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Litter mixture effects on decomposition change with forest succession and are influenced by time and soil fauna in tropical mountain Andes

Dennis Castillo-Figueroa*

Biology Department, Faculty of Natural Sciences, Universidad Del Rosario, Carrera 24 # 63C–69, 111321,
Bogotá, Colombia

Abstract

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In highly transformed regions, such as the tropical Andes, identifying the influence of forest succession and soil fauna on non-additive effects of litter decomposition is crucial for gaining a more realistic understanding of carbon dynamics and nutrient cycles. The objective of this paper was to analyze the changes of litter mixture effects on decomposition between different soil fauna treatments (macrofauna inclusion vs macrofauna exclusion) and successional stages (mature forests vs secondary forests) in upper Andean tropical forests along time by using a reciprocal translocation experiment of 1,344 litterbags that ran for 18 months with six common native Andean species. Thought *t*-tests, linear regressions, and linear mixed models, I found that litter mixture effects vary among sites and increase with time in secondary forests until the year of decomposition in litterbags with macrofauna exclusion. Mature forests exhibited strong antagonistic effects, while pronounced synergistic effects were observed in secondary forests. Although soil macrofauna did not increase significantly litter decomposition and synergistic effects in the mixtures at any of the stages of decay, it is likely that soil macrofauna may impact litter mixtures through top-down effects within soil food webs, rather than exerting a direct effect in the litter consumption as has been reported in tropical lowland ecosystems. Overall, this study supports the idea that litter mixtures exhibit significant variability across sites, can change with successional stage, and are influenced by soil fauna depending on the stage of decay in tropical Andean montane forests.

Keywords

Andean forests, ecological succession, litter decomposition, litter mixture, non-additive effects, soil fauna

Introduction

Litter inputs from terrestrial ecosystems constitute the basis of detrital food webs through their central role in breaking down the organic material into mineral components and reduced organic molecules (Berg and McClaugherty, 2020). This process, commonly known as litter decomposition, is fundamental in the global carbon cycle and soil fertility of terrestrial ecosystems (Swift et al., 1979; Krishna and Mohan, 2017; Giweta et al., 2020). Over the last decades, several field experiments have focused on single litter decay, collectively demonstrating that litter quality is a key determinant of decomposition (Bakker et al., 2011; Esquivel et al., 2020; Canessa et al., 2021), along with climate (Zhou et al., 2020; Canessa et. al., 2022), and soil fauna communities (Cardenas et al., 2017; Peguero et al., 2019; Yang et al., 2022). Nevertheless, few natural ecosystems are dominated by a single species,

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*Corresponding author:
e-mail: dennis.castillof@gmail.com

and instead, litter is typically a mixture of various plant species, implying that decomposition rates are shaped by the interactions between litters from different species. Hence, the study of mixtures in litter decomposition is essential to better understand carbon dynamics and nutrient cycles in a more realistic scenario (Liu et al., 2020; Porre et al., 2020).

Litter mixtures from different plant species often result in non-additive effects, which can be positive (synergistic) or negative (antagonistic) when the observed decomposition rates of mixtures are higher or lower than the predicted from the mean value decomposition of each litter species, respectively (Butenschoen et al., 2014; Zhou et al., 2020; Canessa et al., 2022). These non-additive effects can be attributed to a range of mechanisms, which are not mutually exclusive. For example, the combination of physical litter traits that creates improved microclimatic conditions for decomposers (Makkonen et al., 2013), the transfer of nutrients or recalcitrant compounds between litter species (Butenschoen et al., 2014; Canessa et. al., 2022), and the interaction across trophic levels (Hättenschwiler et al., 2005; Liu et al., 2020). Some studies have demonstrated that litter mixture effects are more pronounced in early stages of decay, diminishing over time due to the decline in litter quality for all species in the mixture as decomposition progresses (Butenschoen et al., 2014; Patoine et al., 2017; Njoroge et al., 2023). However, this can vary depending on the environmental conditions of the incubation site and the litter species composition which determine the combination of chemical and physical traits in the mixtures (Canessa et. al., 2022).

Soil macrofauna plays a major role in decomposition by: (1) increasing the surface area available for microbial decomposers (Peguero et al., 2019), (2) introducing nitrogenous compounds from their excreta and dead tissue (Ristok et al., 2019), and (3) releasing soil enzymes that promote fungal and bacterial populations (Patoine et al., 2020). In mixing litters, soil macrofauna accelerates the mixture effects by interacting with initial litter quality and the decay stage (Yang et al., 2022; Njoroge et al., 2022, 2023). Nonetheless, the effect of soil macrofauna on litter decomposition varies across biomes (García-Palacios et al., 2013; Njoroge et al., 2022). For instance, unlike most lowland forests where soil macrofauna significantly enhances litter decomposition rates (Cardenas et al., 2017; Peguero et al., 2019), in tropical montane ecosystems microarthropods and mesofauna have been recognized as the primary decomposers because of their ability to break down large litter pieces and disperse fungi and bacteria that colonize litter fragments, thus accelerating decomposition (Illig et al., 2010; Sánchez-Galindo et al., 2022). Nevertheless, the inclusion of micro-, meso-, and macrofauna in long-term litter mixture decomposition experiments in tropical montane ecosystems remains understudied.

The Andean tropical mountain forests host one of the most hyper-diverse and distinctive floristic compositions in the Neotropics (Rahbek et al., 2019), constituting the "hottest" hostspot with the highest levels of plant beta-diversity and endemism (Myers et al., 2000; Myster, 2021). Furthermore, Andean forests exhibit a high heterogeneity in several factors, including topography (Pierick et al., 2021), climate (Malhi et al., 2010), vegetation (Calbi et al., 2021), and soil (Moser et al., 2011). This heterogeneity has the potential to influence the environmental conditions related to crucial ecosystem functions linked to water and carbon cycles, which can vary from one forest to another. In particular, these ecosystems are paramount for climate change mitigation given their substantial net carbon stocks (Duque et al., 2021). Nonetheless, our understanding of litter decomposition in the upper slope of Andean forests between 2,600–3,200 m remains limited (Castillo-Figueroa, 2021), and there are no studies analyzing litter mixture effects at this elevation range. Considering that strong environmental filters in upper Andean montane forests shape communities characterized by plant functional traits associated with conservative strategies—such as low litter quality, high toughness, and high thickness (Homeier et al., 2021)—research that incorporates mixed litters from common native Andean mountain species are useful for quantifying the magnitude of mixture effects and their variability across different locations within Andean forests.

Upper Andean tropical mountain forests of Northern South America have been largely transformed since the Spanish colonization (Etter et al., 2008; Etter et al., 2021), which makes them conservation priority ecosystems with high levels of irreplaceability and vulnerability (Bax and Francesconi, 2019; Homeier et al., 2021). In this context, the largest city within the upper Andean mountain forest region is Bogotá, the capital of Colombia (Calbi et al., 2021). Situated at an elevation of 2,600 m, Bogotá and its surrounding natural areas are distinguished by extensive human-induced modifications that have resulted in a mosaic of forest patches with different successional stages, encompassing small and isolated old-growth forest fragments and early-secondary forests (Calbi et al., 2020; Hurtado-M et al., 2021).

