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Identifying major environmental factors of early-stage decomposition dynamics in *Pinus halepensis* and *Pinus brutia* stands

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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. Atmospheric temperature and soil water content interaction had prominent effect across all regions and materials, along with a positive effect of soil pH. The analysis of the decomposition rates of cellulose papers revealed an across-region effect of microclimate (air temperature and soil water content) and stand structure (total basal area and leaf area index). For wood sticks, air temperarute interaction with soil water content and pH were the dominant across-plot predictors of decomposition.

Conclusion

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

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 (°C)
T_{soil}	Mean daily soil temperature (°C)
VIF	Variation Inflation Factor
VPD	Mean daily Vapor Pressure Deficit (kPa)
WHC	Soil Water Holding Capacity

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 Pg 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 20-35ºC 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. 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 and site characteristics 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 has continental characteristics (with mean temperatures ranging from 2 to 8ºC during winter and from 21 to 31ºC 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 broadleaved 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 6-12ºC during winter and 27.5 up to 39ºC 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), like reflects differences in management practices, disturbance history and local environmental conditions. Across all plots, soil, tree and stand characteristics are systemically monitored (Table 1).

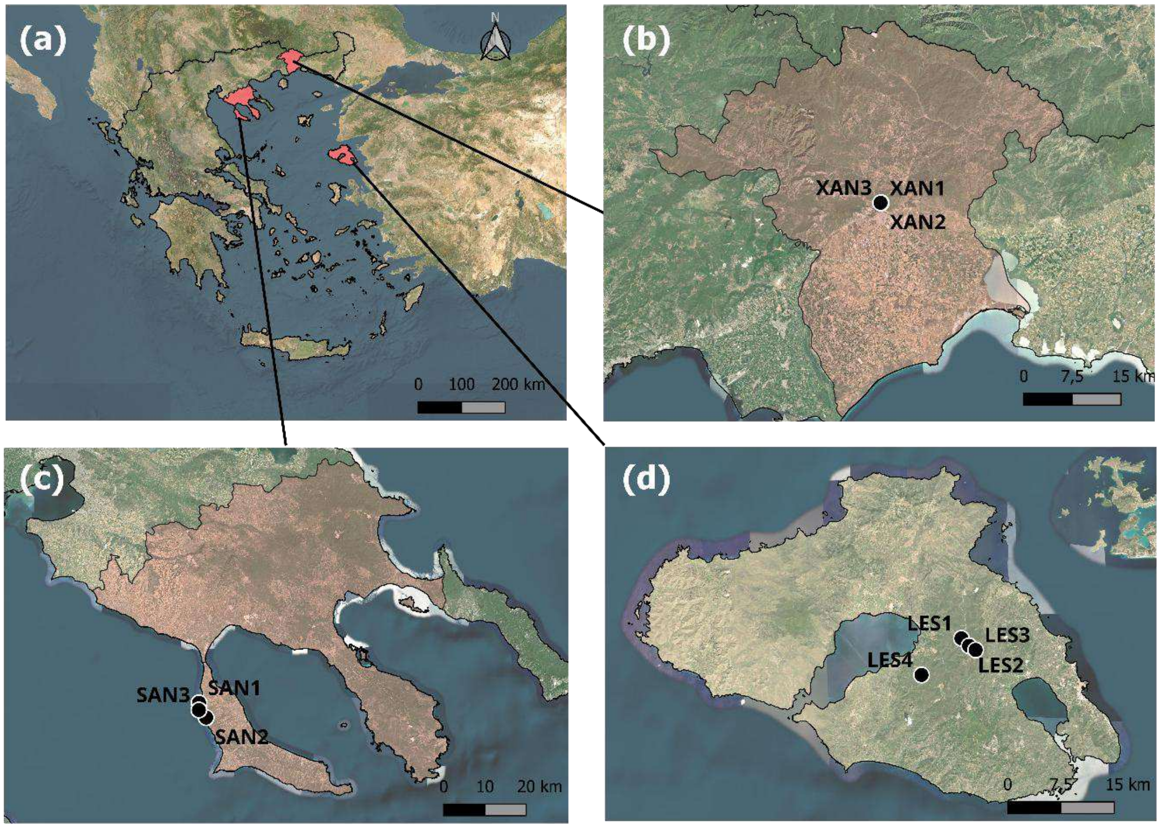

Fig. 1: Study sites and plots across Greece: a) Study areas, b) *P. brutia* stands in Xanthi, c) *P. halepensis* stands in Sani, Chalkidiki, d) *P. brutia* stands on Lesvos Island

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	9.7 ± 3.9	20	7.36	3.34	CL	6.7	Natural post-fire regeneration	None
		LES2	26.29545	39.12662	1.66	22.2 ± 5.5	46	7.76	4.16	SCL	6.6		
