

# Countervailing effects on pine and oak leaf litter decomposition in human-altered Mediterranean ecosystems

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**Abstract** Species affect the dynamics of litter decay through the intrinsic properties of their litter, but also by influencing the environmental conditions imposed by their canopy, roots, and litter layers. We examined how human-induced changes in the relative abundances of two dominant Mediterranean trees—*Pinus halepensis* and *Quercus calliprinos*—impact leaf litter decomposition. A reciprocal transplant experiment tested decomposition of pine, oak, and mixed leaf litter in oak woodland and pine forest ecosystems with different relative abundances of pine and oak. Using likelihood methods, we tested the importance and magnitude of the environmental effects of local species abundance, litter layer composition, and soil properties on

litter mass loss. Oak litter decomposition was slower than pine, and had an antagonistic effect on mixed litter decay. These results differ from other reported pine–oak associations, and are probably associated with a higher content of tannins and phenols in oak compared to pine litter in our study sites. The environmental effects of the two species were opposite to their litter decomposition dynamics. An increased proportion of pine in the oak woodlands and a higher content of pine needles in the litter layer of pine forests reduced decay rates. The presence of more oak and broadleaf litter in the litter layer accelerated decomposition in pine forests. Our results highlight the importance of considering multidimensional species effects mediated by both chemical and physical properties, and imply that man-made changes in the composition and configuration of plant communities may result in complex unpredicted consequences to ecosystem biogeochemistry.

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## Introduction

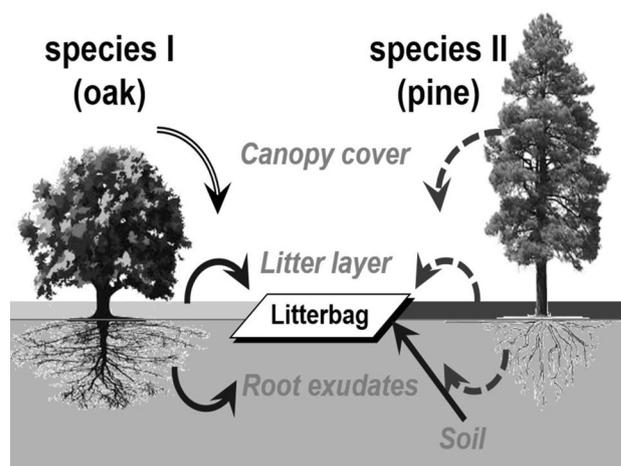
The spatial distributions and abundances of species within ecosystems contribute to the enormous variation observed in ecosystem structure, function, and dynamics (Canham and Pacala 1995; Eviner 2004; Cortez et al. 2007; Gomez-Aparicio and Canham 2008; Vivanco and Austin 2008; Makkonen et al. 2012; Tilman et al. 2012). Research on the consequences of species loss for ecosystem dynamics has generally led to the conclusion that responses are idiosyncratic and vary according to species (Hector et al. 2000; Hättenschwiler et al. 2005; Ball et al. 2008). However, in most cases, species loss has negative consequences

for ecosystem functioning (e.g., Cardinale et al. 2012). The idiosyncrasy of species-specific effects highlights the problem of searching for generalities that can be used in scaling from local community dynamics to ecosystem-level or even global biogeochemical models (Parton et al. 1993; Cox et al. 2000; Adair et al. 2008).

Global change (climate and land-use changes) is threatening to alter the composition of species in most plant communities. Specifically, changes in land use can potentially change species composition (through species loss or the addition of new species) within and among ecosystems (Foley et al. 2005). Variation in the spatial distribution of species within an ecosystem combined with species-specific spatial and temporal patterns of litter fall create complex three-dimensional heterogeneity in litter layers.

Mixing litter of different species can cause nonlinear, synergistic, or antagonistic effects on litter decomposition (Gartner and Cardon 2004). Non-additive effects are typically mediated by species-specific impacts on (1) litter quality, (2) decomposer abundance and community composition, (3) litter layer microclimatic conditions and habitat structure, and (4) interactions across trophic levels (Gartner and Cardon 2004; Hättenschwiler et al. 2005 and references therein). Although litter decay is sensitive to the relative amounts of different litter types within the mixture (e.g., De Marco et al. 2012), the effects of complex vegetation patterns on litter mixing and decomposition are usually overlooked. When species combinations give rise to non-additive effects, understanding neighborhood dynamics—i.e., the fine-scale relative abundances and spatial configurations of different species in the ecosystem (Canham and Uriarte 2006)—is essential when assessing ecosystem-scale processes.

Species affect local litter decomposition dynamics via various mechanisms (Fig. 1). A species' litter can decompose faster under its canopy or where it is abundant, as postulated by the home-field advantage hypothesis (Ayres et al. 2009). Furthermore, species can indirectly affect decomposition by modifying the microclimate at the litter layer, altering the structure of the forest floor, and by changing the conditions in the upper soil layers through resource uptake or other below-ground interactions (Hättenschwiler et al. 2005; Ball et al. 2008; Fig. 1). These species-specific effects are not constant under all circumstances. The magnitude and direction (null, positive, or negative) of a species' effect can change among ecosystems and depending on the identities of other species in its neighborhood (e.g., Gomez-Aparicio and Canham 2008). Therefore, changes in the distribution of species within and among ecosystems can have varying and unpredictable impacts on ecosystem functioning. Plant invasion, for instance, can increase (Ashton et al. 2005), decrease (Cornwell et al. 2008; Godoy et al. 2010), or have no impact (Berger and Berger 2012) on



**Fig. 1** Plant species effects on litter decomposition. Species affect the rate of litter decomposition by various modes, including intrinsic effects of the litter type (whithin the litterbag) and environmental effects. The environmental effects imposed by the canopy, litter layer, and root exudates of each species as well as abiotic factors such as soil characteristics can modify the conditions for decomposition. The results of our best model for the effects of soil clay and *Quercus calliprinos* (I) and *P. halepensis* (II) on litter mass loss are summarized by dashed arrows for negative effects, solid arrows for positive effects, and hollow arrows for non-significant effects

nutrient cycling at the ecosystem scale. These contrasting findings strengthen the importance of species-specific and context-specific effects and make it more difficult to search for general rules of ecosystem dynamics, especially in light of future changes in species distributions (Strayer 2012).