In the last few years, different studies have pointed out the importance of secondary forests in carbon gaining (Chazdon, 2014; Chazdon et al., 2016; Poorter et al., 2021a), however, we still have a poor understanding in the role of these young forests in carbon release and litter decomposition (Xuluc-Tolosa et al., 2003; Paudel et al., 2015). Bearing in mind that secondary forests are usually characterized by microclimate conditions influenced by open canopies and pioneer species with high-quality litter (Seidelmann et al., 2016; Poorter et al., 2021b), it is likely that early successional forests enhance environmental conditions that increase litter decomposition and mixture effects. That is, in secondary forests the absence of a well-developed canopy cover typically results in higher soil temperatures (Seidelmann et al., 2016), and given the prevalence of acquisitive plant species in such environments (Poorter et al., 2021b), one would anticipate to observe a litter matrix in the soil primarily composed of nutrient-rich leaves. These conditions, in turn, attract soil fauna and microbial decomposers, enhancing decomposition rates and fostering synergistic effects within the mixtures through nutrient transfer if soil moisture is adequate. Conversely, mature forests are typically composed of species that use more efficiently nutrients for longer time periods and contain recalcitrant compounds, such as secondary metabolites in their leaves, which are difficult to degrade (Wright et al., 2004; Chua and Potts, 2018). Consequently, one would expect to observe a litter matrix in the soil with limited nutrient transfer, and a high presence of antagonistic compounds that retard decomposition. Additionally, due to the dominance of conservative plant species with low leaf functional dispersion in mature forests (Pinho et al., 2018; Poorter et al., 2021b), litter physical traits tend to exhibit a narrow combination that may not favor microclimatic conditions for decomposers. Collectively, these factors possibly contribute to an antagonistic effect within the mixtures in mature forests.

While many studies of litter mixture effects have primarily focused on analyzing the influence of functional traits and environmental conditions across various temperate ecosystems (Zhou et al., 2020; Porre et al., 2020; Liu et al., 2020), there is currently a gap in research regarding the effect of succession and soil fauna on litter mixtures over time in Andean tropical mountain forests. Considering that decomposition is fundamental for nutrient and carbon fluxes, which are critical functions for maintaining ecological integrity during forest recovery (Rosenfield et al., 2023), it is imperative to conduct studies examining mixture effects between successional stages and involving soil micro-, meso-, and macrofauna in highly diverse and threatened ecosystems such as the upland Andean tropical forests.

In this paper, I aimed to analyze the changes of litter mixture effects on decomposition between different soil fauna treatments (macrofauna inclusion vs macrofauna exclusion) and successional stages (mature forests vs secondary forests) of upper Andean tropical forests along time by using a reciprocal translocation experiment that ran for a year and a half with six common native Andean species. Specifically, I expected that: (1) litter mixture effects will vary among sites and decrease over time as the result of diverging environmental characteristics among sites and converging litter quality in the late stages of decay, (2) secondary forests will predominantly display synergistic effects, while mature forests will exhibit antagonistic effects due to the environmental conditions and plant species composition that influence the transfer of nutrients in the former and the exchange of recalcitrant compounds in the later, and that (3) soil macrofauna will increase the mixture effects as they are essential in litter fragmentation and nutrient transfer.

Materials and methods

Study area

This study was conducted in the Cundiboyacense high plains of the Eastern Colombian Andes, which is the most densely populated region of the country (>70% population) (DANE, 2005), and the most transformed with different human activities including livestock, agriculture, urban expansion, and mining (Etter et al., 2021). In this region, 14 permanent plots (20 × 20 m) were established since 2013 in secondary (7 plots) and mature upper Andean forests (7 plots) in four study sites between 2,685 and 3,140 m (Fig. 1). These plots are part of a larger network consisting of 36 20 × 20 m plots and eight 50 × 50 m plots. Mature and secondary forests were differentiated based on their floristic composition and structural attributes including basal area, tree height, and tree density (see Castillo-Figueroa et al., 2023; Hurtado-M. et al., 2021). Soil temperature and moisture was recorded every 15 minutes from TOMST (Czech Republic) dataloggers installed in each plot for 18 months (October 2021 to April 2023). The main characteristics of the four study sites are as follows:

1. Guatavita (4°56’9.716”N, 73°53’54.237”W, 3,028–3,036 m): situated in a private land in the rural area of *Tominé de Blancos*. The mean atmospheric temperature (MAT) is 10.46 °C (0 °C to 27.75 °C), and the mean soil moisture (MSM) is 39.47% (26.88% to 53.88%). Common agricultural activities in this area include the crops of potatoes and legumes, and the raising of cattle, including sheep and cows. This site contains two plots of secondary forests.
2. Guasca (4°47’20.318”N, 73°54’31.812”W, 3,086–3,140 m): located in the Encenillo Biological Reserve, a 206-hectare civil society reserve managed by the NGO Fundación Natura. MAT is 9.35 °C (0.12 °C to 30.125 °C), and MSM is 33.81% (27% to 53.84%). In this site, there are two plots of each successional stage.
3. Tabio (4°55’33.961”N, 74°6’47.225”W, 2,685–2,821 m): located in a private land of Tabio’s rural area, with extensive secondary forests along with some patches of old-growth forests. Common agricultural activities include the crops of potatoes and maize, as well as cattle ranching and abandoned paddocks. MAT is 11.88 °C (2.5 °C to 26.5 °C), and MSM is 42.14% (25.20% to 56.60%). This site contains two plots for each successional stage.
4. Torca (4°48’48,674”N, 74°0’58.527”W, 2,709–2,966 m): this site is part of the condominium *Floresta de la Sabana*, located in the Eastern hills or “*Cerros orientales*” of the Capital city (Bogotá), and is part of the *Reserva Forestal Protectora y Productora del Río Bogotá* that connects with the *Área de Reserva Forestal Regional de Bogotá*. MAT is 10.91 °C (3.43 °C to 32 °C), and MSM is 37.97% (13.87% to 45.70%). These reserves were established to create a protective connection strip between the Eastern hills and the alluvial valley of the Bogotá River (Ministerio de Ambiente, 2020). This site includes three plots from mature forests and one from secondary forests.

Decomposition experiment

Between October 2021 and April 2023, I conducted a reciprocal translocation experiment in the 14 permanent plots using the litterbag technique. Litterbags were made of fiber glass (10 × 15 cm) with a mesh size of 2 mm,