		LES3	26.38450	39.15641	2.13	31.8 ± 9.1	78	27.20	10.20	SCL	6.6		
		LES4	26.37402	39.16189	2.50	31.2 ± 8.5	97	38.60	16.20	SiL	7.1		
P. halepensis	Sani	SAN1	23.31355	40.10853	2.14 (1.88)	23.5 ± 15.7	85	40.50	15.00	S	7.6	Natural forest	None (low density)
		SAN2	23.33419	40.07637	2.29	27.4 ± 7.6	64	28.20	15.70	C	7.2		Understory removal
		SAN3	23.31331	40.09282	3.06 (4.76)	25.3 ± 7.1	72	26.50	15.20	SCL	7.1		None (high density)
P. brutia	Xanthi	XAN1	24.88772	41.15615	1.29	49.3 ± 16.2	72	36.60	20.70	SL	6.1	Planted forest	None
		XAN2	24.88650	41.15597	1.38	43.3 ± 12.5	72	29.90	15.60	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, as part of a unified protocol as described in Eleftheriadou et al. (2026). 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 70ºC 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 (ºC) and soil water content (m^3m^{-3}), while air sensors measure air temperature (ºC), relative humidity (%) and dew point (ºC), 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 "nls()" function in R (R Core Development Team 2025). The rates inferred by the models were assigned as starting values into non-linear mixed effect models (NLMM) for each material. Following the optimum structure for our data, species were set as fixed effect and plot as random, to produce a general decomposition dynamic throughout the incubation period for each material.

We then used 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) 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 furthermore added a "temperature- soil water content" interaction term (T_{air}*SWC) in order to represent possible effect of the warm and humid

Mediterranean climate. We then fitted a maximal nonlinear mixed effect model, including all non-collinear fixed effects after scaling, and proceeded to a stepwise elimination by sequentially removing nonsignificant predictors (at $p<0.05$).. 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. 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 when all final predictors' coefficients have been unscaled.

3. Results

3.1 Microclimatic Conditions

During the July 2024 – August 2025 period, the average daily temperature ranged from -0.2 to 32.9 ºC at Lesvos, from 3.8 to 32.9 ºC at Sani and from -1.2 to 33.1 ºC 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.

