimes on litter decomposition rates (Santonja et al. 2022), the nutrient release during decomposition (García-Plé et al. 1995; Viros et al. 2021), as well as the effect of different silviculture practices on nutrient availability (Lado-Monserrat et al. 2015). Most of these studies have used methods that monitor the rate of mass loss of litterbags (Berg 2014) and/or of standardized materials (cellulose papers, fabric clots, wood sticks etc.), aiming to distinguish environmental effects from those regulated by the quality of litter. Some studies have

implemented a common decomposition protocol for several climatic regions (Joly et al. 2023) however Mediterranean pine forests were not included or the variety of management practices implemented were not specifically taken into account. Even though recent studies have investigated litterfall composition and carbon accumulation in Mediterranean pine forests under discrete management regimes (Doukalianou et al. 2022; Ganatsas et al. 2024; Bueis et al. 2018), none has focused on the process of decomposition through the implementation of common across-sites decomposition protocol.

In the present study we implemented a common decomposition monitoring protocol in *P. brutia* and *P. halepensis* dominated forests at three different geographic regions in Greece. Within these regions, different plots are characterized by discrete management practices and thus provide a natural laboratory to disentangle the effect of climate, dominant species identity and thus litter quality, and management on decomposition dynamics. Our aim was to identify the main drivers of decomposition dynamics in Mediterranean pine forests and to rank the magnitude of their effects and their interactions. To the best of our knowledge, this study represents the first multisite and multiregional decomposition experiment in Greece.

2. Materials & methods

2.1 Study sites

We used a network of 10 permanent monitoring plots (ca 0.1 ha each) established across three study sites in northern Greece. The four (4) plots on the island of Lesvos and the three (3) plots at the continental area of Xanthi are dominated by *P. brutia.* The three (3) plots at Sani are dominated by the sympatric *P. halepensis* pine (Figure 1). At Lesvos there is no understory vegetation, at Sani there is an understory shrub layer (0.5-2.0 m height), consisting mainly of the evergreens *Pistacia lentiscus, Phyllirea latifolia* and *Quercus coccifera*, and at Xanthi there is an at least 5 m-high floor below the pines, consisting of deciduous broadleaves trees (mainly *Carpinus orientalis, Fraxinus ornus, Quercus coccifera, Q. frainetto*).

Sani experiences a Mediterranean climate with typical hot dry summers and mild, cool winters (with temperatures ranging from 2^{o}C to 10^{o}C in the winter and 20-32^{o}C in the summer, with maximum precipitation of ~60mm in November and December). In the area, three *P. halepensis* plots, all at sea level, are systematically monitored as part of the European LTER network (*Sani Environmental Observatory – LTER-Greece*). Each plot is managed with a different intensity of overstory thinning / understory removal aiming to reduce fire risk (Table 1).

At Xanthi, three study plots are established approximately 4 km north of the city, at an elevation of 290m asl. The climate of Xanthi approaches a continental status with Mediterranean features (with mean temperatures ranging from 2 to 8^{o}C during winter and from 21 to 31^{o}C in the summer). Summers are short, hot and dry, while winters are cold, with significant rainfall and snowfall, particularly in nearby mountains. Xanthi also faces strong stormy winds, especially during winter months. The forest plots at Xanthi are dominated by *P. brutia*, with a significant contribution of various deciduous and broadleaves species. These plots have been subjected to three different thinning practices since 2016 (Table 1): no thinning (control), traditional thinning (~20% removal of total basal area) and intensive thinning (~40% removal of the total basal area) (Doukalianou et al. 2022).

On Lesvos Island, four *P. brutia* plots are established within the island ‘s central pine forest. Lesvos experiences typical Mediterranean climate conditions with mild, rainy winters and hot dry summers. Temperatures range from 6-12^{o}C during winter and 27.5 up to 39^{o}C during the summer, while most precipitation of 115-140mm occurs from December to February. Throughout the year the climate is relatively humid, except during the summer months, when aridity increases due to high temperatures along with strong northerly winds from the Sea of Marmara. The four monitoring plots represent a post-fire chronosequence ranging from approximately 20 to 90 years after stand-replacing fires. These plots are relatively unmanaged and thus provide an example of natural post-fire Pine forest dynamics (Sazeides et al. 2021b).

Variability of stand structure among the plots, as expressed through variation in Basal Area (BA) and Leaf Area Index (LAI), has been shaped by the different management practices, disturbance history and microclimatic conditions. Across all plots, soil, tree and stand characteristics are systemically monitored (Table 1).

Table 1. Characteristics of the permanent monitoring plots.

Species	Site	Plot	Longitude	Latitude	LAI *	Basal area (m^2/ha)	Age	Tree DBH (cm)	Tree height (m)	Soil texture	Soil pH	Origin	Management
P. brutia	Lesvos	LES1	26.36179	39.17160	1.06	9.69 ± 3.86	20	7.36	3.34	CL	6.7	Natural post-fire regeneration	None
		LES2	26.29545	39.12662	1.66	22.2 ± 5.48	46	7.76	4.16	SCL	6.6		
		LES3	26.38450	39.15641	2.13	31.8 ± 9.09	78	27.2	10.2	SCL	6.6		
		LES4	26.37402	39.16189	2.50	31.2 ± 8.54	97	38.6	16.2	SiL	7.1		
P. halepensis	Sani	SAN1	23.31355	40.1085	2.14 (1.88)	23.5 ± 15.7	85	40.5	15.0	S	7.6	Natural forest	None (low density)
		SAN2	23.33419	40.07637	2.29	27.4 ± 7.58	64	28.2	15.7	C	7.2		Understory removal
		SAN3	23.31331	40.09282	3.06 (4.76)	25.3 ± 7.10	72	26.5	15.2	SCL	7.1		None (high density)
P. brutia	Xanthi	XAN1	24.88772	41.15615	1.29	49.3 ± 16.2	72	36.6	20.7	SL	6.1	Planted forest	None
		XAN2	24.88650	41.15597	1.38	43.3 ± 12.5	72	29.9	15.6	LS	6.2		Moderate thinning
		XAN3	24.88765	41.15548	0.73	36.3 ± 11.2	72	30.7	16.0	SL	5.6		Intensive thinning

(*) In plots SAN1 and SAN3 the LAI of the understory shrub vegetation is given in parentheses

2.2 Plot-level measurements

Across the ten study plots tree diameter at breast height (DBH- cm) and (H- m) are systematically recorded (since 2017 at Sani, since 2016 in Xanthi and since 2020 on Lesvos) for all individuals with D > 5cm. Tree diameters were used to calculate the plot-level basal area (BA- m^2 ha^{-1}). LAI (m^2 m^{-2}) was estimated using a ceptometer (ACCUPAR LP-80; Decagon Devices Inc, WA, USA), by systematically measuring photosynthetic active radiation (PAR – μmol quanta m^{-2} s^{-1}) at 36 points above the forest floor (1.3 m) and comparing each PAR with that measured outside of the canopy under full light conditions. All LAI measurements were made around solar noon, and the leaf distribution parameter was set to X = 1. Key soil parameters (soil texture, soil pH, soil organic carbon (SOC), soil nitrogen (N), total plant available phosphorus (Olsen P) and soil water holding capacity (WHC)) were measured at soil samples collected at a depth ranging from 5 to 20 cm, depending on local conditions in each plot, using ISO lab techniques (Soil and Water Resources Institute (SWRI) of the Hellenic Agricultural Organization Dimitra).