Mediterranean landscapes are characterized by highly heterogeneous spatial mosaics as a result of past and present human impacts (Blondel 2006). These landscapes are home to a wide diversity of ecosystems, mainly composed of (1) natural maquis shrublands regenerating after intense human degradation (grazing and wood cutting), with sclerophyllous shrubs and trees (dominated by an evergreen oak species), and (2) planted pine forests (Blondel and Aronson 1999). The spatial juxtaposition of oak-maquis and pine forests has created opportunities for the reciprocal colonization of each ecosystem by dominant species from neighboring ecosystems. Interactions within these landscapes are leading to the formation of mixed pine–oak ecosystems as a result of either pine colonization in natural oak maquis (Sheffer et al. 2014) or due to the colonization of planted pine forests by oaks (Sheffer et al. 2013). Different pine and oak colonization dynamics result in the emergence of a suite of new plant communities with different proportions of pines and oaks in the canopy and understory (Sheffer 2012).

Here we examine how changes in the abundance of two dominant species, as a result of the formation of pine–oak ecosystems, affect the functioning of those ecosystems,

focusing on litter decomposition as a key process in nutrient cycling. Our hypothesis is that litter decomposition processes will differ between the “natural” oak maquis and man-made pine forests, and that the development of pine–oak ecosystems in places that were historically dominated by only one of these species will result in non-additive effects on decomposition of mixed litter types. We performed a litter transplant experiment to investigate how the neighborhood dynamics of two different tree species affect the decomposition of their litter. We compared the dominant pine (*Pinus halepensis*) and oak (*Quercus calliprinos*) species in terms of leaf litter decomposition and examined the chemical effect of mixing pine and oak litter on their decomposition. Using maximum likelihood methods, we further examined how each of the dominant species affects the rate of leaf litter mass loss through physical–environmental effects imposed by (1) the composition of the standing litter layer and (2) local species abundances, and how these impacts vary in the two types of ecosystems (oak–maquis vs. pine forest). We also compared the soil properties among these ecosystem types and tested the effect of soil properties on the rate of decomposition, as this is another indirect effect that may be mediated by species composition. We studied forests that varied along a gradient of densities of the resident species (oak–maquis vs. planted–pine forest) and the density of colonization by the reciprocal species, to better understand the relative magnitude of the differences in the effects of the colonist versus the local dominant species.

## Methods

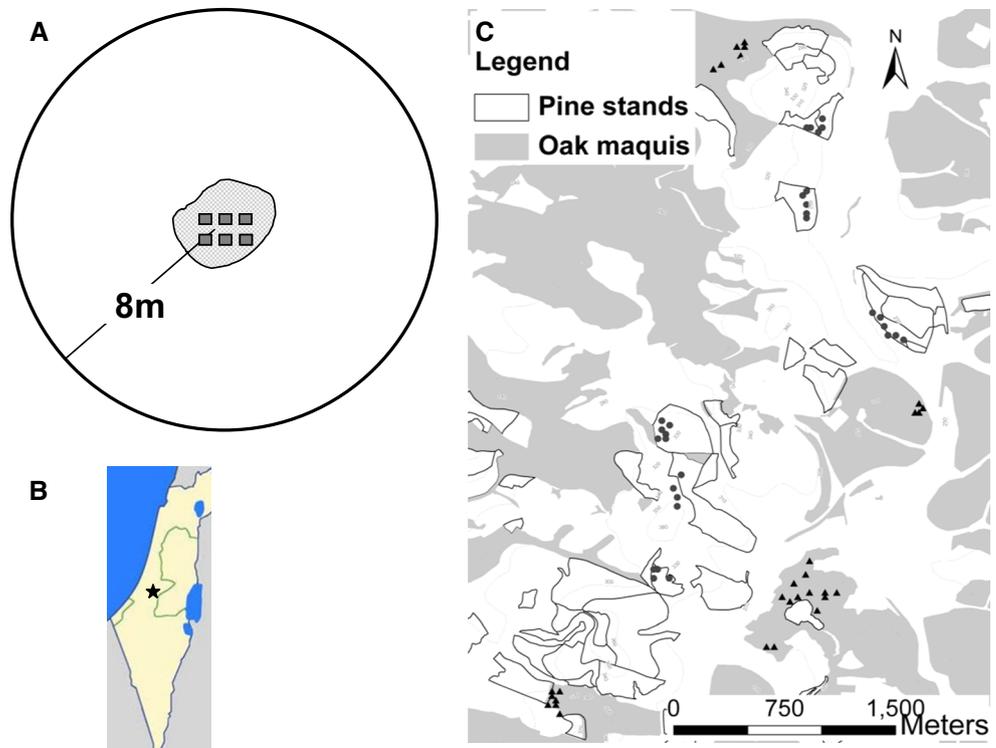
### Study site

The study was conducted in Britannia Park (4000 ha, 34°55′49″E 31°40′54″N), located in the Judean lowland, Israel (Fig. 2b). The altitude of the park ranges between 200 and 400 m above sea level. The climate is typical Mediterranean, with hot dry summers and mild rainy winters and a mean annual precipitation of 480 mm. The soil is brown forest Rendzina (Haploxeroll or Xerothent, USDA) formed on rolling hills of early Eocene chalk sediments covered by a petrocalcic horizon (or calcrete, locally termed “Nari”) (Dan et al. 2007). Vegetation in the park is composed of areas of natural oak maquis dominated by *Quercus calliprinos* Webb. and 60-year-old planted stands of the native *Pinus halepensis* Miller (Fig. 2c). The local oak maquis includes large trees and shrubs (e.g., *Pistacia lentiscus* and *Pistacia palestina*) and dwarf shrubs (e.g., *Calicotome villosa* and *Sarcopoterium spinosum*), intermingled with patches of ephemeral herbaceous vegetation and some planted carob trees (*Ceratonia siliqua*). The forests were planted in the 1950s as monospecific dense pine stands.

### Experimental design

We used an inverse modeling approach to examine how ecosystem dynamics vary along the range of oak–maquis to

**Fig. 2** Study design. **a** Six litterbags (3 litter types  $\times$  2 incubation periods) were incubated at each plot. The structure of the vegetation canopy cover was measured in 8-m-radius plots surrounding the litterbags, and soil and litter-layer samples were collected near the center of the plot (gray patch, <2 m distance from the litterbags). **b** Location of Britannia Park study area on a map of Israel. **c** Distribution of experimental plots in oak–maquis and planted–pine forest stands throughout the area of the park



pine-forest ecosystems with different degrees of reciprocal pine and oak colonization (e.g., Gomez-Aparicio and Canham 2008). We selected 60 sampling plots (30 plots in oak-maquis ecosystems and 30 plots in planted *P. halepensis* stands) using a map of vegetation cover and forest stands; these plots were distributed throughout the park in a total area of 12 ha (Fig. 2c). Plots were stratified along the range of pine–oak coexistence ranging from pure pine forest to pure oak maquis with intermediate states of cross-colonization. Four to ten plots were selected in several stands throughout the study area, with a distance of at least 50 m maintained between plots to ensure independence.