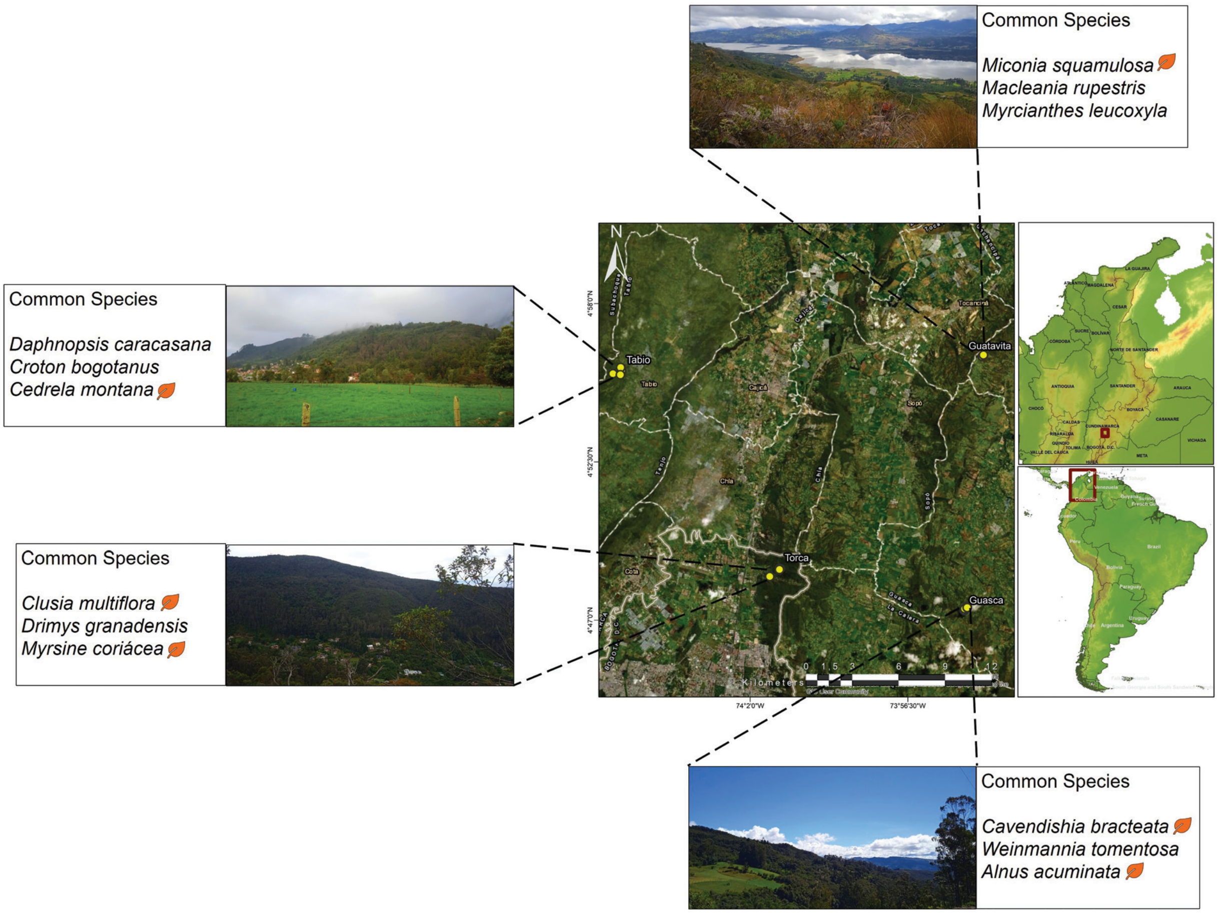

Fig. 1. Study area in the Andean mountains of Colombia. Yellow circles represent the plots of each site where the litter mixture experiment was conducted. In each site, some of the common plant species are pointed out. The six plant species with orange leaf symbol were the species selected to conduct the litter mixture experiment.

which allow the access of micro- and mesofauna but at the same time prevents the loss of litter fragments (Swift et al., 1979; Bakker et al., 2011). The litter mixture translocation experiment comprised two soil fauna treatments. The first treatment allowed the entry of micro- and mesofauna (macrofauna exclusion), while the second treatment enabled access for micro-, meso-, and macrofauna (macrofauna inclusion). This latter was done by opening 6 mm diameter holes in each corner of the bag, thus ensuring the access of macrofaunal decomposers but preventing losses of litter caused by the holes (Salinas et al., 2011). The litter mixture consisted of 1 g of dry weight from some of the dominant species of the study sites: *Alnus acuminata* Kunth, *Cavendishia bracteata* (Ruiz & Pav. ex J. St.-Hil.) Hoerold, *Clusia multiflora* Kunth, *Cedrela montana* Moritz ex Turcz., *Miconia squamulosa* (Sm.) Triana and *Myrsine coriacea* (Sw.) R. Br. ex Roem. & Schult (Fig. 1). All the litter material was collected in the study sites from freshly fallen senescent leaves, discarding those with conspicuous damages such as fungal infections, insect galls or high herbivory (>30%), as well as very bright young leaves and highly rooted leaves with extended necrotic area (Cardenas et al., 2017; Four et al., 2019). The collected litter material was oven-dried at 60 °C during 72 h and weighted using a 0.1 mg precision scale (LX 220A scs) to measure the initial and final weights.

In each of the 14 plots, I prepared three independent litterbeds (n = 42), placing them directly on the forest floor to minimize disturbance to the soil. Within these experimental units, I incubated four litterbags for each of the six litter species, along with the litter mixture treatments, arranged in a clockwise fashion corresponding to consecutive harvesting times (3, 6, 12, 18 months). This resulted in a total placement of 1,008 litterbags containing single litter from each species (2 forest successional stages × 7 permanent plots in each forest successional stage × 3 decomposition beds in each plot × 6 litter species × 4 harvesting times), as well as 336 litterbags containing mixtures (2 forest successional stages × 7 permanent plots in each successional stage × 3 decomposition beds in each plot × 2 soil fauna treatments × 4 harvesting times).

Data analysis

Litter mass loss of the six species assessed was calculated for each plot and decomposition time. Mass loss (%) was estimated as $((Wi–Wf) \times 100)/Wi)$), where Wi is the initial dry weight of the sample, and Wf is its final dry weight (Njoroge et al., 2023). After assumption checks of normality (Shapiro-Wilk test) and equality of variances

(Brown-Forsythe test), ANOVA test and *t*-test were used to analyze differences among litter species and between soil fauna treatments in each decomposition time, respectively. To estimate predicted mass loss of litter mixture (*Mp*), the average of single-species mass loss from all the six species was computed for each litterbed and plot. Litter mixture observed (*Mo*) was divided in the two soil fauna treatments: (1) macrofauna exclusion (2) and macrofauna inclusion. Thus, linear regressions were conducted between *Mo* and *Mp* for each decomposition time and soil fauna treatment. To assess the direction and significance of litter mixtures' effects, *t*-tests were applied for each of the factors analyzed (i.e., time, succession, sites, soil fauna). The relative difference between *Mo* and *Mp* was determined using the *t*-statistic, where $t < 0$ indicates an antagonistic non-additive effect, $t = 0$ implies additive effect, and $t > 0$ suggests a synergistic non-additive effect. Size effects of the statistical tests were calculated from eta-squared η^2 (ANOVA), Cohen's d (*t*-test), and R^2 (linear regressions).

Litter mixture effect (%), which is the percentage difference between the observed mass loss of litter mixture and the predicted mass loss of the litter mixture, was calculated as $[(Mo–Mp)/Mp \times 100]$ for each of the two soil fauna treatments. Non-additive effects were detected when observed mass loss of litter mixture was higher (synergistic) or lower (antagonistic) than predicted mass loss of litter mixture (Butenschoen et al., 2014; Canessa et al., 2022). To assess how the significance of site, succession, and their interaction influenced litter mixture effects across different stages of decomposition and soil fauna treatments, linear mixed models were conducted for each decomposition stage and soil fauna treatment separately. The fixed effects were site and succession, while the random effects were the plots. All the analyses were performed using JASP 0.17.2.1 (JASP Team, 2023).

