







RESEARCH ARTICLE

Liana litter decomposes faster than tree litter in a multispecies and multisite experiment

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Abstract

1. Lianas account for a small fraction of forest biomass, but their contribution to leaf or litter biomass and thus to food webs can be substantial. Globally liana exhibit fast life-history traits. Thus, liana litter may decompose faster than tree litter, and could enhance the decomposition of tree litter (complementarity effect). The differences in decomposition may also vary with mesofauna access or across forest communities. The contribution of these factors to nutrient biogeochemical cycling is poorly understood.
2. We examined the decomposition of litter of 20 liana and 20 tree species of three different tropical forest communities in southern China, over 1 year. (i) We incubated the litter in bags with coarse and fine mesh to distinguish mesofaunal and microfaunal effects. (ii) We used single-species litter bags to compare decomposition rates of lianas and trees, to test which functional traits best explained decomposition, and whether those traits differed between lianas and trees, and among forest types. (iv) We used mixed-species litter bags to test whether liana litter enhances decomposition in litter mixtures. (v) We evaluated how leaf litter nutrients decayed in relation to litter mass.
3. Litter decayed faster in coarse-mesh than fine-mesh bags, but there was no interaction effect with forest type or growth form. Liana litter decayed faster than tree litter in single-species bags with mesofauna access and in mixed bags (liana-only mix, tree-only mix) without mesofauna. Lianas had higher nitrogen content and specific leaf area and lower leaf dry matter content (LDMC) and toughness than trees. Decomposition rate was significantly negatively related to LDMC. Litter of evergreen broadleaved forest decomposed slower than that of other forest types. Liana litter did not enhance the decomposition of tree litter in mixtures. Liana litter released calcium slightly faster than trees.

4. **Synthesis:** Leaf litter decomposes faster for lianas than trees, despite high variability of traits and decomposition rates within each growth form and overlap between growth forms, and we found no evidence for the complementarity hypothesis. Our study sheds light on the potential role of lianas within brown food webs and their importance on terrestrial biogeochemistry.

KEYWORDS

complementarity, leaf dry matter content, mesofauna, nutrients, specific leaf area, woody growth forms

1 | INTRODUCTION

Lianas contribute significantly to the dynamics of tropical and subtropical forests (Paul & Yavitt, 2010; Putz & Mooney, 1991; Schnitzer & Bongers, 2002), but our understanding of their contribution to food webs and biochemical cycling remains limited. In liana-rich forests, lianas provide substantial food resources and habitats for animals (Odell et al., 2019). To date, most studies have focused on 'green' food webs associated with living liana organs. By contrast, we know very little about the role of lianas in 'brown' food webs and associated biogeochemical nutrient turnover, including limited knowledge of how differences between microbial and invertebrate organisms impact the decomposition of liana organs.

The role of lianas in biogeochemical cycling may be understood from their contribution to total litter biomass and by the difference in functional traits of their organs compared to co-occurring trees (Powers, 2014). These trait differences may affect rates of decomposition and, in turn, nutrient turnover in forests (Cornwell et al., 2008). The contribution of lianas to total forest biomass is small, usually below 5% (van der Heijden et al., 2013; van der Heijden et al., 2014), but their contribution to specific components of the total forest litter pool may be much greater. For example, liana contribution to leaf litter fraction can be as high as 20–40% (Hegarty, 1991; Hora et al., 2008; Kusumoto & Enoki, 2008; Pragasan & Parthasarathy, 2005; Putz, 1983), and lianas have been found to contribute ~50% of seed and flower fall in seed traps in a tropical Dipterocarp forest (Wright et al., 2015). Global functional trait datasets suggest that liana leaves are richer in nutrients (higher nitrogen (N) and phosphorus (P) content per leaf mass) and have higher specific leaf area (SLA) than trees (Asner & Martin, 2012; Kazda, 2014). Comparisons to date include liana-host pairs (Cai & Bongers, 2007; Kazda et al., 2009; Kazda & Salzer, 2000), congeners (Cai et al., 2007), dominant species in forests (Cai & Bongers, 2007; Kusumoto & Enoki, 2008) or global datasets of leaf traits (Asner & Martin, 2012). Due to these structural and chemical characteristics, liana leaves as well as the litter lianas produce likely represent a more palatable food source for invertebrates and microbes compared to those of co-occurring trees in tropical and subtropical forests. Moreover, soil macro- and mesofauna, which in concert, can consume up to 50% of litter (Frouz, 2018), might benefit from enhanced

litter quality provided by lianas. If that is the case, then a mixture of litter from lianas with litter from trees may enhance litter mixture decomposition rates and speed up biochemical cycling.