#### Litter collection and incubation

Leaf litter decomposition was measured using the litter-bag experimental method (Karberg et al. 2008) to compare the mass losses of three litter types: pure oak leaf litter, pure pine needle litter, and mixed pine–oak leaf litter. We collected *P. halepensis* needle and *Q. calliprinos* leaf litter underneath pine and oak trees in two forest and two maquis stands in the study area. Litter was collected immediately at the end of the summer leaf deposition period and before the beginning of the rainy season. Pine needles and oak leaves were collected from the upper layer of the litter on the floor so that they comprised only the most freshly senesced leaves. Collected litter was then sorted to remove stones, soil, litter of other species, and any leaves or needles with different colors (which may indicate older litter). Clean material from the two stands per species was thoroughly mixed for litter homogeneity and air-dried for subsequent chemical analyses and field incubations. A subsample was oven-dried (60 °C, 72 h) to correct the air-dry mass for residual humidity.

Litter bags (15 × 15 cm fiberglass net bags, 1-mm mesh) were filled with a total of 5 g of either pine needles (pure pine), oak leaves (pure oak), or a mix of oak and pine (2.5 g oak, 2.5 g pine). Reciprocal litter transplants consisted of field incubations of pine, oak, and mixed litterbags in both pine forests and oak-maquis plots, representing their ecosystems of origin and the ecosystems that they are colonizing. Two litterbags of each type (2 bags × 3 litter types × 60 plots, Fig. 2a) were deployed on the ground in each plot, in direct contact with the decomposed litter layer, at the beginning of the wet season. We collected one of the two litterbags of each litter type after 6 months and the second set after 13 months of field incubation to measure mass loss. After collecting the litterbags, the adhering soil and other non-litter material were gently removed from the decomposed litter and the samples were dried and reweighed. Ash-free dry mass was determined for all samples to correct for soil contamination (Harmon and Lajtha 1999). Percent mass loss was calculated as the ash-free

mass ( $M$ ) difference between times 0 and  $t$  as a percent of the initial mass at time zero, i.e.,

$$\% \Delta M = \frac{(M_0 - M_t)}{M_0} \times 100,$$

for the three litter types at each time point.

#### Initial litter characteristics

The chemical composition of a subsample of the collected pine and oak leaf litter was determined using near-infrared spectroscopy (NIRS, Deaville and Flinn 2000), with a Foss NIR Systems 5000 NIR reflectance monochromator spectrometer (Foss Tecator, Hoganas, Sweden) and standard laboratory procedures. Finely ground dry litter powder of each of the litter types used in the experiment was analyzed for the percentage of tannin, fiber, lignin, cellulose, hemicellulose, and phenols, using calibrations from previously collected *P. halepensis* and *Q. calliprinos* samples (Landau et al. 2004). Total nitrogen concentration was determined using the Nessler colorimetric method and spectrophotometric analysis (Jones and Case 1990).

#### Soil and litter layer characteristics

We collected samples of the soil and the accumulated litter layer in each plot, close to the incubated litter bags (within <2 m distance, Fig. 2a). Soil was collected by digging 20-cm-diameter pits to a depth of 15 cm at three positions in the center of the plot. The three soil samples were pooled for laboratory analysis. We analyzed soil texture (using the hydrometer method after dispersion with sodium hexametaphosphate), pH, conductivity, water-holding capacity (gravimetrically), and nutrient concentration. Phosphorus availability was measured with the Olsen P method (Olsen et al. 1954). Inorganic nitrogen concentration was determined by colorimetric methods: ammonium–N ( $\text{N-NH}_4^+$ ) by the silicate-hypochlorite method in soil KCl solution extract, and nitrate–N ( $\text{N-NO}_3^-$ ) by the dual-wavelength ultraviolet spectrophotometric method in soil aqueous extract. Total organic matter was measured by weight loss on ignition, by burning soil samples in a 550 °C furnace for 5 h. All soil chemistry analyses were conducted according to Sparks (1996) at Gilat Field Services Laboratory, The Agricultural Research Organization, Israel.

Samples of the litter layer were collected in four 20 × 20 cm quadrats within each plot. Sample locations were randomly placed within <2 m of the incubated litterbags. Material from the litter layer was separated into its species components, distinguishing among oak litter (leaves, branches, and acorn parts), pine litter (needles, branches, cones, and kernels), and litter from all other species (including unidentified litter fragments). Litter-layer fractions were oven-dried and weighed.

## Species neighborhood abundance

In each plot, we measured the abundance of pines, oaks, and all other woody vegetation in a circular 8-m-radius plot (~200 m<sup>2</sup>) surrounding the location of litterbag incubation (Fig. 2a). We measured diameter at 130-cm trunk height of all pine trees in the plot and calculated the basal areas of all mature planted pines. The total basal area was used as a measure of *P. halepensis* abundance in the forest neighborhood of each of our experimental sites. We estimated oak abundance using canopy cover instead of basal area due to the complex multi-stemmed structure of *Q. caliprinos*. We tallied all oaks in the plot and measured their sizes (height and canopy diameter at two random perpendicular axes). We calculated the total abundance of oaks in each plot as the sum of ellipse areas calculated using the two measured diameters for each oak tree. We assessed the abundance of all other woody vegetation in the plot by identifying and counting all woody species and categorizing them into four canopy-diameter categories (0–50, 51–150, 151–450, and >500 cm canopy diameter). Woody vegetation in these ecosystems included only broadleaf species. We calculated the total abundance of all woody vegetation (other than pines and oaks) by summing the calculated circular cover areas of each plant using the mean radius for each size category.

## Maximum likelihood models of leaf litter mass loss

We used maximum likelihood estimation methods to examine how litter mass loss is controlled by species identity and environmental effects. The environmental effects included physical conditions imposed by the soil and biotic impacts imposed by species. The effects of the species included: (1) the intrinsic effect of the properties of the three litter types within litter bags, and the extrinsic effects of (2) the composition of the accumulated litter layer and (3) the local abundance of trees in the stand neighborhood. Our models test how the dynamics of litter decomposition vary across different pine–oak mixtures, ranging from pure pine stands to pine stands with different densities of oaks in the understory to oak maquis with different densities of pine colonists and to oak maquis without pines.