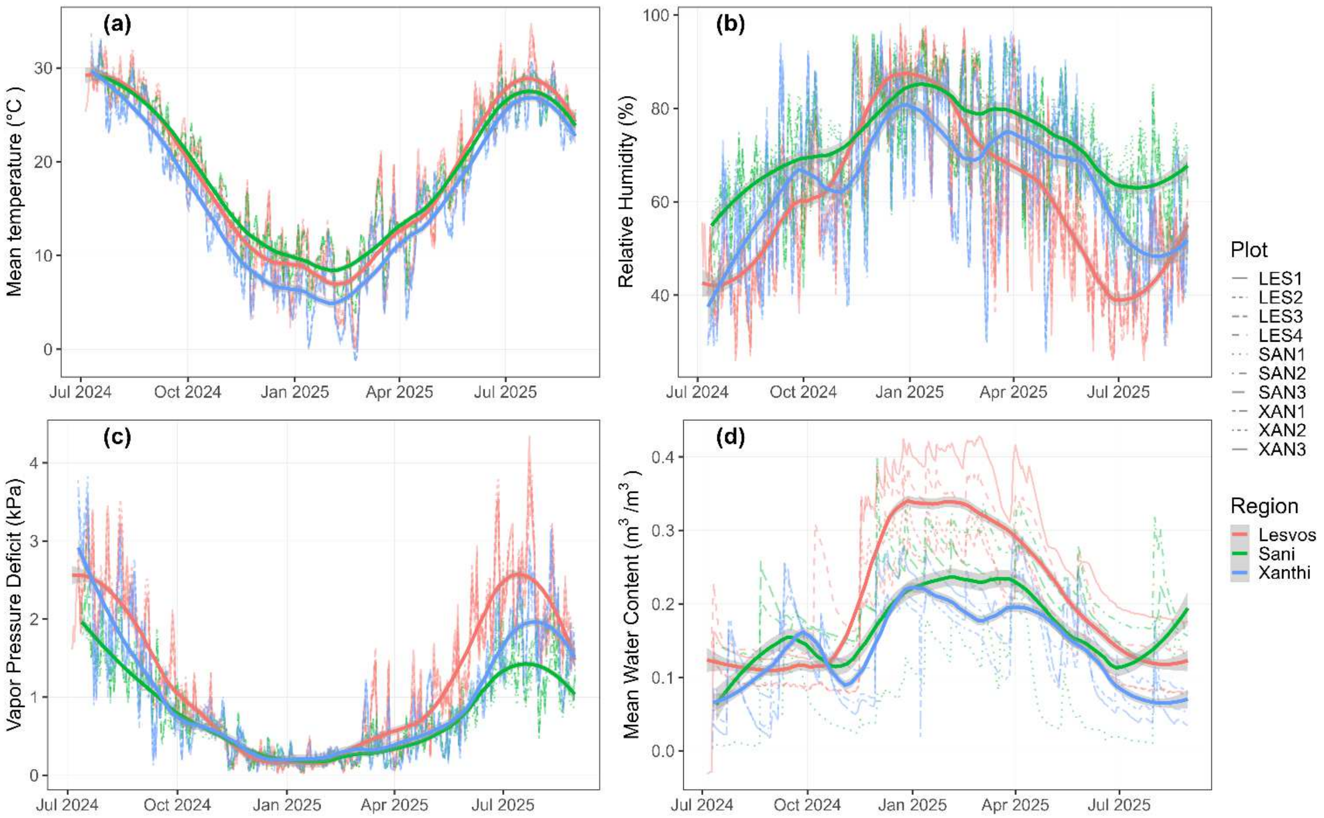

Fig. 2: Climate data per site and plot. Plots illustrate: a) the mean daily temperature (^{o}C), b) the mean daily relative humidity (%), c) the average daily vapor pressure deficit (kPa) and d) the mean daily water content (m^3m^{-3}). Number of days with VDP<1.5 kPa and SWC<0.15 m^3/m^3 for each plot 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.

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}≈0.00173 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}≈0.0025 d^{-1} vs Lesvos k_{paper}≈0.0005 d^{-1}, Table 2). 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).

The plot-specific non-linear mixed effect models provided a good fit for the needle litter (Fig.3), paper sheets (Fig. 4) and wood sticks (Fig. 5) data. 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 (see Supplementary Material A).

Table 2: Mean decomposition rates (day^{-1}) for pine litter, papers and wood sticks estimated through non-linear mixed effect models on each site. Marginal and conditional R^2 represent the variation attributed to species and to species in each plot, respectively.