Results

Litter decomposition increased with time, but after 18 months no species decomposed half of the initial mass on average. Strong differences in mean mass loss were found among species after 3 months (F = 107.017, $p < 0.001$, $\eta^2 = 0.685$, df = 5), 6 months (F = 127.131, $p < 0.001$, $\eta^2 = 0.721$, df = 5), 12 months (F = 117.188, $p < 0.001$, $\eta^2 = 0.704$, df = 5), and 18 months (F = 72.536, $p < 0.001$, $\eta^2 = 0.596$, df = 5). After a year, the species with the fastest decomposition on average was *A. acuminata* (37%), while the species with the lowest decay rate was *M. coriacea* (17%), which even did not further increase after 18 months (Fig. S1).

In all the litter mixtures, regardless of soil fauna treatment, mean decomposition rates showed an increase from 11.9% at 3 months to 30.9% at 18 months, and variations in mass loss were detected across different sites at every stage of decay ($p < 0.001$, Table 1). Specifically, Torca showed higher decomposition rates during the initial stages of decay (3 months and 6 months), while Guasca exhibited higher values during the later stages of decay (12 months and 18 months). Conversely, Guatavita consistently displayed the lowest values across all decomposition times (Table 1). However, no significant differences were found between mature and secondary forests in the mass loss of litter mixtures ($p > 0.1$, Table 1), and there was no substantial increase in litter decomposition attributed to soil macrofauna at any stage of decay ($p > 0.1$, Fig. S2, Table 1).

Linear regressions between predicted and observed values revealed non-additive effects in mature forests that varied over time, while secondary forests demonstrated a closer alignment with additive effects (Fig. 2, Table S1). Notably, *t*-tests exhibited significant differences in mature forests between predicted and observed decomposition at 3 months ($t = –2.511$, p = 0.021, Cohen's d = –0.235) and 6 months of decay ($t = –2.861$, p = 0.010, Cohen's d = –0.296), while secondary forests only showed differences at 12 months of decay ($t = 2.251$, p = 0.036, Cohen's d = 0.491, Table S2). In this sense, mature forests showed a pronounced antagonistic effect at the initial stages of decomposition (Fig. 3, Table S2). This effect, along with the observed additivity in secondary forests during these initial phases of decay, as well as the subsequent emergence of positive non-additive effects at 12 months, collectively explain the differences observed in litter mixture effects between successional stages within the first year of decomposition. However, it's worth noting that this effect was exclusively observed in mixtures without macrofauna. When macrofauna was included, additivity consistently prevailed (Figs 2 and 3, Tables S1 and S2).

Accordingly, litter mixture effects varied between mature and secondary forests along time. Out of the 336 mixtures, more than half presented antagonistic effects (n = 180, 53.57%), from which 57% corresponded to mature forests (n = 103), with a decreasing number of negative effect cases from 3 months (n = 30, 71.42%), 6 months (n = 27, 64.28%), and 12 months of decomposition (n = 23, 54.76%). Interestingly, after 18 months, antagonistic effects in mature forests remained constant, showing no reduction (n = 23, 54.76%). Conversely, secondary forests showed fewer negative cases at 3 months (n = 20, 47.62%), 6 months (n = 19, 45.24%) and 12 months of decay (n = 15, 35.71%) despite following a similar decreasing trend as observed in mature forests, but with an increase at the final incubation time of 18 months (n = 23, 54.76%). In line with this pattern, positive mixture effects were stronger in secondary forests than mature ones and increased over time until the year of decomposition, but then declined at 18 months (Fig. 4, Table 2). Soil macrofauna didn't increase the synergistic effects on decomposition and exhibited no consistent effect, neither in sites nor between successional stages (Table 2, Figs 3 and 4).

Litter mixture effects varied among sites during the first year of decay in mixtures where macrofauna was excluded (Figs 3 and 5, Table 2, Table S3). Remarkably, Guasca consistently displayed the highest synergistic effect at all stages of decay, regardless the influence of soil macrofauna (Fig. 3, Table S3). In contrast, Torca consistently exhibited a primarily antagonistic effect over time under both soil fauna treatments. Lastly, Tabio and Guata-

Table 1. ANOVA and *t*-test assessing the mass loss (%) among sites and successional stages at every stage of decay, respectively. Means and ± standard deviations are shown in each of the sites and soil fauna treatments. Significant differences are depicted in *($p < 0.05$), **($p < 0.01$), ***($p < 0.001$). Size effects for ANOVA (η^2) and *t*-test (Cohen's d) are also shown in the table. In the column soil fauna "General" represents the analysis of mass loss (%) using all the litter mixtures regardless soil fauna treatments. Symbols "–" and "+" represent macrofauna exclusion and inclusion, respectively.

Soil fauna	Stage of decay	F (sites)	η^2	Guatavita	Guasca	Tabio	Torca	Secondary	Mature	*t* (succession)	Cohen's d
General	3	7.72***	0.22	9.42 ± 2.15	11.12 ± 2.74	12.23 ± 2.91	13.46 ± 2.04	11.54 ± 3.05	12.19 ± 2.58	1.05	0.23
	6	3.54**	0.12	14.46 ± 3.91	17.76 ± 2.73	15.95 ±4.47	18.07 ± 3.52	16.58 ± 4.38	17.14 ± 3.26	0.67	0.15
	12	6.06***	0.19	23.70 ± 4.24	28.54 ± 5.61	26.73 ± 6.89	22.54 ± 3.05	25.52 ± 5.86	25.71 ± 5.68	0.03	0.15
	18	6.03***	0.19	26.68 ± 2.95	33.76 ± 5.44	32.21 ± 7.43	28.66 ± 4.01	29.99 ± 5.95	31.72 ± 5.99	1.33	0.29
–Macrofauna	3	4.64**	0.15	11.88 ± 3.81	13.39 ± 3.48	14.75 ± 4.00	16.31 ± 3.58	11.35 ± 2.94	12.01 ± 2.28	0.82	0.25
	6	3.11*	0.10	16.37 ± 4.71	21.61 ± 4.36	19.90 ± 6.29	21.09 ± 4.69	16.91 ± 4.97	16.07 ± 2.39	–0.70	–0.21
	12	4.05**	0.13	26.82 ± 5.63	31.90 ± 7.35	29.16 ± 7.72	25.67 ± 4.25	25.86 ± 6.55	24.31 ± 5.21	–0.85	–0.26
	18	2.08	0.07	30.19 ± 4.64	36.04 ± 6.38	35.69 ± 10.35	33.11 ± 6.35	29.57 ± 6.40	31.04 ± 5.75	0.78	0.24
+Macrofauna	3	2.73	0.18	9.73 ± 1.69	11.29 ± 3.51	12.49 ± 3.02	13.51 ± 2.37	11.73 ± 3.21	12.36 ± 2.90	0.67	0.21
	6	1.08	0.08	15.62 ± 3.87	17.72 ± 3.05	16.29 ± 4.07	18.47 ± 4.21	16.24 ± 3.79	18.21 ± 3.70	1.70	0.52
	12	4.13**	0.25	24.59 ± 3.47	28.96 ± 5.76	27.87 ± 6.35	22.39 ± 2.99	25.19 ± 5.22	27.11 ± 5.90	1.12	0.35
	18	3.78**	0.23	27.00 ± 3.42	34.06 ± 6.02	33.52 ± 6.17	28.82 ± 4.74	30.41 ± 5.58	32.40 ± 6.29	1.08	0.33