2.3 Experimental design

A common experimental design that included two decomposition protocols was implemented simultaneously across all regions and study plots. The litterbag method focuses on the decomposition of pine needles from each site (Berg 2014; Krishna and Mohan 2017), including the effect of litter quality on the decomposition rate. The standard material protocol, using paper sheets and wood sticks (Joly et al. 2017) focuses on the decomposition of common materials across sites, emphasizing the effect of microenvironmental conditions on decomposition dynamics.

In the litterbag protocol eighteen (18) litterbags (15x15 cm) containing pine needles (~1g of air-dry mass per litterbag) were placed in a subplot within each study plot. The litterbags were placed below the surface of the forest floor and above the humus layer. They were fixed with fine plastic mesh parallel to the ground. Each litterbag featured a double mesh design, with the upper side made of plastic wire (mesh size 0.15x0.15 cm), to facilitate micro-fauna interaction with litter, and the underside constructed from non-degradable organic material with a finer mesh size of approximately 0.05x0.05 cm. Every 90 days 3 litterbag samples were collected.

The same type of litterbags was used for the paper sheets. We used non-recycled, chlorine-free, A3 printing paper, of an indicative size of 297 x 420 mm and weight ~10g, folded in 1/6 of their size to fit the litterbags These represent decomposition materials of high cellulose concentration. For wood sticks (low lignin, recalcitrant compounds of organic matter proxy), we used common tongue depressors (made of birch wood) of indicative size of 149 x 19 x 1 mm and weight of 2.5g. In the standard material protocol, eighteen (18) paper sheets and eighteen (18) wood sticks were placed adjacent to the pine litter subplot within each study plot. Every 90 days, three (3) paper sheets and three (3) wood sticks samples were collected. For this protocol, a supplementary subplot was also installed, to determine the incubation period needed in each plot to reach the same proportion of mass loss across all sites. This threshold was defined at 30-45% for cellulose papers and 7-28% of initial mass for wood sticks (Joly et al. 2017). Samples from the supplementary subplot were collected every 60 days.

After retrieval, all samples (both pine needles and standard material) were dried for 48 hours at a temperature of 70^{o}C and then weighed after carefully removing them from the litterbags and separating them from soil debris. The experiment was initiated in all study sites in July of 2024.

2.4 Monitoring of micro-climate conditions

Micro-climate conditions on each plot were measured using a set of HOBO® data loggers. The MX230x soil moisture and temperature sensors were established at a depth of 5cm in every subplot. The MX2031A air temperature and relative humidity sensors were placed on trees adjacent to the decomposition subplots. Soil sensors measure soil temperature (^{o}C) and soil water content (m^3m^{-3}), while air sensors measure air temperature (^{o}C), relative humidity (%) and dew point (^{o}C), at a 30 minute step. Mean, maximum and minimum values of all parameters were calculated both daily and for the 90 days period on each plot. The latter occurred to follow the number of samples collected to ensure their incorporation into the statistical analysis.

2.5 Statistical analysis

We initially used non-linear regression to fit the Olson decay model (Olson 1963), for each study plot and type of decomposition material:

$$M(t) = M_0 e^{-k \cdot t} \; or \; RM(t) = e^{-k \cdot t} \qquad (1)$$

with $M(t)$ (g) the mass remaining after incubation time t (days), M_0 is the initial incubated mass (g), RM the remaining mass portion ($M(t)/M_0$) and k the decomposition rate (day^{-1}). In this model, incubation time (t) was the single predictor and the estimated k's represents the average (constant) decomposition rate over the study period. Non- linear regression models were fitted using the "nlsList" function in R (R Core Development Team 2025).

We then used a non-linear mixed effects model (NLMM) analysis, in which the decomposition rate was allowed to vary with the microenvironmental conditions, and the hierarchical structure of our dataset was specifically considered. Mixed effect analysis was chosen since it is considered suitable for handling ecological data, due to its resilience to spatial dependence (Fletcher et al. 2018), its ability to produce consistent results from clustered data, and its flexibility to incorporate site-specific parameters and their contribution to decomposition dynamics (Oberpriller et al. 2022).

For each type of material, we initially fitted alternative NLMMs setting plot, species and plots nested in species as random effects, using the "nlme" package (Pinheiro et al. 2025). By considering the variance associated with each random term and the overall model performance we decided to proceed with our analysis using plot as the only random term. For the fixed part of the model, we initially tested for the multicollinearity of all potential fixed terms i.e. T_{air} *RH*, T_{soil} *SWC*, elevation, total stand BA and average LAI, soil pH, soil organic carbon (*SOC*), soil nitrogen (N) and phosphorus (P) concentration as well as soil water holding capacity (WHC), by considering the Variance Inflation Factors (VIF) through the "*car*" package (Fox et al., 2001). We then fitted a maximal nonlinear mixed effect model, including all non-collinear fixed effects, and proceeded to a stepwise elimination by sequentially removing nonsignificant predictors (at $p<0.05$) and comparatively considering the value of the model's Akaike Information Criterion (AIC). During the elimination process of collinear variables (from a maximum to minimal structure), we chose to keep at least one from each group (e.g. micro-climatic, soil, stand structure) providing us with ecological meaning. In all cases we retained the simplest model that had a ΔAIC lower than 4 from the previous model. The outcome of our model fits represents the decomposition rate as a linear function of the fixed effect terms (F_i), i.e.

$$k = a + bF_1 + cF_2 + \cdots nF_n \qquad (2)$$

with the overall model for the remaining mass (RM):

$$RM(t) = e^{(-k+p_j)\cdot t} \quad (3)$$

and p_j the random (plot-specific) effect.

3. Results

3.1 Microclimatic Conditions

During the July 2024 – August 2025 period, the average daily temperature ranged from -0.2 to 32.9 ^{o}C at Lesvos, from 3.8 to 32.9 ^{o}C at Sani and from -1.2 to 33.1 ^{o}C at Xanthi (Fig 2a). Average daily RH ranged from 25.9 to 98.2% at Lesvos, from 37.1 to 96.9 % at Sani and from 27.9 to 96.5 % at Xanthi (Fig 2b). We estimated that at Lesvos there were 94 to 104 days with an average atmospheric vapor pressure deficit (VPD – kPa) higher than 1.5 kPa, thus the forest there seem to be under the driest atmospheric conditions, compared with 50 to 61 days at Xanthi and 15 to 34 days at Sani (Fig 2c), probably due to proximity of the stands at Sani to the coastline.

3.2 Average Decomposition Rates

Among the used materials, decomposition rates followed the expected ranking (from fast to slow) across all sites: cellulose papers > pine litter > wood (lignin material). At Lesvos and Xanthi, the needle litter of *P. brutia* had an almost three times lower decomposition rate compared to the *P. halepensis* litter at Sani (k_{litter}≈0.0017 d^{-1} vs k_{litter} ≈0.0006 d^{-1}, Table 2). At Sani and Xanthi, cellulose papers had a similar incubation period of 180 days and presented a faster decomposition compared to Lesvos (Xanthi: k_{paper}≈0.0026 d^{-1}, Sani k_{paper}≈0.0022 d^{-1} vs Lesvos k_{paper}≈0.0005 d^{-1}, Table 3). On the other hand, the decomposition of recalcitrant wood sticks followed a more distinct regional pattern. On Lesvos, the recorded wood sticks' decomposition rates were the slowest (incubation period of ~240 days), at Sani the fastest (~120 days) with Xanthi in between (~180 days). When data were grouped per species, litter of *P. halepensis* stands decomposed ~2.83 times faster than litter of *P. brutia stands*, papers in *P. halepensis* stands decomposed ~1.8 times faster than papers in *P. brutia* stands. The wood sticks in *P. halepensis* stands decomposed ~2.8 times faster than the woods in *P. brutia* stands.