Liana litter in forest communities may enhance tree litter decomposition, as decomposers can access different resources from various litter sources and qualities; this is known as the complementarity effect or positive non-additive effect. Complementarity effects have been detected in several decomposition studies on tree litter (Gartner & Cardon, 2004; Guo et al., 2019; Hättenschwiler et al., 2005; Meier & Bowman, 2008; Vos et al., 2013, but see Pan et al., 2015). One mechanism supporting the complementarity effect is nitrogen transfer which can enhance decomposition rates (Bonanomi et al., 2014). The broad range of trait diversity across both lianas and co-occurring trees represents an opportunity to test complementarity effects. Yet, decomposition studies leveraging this opportunity remain rare. Only a handful of studies examined the decomposition of liana litter of single invasive species, finding accelerated decomposition rates compared to native woody species or communities of non-infested areas (Ashton et al., 2005; Leicht-Young et al., 2009; Scowcroft, 1997). Few studies have considered liana litter decomposition at the community scale and the results regarding decomposition rates differ. On the one hand, Cornelissen (1996) found that woody climbers s.l. had relatively fast decaying litter in a temperate flora and Jo et al. (2020) assigned half of the liana species in a temperate forest to the group of rapidly decaying species. On the other hand, Santiago (2009) found no difference in decomposition rate of litter between lianas and canopy trees in a tropical community.

To date, we have little understanding of how liana and tree litter decomposition change across forest types or environmental gradients. Forest communities which host lianas can differ in many abiotic and biotic aspects, which, in turn, may affect decomposition properties. First, plant communities consist of different plant species (e.g. Pasion et al., 2018). These representative species might differ in their functional traits, even within the same growth form (e.g. Roeder et al., 2019). And it is well established that functional traits drive decomposition rates (Cornwell et al., 2008; Dias et al., 2017). Second, different communities arise because of underlying variation in soil and climate properties (Liu & Slik, 2014), which also affect decomposition; high soil moisture, temperature

and air humidity will increase the decomposition rates of plant material (Swift et al., 1979).

In this study, we investigated the decomposition of liana and tree litter at community level across three forest types. We tested the following hypotheses:

H1: Liana litter generally decomposes faster than tree litter because liana leaves have higher litter quality than trees (Asner & Martin, 2012; Mello et al., 2020), and mesofauna contribute significantly to this process.

H2: Litter of lianas and trees decomposes differently across different forest types (significant forest x growth form interaction) due to differences in litter traits, microclimate or soil fertility.

H3: As a consequence of H1, liana leaf litter mixed in tree leaf litter enhances total litter decomposition (complementarity or positive non-additive effect e.g. Vos et al., 2013).

H4: As a consequence of H1, lianas release nutrients faster than trees (Hobbie, 2015).

We tested these hypotheses using liana and tree species growing in three different tropical forest communities that are interspersed in tropical southwest China. These forest types differ in tree, liana and herb species composition (Pasion et al., 2018) and vary in several abiotic aspects such as water availability, elevation and soil fertility (Liu & Slik, 2014; Roeder et al., 2019). We collected community-level data of 40 species (20 lianas and 20 trees), using mixed species bags as well as single species bags, to get a comprehensive understanding of liana and tree litter decomposition.

2 | MATERIALS AND METHODS

2.1 | Location and forest types

The study was conducted in the tropical forests around Xishuangbanna Tropical Botanical Garden, Menglun, Yunnan, China (21°54' North, 101°46' East), within a radius of 10 km of the garden. The area has a hilly topography with steep slopes, and altitude ranges between 540 and 1400m. Annual rainfall averages 1500mm, and mean temperature is 21.8°C. Our study site encompasses three communities (Cao & Zhang, 1997; Pasion et al., 2018): (A) forest situated on rocky limestone with shallow soil and low tree diversity (hereafter called 'LIM'), (B) evergreen broadleaved (EBL) forest on sandstone, dominated by *Castanopsis* and *Lithocarpus* species, mainly occurring on ridges at middle to high elevation ('EBL'), (C) tropical seasonal forest on sandstone, often located in valleys and at low elevation with high tree species richness (tropical rain forest ['TRF']). In each forest type, we used five locations (Figure 1). The elevation ranges of the plots of the different forest types overlapped. The highest plots were in EBL forest (714–1148m asl), followed by LIM forest plots (670–869m), with TRF lowest (541–817m asl). Due to the small area encompassed, average rainfall can be assumed to be similar across forest types, but temperature likely differs between EBL and TRF due to their elevational differences (0.65°C decrease per 100m

elevation). The cumulative precipitation in Menglun municipality was 164mm for the collection after 1 month, 816mm after 3 months, 1118mm after 5 months and 1660mm after 11 months (source: XTBG weather station).