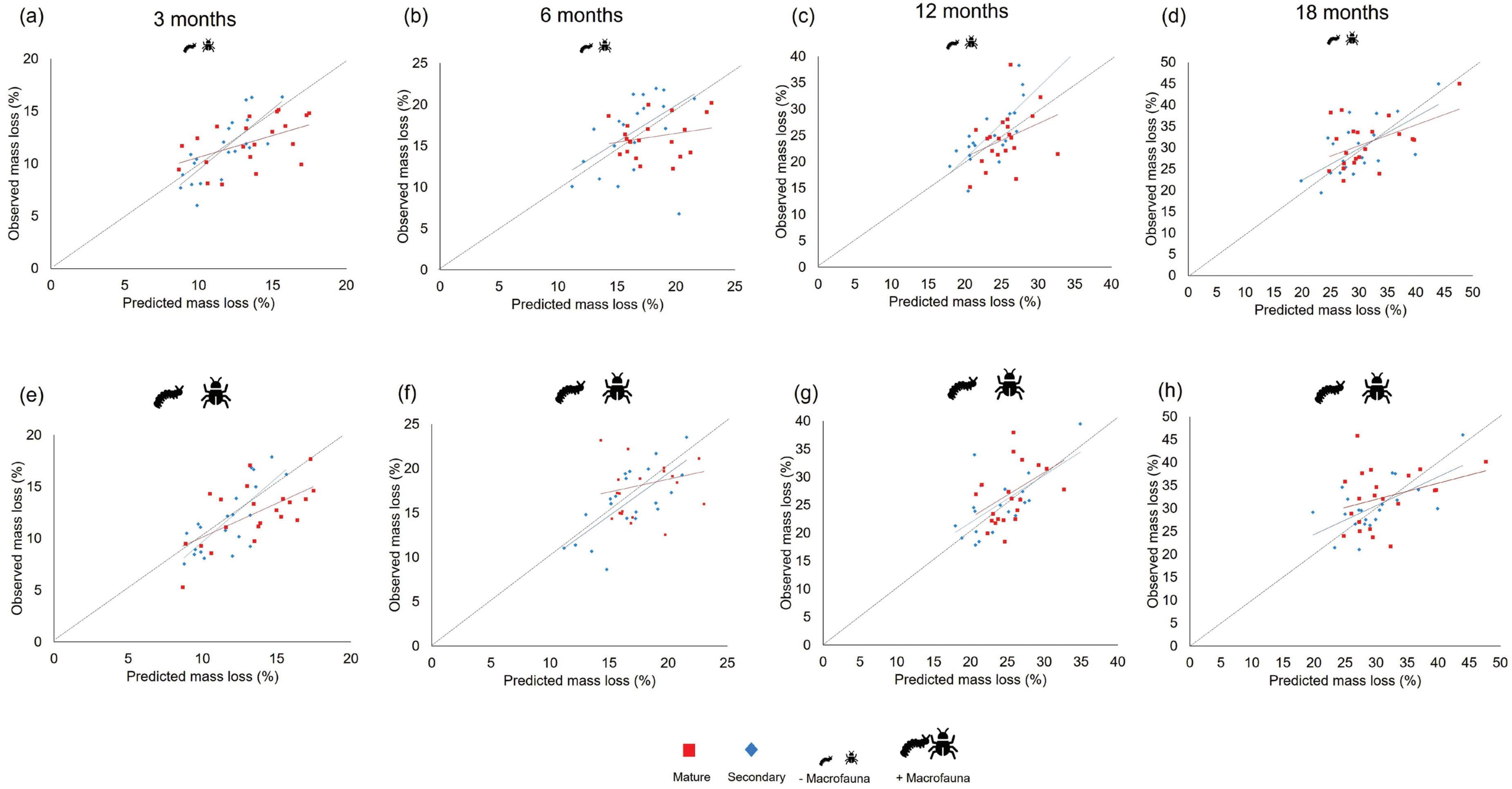

Fig. 2. Observed mass loss of litter mixtures against predicted mass loss in mature (red squares) and secondary forests (blue diamonds) in upper Andean forests of Colombia at 3, 6, 12 and 18 months of decomposition (columns). Dashed line in each regression represents the 1:1 relationship (additive mixture effects). Top of the panel shows macrofauna exclusion (a–d) and the bottom of the panel macrofauna inclusion (e–h). The predicted mass loss of the mixture is the outcome of averaging the mass loss of the six individual litter species that constitute this mixture. Values above the dashed lines indicate positive non-additive effects (synergistic effect), while values below the dashed lines indicate negative non-additive effects (antagonistic effect). Size effects (R^2), statistical significances (p), and confidence intervals for the slope (CI slope) of each linear regression are available in Table S2.