Region	k_{litter}	R_M^2	R_C^2	k_{paper}	R_M^2	R_C^2	k_{wood}	R_M^2	R_C^2
Lesvos	0.000611 ± 0.000064			0.000511 ± 0.000159			0.000401 ± 0.000048		
Sani	0.001730 ± 0.000108	59.92%	79.96%	0.002530 ± 0.00157	46.86%	73.43%	0.001670 ± 0.000246	43.48%	71.74%
Xanthi	0.000625 ± 0.000072			0.00259 ± 0.000309			0.000700 ± 0.000052		

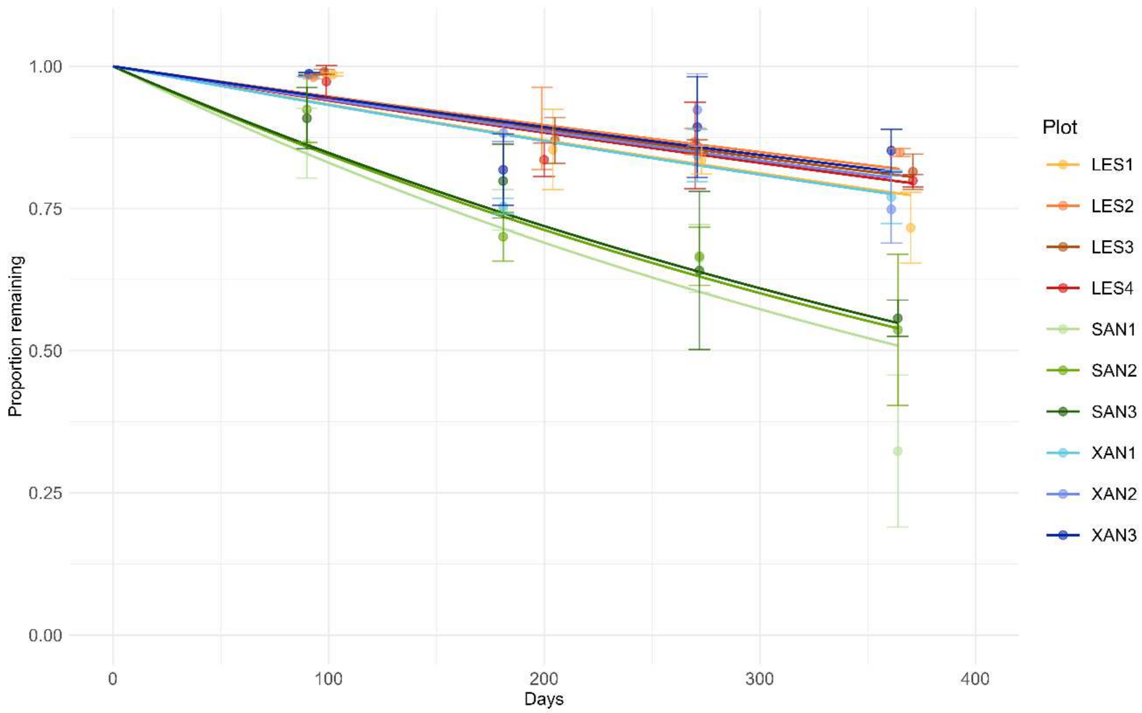

Fig. 3: Pine needle litter proportion of remaining mass over the incubation period. Dots represent the mean of pine needle litter samples collected on each sampling period and curves represent predicted mass loss inferred by the NLMM analysis. Error bars indicate standard error of the mean.