To analyze the intrinsic effect of the type of litter, we tested for a non-additive effect of pine–oak litter mixing by comparing the measured mass loss of mixed litter with the additive mass loss calculated according to the mass loss of each litter decomposing separately, as:  $\% \Delta M_{\text{mixed}} = 0.5\% \Delta M_{\text{pine}} + 0.5\% \Delta M_{\text{oak}}$ .

We used linear models to test the magnitude and the importance of each of the environmental effects. The models take the form

$$\begin{aligned} \% \Delta M_{ijk} = \% \Delta m_k + \alpha_j C1_i + \beta_j C2_i + \tau_j C3_i \\ + \omega_j L1_i + \delta_j L2_i + \rho_j L3_i + \phi_j S_i, \end{aligned} \quad (1)$$

where the percent mass loss  $\% \Delta M_{ijk}$  of litter type  $k$  in the  $i$ th plot in ecosystem type  $j$  (pine forest vs. oak maquis) is a function of the intrinsic expected mass loss  $\% \Delta m_k$  of litter type  $k$  (three estimated intercept parameters); and the additive effects of the abundances of pine, oak, and all other broadleaf vegetation ( $C1_i$ ,  $C2_i$ , and  $C3_i$ , respectively), the pine, oak, and other broadleaf components of the litter layer ( $L1_i$ ,  $L2_i$ , and  $L3_i$ , respectively), and soil property  $S_i$  in the  $i$ th plot.  $\alpha$ ,  $\beta$ ,  $\tau$ ,  $\omega$ ,  $\delta$ ,  $\rho$ , and  $\phi$  are estimated linear slope parameters that quantify the magnitudes of the effects of the environmental variables. The effect of ecosystem type  $j$  (pine forest vs. oak maquis) was tested using different  $\alpha_j$ ,  $\beta_j$ ,  $\tau_j$ ,  $\omega_j$ ,  $\delta_j$ ,  $\rho_j$ , and  $\phi_j$  slope parameters. The composition of the litter layer ( $L1$ ,  $L2$ , and  $L3$ ) was modeled as either the total mass of each type of litter or the fraction of each litter type from the total accumulated litter-layer mass. For the soil, we examined the variability of different soil properties in our dataset, and selected soil clay content as representing the largest source of variability.

## Hypothesis testing by model comparison

We compared different models representing alternative hypotheses of the factors that control litter decomposition (Burnham and Anderson 2002). We compared three sets of models: (1) mean models, which test only for the categorical effects of litter and/or ecosystem types (models 1–4 in Table 1, employed as a maximum likelihood alternative to ANOVA); (2) linear models, which test the continuous effect of an environmental variable as in Eq. 1 (models 5–10 in Table 1); and (3) Gaussian models, which allow more flexible unimodal responses to the environmental variables. To understand the relative importance of each of the independent variables, we searched for the most parsimonious grouping of the effects and different partial combinations of them (Table 1), using model comparison methods. We searched for the most parsimonious set of factors that control the rate of litter decomposition in two steps. First, we tested different combinations of the environmental effects (models 5–9 in Table 1). For instance, we tested models with different effects for the litter layer and abundance of oaks ( $L2$  and  $C2$ , respectively) and those of the rest of the broadleaf vegetation in our plots ( $L3$  and  $C3$ ). But, after finding similar slope parameters for the two components separately, we combined oak abundance with the abundance of all other broadleaf vegetation in the plot and the accumulated litter of oak with the components of all other broadleaves in the litter layer, for reasons of parsimony. Then, we further simplified the model represented by Eq. 1 by (1) lumping together the variables that showed

**Table 1** Comparison of alternative models for leaf litter mass loss

Model	Effect variable		Environmental effects					Model evaluation				
			Litter layer composition		Canopy cover		Soil	Parameters	AICc	Slope	$R^2$	
			Pine	Oak + broadleaf	Pine BA	Oak + broadleaf	Soil clay					
1	Mean	None						2	1,060.908	–		
2	Mean	Ecosystem type						3	1,061.807	1.00	0.007	
3	Mean	Ecosystems $\times$ litter type						7	1,061.969	0.99	0.054	
4	Mean	Litter type						4	1,057.815	1.00	0.041	
5	Linear	Litter type					All	5	1,054.386	1.00	0.07	
6	Linear	Litter type			OM & PF	OM & PF	All	9	1,054.601	1.00	0.12	
7	Linear	Litter type	OM & PF	OM & PF				8	1,044.138	0.99	0.158	
8	Linear	Litter type	OM & PF	OM & PF			All	9	1,036.387	1.00	0.21	
9	Linear	Litter type	OM & PF	OM & PF	OM & PF	OM & PF	All	13	1,038.294	1.00	0.24	
10	Linear	Litter type	PF only	PF only	OM only		All	8	1,024.778	1.00	0.25	

Mean and linear models are compared using the AIC corrected for a small sample size (AICc), and are listed in order from the worst to the best model. Mean models 1–4 use different categorical classes to group the effects of ecosystem and litter types. Linear models 5–10 are composed of the estimated basal mass loss of each litter type (three constant intercepts) and the linear effects of additional explanatory variables. The linear effects of the explanatory variables (columns 2–6; note that “Pine BA” is the pine basal area) were either similar in both oak-maquis and pine-forest ecosystems, i.e., using a single estimated slope parameter (marked as “All” in the table); they showed different effects in each of the ecosystems, using two estimated slope parameters (marked “OM & PF” in the table); or they were significant in only one ecosystem (marked “OM” or “PF” in the table)

the same effect (e.g., similar slope parameters  $\alpha_j$ ,  $\beta_j$ ,  $\tau_j$ , etc.) for both ecosystem types, and (2) omitting the factors for which the slope of the effect was not different from zero (e.g., mean  $\alpha_j \approx 0$ , model 10 in Table 1).