2.2 | Species selection and litter collection

We aimed to include representative species in each forest type. Using several data sources (Cai et al., 2009; Cao & Zhang, 1997; Chen et al., 2015; Lü et al., 2010; Pasion et al., 2018; Zhu, 2008), we checked for abundance data, basal area or Importance Value Index of tree and liana species of the region and ranked all species in each study. Species were pre-selected if they had a high average ranking and if they occurred in many/most sources. We then checked for abundance of litter for each species during the dry season in February to May 2017 and subsequently chose a final list of 40 species. Litter was collected during the same period. We used 17 species in the TRF (7 liana, 10 tree), 10 species in the EBL (5 tree, 5 liana) and 9 species (5 tree, 4 liana) in the LIM. Four more liana species with less litter were included for the first 1–2 collection times (2 liana species in TRF, 1 in EBL, 1 in LIM). Species numbers were different per forest type, which reflects the richness differences between the forest types. Species names, family, growth form and habitat are listed in Appendix Table S1.

2.3 | Field experiment

We used single-species litter bags and mixed species bags to measure decomposition rates of liana and tree species (H1) across different forest types (H2). We also used bags only containing filter paper as an additional neutral assay to measure decomposition across forest types (H2). We used mixed-species litter bags to test whether liana litter enhances decomposition rates in litter mixtures (necessary for H3). We placed litter bags of single species and of mixed species only in the forest type they represented (thus bags only contained species sampled from a particular forest type). We also placed litter into bags with two mesh sizes, fine-mesh bags (~0.1mm mesh) and coarse-mesh bags (2mm mesh). The different mesh sizes allowed us to measure the contribution of mesofauna to decomposition, as these would be excluded by the fine mesh but allowed access in the coarse mesh. All bags were 16cm x 20cm in dimensions.

For bags containing litter of single species, we weighed 5 g of air-dried litter. We had four collection dates (1, 3, 5, 11 months of field incubation), and 5 replicates, resulting in 40 bags per species. Four liana species did not have sufficient litter for all time steps and were only sampled at the first two collection dates (see Appendix S1). Additionally, we had one replicate of the coarse mesh for month 0, to determine the loss of biomass through handling (transport to field and back) and by oven drying. For the filter paper test, used as a neutral standard material to measure decomposition differences across forest types and locations, we used Whatman filter paper