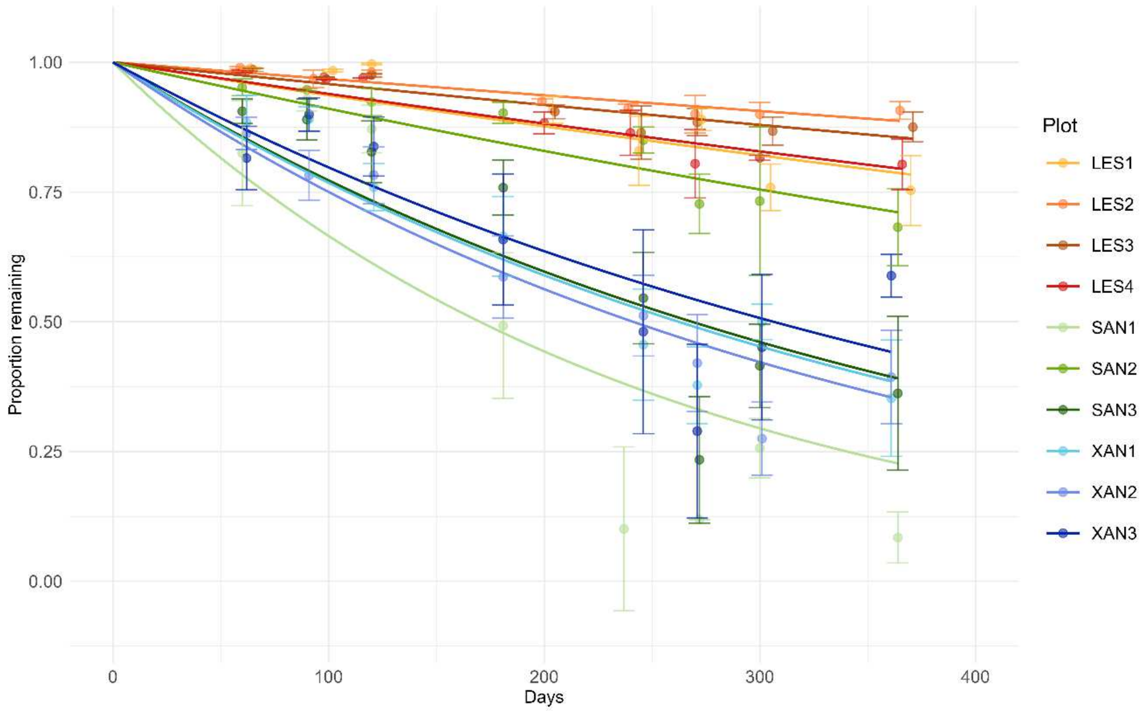

Fig. 4: Paper sheet proportion of remaining mass over the incubation period. Dots represent the mean of paper sheet samples collected on each sampling period and curves represent predicted mass loss inferred by the NLMM analysis. Error bars indicate standard error of the mean.