The plot-specific non-linear regression models provided a good fit for the needle litter (Fig.3) and paper sheets (Fig. 4) data. For wood sticks, nonlinear regression did not provide a good fit and thus linear regression was applied (Fig 5). For the pine needles litter and papers, the estimated decomposition rate was highest at SAN1 and lowest at LES2. For wood sticks the fastest rate was also at SAN1, while the slowest at LES1 (Table 3).

Table 2: Decomposition rates (day^{-1}) for pine litter, papers and wood sticks estimated through nonlinear regression, grouped by region (left columns) and dominant species (right columns). R^2 was traditionally calculated by the ratio of the sum of squares of the difference between observed and predicted values to the sum of squares of the difference between the observed values and the mean observed value per grouping variable.

Region	k_{litter}	R^2	k_{paper}	R^2	k_{wood}	R^2	*Dominant species*	k_{litter}	R^2	k_{paper}	R^2	k_{wood}
Lesvos	0.000607 ± 0.000048	66.10%	0.000504 ± 0.000006	55.70%	0.000357 ± 0.000012	86.90%	***P. brutia***	0.000617 ± 0.000037	53.37%	0.001243 ± 0.000079	53.38%	0.000495 ± 0.000026
Sani	0.001745 ± 0.000079	71.86%	0.002245 ± 0.000118	43.14%	0.001387 ± 0.000073	80.53%	***P. halepensis***	0.001745 ± 0.000079	71.86%	0.002245 ± 0.000168	71.86%	0.001387 ± 0.000073
Xanthi	0.0006312 ± 0.000058	40.74%	0.002612 ± 0.000124	66.34%	0.000689 ± 0.000054	64.57%						

Table 3: Decomposition rates (day^{-1}) for pine litter, papers and wood sticks estimated through plot-specific nonlinear regression (pine litter and papers) and linear regression (wood sticks). Coefficient of determination R^2 is also provided (and calculated similarly as mentioned in Table 2).

Plot	k_{litter}	R^2	k_{paper}	R^2	k_{wood}	R^2
LES1	0.000764 ± 0.000095	74.51%	0.000654 ± 0.000092	64.71%	0.000295 ± 0.000024	83.49%
LES2	0.000485 ± 0.000089	68.69%	0.000322 ± 0.000085	69.11%	0.000391 ± 0.000027	87.58%
LES3	0.000556 ± 0.000089	79.24%	0.000422 ± 0.000086	67.24%	0.000344 ± 0.000024	87.49%
LES4	0.000624 ± 0.000092	63.90%	0.000623 ± 0.000093	74.10%	0.000400 ± 0.000022	92.01%
SAN1	0.002011 ± 0.000144	72.05%	0.004146 ± 0.000267	69.48%	0.001657 ± 0.000111	88.47%
SAN2	0.001633 ± 0.000126	78.44%	0.000924 ± 0.000103	68.19%	0.001128 ± 0.000095	83.35%
SAN3	0.001513 ± 0.000122	79.86%	0.002582 ± 0.000162	78.63%	0.001368 ± 0.000152	74.18%
XAN1	0.000793 ± 0.000099	44.55%	0.002668 ± 0.000165	78.62%	0.000611 ± 0.000059	78.66%
XAN2	0.000593 ± 0.000094	58.10%	0.002908 ± 0.000176	79.14%	0.000713 ± 0.000075	75.77%
XAN3	0.000515 ± 0.000092	22.22%	0.002278 ± 0.000149	45.39%	0.000742 ± 0.000136	52.00%

3.3 Environmental Effects on Decomposition Rates

A summary of the mixed effect model analysis used to decide for the optimum hierarchical structure of our dataset is presented in Supplementary Material (A). Using plot as the only random term, the NLMMs yielded the best fitting results with similar estimates for the plots' decomposition rates to the nonlinear simple plot-level analysis (Table S1). By using species as the only random term, thus grouping together all data from Xanthi and Lesvos (*P. brutia*) in one group and all data from Sani (*P. halepensis*) in another one, the NLMM analysis suggested that litter from the *P. halepensis* stands decomposed 2.79 times faster than the litter from *P. brutia* stands ($k_{Phalepensis}$=0.001734 d^{-1}, $k_{Pbrutia}$=0.0006195 d^{-1}) (Fig. S1). Similar results were obtained when a random structure of plot- nested within species was used (Table S2). Even though the "plots nested in species" random term probably represents in a more informative way the structure of our dataset, the simpler "plot only" random effect model was used to avoid unnecessary complexity when micro-environmental fixed effects terms were added.

The correlation and the VIF analysis revealed intercorrelation between the micro-climatic, edaphic and stand structure variables (Supplementary Material B, Fig. S2). Thus *RH*, *VPD* and *WHC* were excluded from the set of variables used as fixed terms. For all materials, the elimination process was finalized when the most significant factors were identified, multicollinearity among predictors was low VIF <5, and the optimum R^2 and AIC were achieved (Supplementary Material C, Table S3, S4 and S5).

The effect of the maintained fixed effect terms on the decomposition rate of each material is summarised in Table 4. *pH* presented a universal positive effect on the decomposition rate across all materials. T_{air} and *SWC* presented positive effects on the decomposition rate for pine litter and paper sheets. The effect of stand structure, expressed through total stand *BA* and *LAI*, affected significantly only the decomposition rate of paper sheets in a positive and a negative way respectively. On the other hand, the decomposition rate of woods sticks was only significantly (positively) affected by the *pH* of the soil.

To summarize the seasonal variation in the decomposition rate of each material we used the estimated coefficients of the environmental (T_{air}, *SWC, pH*) and stand structure (*BA*, *LAI*) predictors and inferred the plot specific *k*'s for each decomposing material (Fig. 6). The predicted decomposition rates at Sani present the wider variation, in contrast to Lesvos. For example, k_{paper} varies from less than 0.001 d^{-1} to SAN2 to more than 0.004 d^{-1} at SAN1, underlying the importance of plot specific conditions, even within the site. The smallest seasonal variation in the decomposition rates was found at Lesvos, with the *k*'s for all materials not exceeding in any season the value of 0.001 d^{-1}. Xanthi on the other hand illustrated systematically low *k*'s for needle litter and wood sticks (below of 0.001 d^{-1}) but had higher decomposition rates for paper (from ca 0.002 to 0.003 d^{-1}). For plots at Lesvos and Sani, the fastest decomposition rates of litter and papers were shown for the plots with the smallest *BA* (LES1 and SAN1 respectively), a pattern which was not observed at Xanthi 's plots.

In terms of seasonality, the decomposition rate at Lesvos seemed to be higher during the winter 2025 period, reaching a plateau or even reducing during the spring and summer 2025 periods. At Sani the estimated decomposition rates seem to progressively increase from autumn 2024 to summer 2025. At Xanthi the decomposition rates seem to progressively increase at XAN1 and XAN2 but reach a plateau during spring 2025 at XAN3.

Table 4: Optimum fixed effect structure for decomposition of each material. Marginal (R^2_M) and conditional (R^2_C) coefficient of determination are also reported. Both R_M^2 and conditional R_C^2 coefficients use the same total variance (sum of predicted fixed, random and residuals variances) as denominator. R_M^2 uses only the predicted fixed effect variance in its numerator, while (R_C^2) uses the sum of fixed and random effect variance in its numerator.