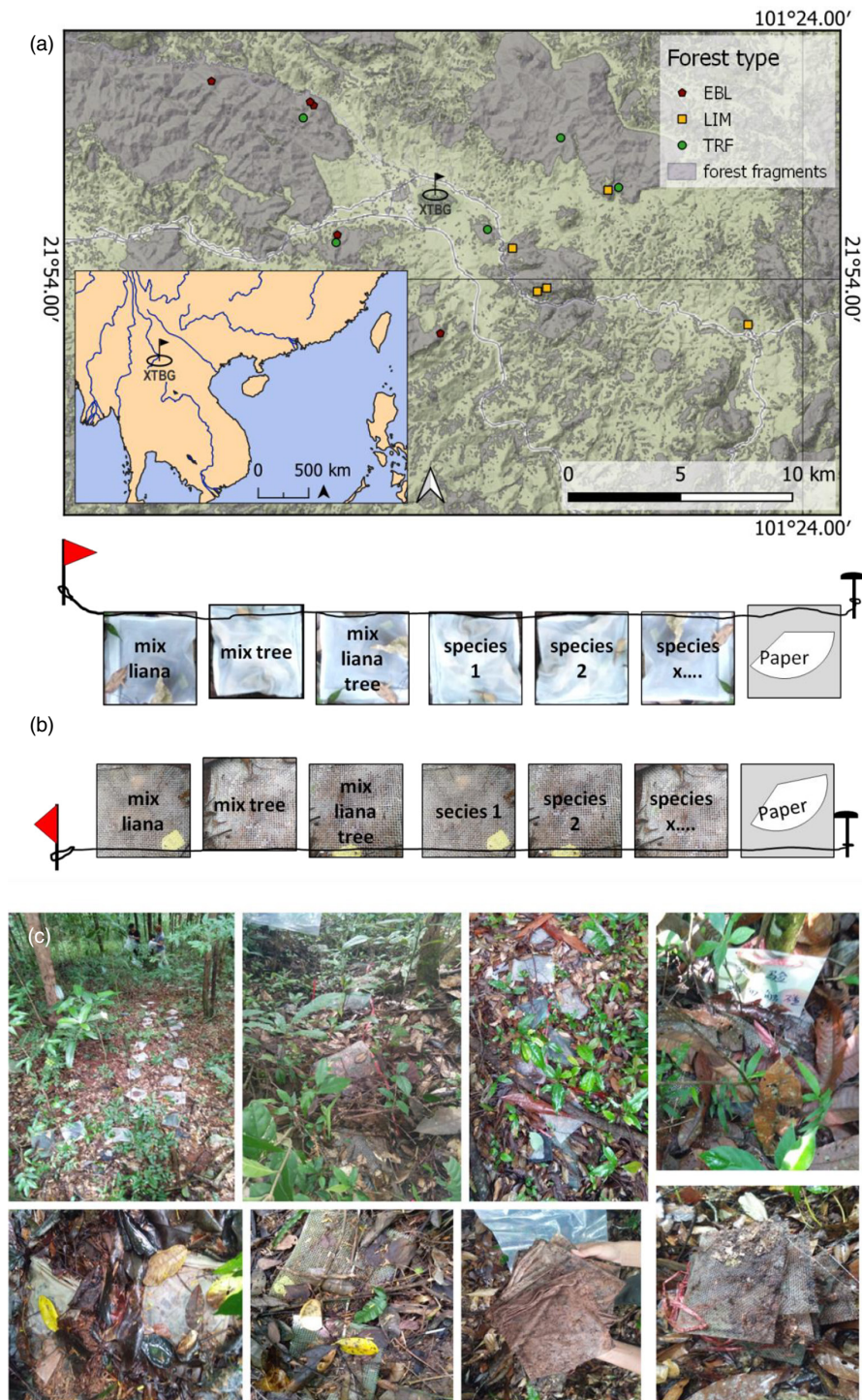


FIGURE 1 (a) Geographical location of the study plots around Xishuangbanna tropical botanical garden (XTBG), Menglun, Xishuangbanna prefecture, Yunnan Province, China. Brown pentagons represent evergreen broadleaved forest (EBL), green circles represent tropical rain forest (TRF) and yellow squares represent limestone forest (LIM). (b) Schematic set up of one replicate of litter bags, consisting of mixed litter bags and single species bags in fine- and coarse-mesh bags, and filter paper in a medium mesh-size bag. Each plot contained four replicates, at 2–10 m distance from each other. (c) Aspects of the litter bags in the field at various incubation times until the last harvest.

(Qualitative circles, 110mm diameter), cut into quarters, which was weighed and then put into 1 mm mesh bags.

Mixed species bags contained 10 g of air-dried litter of (a) several liana species or (b) several tree species or (c) several liana and tree species, with equal litter amounts for each component species of the mixture. We also used the two mesh sizes. For the forest types EBL and LIM, mixed bags contained all species, for example, EBL liana mix = 5 species, EBL tree mix = 5 species, EBL tree & liana mix = 10 species. In case of TRF, only 9 of the 19 available species were used for the mixed bags (5 tree, 4 liana); otherwise, the litter

amount per species per bag would have been very small. Every bag had a unique label inside. We tacked all bags of one replicate per mesh size together on a string to facilitate rapid relocation of samples during harvesting (e.g. for TRF fine mesh: 17 single species bags +3 mixtures bags +1 filter paper bag) and fixed these strings onto the forest floor with nails. The bags were laid out in May 2017 shortly prior to the start of rainy season and subsequently collected up to beginning of May 2018. Bag placement and each harvest date were accomplished within 1 week. We placed a total of 2071 bags in the field, of which more than 99.5% were recovered during harvests.

After collection, litter bags were opened, all soil and ingrown roots were carefully removed from the samples, and then the samples were oven-dried at 65 °C until constant weight (weighed to 0.001 g accuracy). When we removed the fine-mesh bags, we noticed that several had holes. Therefore, hole damage was recorded for each bag in terms of size and number of holes and assigned roughly to three categories according to size: small (≤ 3 mm), medium (~ 4 – 9 mm) and large (≥ 10 mm) holes. We excluded fine-mesh bags with large holes (≥ 10 mm) from the dataset (39 samples removed), and checked if mass loss for the remaining bags was influenced by damage using a Linear Mixed-effect Model (LMM) with species, site and damage as random factors. Damage had no significant influence, and was not further considered (Appendix S2).