#### Parameter estimation and model evaluation

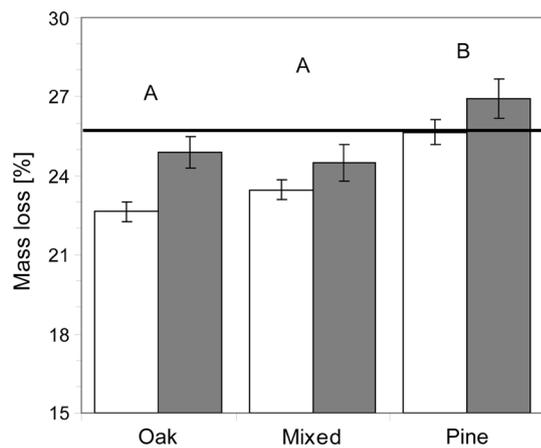
We solved for the maximum likelihood parameter values using simulated annealing in the “likelihood 1.3” package in R (Murphy 2012). Residuals ( $\varepsilon$ ) for the different variables were normally distributed, so the error terms were modeled accordingly. Although we analyzed mass loss percentage data, no angular transformation was needed since the response variables were normally distributed. We compared alternative models on the basis of the Akaike information criterion corrected for a small sample size (AICc). We used asymptotic 2-unit support intervals to assess the strength of evidence for individual maximum likelihood parameter estimates (Edwards 1992). To simplify our linear models (e.g., full model 9 in Table 1), we excluded the effects of the variables for which the upper and lower support intervals of the maximum likelihood estimate of the slope parameter bounded zero (model 10 in Table 1). This elimination process allowed us to find a partial but parsimonious model (lower AICc) which included only the significant effects. To evaluate each alternate model, we calculated the slope and the  $R^2$  of the regression of observed vs. predicted as measures of model bias and goodness of fit, respectively. All analyses were done using the R

programming environment version 2.8.0 (R Development Core Team 2006).

#### Results

In spite of varying levels of reciprocal pine and oak colonization, there are still distinct differences between the ecosystems that were initially oak-maquis and planted-pine forests in our study. The abundance of pines in the maquis communities was an order of magnitude smaller than the pine abundance in the planted forests (mean basal area 1.434 m<sup>2</sup> ha<sup>-1</sup>, range 0–5.089, and 13.958 m<sup>2</sup> ha<sup>-1</sup>, range 0.261–28.349, respectively). Oak abundance in pine forests was about half of that in oak-maquis plots (average canopy cover 18 %, range 0–77 %, and 30 %, range 0.6–88 %, respectively). The abundance of other broadleaf woody vegetation was similar (~5 % mean cover) in both oak-maquis and pine-forest plots (2.726–10.5 % and 1.751–13.098 %, respectively). However, when we compared the mean rates of leaf litter decomposition of these two ecosystems without taking into account additional environmental species-specific influences at the neighborhood scale, we found no significant difference (pine forest vs. oak maquis:  $\Delta$ AICc = -0.899, model 2 vs. 1, Table 1).

Most of the decomposition occurred during the wet season (first 6 months, Fig. 3). We found very similar results and models for decomposition in the wet season alone compared to decomposition after a full year. Thus, we present



**Fig. 3** Average pine, oak, and mixed pine–oak leaf litter mass loss ( $\pm$ SE) after 6 (white bars) and 13 (dark bars) months of field incubation ( $N = 60$ ). The line at 25.9 % mass loss is the calculated additive mass loss for mixed pine and oak litter based on the mean measured mass losses of each litter type separately after 13 months. Bars with different letters next to them are significantly different according to a model comparison, and similar differences are seen after both 6 and 13 months

**Table 2** Initial leaf litter chemistry (mean  $\pm$  SD,  $N = 10$ )

	Pine	Oak	
Ashes	<b>6.580 <math>\pm</math> 1.020</b>	<b>7.570 <math>\pm</math> 0.242</b>	$p = 0.0079$
Total fiber (NDF)	53.678 $\pm$ 6.628	55.600 $\pm$ 3.437	ns
Acid detergent fiber	33.947 $\pm$ 5.170	34.846 $\pm$ 2.683	ns
Lignin	<b>14.066 <math>\pm</math> 1.306</b>	<b>13.025 <math>\pm</math> 0.592</b>	$p = 0.034$
Nitrogen	<b>0.732 <math>\pm</math> 0.270</b>	<b>0.916 <math>\pm</math> 0.097</b>	$p < 0.0001$
Digestibility	<b>36.059 <math>\pm</math> 2.174</b>	<b>33.216 <math>\pm</math> 0.874</b>	$p = 0.0012$
Condensed tannins	<b>3.436 <math>\pm</math> 1.609</b>	<b>8.571 <math>\pm</math> 1.766</b>	$p < 0.0001$
Total phenol	<b>4.445 <math>\pm</math> 1.486</b>	<b>9.288 <math>\pm</math> 1.595</b>	$p < 0.0001$
Cellulose	39.612 $\pm$ 7.849	42.575 $\pm$ 3.944	$p = 0.3003$
Hemicellulose	19.731 $\pm$ 1.571	20.754 $\pm$ 0.858	$p = 0.0876$
Lignin:N	<b>19.223 <math>\pm</math> 4.843</b>	<b>14.225 <math>\pm</math> 4.8432</b>	$p < 0.0001$

All measures are given in units of % ash-free dry matter  
Significant differences are indicated in bold ( $t$  test)

only the results for the full year as representing the longer-term decomposition process. We found greater support for our linear models (lower AICc in models 5–10 in Table 1) and very low support for Gaussian models (AICc  $\geq$  1,060). The most parsimonious model (model 10 in Table 1,  $R^2 = 0.25$ ,  $N = 172$  and only the 8 parameters shown in Table S1 of the Electronic supplementary material, ESM) contained the different intrinsic effects for the three litter types and a set of environmental effects. Some environmental effects that appeared in the full model (model 9 in Table 1) had no significant influence on litter decay (e.g., the composition of the litter layer in oak maquis, pine

abundance in the pine forest, and oak and broadleaf abundance in the two ecosystems) and were excluded for parsimony from the best model, model 10.