-	Intercept	T_{air}	SWC	pH	BA	LAI	R^2_M	R^2_C
k_{litter}	0.005896	+0.000029	+0.003226	+0.000560			64.46%	81.24%
p		**0.026**	**0.019**	**0.013**				
k_{paper}	0.020061	+0.000054	+0.005676	+0.002902	+0.000130	-0.002035	65.89%	82.94%
p		***<0.001***	***<0.001***	**0.002**	***<0.001***	**0.002**		
k_{woods}	0.003055			+0.000594			28.02%	64.02%
p				0.038				

4. Discussion

In this study we present the results of an early-stage decomposition experiment in Mediterranean pine forests. The common monitoring protocol identified between regions and dominant species differences in the decomposition rate of different materials. Across regions, soil pH emerged as a consistent predictor of the process of early-stage decomposition. Within the relatively narrow range of climatic conditions that our monitoring protocol was implemented, microclimate conditions seem to partially control the rates of early-stage decomposition. The effect of litter quality as expressed through the chemical composition of litter from the two study species could only be indirectly considered as the latter was not measured throughout the implementation period. However, differences in the decomposition rates of standard material, where the effect of litter quality is by-passed, highlighted the effect of soil pH as a common predictor of across region differences in the rates of decomposition.

Our results show that litter *P. halepensis* stands decomposed significantly faster than litter of *P. brutia* stands. We estimated an average decomposition rate of k_{NLR}= 0.001745417 d^{-1} for *P. halepensis* and k_{NLR}=0.000617105 d^{-1} for *P. brutia*. The estimated decomposition rate for *P. halepensis* is close to those reported in other studies. For example, Gliksman et al. (2018b) reported an average decomposition rate ranging from 0.001338 d^{-1} in large forest gaps, to -0.001057 d^{-1} in shady areas, for *P. halepensis* after a one-year incubation period under relatively warmer conditions. In Greece, Arianoutsou and Radea (2000) reported a *k* around 0.00029 d^{-1} for *P. halepensis* litter, estimated through monthly litterfall production and accumulation. Plots at Sani presented decomposition rates ranging from 0.002011 d^{-1} to 0.001633 d^{-1}, which is an order of magnitude greater than the decomposition rates of *P. halepensis* stands of various silvicultural treatments reported in Lado-Monserrat et al. (2016) (from k=0.00078 d^{-1} of the densest plot to k=0.00066 d^{-1} on the clear-cut plot). On the other hand, decomposition rates of *P. halepensis* measured by García-Plé et al. (1995) were significantly faster than the ones reported here (ranging from 0.0170 d^{-1} to 0.0120 d^{-1} in their case). Litter mass loss in *P. brutia* stands yielded an average decomposition rate from k_{NLR} =0.000485 d^{-1} to k_{NLR} =0.000764 d^{-1} across our monitoring plots at Lesvos and Xanthi. Our estimates are within the range reported by Tsiafouli et al. (2018) under different drought treatments (from 0.0001999 d^{-1} to 0.0009001 d^{-1}) for similar incubation period, but with their litterbags intercepting micro-fauna. Unfortunately, few decomposition

studies on *P. brutia* were found, with some concerning woods decomposition (De Meo et al. 2019). This variation in the observed decomposition rates at different areas around the Mediterranean basin suggests that microenvironmental conditions could significantly affect the process of early decay, as also highlighted by the results of this study.

From the two to three times higher k_{litter} in Sani compared to Lesvos and Xanthi and assuming "all else being equal", we could hypothesize that *P. halepensis* litter should be of higher quality than that of *P. brutia*. *P. brutia* is encountered in more arid and semi-arid zones in the eastern Mediterranean basin, hence it could be considered to require lower amounts of precipitation and humidity to grow than *P. halepensis* (Boydak 2004; Ne'eman and Trabaud 2000). Differences in their needle water retention have been reported, with *P. brutia* being able to retain more water under drought stress (Houminer et al. 2022). Although we did not specifically measure litter quality, needle chemical concentration data from previous studies (Michelaki et al. 2019; Fotelli et al. 2020) suggest that fresh *P. brutia* needles have a slightly non-significant higher C/N ratio compared to *P. halepensis* across different sites in Greece. Nevertheless, this difference does not seem rigid enough to explain the observed differences in the decomposition rates between our study species, in the lengths that higher leaf C/N ratios could slow down decomposition rates (McClaugherty and Berg 1987; Aber et al. 1990; Arianoutsou 1993; Berg et al. 1993; Arianoutsou and Radea 2000), even before moisture conditions and their attribution to C/N ratio are considered (Aerts 1997; Petraglia et al. 2019). Furthermore, C/N ratio has been reported as partially insufficient to estimate predicted mass loss of decomposed material (Bonanomi et al. 2013). Additionally, differences in leaf flavonoids concentration that control litter UV sensitivity or microbial activity (Buer et al. 2010), could potentially explain the between species k_{litter} difference, but do not seem to be of an adequate magnitude between these two sympatric species (Kaundun et al. 1997). Unfortunately, since a chemical analysis (including C/N, lignin, cellulose composition etc.) of leaf litter during the implementation period of this set-up was not available, a definitive distinction of species versus microclimatic conditions effects cannot be derived.

However, by considering the results from the decomposition of the standardized material, where the effect of litter quality has been excluded, "all else is not equal". Cellulose papers decomposed significantly faster at Sani and Xanthi with k_{paper} at SAN1 being almost an order of magnitude higher than the average k_{paper} at Lesvos. During the incubation period SAN1 had the least atmospherically dry conditions across all plots, and in general plots at Sani and Xanthi experienced a lower amount of atmospheric dry days. Thus, microclimatic conditions and in particular *RH* and/or *VPD* could be considered a candidate for explaining differences across sites. However, in the case of paper sheets, the per-plot ranking of k_{paper} does not follow the same order as the estimated indexes of atmospheric dryness, with k_{paper} at Sani illustrating a wide range that included all the respective decomposition rates at the relatively drier plots at Xanthi. For wood sticks however, a clear regional separation based on atmospheric dryness is achieved, although no climate variable was maintained as significant in the NLMM analysis. In general, the effect of microclimatic conditions on the decomposition process seems to agree with previous studies, identifying air temperature and soil moisture as important predictors (Moore 1986; Laskowski 2012; Sierra et al. 2017; Wallace et al. 2018; Schwieger et al. 2025), through their influence on micro-fauna activity and thus decomposition rates (Cortez 1998; Bonanomi et al. 2023; Villazón-Orozco et al. 2025).

Soil *pH* was the single predictor that was systematically retained in our NLMM analysis and could be used to separate regional level differences in the early decomposition stage. All plots at Sani had a *pH*> 7 in contrast with the more acidic plots at Lesvos and Xanthi. Thus, the higher atmospheric wetness and the favorable edaphic condition at Sani could explain the regional differences in the observed decomposition rates, suggesting that between these two sympatric species, litter quality could not be a strong determinant. Microbial activity is relatively higher in more alkaline soils rather than acidic ones (Cao et al. 2016). Soil *pH* is related to local bacterial and fungal diversity (Romanowicz et al. 2016), their phylogenetic structure (Freedman and Zak 2015) and has been suggested as the primary driver for microbial communities' composition and richness, even stronger than plants' phylogenetic diversity (Ni et al. 2021). This could be particularly important for wood sticks, with the positive effect of *pH* likely linked to the composition of recalcitrant compounds at this early-decay stage, with the influence of climatic conditions and nutrients availability expected to emerge over longer incubation periods (Bonanomi et al. 2021), probably explaining the better fit of linear regression at this stage of decay. The common positive effect of *pH* across all materials could be associated with the synthesis and activity of fungal and soil bacteria communities (Sinsabaugh et al. 2008; Rousk et al. 2010), with Malik et al. (2018) also highlighting the role of *pH* in explaining two fundamental mechanisms of soil organic carbon accumulation in soils with varying land use intensities.