2.4 | Litter traits and nutrient decay measurements

Leaf traits (H1) were measured at the beginning of the experiment on the same litter material used in the litter bags. We estimated SLA (fresh area per dry weight) and dry matter content (dry weight/saturated weight), using 10 leaves per species. These were moistened overnight in towels in a fridge. After blotting excess water, leaves were weighed and scanned, oven-dried at 65 °C, and weighed again. Image J software was used to measure leaf area. We measured leaf toughness with the puncture method, which measures the force used when a leaf is penetrated (IMADA digital force gauge Model DS2-50N), using moistened and dry leaves for each species. The toughness values of wet and dry litter were highly correlated across species ($r^2 = 0.92$); therefore, we proceeded with dry litter toughness as a trait. We analysed the total content of several macro- and micro nutrients (N, P, K, C, Mg, Ca, S) as well as (soluble) tannin and lignin for each species. These elements and compounds have been widely shown to be potentially important drivers of decomposition rates (Cadish & Giller, 1997; Makkonen et al., 2012; Swift et al., 1979). Details for the methods used for respective compound content are provided in Appendix S3.

To address H4 (differences in nutrient decomposition between liana and tree litter), the same chemical analyses were done on the remaining material in coarse- and fine-mesh bags after 3-month and 5-month incubations: After 11 months, too little litter mass was left to conduct these chemical analyses. After 3 and 5 months, some rapidly decomposing species had insufficient material left for all chemical analyses, so we conducted nutrient analyses following a priority order: C & N > P & K & S & Ca & Mg > tannin > lignin.

2.5 | Statistical analysis

All data analysis was conducted in R 3.6.1 (R Core Team, 2019). Our data analysis included a large number of models with fixed and random effects (*lmer* function, *lme4* package, Bates et al., 2015). In all cases, we started with the full LMM of fixed and random effects (provided below), then removed non-significant random effects

term-wise using bootstrapped confidence intervals. In some cases, models were reduced to simple linear models with no random effects. Subsequently, we simplified interaction terms of the fixed effects part of the model, and selected the best model based on AICc rank (*model.sel* function, *MuMIn* package [Barton, 2020]). Only the final selected models are provided in the results below.

2.5.1 | Differences in decomposition rate between mesh sizes

We first tested whether there were differences in the decomposition rates of litter in fine- versus coarse-mesh bags; if so, then all other analyses would be done separately for each mesh size. For this analysis, we estimated decomposition rates for each species, k , a species-level variable. Species' k was calculated using individual species bags per mesh size per species, using the formula: $k = \ln\left(\frac{m_1}{m_0}\right)^{-t}$ (Olson, 1963; Silver & Miya, 2001), where m_0 is the dry mass at the beginning of the experiment, m_1 is the dry mass at harvest time and t is the duration of the experiment. A larger k indicates that decomposition is more rapid. We used a negative exponential function fitting all values (4 harvest times \times 5 locations) to calculate k per species per mesh size, using the package *litterfitter* (Cornwell et al., 2020). We used the following linear model to test for differences in decomposition rate across mesh sizes, growth forms and forest types: $k \sim \text{growth form} \times \text{forest types} \times \text{mesh size}$. This analysis showed that mesh size substantially impacted decomposition rate (see Results), and the best model included no interaction term, so all subsequent analyses were conducted separately for each mesh size.

2.5.2 | Differences in decomposition rate of growth forms and relation to leaf functional traits

To test whether lianas had greater decomposition rates than trees and whether this difference was associated with differences in functional traits (H1), we ran several analyses. First, we used the results of the previous linear model analysis to establish whether lianas and trees differed in decomposition rate. Second, we used the initial chemical and physical leaf litter trait values (month 0) per species to test if traits differed between forest types and between growth forms (H1). For this, we used one linear model per trait with 'forest type * growth form' as fixed predictors. Leaf area and leaf toughness were log transformed prior to analysis. Additionally, we carried out a permutational analysis of variance (PERMANOVA, *adonis* function, *vegan* package [Oksanen et al., 2019]) to test for differences between growth forms, forest types and their interaction, in multivariate space (measured as Euclidean distances). We used Principal Component Analysis (PCA) ordination on centred and scaled data to visualize any differences between forest types and growth forms, and correlated decomposition rate k to the first two PCA axes. Third, we also related decomposition rate k to all litter traits using a multilinear model. Because there were

so many predictor variables in this model, we used model averaging (*model.avg* function, MuMin package) and reported conditional averages of coefficients and importance values.

2.5.3 | Decomposition differences in growth form and forest types

To test for decomposition differences in growth form across forest types (H2), we used mass loss over time analyses. Using the single species bags, we calculated the mass loss percentage at each sampling time relative to the estimated original mass placed in the field, and used this as response data in LMM models of the following form: $\text{exp}(\text{mass loss}) \sim \text{time} \times \text{forest type} \times \text{growth form} + (1 | \text{site}) + (1 + \text{time} | \text{species})$. The model separated the effect of time out from the effects of forest type and growth form, and accounted for the random effects of sites and species, where species were allowed individual mass loss responses over time (random slopes). We ran the same model on mixed bag data, replacing growth form by litter mixture type and removing species as a random effect. The full model tested was as follows: $\text{exp}(\text{mass loss}) \sim \text{time} \times \text{forest type} \times \text{mixture} + (1 | \text{site})$.