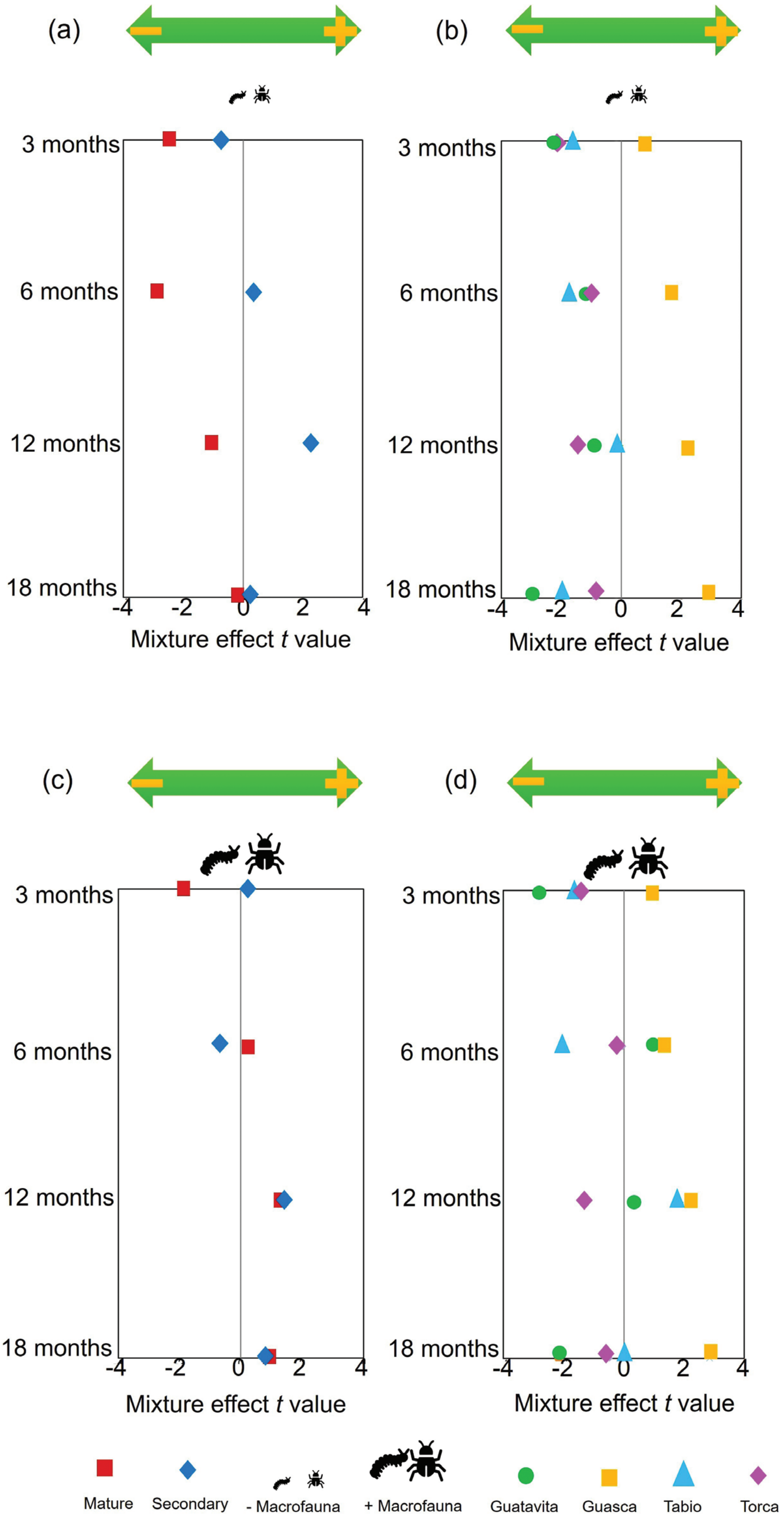

Fig. 3. Distribution of *t*-values for comparisons between observed decomposition and predicted decomposition, analyzing successional stages and sites at 3, 6, 12 and 18 months of decomposition (rows). Top of the panel shows macrofauna exclusion (a–b) and the bottom of the panel macrofauna inclusion (c–d). Note that grey line represents additivity in litter mixtures. When $t > 0$ litter mixtures exhibit a positive non-additive effect (synergistic effect), when $t < 0$ litter mixtures exhibit a negative non-additive effect (antagonistic effect). For successional stages, mature forests are represented by red squares and secondary forests by blue diamonds. For sites, Guatavita is represented by green circles, Guasca by yellow squares, Tabio by blue triangles, and Torca by purple diamonds.

Table 2. Linear mixed models of litter mixtures in upper Andean tropical forests. Symbols "–" and "+" represent macrofauna exclusion and inclusion, respectively. Significant fixed effects on litter mixture are shown in *($p < 0.05$), **($p < 0.01$).

	Fixed effects	Df	F	p
–Macrofauna	3 months			
	Succession	1, 35	2.851	0.100
	Site	3, 35	3.690	0.021*
	Succession*Site	2, 35	5.986	0.006**
	6 months			
	Succession	1, 35	6.240	0.017**
	Site	3, 35	3.514	0.025*
	Succession*Site	2, 35	0.519	0.600
	12 months			
	Succession	1, 35	7.323	0.010**
	Site	3, 35	4.209	0.012**
	Succession*Site	2, 35	2.864	0.070
	18 months			
	Succession	1, 7	1.621e-4	0.990
	Site	3, 7	4.079	0.057
	Succession*Site	2, 7	2.682	0.137
+Macrofauna	3 months			
	Succession	1, 7	1.610	0.245
	Site	3, 7	1.064	0.423
	Succession*Site	2, 7	0.537	0.607
	6 months			
	Succession	1, 35	1.376	0.249
	Site	3, 35	2.058	0.124
	Succession*Site	2, 35	0.026	0.974
	12 months			
	Succession	1, 7	0.280	0.613
	Site	3, 7	2.300	0.164
	Succession*Site	2, 7	0.397	0.687
	18 months			
	Succession	3, 7	2.672	0.128
	Site	1, 7	0.005	0.945
	Succession*Site	2, 7	1.632	0.262

vita predominantly showed a negative non-additive effect on litter mixtures, with some variations in positive and additive effects depending on the time and soil fauna treatment (Fig. 3, Table S3).

Discussion

Positive non-additive effects on decomposition increase in early stages of succession during the first year of decomposition when macrofauna was excluded. Contrary to my expectations and the findings of several studies that have suggested a decrease of mixture effects over time (Butenschoen et al., 2014; Patoine et al., 2017; Liu et al., 2020; Njoroge et al., 2023), I found an increase of synergistic effects as decomposition proceeds (Fig. 3, Table 2). This is probably explained by the combination of the plant species in the litter mixture, bearing in mind that recent studies have revealed the importance of litter mixture types on non-additive effects (Yang et al., 2022; Canessa et al., 2022; Njoroge et al., 2023). In particular, the increase in taxonomical dissimilarity within the litter mixtures amplifies the potential for more pronounced non-additive interactions (Jewell et al., 2015). This likely explain the strong mixture effects found in the experiment (Figs 2–5), as all the species of the mixtures belonged to six different families and genera with different traits (Table S4). Consequently, antagonistic effects observed during the initial stages of decay may be linked to the influence of recalcitrant compounds exchanged among low-quality litter species (Hättenschwiler et al., 2005), which can turn into synergistic effects over time (Liu et al., 2020). These non-additive interactions can also change in response to sites, succession, and soil macrofauna (Table 2).

Despite the six species selected for the mixture experiment are quite common in upper Andean tropical forests (Hurtado-M. et al., 2021; Homeier et al., 2021), most of them are conservative species with a relatively low litter quality and low decomposition that didn't exceed half of the mean mass loss after 18 months (Fig. S1, Table S4). Even the species with the highest decay rates, the common alder (*A. acuminata*), which is a nitrogen-fixing species, did not decompose as faster as expected given its low C:N ratio (Table S4). This could be attributed to the presence of secondary compounds typical of the genus *Alnus*, such as flavonoids, polyphenols, terpenoids, steroids (Ren et