The direct effect of stand structure, through variation in total basal area and leaf area index, was only identified in the paper sheet decomposition rates. A positive effect of *BA* on the decomposition process has been found in other studies (Hutson and Veitch 1985; Kim 2016; Bueis et al. 2018; Liu et al. 2018; Santos et al. 2019). In our study the stand thinning practices at Xanthi (XAN1- XAN3 from control to heavier thinning) seem to affect the decomposition rate with XAN3 experiencing a slower decomposition for needle litter and paper sheets, but a higher rate for wood sticks. This trend aligns with the findings of Bravo-Oviedo et al. (2017) for mixed oak and pine forests, where heavy thinning led to decrease in decomposition rates. On the contrary, across the post-fire chronosequence gradient on Lesvos, the youngest and least dense plot (LES1) illustrated faster decomposition of paper sheet and needle litter, with wood decay rates increasing with stand age. Studies in *P. brutia* plantations have not identified a significant effect of stand structure on litter decomposition even though litter nutrients stocks vary under different treatment intensities (Erkan et al. 2023). The above suggests that although in general an increase in the decomposition rate is expected at denser stands, important interactions with microenvironmental conditions could ultimately determine the process (Latterini et al. 2023).

The effect of climate, soil, litter quality and stand structure on the decomposition of organic material within forests remains an important ecological question. A clear understanding of the relative importance of these key abiotic and biotic factors is often hindered by their interconnections. Ongoing climate change could influence the process of decomposition and the way it is modeled (Ranucci et al. 2022) and highlight the importance of non-rainfall water sources and their incorporation in carbon cycle models (Logan et al. 2022), especially for Mediterranean ecosystems, where climatic variations are more pronounced. Common decomposition studies for dominant Mediterranean pine species under varying canopy status and management treatments could create comparable outcomes and disentangle the species versus environmental effects on litter decomposition. Adding chemical analysis, and/or mixed litter influence (where the latter occurs) throughout the decomposition process, can further inform valuable data-driven simulations of carbon fluxes in terrestrial ecosystems under climate change.

Abbreviations

AIC	Akaike Information Criterion
BA	Plot basal area (m^2/ha)
C	Carbon
C/N	Ratio of carbon to nitrogen
DBH	Tree diameter at breast height (cm)
H	Tree height (m)
LAI	Leaf Area Index (m^2/m^2)
N	Soil nitrogen (%)
NLMM	Nonlinear mixed effects model
P	Soil phosphorus (mg/kg)
PAR	Photosynthetically Active Radiation (μmol quanta m^{-2} s^{-1})
RH	Relative Humidity (%)
sdD	Standard deviation of trees diameters for each plot
SOC	Soil Organic Carbon
SWC	Mean daily soil water content (m^3/m^3)
T_{air}	Mean daily atmospheric temperature (^oC)
T_{soil}	Mean daily soil temperature (^oC)
VIF	Variation Inflation Factor
VPD	Mean daily Vapor Pressure Deficit (kPa)
WHC	Soil Water Holding Capacity

Declarations

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Authors’ Contributions

Conceptualization: EDM, PGD, NMF, MF, KR; Methodology: EDM, PGD, CS, NMF, MF; Investigation: EDM, NE, GX, AG, NK, NM, CS, EBF, GS; Data curation: EDM, NE, GX, AG, EBF; Visualization: EDM, NMF; Formal Analysis: EDM, PGD, NMF; Writing- original draft: EDM, PGD, NMF; Writing - review & editing: NK, PGD, MF, EV, NMF; Project administration: MNF, PGD, KR; Funding acquisition: MNF, PGD, KR.

Data availability

The datasets generated and analyzed during the current study are available from the corresponding authors on reasonable request.

Conflict of interest

Authors declare no conflict of interest.

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Figures

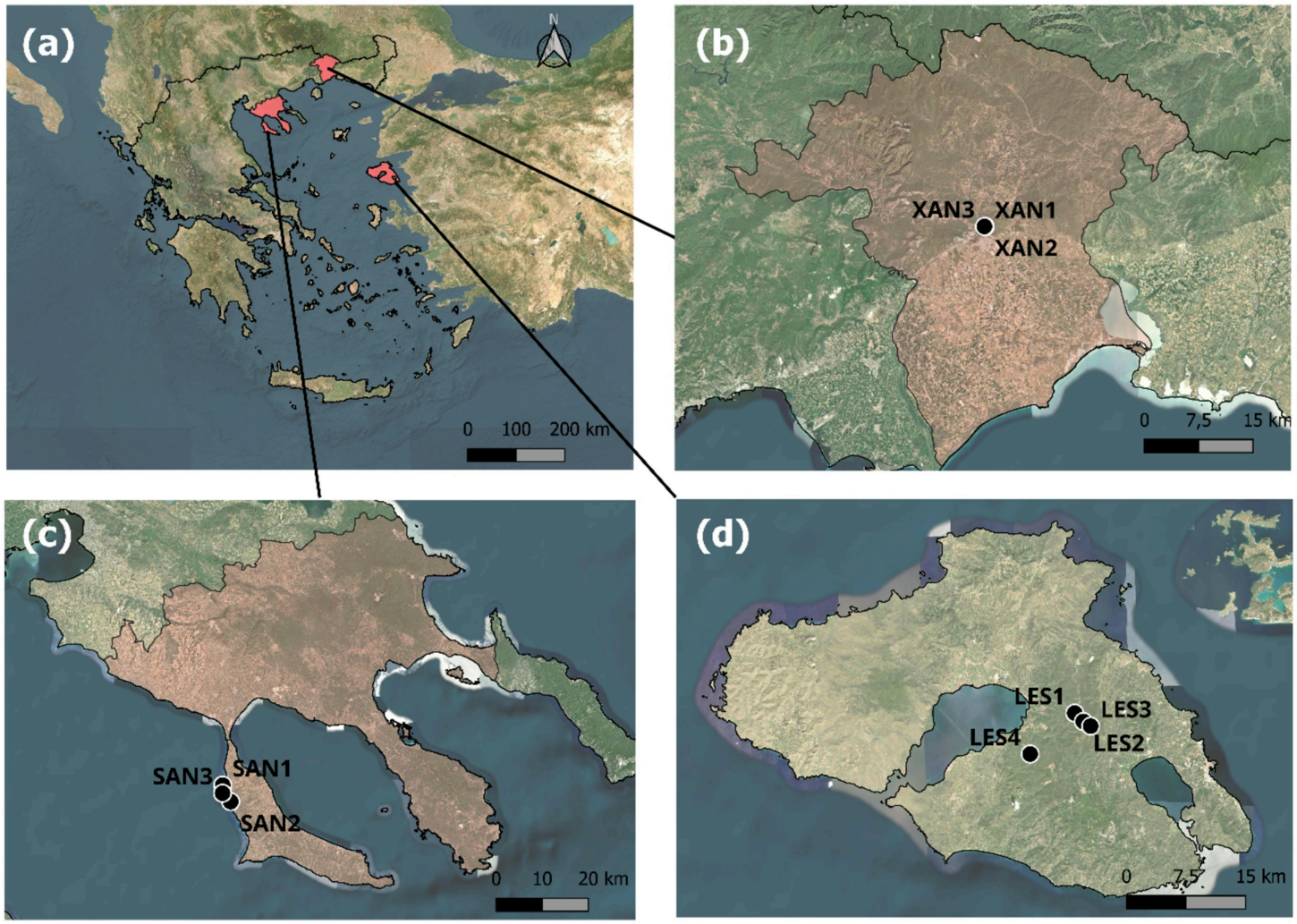

Figure 1

Study sites and plots across Greece: a) Study areas, b) P. brutia stands in Xanthi, c) P. halepensis stands in Sani, Chalkidiki, d) P. brutia stands on Lesvos Island