We conducted an additional analysis using the neutral filter paper data, which did not include growth form or species: $\text{exp}(\text{mass loss}) \sim \text{forest types} \times \text{time} + (1 | \text{site})$. This was supposed to uncover differences in decomposition between forest types related to location (e.g. microclimate, soil type, soil fauna) but not to species identity.

2.5.4 | Complementarity effect analysis

We used the mixed litter bags to test whether there was a complementarity effect caused by mixing the different species and growth forms (H2) in each mesh size. We calculated the expected remaining litter mass M_e for each mixture bag type (mixture, forest type, harvest time, mesh size, $n = 72$) using rates derived for each species from the single species litter bags and summing the estimates together: $M_e = \sum \left(M_i * \frac{R_i}{B_i} \right)$, where M_i is initial mass of species i in a mixed bag, R_i is remaining mass and B_i initial mass of species i in single species bag (Hoorens et al., 2003, modified equation). We compared the observed remaining mass (M_{obs}) to expected remaining mass (M_e) in a paired t-test, conducting one test for each litter mixture in each mesh size. If complementarity is true, then observed litter mass should be less than expected mass ($M_{\text{obs}} < M_e$), and $M_{\text{obs}} > M_e$ would indicate an inhibitory effect of mixing on mass loss.

2.5.5 | Nutrient decomposition in litter

We calculated remaining nutrients at each time point for each species and mesh size as nutrient concentration \times average remaining litter mass. After this, we calculated decomposition rate k for each nutrient per species per mesh size using the R package *litterfitter*. We

correlated log transformed data (Pearson correlation) of nutrient decomposition rate and mass decomposition rate over all species and mesh sizes. We tested if nutrient release from the litter was faster in lianas than in trees (H4) and whether there was a difference among forest types using the maximum LMM model: $\text{nutrient } k \sim \text{growth form} \times \text{forest type} \times \text{mesh size}$.

3 | RESULTS

3.1 | Differences in decomposition among bag mesh sizes

We compared the decomposition rates (k) of all 40 species in both mesh sizes (Table S1) using an additive model ($R^2 = 0.539$, $p < 0.001$). No interaction term (e.g. growth form \times mesh size) was significant and all were excluded from the final model. Mesh size was highly significant and explained most variation ($F_{1,75} = 76.0$, $SS = 15.25$, $p < 0.001$), with leaves in coarse-mesh bags decomposing much faster than fine-mesh bags (Figure 2). Growth form also explained a much smaller portion of variation ($F_{1,75} = 8.8$, $SS = 1.76$, $p = 0.003$), with lianas decomposing significantly faster than trees. Therefore, all analyses were subsequently conducted separately for fine- and coarse-mesh bags (Appendix S4).

3.1.1 | Differences in decomposition rate between growth forms and relation to leaf functional traits

Across all forest types and species, liana litter had higher N content, higher SLA and lower LDMC and lower leaf toughness than trees (Table 1). Litter of the different forest types differed in concentrations of P, K, S, C, Ca, leaf area and SLA; for details see Table 1.

In our multivariate analysis (Figure S5), the first axis of the PCA explained 24% of variation, with S, P, Ca, SLA in the negative direction and LDMC in the positive direction. The second axis explained 19% of variation and was determined by carbon content and SLA (both negative), and leaf toughness (positive). The decomposition rate k (all harvest time points) per species for coarse-mesh bags (k_c) and fine-mesh bags (k_f) was both correlated to PCA axis 1 and 2 ($R^2 = 0.26$, $p < 0.01$; and $R^2 = 0.25$, $p < 0.01$, respectively), with high SLA species associated with fast decomposition rates and tough, high LDMC species associated with slow decomposition rates. PERMANOVA could not distinguish trait groups between growth forms, but could distinguish trait groups among forest types: EBL was significantly separated from TRF and from LIM (forest type $F_{2,36} = 3.34$, $p = 0.036$).

In the multilinear analyses using model averaging (Table S6), decomposition rate per species in coarse-mesh bags (k_c) was positively related to leaf area and negatively related to LDMC (Figure 3, av. coefficient 0.144, $p = 0.024$ and -0.269 , $p > 0.001$, respectively). In fine-mesh bags, decomposition rate (k_f) was negatively related to

FIGURE 2 Decomposition rate (constant 'k', month⁻¹) of litter of 20 liana and 20 tree species in fine- and coarse-mesh bags. (a) Rate of all 40 species, (b–d) Rate of representative liana and tree species of different forest types: Evergreen broadleaved forest (EBL), limestone forest (LIM), tropical rain forest (TRF). * = significant $p < 0.05$, + = $p < 0.1$.