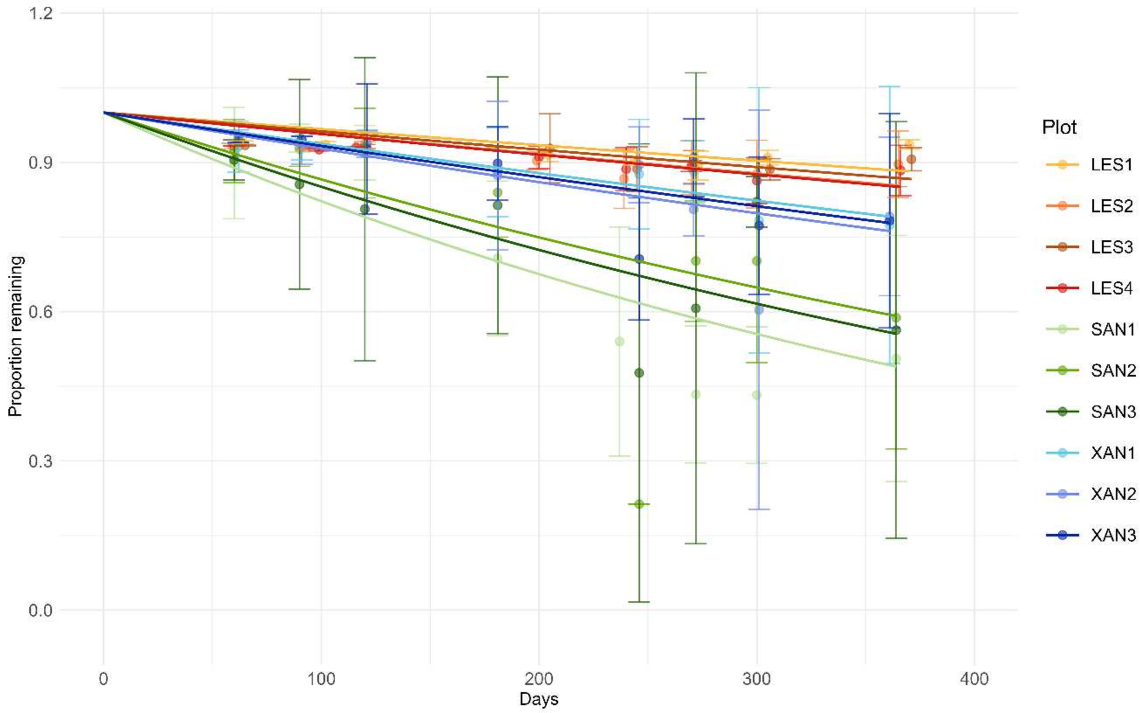

Fig. 5: Wood stick proportion of remaining mass over the incubation period. Dots represent the mean of wood stick samples collected on each sampling period and lines represent predicted mass loss inferred by the NLMM analysis. Error bars indicate standard error of the mean.

3.3 Environmental Effects on Decomposition Rates

Even though the "plots nested in species" random term represented the structure of our dataset in a more informative way, the simpler "plot only" random effect model was used to avoid unnecessary complexity when micro-environmental fixed effects terms were added. Additionally, when using species as fixed effect, the models provided unstable behavior, and the important micro-environmental predictors were masked under the influence of the species presence on each plot.

The correlation and the VIF analysis revealed intercorrelation between the micro-climatic, edaphic and stand structure variables (Supplementary Material B, Fig. S1). 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 <5and the optimum R^2 was achieved (Supplementary Material C, Table S2, S3 and S4). During the elimination process, both T_{air} and *SWC* were kept as long as their interaction remained important, even if they presented high VIFs.

The effect of the maintained fixed effect terms on the decomposition rate of each material is summarised in Table 3. Soil *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 all materials, even though their interaction presented negative effects for paper sheets and wood sticks and positive effect for pine litter. 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. Soil *N* presented a moderate significance in the decomposition of paper sheets.

To summarize and evaluate prediction of the seasonal variation in the decomposition rate of each material we used the estimated coefficients of the environmental (T_{air}, *SWC, pH, N*) 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 widest variation in central estimates across plots and seasons. For example, k_{paper} varies from less than 0.001 d^{-1} to SAN2 to more than 0.003 d^{-1} at SAN1, underlying the importance of plot specific conditions, even within the site. Similarly, Lesvos presents a significant plot-level heterogeneity across the four plots, mostly for papers, while pine litter and wood sticks rates remain lower than or equal to 0.001 d^{-1}. Notably, negative predictions are inferred – carrying no ecological meaning- but represent a NLMM artifact in conditions of great aridity. Xanthi 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 0.0015 to 0.003 d^{-1}).

In terms of seasonality, Xanthi presents the most homogeneity among plots for all materials across the seasons, with lowest pine decomposition rates for summer and winter (when the coupling of high and low temperatures respectively coexist with medium to high moisture levels) At Sani the estimated decomposition rates seem to progressively increase from autumn 2024 to summer 2025, mostly for the standard materials, with a slight decrease of the pine litter rates towards the autumn of 2025, except SAN1, which in general presents a reverse pattern for all materials than all other plots and sites, since it is characterized by moist air conditions, but drier soil conditions (Fig. 2). At Lesvos, rates rise toward winter 2025 before declining or plateauing through spring and summer 2025, in line with the onset of summer drought. However, wood sticks in Lesvos present higher variability towards winter of 2025, when moist conditions and low temperatures occur in the region.