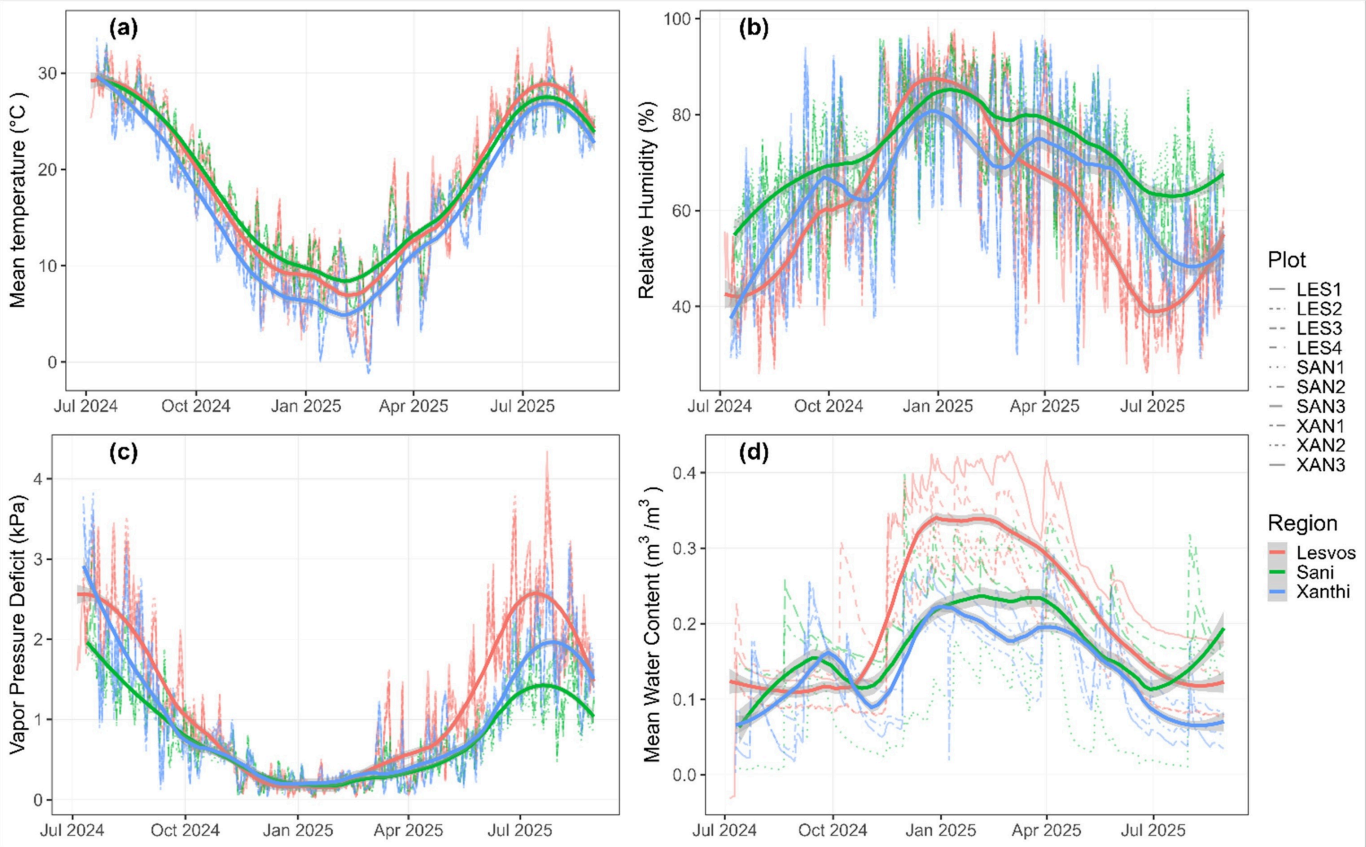

Figure 2

Climate data per site and plot. Plots illustrate: a) the mean daily temperature (°C), b) the mean daily relative humidity (%), c) the average daily vapor pressure deficit (kPa) and d) the mean daily water content (m^3m^{-3}). Number of days with VDP<1.5 kPa and SWC<0.15 m^3/m^3 for each plot respectively: LES1: 102, 107; LES2: 104, 175; LES3: 94, 166; LES4: 96, 102; SAN1: 15, 316; SAN2: 34, 38; SAN3: 25, 57; XAN1: 50, 166; XAN2: 61, 206; XAN3: 59, 169.