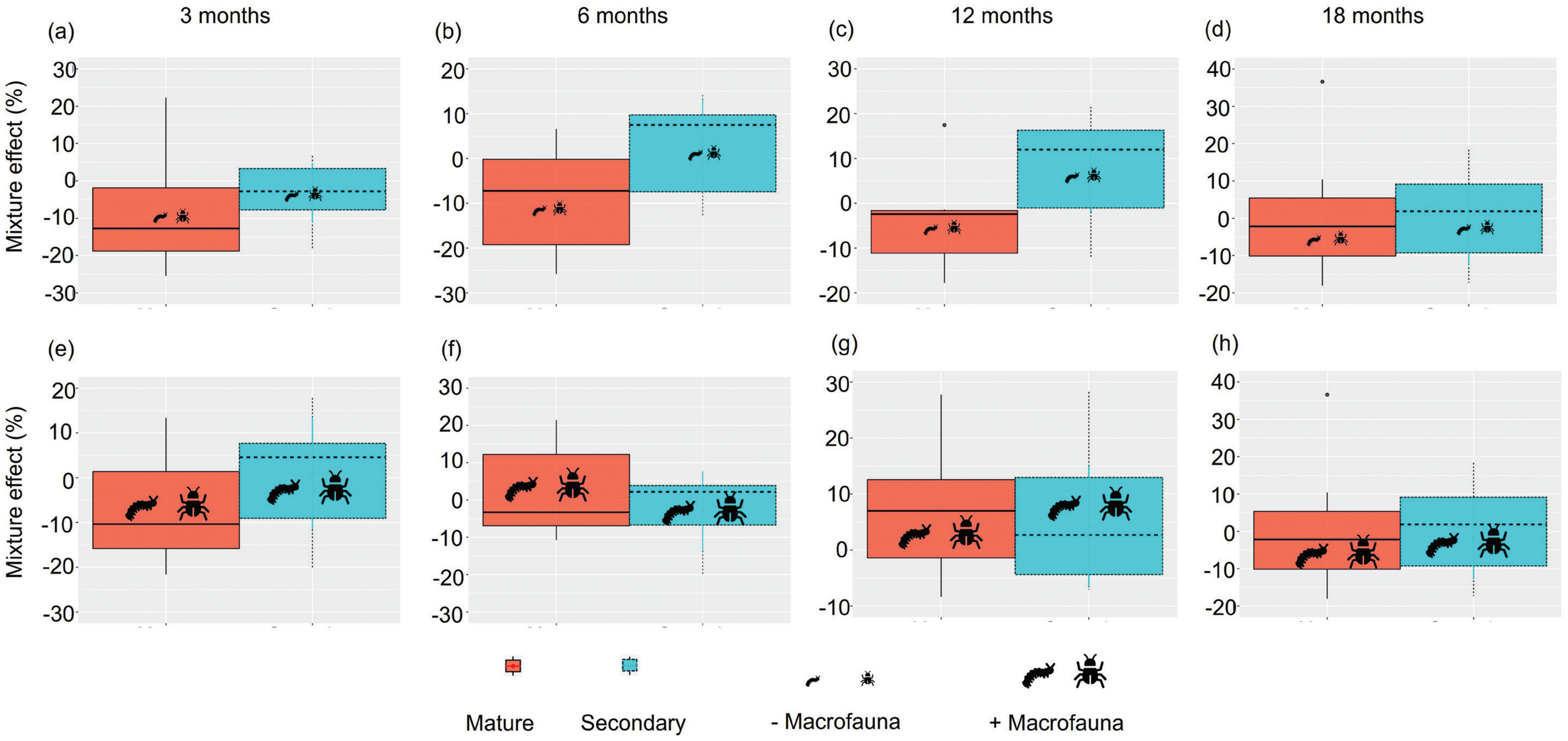

Fig. 4. Mixture effect (%) between mature and secondary forests at 3, 6, 12, and 18 months of decomposition (columns). Top of the panel shows macrofauna exclusion (a–d) and the bottom of the panel macrofauna inclusion (e–h). Mature forests are represented by red colors, while secondary forests are represented by blue colors.

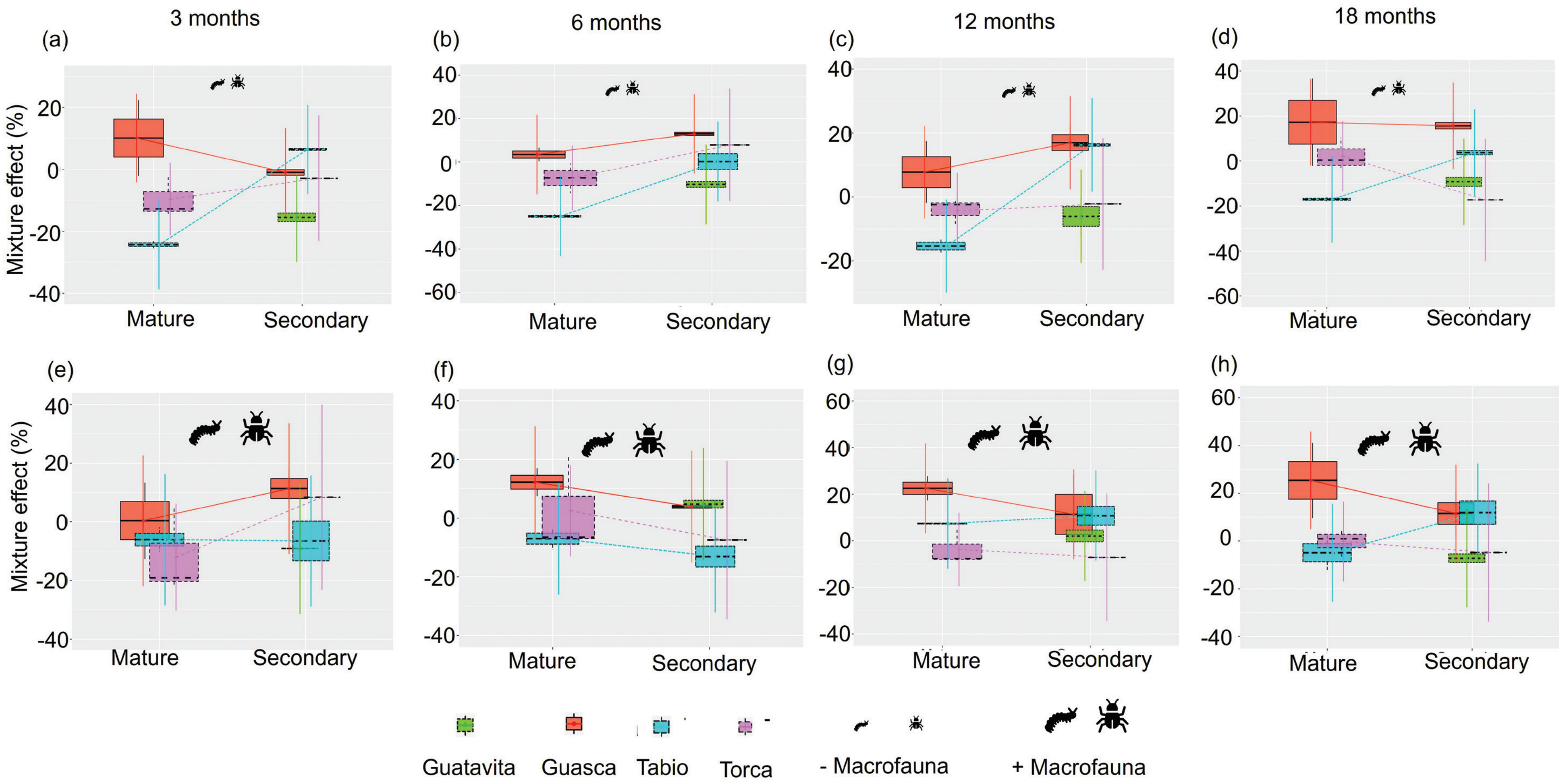

Fig. 5. Mixture effect (%) incorporating successional stage and site as fixed effects at 3, 6, 12 and 18 months of decomposition (columns). Top of the panel shows macrofauna exclusion (a–d) and the bottom of the panel macrofauna inclusion (e–h). Guatavita is represented by green colors, Guasca by red colors, Tabio by blue colors, and Torca by purple colors.

al., 2017), which can slow down decomposition (Berg and McClaugherty, 2020). A somewhat similar situation is observed regarding the chemical constituents of the other plant genera included in the mixture like *Clusia* (Camara et al., 2018), *Myrsine* (Zou et al., 2008), *Cedrela* (Nogueira et al., 2020) and *Cavendishia* (Castrillón-Cardona et al., 2015), because they also present toxic or recalcitrant compounds that inhibit microbial growth, thus collectively affecting the decomposition of other litter species by potentially transferring these secondary compounds and contributing to increased antagonistic effects within the mixtures (McArthur et al., 1994; Canessa et al., 2022). Further studies should explore non-additive interactions by employing different combinations of other Andean plant species and by varying the species richness within the mixture.