#### Species-specific intrinsic effects of litter type

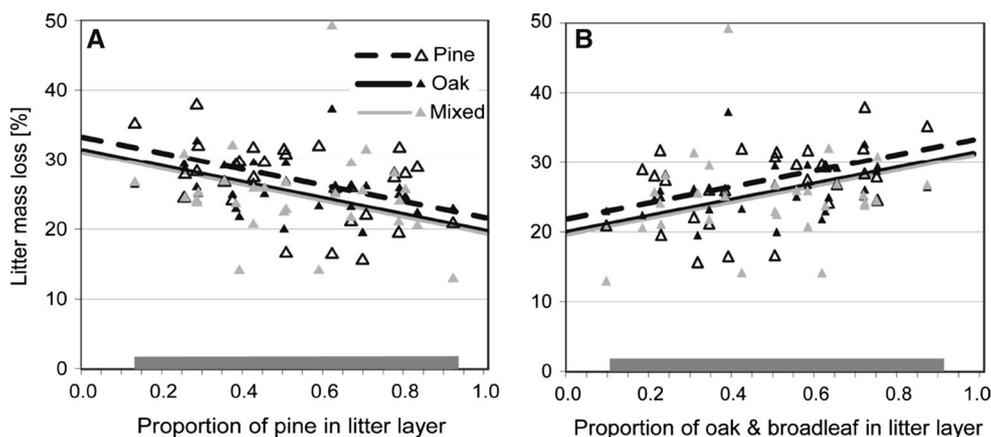
Mass loss of pine needles was greater than that of oak leaves after 6 and 13 months of field incubation (Fig. 3,  $\Delta$ AICc = 3.093 between model 1 with a single mean for all litter types and model 4 with means for each of the three litter types, Table 1; and  $\Delta$ AICc = 2.447 for the same comparison with pine and oak litter only). A comparison of initial oak and pine litter chemistry showed that the slower decomposing oak litter contained more nitrogen and phenols, particularly condensed tannins, compared to the pine leaf litter ( $t$  tests shown in Table 2). Leaf lignin content and the lignin:N ratio were slightly higher in pine litter than in oak litter (Table 2).

Mass loss of mixed pine and oak litter was significantly lower than the additive mean mass loss expected from the mass loss of each species decomposing alone (Fig. 3,  $\Delta$ AICc = 3.449 for a comparison of models with one grand mean vs. two litter-type specific means using the data on pine and mixed litter only). This result indicates a non-additive antagonistic effect of oak litter that slows down the decomposition of mixed pine–oak litter. The mean mass loss of the mixed litter as well as its upper two-unit support intervals were very close to the oak mass loss ( $\Delta$ AICc =  $-1.90$  for a comparison of models with one grand mean vs. two litter-type specific means with the data of oak and mixed litters only) and below the mean mass loss of pine litter (see the parameters  $\% \Delta m_{\text{Pine}}$ ,  $\% \Delta m_{\text{Mixed}}$ , and  $\% \Delta m_{\text{Oak}}$  in Table S1 of the ESM). However, the overall differences are relatively small, with a mean mass loss after a year of decomposition of either mixed or oak litter that is less than 3 % lower than that of pine litter (Fig. 3).

We found no significant interaction between decomposing species and ecosystem type ( $\Delta$ AICc =  $-1.061$  between mean model 1 for all the data and model 3 with means for the six combinations of three litters and two ecosystems, Table 1). This indicates that the decomposition of both pine and oak litter in their “home” ecosystems was similar to the decomposition in their reciprocal ecosystem. These results do not support a clear “home field advantage” for litter decomposition in the two ecosystem types included in our study, but with the caveat that there is a wide range of admixtures of pines and oaks in our individual study sites.

#### Species-specific environmental effects

We found only weak correlations between local neighborhood abundance of each species and the proportions of pine and oak in the litter layer (Pearson correlation coefficients



**Fig. 4** Leaf litter decomposition after 13 months as a function of environmental species effects. Percents of leaf litter mass loss of the pine (dashed black), oak (solid black), and mixed (gray) litter types as functions of the fractions of **a** pine and **b** oak and other broadleaf litter in the litter layer of the planted pine forest. Lines indicate the percent litter mass loss in pine forest as predicted by the best

model (using soil clay content = 32.9 %, the mean value in samples from pine forests, for all calculations, and parameters in Table S1 of the ESM). Triangles represent the actual mass loss measured after 13 months in pine forest incubation plots. Gray shadows on the *x*-axes represent the range of accumulated litter found in the litter layer of examined pine stands

of 0.392 and  $-0.123$ , respectively). These weak correlations probably reflect the patchiness of the litter layer within the 200 m<sup>2</sup> area scale used to measure neighborhood abundance, and indicate that the two variables are independent and not redundant in the analysis.

of litter type mass loss, which was slower for oak and faster for pine litter. This suggests that the environmental impacts of the litter layers alter decomposition dynamics in pine forests through different mechanisms.

#### Composition of the litter layer

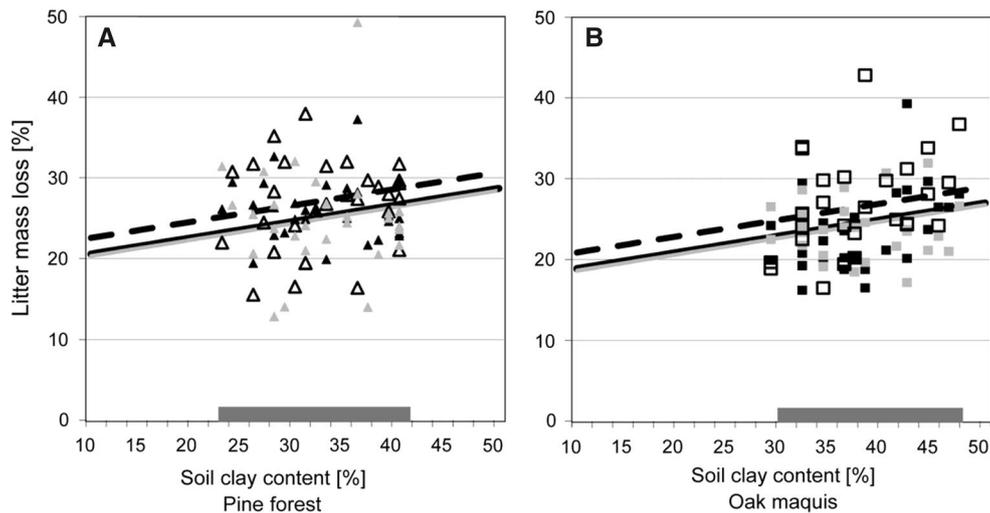
#### Neighborhood species abundance

The proportions of pine, oak, and broadleaved species in the litter layer had a significant effect on the rates of decomposition of all three litter types, but only in the pine forests (see litter layer effects of the most parsimonious model, model 10). The oak and broadleaf litter constituted an average of 10 and 38 % of the litter layers in pine forests, respectively (ranging from 0 to 42 % for oak and from 9 to 87 % for broadleaved species). The litter layer in the oak maquis was mostly composed of oak (mean 35 %, range 0–83 %) and broadleaved species (mean 52 %, range 7–99 %), and less affected by the small proportions of pine litter (mean 12 %, range 0–64 %). The rate of litter decomposition of all litter types was negatively affected by increasing proportions of pine in the litter layer (Fig. 4a and parameter  $\gamma$  in Table S1 of the ESM). On the other hand, the rate of litter decomposition increased as a function of increasing proportions of oak and broadleaves in the litter layer (Fig. 4b and parameter  $\delta$  in Table S1 of the ESM). But the magnitude of the slope of the positive effect of accumulated oak and broadleaves in the litter layer was larger than the negative effect of accumulated pine in the litter layer (Fig. 4a, b). These results indicate that the environmental effects of the accumulation of pine, oak, and broadleaf litters in the litter layer may be countervailing to the pattern