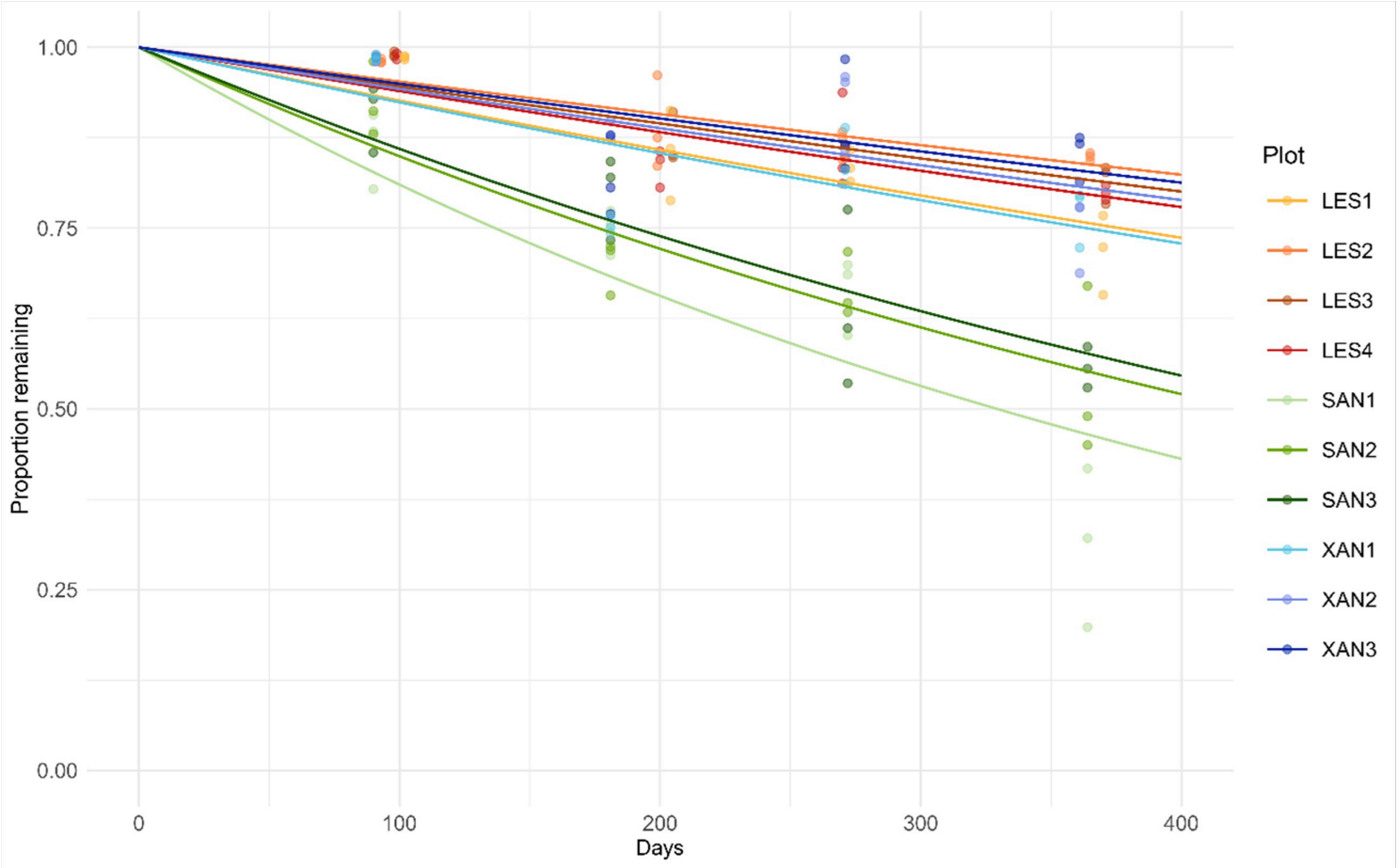

Figure 3

Pine needle litter proportion of remaining mass over the incubation period. Dots represent pine needle litter samples collected and curves represent predicted mass loss using the plot-specific nonlinear regression. Standard errors are not illustrated due to aesthetic reasons. Proportions' standard errors per region: Lesvos varies from 0.98092 ± 0.00168 (days=93) to 0.71609 ± 0.03186 (days=370), Sani varies from 0.89910 ± 0.01719 (day=90) to 0.46857 ± 0.04771 (days=364) and Xanthi varies from 0.98523 ± 0.00117 (days=90) to 0.790121 ± 0.02002 (days=361).

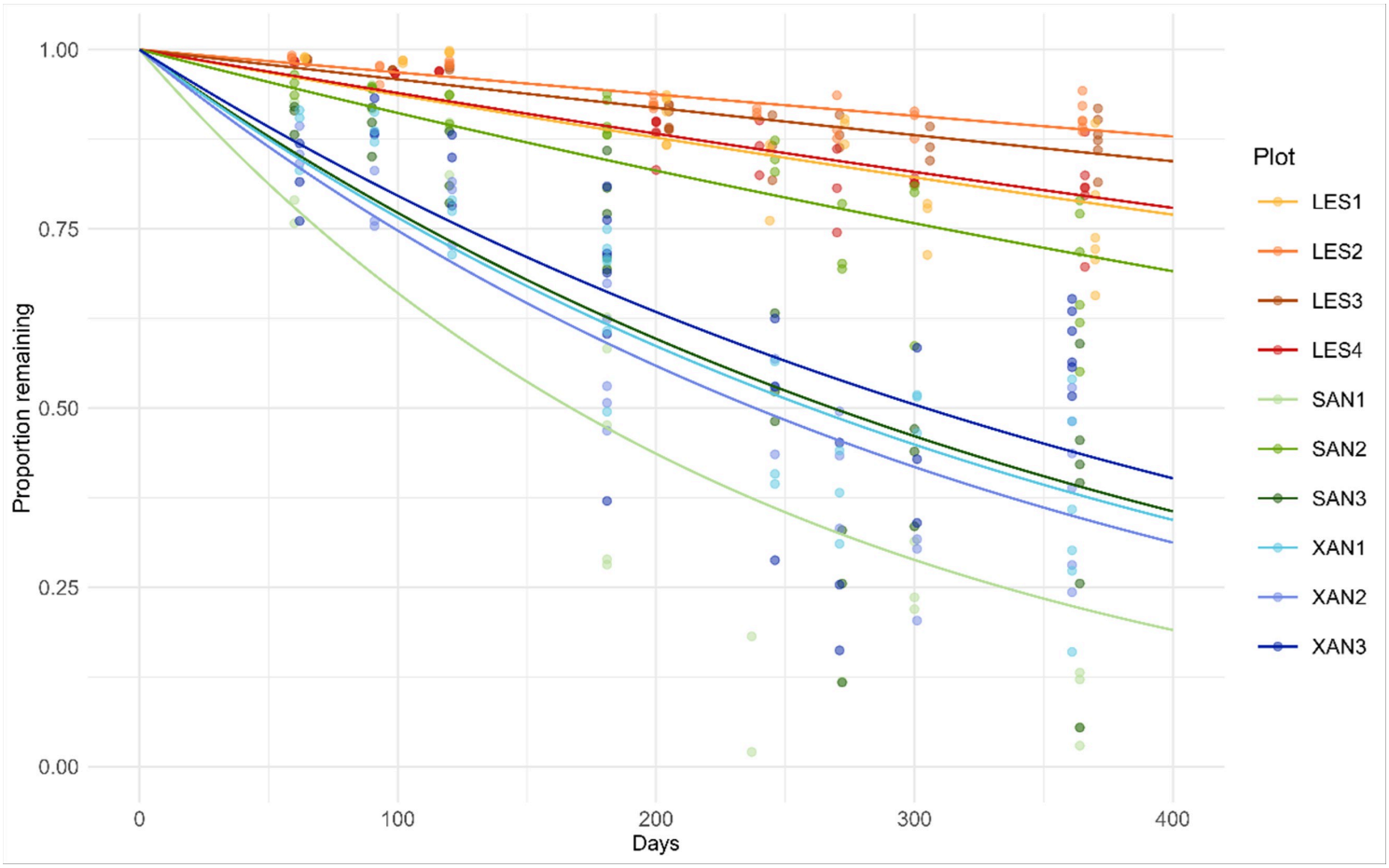

Figure 4

Paper sheet proportion of remaining mass over the incubation period. Dots represent paper sheet samples collected and curves represent predicted mass loss using the plot-specific nonlinear regression. Standard errors are not illustrated due to aesthetic reasons. Proportions' standard errors per region: Lesvos varies from 0.98956 ± 0.00118 (days=59) to 0.75312 ± 0.03436 (days=370), Sani varies from 0.89411 ± 0.02419 (day=60) to 0.42886 ± 0.10963 (days=272) and Xanthi varies from 0.85409 ± 0.016222 (days=62) to 0.40849 ± 0.04151 (days=301).