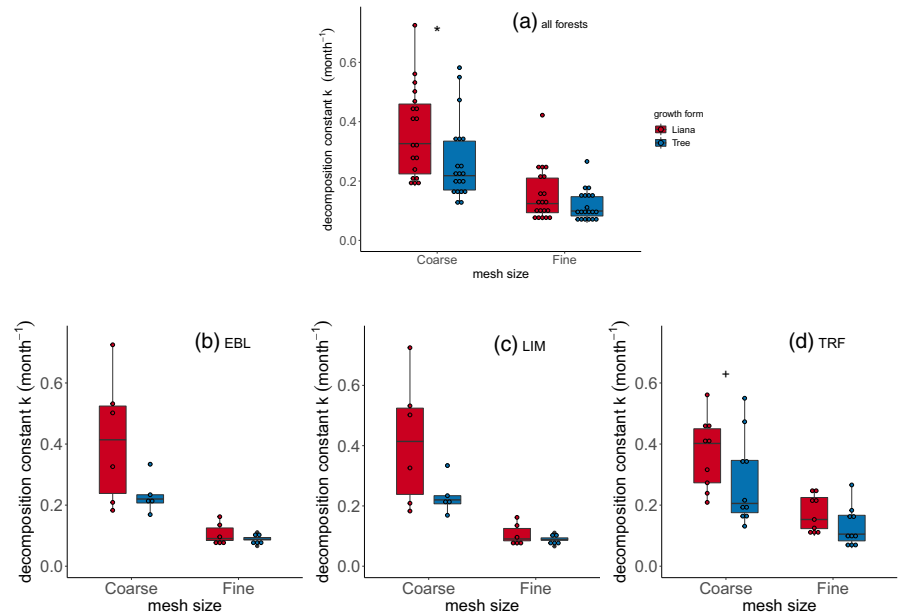


TABLE 1 Mean values of initial litter traits and their differences between forest types and growth forms. Upper letter indicate differences between forest types (tropical rain forest (TRF), a limestone forest (LIM), and evergreen broadleaved forest (EBL))

Litter trait	F-value (df: 3, 37)	Forest type (means)			Growth form (means)			
		EBL	LIM	TRF	p	Liana	Tree	p
N (g/kg)	3.26*	13.4	12.3	15.5		15.6	12.6	*
P (g/kg)	2.44	0.615 ^a	0.802 ^{ab}	1.131 ^b	*	0.888	0.926	
K (g/kg)	6.47**	3.34 ^a	5.02 ^{ab}	8.38 ^b	***	6.32	5.99	
S (g/kg)	1.93	1.47 ^a	1.83 ^{ab}	2.20 ^b	*	1.92	1.89	
Mg (g/kg)	1.03	2.28	2.97	2.98		3.15	2.42	
Ca (g/kg)	4.16*	14.4 ^a	34.0 ^b	22.6 ^{ab}	**	26.4	20.0	
C (g/kg)	2.94*	480 ^a	435 ^b	447 ^b	*	457	450	
Tannin (%)	0.65	5.35	4.14	3.92		4.14	4.59	
Lignin (%)	1.01	17.2	12.1	15.1		15.6	14.2	
SLA (cm ² /g)	7.14***	133	115	143		155	111	***
LDMC (mg/g)	4.46**	472	449	443		418	486	***
Leaf area (mm ²) ⁺	2.75*	4806 ^a	7977 ^b	11550 ^b	*	8823	8782	
Toughness (N) ⁺	3.89*	0.668	0.665	0.523		0.449	0.747	**

Note: F-values are from the additive model, df denotes degrees of freedom, and stars significance of total model.

Significance levels of coefficients: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

⁺Original values given here, in the linear model log transformed values were used.

LDMC (averaged coefficient -0.138 , $p = 0.010$) and positively related to (soluble) tannin, calcium and potassium content (averaged coefficients 0.16 , 0.219 , 0.212 , $p \leq 0.001$).