We found that the decomposition of all litter types decreased as a result of increasing pine abundance, but this effect was only significant in the oak maquis (see comparison of model 9 vs. model 10 in Table 1 and parameter  $\alpha$  in Table S1 and Fig. S1 of the ESM). Thus, in the oak maquis, the environmental effect of pine abundance is negative while the chemical effect of the litter is positive (i.e., faster decomposition of pine litter compared to oak litter). Decomposition rate was not significantly affected by oak and broadleaf abundances in either of the two ecosystems (see model 10 in Table 1). Neither the effect of oak and broadleaf abundance nor that of pine abundance were significant in the pine forest (Table 1), reflecting a significant interaction between the effects of species abundance and type of ecosystem.

#### Physical environment

The soils of the forest and maquis plots were similar in chemistry but differed in soil texture (Table S2 of the ESM). Maquis soils contained more clay (37.4 %  $\pm$  5.2 SD) and less sand (36.9 %  $\pm$  7.3) than forest soils (clay 33.1 %  $\pm$  6.0; sand 42.6 %  $\pm$  6.8). Litter decomposition rates of all three litter types were enhanced in soils with higher clay contents (Fig. 5a, b; see parameter  $\phi$  in Table



**Fig. 5** Leaf litter mass loss of the pine (dashed black, open symbols), oak (solid black, full symbols), and mixed (gray) litter types as functions of the contents of clay in the soils of **a** pine-forest and **b** oak-maquis ecosystems. Lines are based on the calculated mass loss of the best model using the mean fractions of pine (0.52) and oak and broadleaf (0.48) litter in the litter layer in pine-forest plots, or the

mean basal area of pines ( $1.34 \text{ m}^2 \text{ ha}^{-1}$ ) in oak-maquis plots. Triangles and squares represent the actual mass losses measured after 13 months in pine-forest and oak-maquis incubation plots, respectively. Gray shadows on the x-axes represent the range of soil clay contents found in the examined ecosystems

S1 of the ESM). We found no significant difference in the slopes of the effect of soil texture for the two ecosystems, so we used a single slope parameter for that effect in the models (e.g., model 5, Table 1).

## Discussion

Our reciprocal litter transplant experiment shows intrinsic, antagonistic effects of oak litter on pine litter decomposition. But there were countervailing negative effects on the decomposition of all three litter types as a result of increasing abundance of pine in the immediate neighborhood within maquis communities, and as a result of increasing proportion of pine litter relative to oak litter within pine communities. These countervailing effects were presumably mediated by a variety of species-specific effects of admixtures of pines and oaks on the structure and microenvironment of the overall litter layer (Fig. 1).

### Species-specific intrinsic effects of litter type

Our findings of the antagonistic effect of oak litter on the decomposition of mixed oak–pine litter provide an example that differs from previous studies of decomposition in mixed conifer/broadleaved forests (Cornwell et al. 2008; Weedon et al. 2009), and particularly of pine–oak mixtures, where oak leaf litter typically has higher decomposition rates than pine does, and a synergistic effect of oak litter increasing the rates of pine litter decomposition (Conn

and Dighton 2000; Kaneko and Salamanca 1999; Gartner and Cardon 2004). Even within the Mediterranean biome, most studies have shown that the litter of other pine species is more recalcitrant than that of oaks (van Wesemael 1993; Ibrahim et al. 1995; Rutigliano et al. 2004; Arslan et al. 2010). The differences between those studies and our results highlight the importance of understanding the high variability in these processes and the wide range of mechanisms by which different species influence ecosystem processes.

Our results imply that comparisons of functional or phylogenetic groups (e.g., pines vs. oaks or broadleaved vs. conifers) are not always reliable predictors of litter decay rates (Berg et al. 1993; Cornwell et al. 2008; Weedon et al. 2009). Similarly, attempts to predict litter decomposition dynamics based on leaf nutrient contents or leaf chemistry and structure are not always successful. A more flexible approach that incorporates the complexity of species traits and trait interactions seems to offer a more promising avenue for predicting species-specific effects (e.g., Eviner 2004).

The slower decomposition of *Q. calliprinos* compared to *P. halepensis* observed in our experiment is associated with higher contents of secondary metabolites (tannins and total phenols) in the oak leaf litter compared to pine, but not with lignin and nitrogen contents (Makkonen et al. 2012). Phenolic compounds are typically produced as a plant defense against herbivory (Heil et al. 2002). When these phenolics leach during decomposition, they complex with the enzymes of decomposing bacteria and fungi

and inhibit their activity (Lambers 1993). This inhibition should also affect the decomposition of other litters mixed with oak litter, thus explaining the proposed antagonistic effect in the mixture with pine. Leaf litter consumption by macrofauna (millipedes and snails) serves to eliminate tannins from decomposing litter (Coulis et al. 2009), but this was prevented in our experiment by the litterbag mesh (Milcu and Manning 2011). Controlled decomposition experiments with appropriate macrofauna would examine whether consumption by soil fauna prevents the reduced decay caused by oak litter and even increases overall rates of mass loss.

Other factors that may explain the recalcitrance of *Q. calliprinos* litter (as well as other broadleaved plants in the maquis) are related to the poorer quality of long-lived leaves, and to sclerophyllous leaf properties (Aerts 1997). The leaves of slow-growing sclerophyllous plants that grow in water and nutrient-limited conditions produce low-quality litter because their litter is (1) poor in nutrients due to nutrient conservation, (2) less water absorbent due to their sclerophyllous properties (Ibrahima et al. 1995), (3) better-defended (Cornelissen et al. 1999), and (4) dense in biomass, with a low leaf area to leaf dry mass ratio (Garnier et al. 2004). On the other hand, although pine needles have higher lignin to N ratios, they contain less defense compounds in the leaves (or different defense compounds, e.g., resins) and have less efficient nutrient- and water-conservation mechanisms. Gressel et al. (1995) even found that salt accumulation on the needles while still on the canopy facilitated enhanced breakdown of *P. halepensis* compared to *Q. calliprinos* leaves.