Nevertheless, mixture effects varied strongly among sites and successional stages as predicted (Figs 3–5, Table 2). Previous studies conducted in the same plots of this experiment have highlighted a remarkable plant beta-diversity (Hurtado-M et al., 2021; Calbi et al., 2021). These pronounced differences in floristic composition can largely influence microenvironmental conditions and soil decomposers, which are essential for determining litter mixture effects (Hättenschwiler et al., 2005; Zhou et al., 2020; Canessa et. al., 2022). This is especially true for secondary forests, where positive non-additive effects were detected as decomposition advanced (Fig. 4, Table 2). Thus, the interplay between site and succession could be explained because of improved conditions for decomposers, such as temperature and soil moisture in secondary forests of the study sites, facilitating more efficient nutrient transfer between litter species within the mixture. For instance, despite no significant difference in soil temperature between the secondary forest plots and mature forest plots, the maximum soil temperature in the former exceeded that of the latter by more than half a degree (Secondary = 13.822 °C, Mature = 13.091 °C, Table S5), and soil moisture levels were notably higher in secondary forests than in old-growth forests ($p = 0.003$, $t = –3.074$, df = 54, Table S5). Several studies have emphasized that higher soil moisture and temperature can enhance biological activity of soil microorganisms (Salinas et al., 2011; Zhang et. al., 2008; Liu et al., 2020), leading to increased nutrient transfer and litter decomposition (Berg and McClaugherty, 2020). Moreover, the higher input of litterfall with a high nitrogen content, typically associated with acquisitive species in early succession (Poorter et al., 2021b), is preferred by decomposers since nitrogen is a limiting resource for their metabolism (Bakker et al., 2011). That said, it is plausible to suggest that in secondary forests, the combination of higher soil moisture, maximum temperature, and a litter matrix of high quality could result in a positive non-additive effect through nutrient transfer between different types of litter. This, in turn, could lead to an increase in decay rates of the mixtures beyond what was initially expected (i.e., synergistic effect), which could have implications for nutrient cycling in Andean second-growth forests.

In contrast, mature forests are predominantly composed of shade-tolerant plants known for their efficient nutrient conservation, characterized by high levels of secondary compounds and thicker leaves that decelerate decomposition and increase carbon accumulation (Wright et al., 2004; Chua and Potts, 2018; Poorter et al., 2021a). Consequently, in mature forests, negative non-additive effects occur within litter mixtures possibly due to the low nutrient quality in the litter matrix, making it less readily transferable between different litter types. Furthermore, instead of nutrients, the prevalent recalcitrant compounds found in these conservative species may facilitate easier exchange between litter species, exacerbating the negative effects of mixing. As a result, this could lead to a reduction in litter decay within these mixtures, contrary to the expected litter decomposition rates (i.e., antagonistic effect). This phenomenon may contribute to increased soil carbon storage within Andean old-growth forests, establishing them as crucial carbon sinks.

One of the most striking findings of this experiment is that the effect of succession on litter mixtures was only significant when macrofauna was excluded, while no effect of site or successional forest was found when macrofauna was included (Fig. 4, Table 2). Even though this result contradicts my initial expectations, it is consistent with a recent meta-analysis that suggested stronger synergistic effects in litterbags with micro- and mesofauna inclusion, while those with macrofauna inclusion displayed either no effect or only a minimal synergistic effect (Liu et al., 2020). One potential explanation for this result is that macrofauna could have a negative effect on litter decomposition by preying on small decomposers, thereby diminishing the positive non-additive effect of litter mixture on decomposition. In other words, macrofauna may exert an antagonistic indirect effect on decomposition via top-down effect in soil detrital webs, thus weakening the synergistic effects on decomposition observed in litterbags with micro- and mesofauna inclusion (Liu et al., 2020). Having that decomposer communities in upper Andean montane forests are primarily composed of soil microarthropods and microorganisms (Illig et al., 2008; Scheu et al., 2008; Sánchez-Galindo et al., 2022), the predation of these organisms could largely decrease litter decomposition. Indeed, some of the most common soil microarthropods, such as oribatid mites, millipedes, and springtails play essential roles in litter decomposition and nutrient cycling within tropical montane forests through the consumption of litter fragments, the stimulation of microbial growth, and the dispersion of bacterial and fungal propagules (Ruess and Lussnhop, 2005; Illig et al., 2010; Sánchez-Galindo et al., 2022).

However, it has been posed that soil macrofauna do not play a central role in decomposition in upper montane forests (Varela et al., 2007; Illig et al., 2008; Maraun et al., 2008; Scheu et al., 2008). In these ecosystems, macrofauna may not directly accelerate decomposition to the same extent as observed in studies conducted in tropical lowland ecosystems (Cardenas et al., 2017; Peguero et al., 2019). In line with this idea, I found no significant increase in litter decomposition by macrofauna at any stage of decay (Fig. S2). Nonetheless, recent studies have pointed out the relevance of indirect effects caused by different invertebrate groups in soil food webs and their potential role on litter decomposition (Laigle et al., 2021). Thus, it is possible that macrofauna may influence litter decomposition and mixture effects by interacting with microorganisms and microarthropods, potentially triggering substantial effects on trophic cascades within soil food webs. Further research on soil food webs in upper Andean mountains should delve into the direct and indirect roles of soil fauna in litter decomposition and non-additive effects.

Conclusion

In this study, using a reciprocal translocation experiment, I found that litter decomposition in upper Andean tropical forests is slowed down when common native conservative species are mixed, and this can turn from antagonistic to synergistic effect over time in secondary forests when macrofauna is excluded. However, the magnitude and direction of mixture effect on litter decomposition can vary among different sites due to the high spatial heterogeneity and diverse floristic composition characteristic of the Andean region. Secondary forests exhibited more pronounced synergistic effects compared to mature forests. This can be primarily attributed to environmental conditions, including soil moisture, maximum temperature, and the quality of the litter matrix in the soil, which likely create more favorable conditions for decomposer communities in secondary forests, thus facilitating nutrient transfer among different litter types. Conversely, mature forests are composed of species that produce leaves with limited nutrient quality, impeding their effective transfer between diverse litter types. Moreover, the presence of abundant recalcitrant compounds in these leaves may increase the antagonistic effects within litter mixtures when exchanged. These results imply that mixture effects may have implications for nutrient cycling and carbon accumulation depending on the forest successional stage.

Regarding the role of soil macrofauna, the results suggest that it exerts an indirect effect on litter mixtures through trophic cascades rather than a direct effect by consuming litter, as demonstrated in tropical lowland ecosystems, but further research should address this issue. Collectively, these findings represent an initial step toward a better understanding of litter mixtures and the role of soil fauna in successional forests of the tropical mountain Andes. Additional research is needed to delve deeper into the mechanisms that control mixture effects along successional gradients in Andean forests.

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Data availability

The data and supplementary material that support the findings of this study are openly available in Open Science Framework repository at https://osf.io/97bzj/

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