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*	T_{air}*SWC	*pH*	*N*	*BA*	*LAI*	R^2_M	R^2_C
***k** litter*	0.006337	+0.000021	+0.003470	+0.00614	+0.000702				64.93%	83.16%
p		0.556	0.409	**0.004**	**0.001**					
***k** paper*	0.015474	+0.000054	+0.019497	-0.000920	+0.002470	-0.000811	+0.000089	-0.002748	72.94%	84.82%
p		0.249	***<0.001***	**0.007**	***<0.001***	**0.020**	***<0.001***	**<0.001**		
***k** woods*	0.001436	+0.000012	0.004467	-0.000971	+0.000586				39.25%	65.12%
P		0.728	0.259	*<**0.001***	**0.015**					

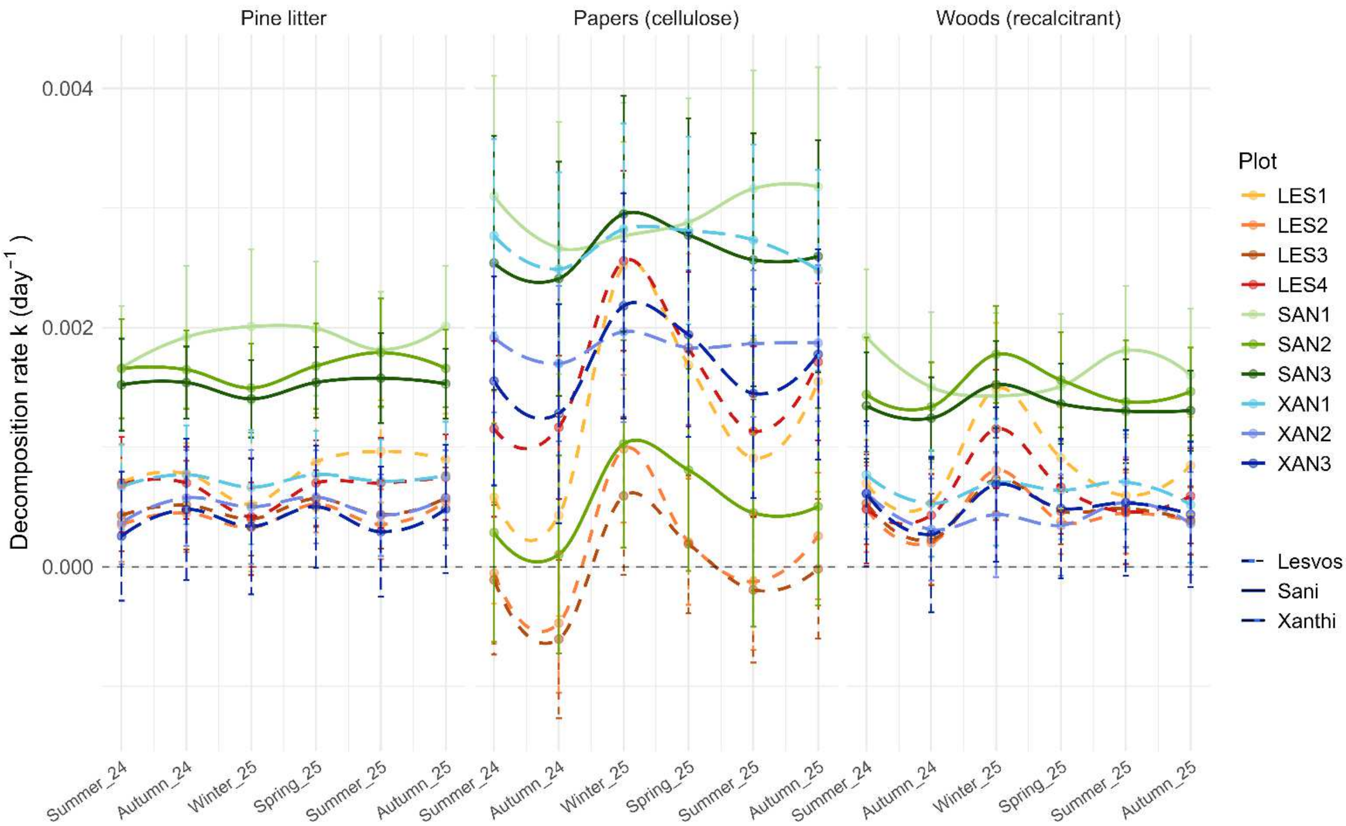

Fig. 6: Seasonal variation of decomposition rates k for each material, as inferred from the NLMM analysis. Solid lines represent plots in Sani; dashed lines represent plots in Lesvos and long- dashed lines represent plots in Xanthi. Error bars represent both fixed and random effects' standard errors.

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 differences and significant predictors in the decomposition rate of different materials. Across regions, soil pH and $T_{air}*SWC$ interaction emerged as consistent predictors of the process of early-stage decomposition in these ecosystems. 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 not be considered as the latter was not measured throughout the implementation period and a more mechanistic approach was applied. Differences in the decomposition rates of standard material, where the effect of litter quality is by-passed entirely, highlighted the effect of the coupling effect of temperature and soil water content along with soil pH as common predictors of across region differences in the rates of decomposition.

We estimated an average decomposition rate of k= 0.00173 d^{-1} for *P. halepensis* in Sani and k=0.0006 d^{-1} for *P. brutia* in Lesvos and Xanthi. 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 0.0019 d^{-1} to 0.0016 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). Our estimates for *P. brutia* stands in Lesvos and Xanthi 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.

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. Additionally, our experimental set-up, where regional variance co-existed with species establishment, species effects on decomposition rates could not be attributed.

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. 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).