#### Species-specific environmental effects

Understanding the intrinsic decomposition dynamics of single and mixed litters is clearly not sufficient for understanding and predicting multi-species effects on decomposition in complex ecosystems (Weber and Bardgett 2011). We found counterintuitive effects of the same species, where the environmental effects of the abundance of a tree species in the litter layer and neighboring stand composition on leaf litter decomposition differed from the litter decay dynamics of the same species. Although pines have the faster decomposing litter type, increasing presence of pines in the oak maquis actually reduced overall litter decay rates. Similar results were reported by Rutigliano et al. (2004) for a Mediterranean maquis. As to the environmental effect of the surrounding litter layer, the effect of more pine in the litter layer was also negative, reducing litter decomposition in the planted pine forest. Accumulated oak and broadleaf litter in the litter layer, although more recalcitrant, actually increased the decomposition of both species, but only in the pine forest.

Several mechanisms could explain these contrasting effects (Hector et al. 2000). First, both the presence of the tree (canopy) and the litter layer it produces can alter the microclimate at the site of decomposition. Pine canopies are sparse and open compared to the thick canopies of evergreen broadleaf trees and shrubs such as *Q. calliprinos*. Therefore, pines growing in the maquis create canopy “gaps” that allow more light to penetrate into and water to evaporate from the forest floor (e.g., Gabay et al. 2012). Colonizing pine trees in the oak maquis can increase the temperature and reduce the water availability at the litter strata and thus limit litter decomposition in the colonized maquis (Rutigliano et al. 2004). Similarly, the characteristics of the accumulated litter layer can influence its microclimate (temperature, moisture, and light) and indirectly control decomposition (Eckstein and Donath 2005). A layer of oak litter (and other sclerophyllous broadleaved plants) is usually thicker and denser than that of pine needles, and may therefore hold more water and maintain a more stable moisture regime. In contrast, water quickly evaporates from pine litter and from the soil underneath it (e.g., Garcia-Pausas et al. 2004).

Changes in the composition and abundance of soil biota could be a second mechanism by which plant species affect decomposition at larger scales (Chapman and Newman 2010). Exudates from pine litter or roots (e.g., Fig. 1) may alter the composition of the decomposer community or reduce its activity and thus reduce the efficiency of litter breakdown. The macro- and microfauna that develop in litter layers containing a larger proportion of sclerophyllous broadleaf litter (the dominant native type in these ecosystem for thousands of years), on the other hand, are probably composed of species adapted to decompose litters with high contents of secondary metabolites (Baldrian 2006). Therefore, increased contents of oak and broadleaf in the litter layer in the pine forest can change the decomposer community, with implications for both oak and pine litter decomposition.

#### Habitat effects: ecosystem type and human impact

Our finding that there were no overall differences in the decomposition of specific litter types placed in oak-maquis vs. pine-forest ecosystems, in combination with the small magnitude of the absolute differences in decomposition rates between our oak and pine species, suggest that their decomposition dynamics, and possibly their decomposing communities, are relatively similar. Thus, although we did not find any significant affinity between litter type and the decomposing community (a “home-field advantage” sensu Ayres et al. 2009), or a significant interaction with the matrix that surrounds the site of decomposition (Freschet et al. 2012), these results could be simply due to

a combination of the overall similarity among our studied ecosystems and the restriction of the macrofaunal activity in our fine-mesh bags. The similarity in decomposition rates in what is considered the “natural” oak-maquis vs. the monospecific planted-pine forests is by itself surprising, especially in light of the expected differences between natural and man-made ecosystems (Chazdon 2003; De Fries et al. 2004). Further examination of soil biota and microflora in maquis and forest ecosystems could resolve these questions and improve our understanding of how ecosystem functioning is altered as a result of cross-colonization between these ecosystems.

#### Litter decomposition in human-altered Mediterranean ecosystems

Overall, litter mass loss in Mediterranean ecosystems is typically very low (<30 % mass lost within a year) compared to decay rates in mesic and humid ecosystems. Processes in Mediterranean ecosystems are constrained by both climatic conditions and low nutrient availability (mainly N and P) (Blondel and Aronson 1999). This implies that understanding the effects of changes in the composition and structure of Mediterranean systems on their function should take into account that these ecosystems are limited in the rates of key processes (e.g., Godoy et al. 2010). Nevertheless, many studies have found impacts of Mediterranean ecosystem type and land-use history on soil fertility. Soils were usually more fertile in pine forest (Fernández-Ondoño et al. 2010; Gelfand et al. 2011) and in oak maquis (Aranda and Oyonarte 2006; Arslan et al. 2010; Aponte et al. 2011) compared to the soils in Mediterranean shrublands. Differences in soil properties can further affect decomposition as the system is changing. However, from our analysis, the formation of mixed pine–oak communities in this system is not likely to have large effects on ecosystem functioning as measured by decomposition.

We found that oak-maquis soils contained more clay, which had a positive effect on litter decomposition rates. Improved decomposition with increased soil clay content is a well known phenomenon in temperate and tropical forests (Chapin et al. 2011) but, as far as we know, our experiment is the first to report the same effect in a semi-arid ecosystem. Litter breakdown by UV radiation is another important process in dry ecosystems (Aerts 1997; Austin and Vivanco 2006). Photodegradation contributes to litter decay mainly in open habitats such as grasslands and shrublands (e.g., Dirks et al. 2010), whereas in forests and woodlands tree canopies intercept much of the incoming radiation and decrease the contribution of dry season UV-mediated decomposition.

## Conclusions

We have shown that leaf litter decomposition dynamics are both species- and context-specific (e.g., community-level species mixtures), and are controlled by several, sometimes opposite, mechanisms. The litter decay dynamics of our pine and oak species could not be predicted from general rules of leaf lignin and nitrogen content. Furthermore, interactions among the species within a community affected litter decomposition via (1) nonlinear effects of litter mixing on litter decay rates and (2) environmental impacts of each species. The primary driver of litterbag dynamics appear to be chemically mediated, whereby oak chemistry retards decomposition in a non-additive manner. Conversely, the driver of the effect of local forest composition on decomposition dynamics appear to be environmentally mediated, such that the physical conditions created by increasing oak presence increases decomposition whereas increasing pine presence decreases it. Our results highlight the potential impacts of human-induced changes in community composition on ecosystem functioning, with different mechanisms acting simultaneously. It also highlights the problems involved in predicting the implications of changes in species composition as a result of global changes in climate and land use on ecosystem processes.

**Author contribution statement** ES, CDC, JK and AP conceived and designed the experiments. ES performed the experiments and analyzed the data. ES, CDC wrote the manuscript; other authors provide editorial advice.

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