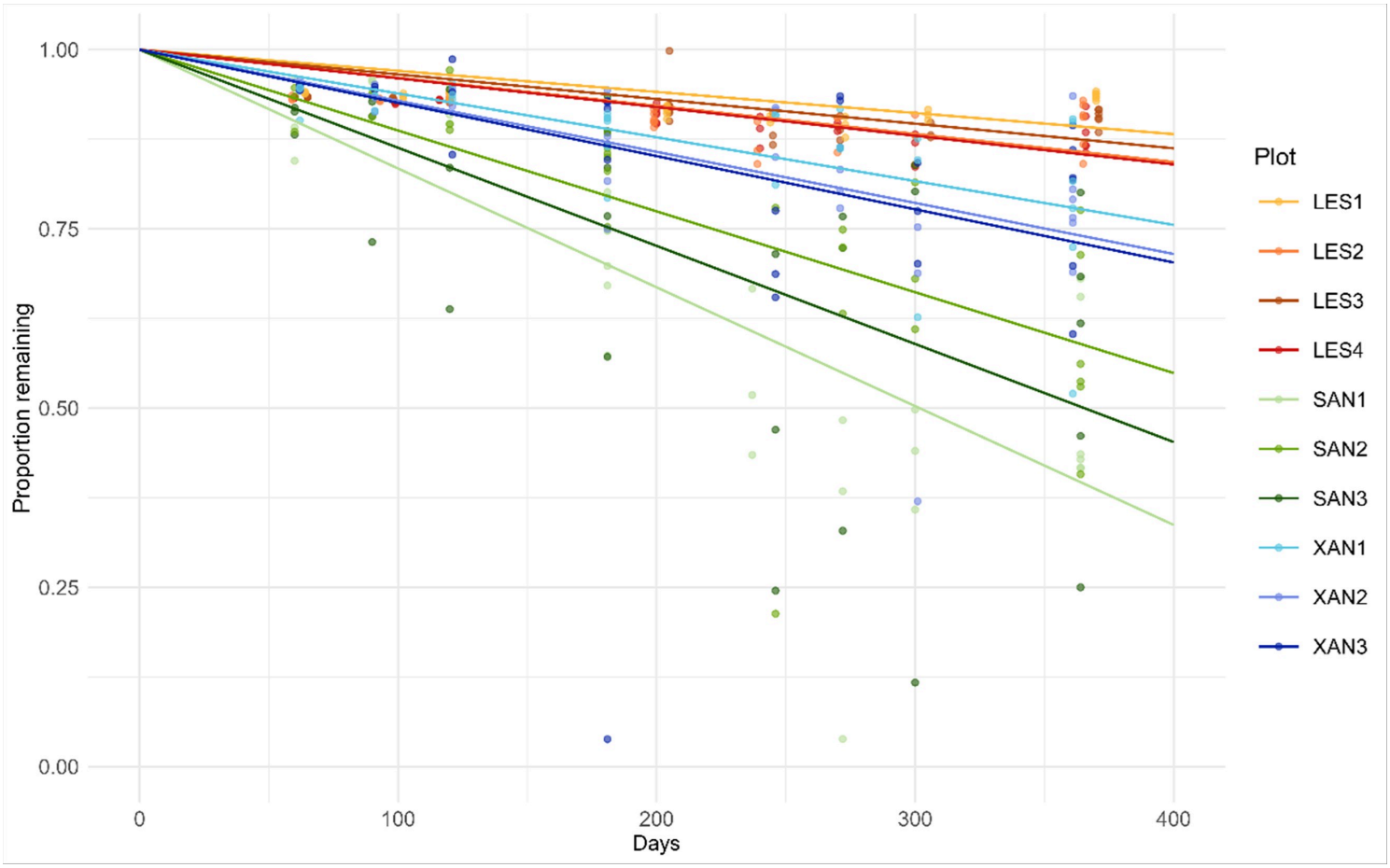

Figure 5

Wood stick proportion of remaining mass over the incubation period. Dots represent wood stick samples collected and lines represent predicted mass loss using the plot-specific linear regression. Standard errors are not illustrated due to aesthetic reasons. Proportions' standard errors per region: Lesvos varies from 0.93289 ± 0.00020 (days=64) to 0.89595 ± 0.01400 (days=365), Sani varies from 0.90856 ± 0.01203 (day=60) to 0.48456 ± 0.11644 (days=246) and Xanthi varies from 0.93455 ± 0.0.00503 (days=91) to 0.71982 ± 0.05161 (days=301).

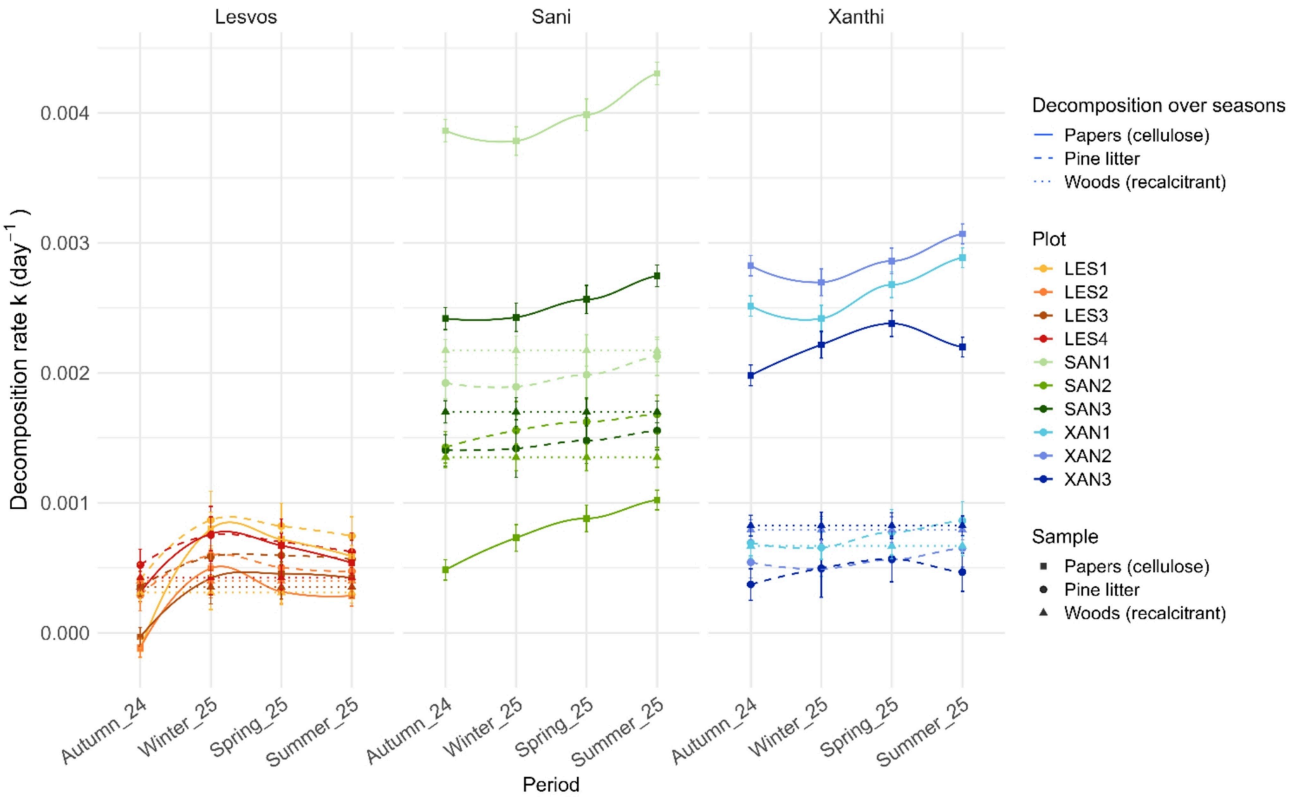

Figure 6

Seasonal variation of decomposition rates k in each site, as inferred from the NLMM analysis. Solid lines represent paper sheets; dotted lines represent woods sticks and dashed lines represent pine needle litter decomposition.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- MantzarietalSupplementaryInformation.pdf