Especially for Mediterranean ecosystems, the combined non-linear effect of temperature and soil moisture in decomposition rates has been previously noticed (Incerti et al. 2011; Petraglia et al. 2019). The divergence emerged between the positive effect of $T_{air}*SWC$ on pine litter rates and the negative effect on the standard materials rates reflects the response of decomposition pattern to climatic variations in different substrate materials (Manzoni et al. 2012; Ågren et al. 2013) and in subsequent stages of decomposition (Berg 2014). Labile compounds- such as cellulose- are the first to decompose and are highly moisture-driven (Djukic et al. 2018), which aligns with our finding of *SWC* significance in papers. However, when T_{air} rises, evapotranspiration is enhanced, reducing moisture signals and suspending decomposition (Curiel Yuste et al. 2007). Furthermore, recalcitrant materials, like wood sticks, demand important amount of thermal energy to break down which combined with moderate moisture (A'Bear et al. 2014), provides either stable rates of decomposition (for moderate moisture) or high variability when low temperatures and significant moisture appear (mostly noted for winter and spring in Lesvos, in contrast to the other sites). Hence, pine litter represents an intermediate state where both labile and recalcitrant compounds coexist and a more sustained pattern is emerge in different phases (Berg and McClaugherty 2008).

Soil *pH* was the single edaphic predictor that was systematically retained in our NLMM analysis across materials 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. Microbial activity is relatively higher in more alkaline soils rather than acidic ones (Cao et al. 2016). 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. Additionally, soil N negative effect on papers' decomposition has been reported in cellulose-rich environment, as an attempt to stabilize substrate C/N ratio available to decomposers (Fog 1988; Knorr et al. 2005; Hobbie et al. 2012),

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). 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). However, in order to examine the direct effects of management in decomposition rates of pine species, an experimental set up combing both micro-climatic variations along with the repetition of management treatments should be used. This investigation was not feasible in our experimental design.

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/or 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.

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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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