3.2 | Decomposition differences in growth form and forest types

There were no significant interactions among growth form, forest type or time, on the mass loss of individual species in either mesh size

(Table 2; Figure 4). In single species bags, mass loss over time differed significantly between growth forms in coarse-mesh bags (faster for lianas than trees) but not in fine-mesh bags. Mass loss over time differed significantly among forest types for single species in fine-mesh bags (mass loss was lower in EBL than in LIM and TRF) but not in coarse-mesh bags. In mixed litter bags with fine mesh, the liana mixture decomposed faster than the tree mixture, both did not differ significantly from liana-tree mixtures and mass loss of litter was slightly slower in forest type EBL than in TRF and LIM (Table 2; Figure 4). In coarse-mesh mixed bags, litter of EBL decomposed slower than TRF litter (Appendix S7).

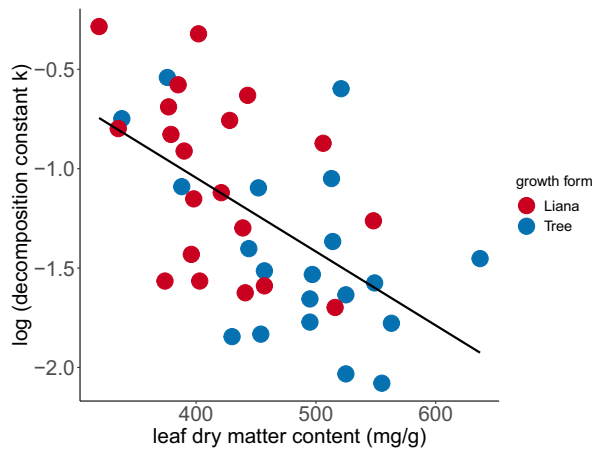


FIGURE 3 In coarse-mesh bags, leaf dry matter content (LDMC) was the best predictor for the decomposition rate (constant k) in a linear model with various litter traits, (see Table S6). Note the log scale for decomposition constant k . LDMC over all species was significantly higher in trees (blue) than in lianas (red) (Table 1).

For the filter paper, the cellulose material in medium mesh size bags, no difference between forest types was detected. Filter paper in EBL had lower mass loss percentage, but this was not significantly different from other forest types ($R^2 = 0.614$, forest type: $F_{2,66} = 0.916$, $SS = 0.277$, $p = 0.1405$), Appendices S8.1 and S8.2.

3.3 | Tests for complementarity using mixed bags

Observed remaining biomass in the mixture bags was not significantly different from the expected biomass for any of the three mixture types (tree only, liana only, tree and liana together) (Figure 5), with the exception of one case: decomposition of mixed tree-only litter in coarse-mesh bags was slower than expected from single bag values ($t = -3.47$, $df = 77$, $p < 0.001$; for the other non-significant tests see Appendix S9). Thus, we did not find any positive non-additive mixture effect. In other words, there was no evidence for a complementarity effect (H3).

TABLE 2 Influence of forest type and growth form on the mass loss of the 20 liana and 20 tree species in single-species litter bags or in mixed litter bags. Summary results of linear mixed-effect models (LMMs) (single bags) of fine- and coarse-mesh bags with species and site as random effect, or results of linear model (LM) (mixed bags). R^2 marginal (R_m^2) represents variation explained by fixed effects in the model. R^2 conditional (R_c^2): Total variation explained by model. Bold values show significant predictors, which confidence interval did not overlap with 0 (random effect LMM), or $p < 0.05$ (fixed effects). df denotes degrees of freedom (details Appendix 2.3)

Bag type	Response	Mesh size					
		Coarse mesh		Fine mesh			
Single-species litter	Random effects	Variance	Standard deviation		Variance	Standard deviation	
	Site (Intercept)						
	Species (Intercept)	0.047	0.217		0.011	0.107	
	Time (Intercept)	0.000	0.004		0.000	0.011	
	Fixed effects	Sum of squares	F-value	p	Sum of squares	F-value	p
	Time	82.477	667.890	<0.001	17.668	561.498	<0.001
	Forest type	0.089	0.359	0.701	0.343	5.447	0.007
	Growth form	0.606	4.906	0.033	0.013	0.404	0.528
		$R_m^2 = 0.423$			$R_m^2 = 0.481$		
		$R_c^2 = 0.565$ (LMM)			$R_c^2 = 0.723$ (LMM)		
Mixed litter	Random effects	Variance	Standard deviation		Variance	Standard deviation	
	Site (Intercept)				0.004	0.062	
	Fixed effects	Sum of squares	F-Value (df:5, 174)	p	Sum of squares	F-value	p
	Time	19.789	241.179	<0.001	7.780	372.269	<0.001
	Forest type	0.510	3.107	0.047	0.125	2.984	0.089
	Mixture	0.234	1.422	0.244	0.166	3.973	0.021
		$R^2 = 0.590$			$R_m^2 = 0.664$		
	$p > 0.001$ (LM)			$R_c^2 = 0.716$ (LMM)			

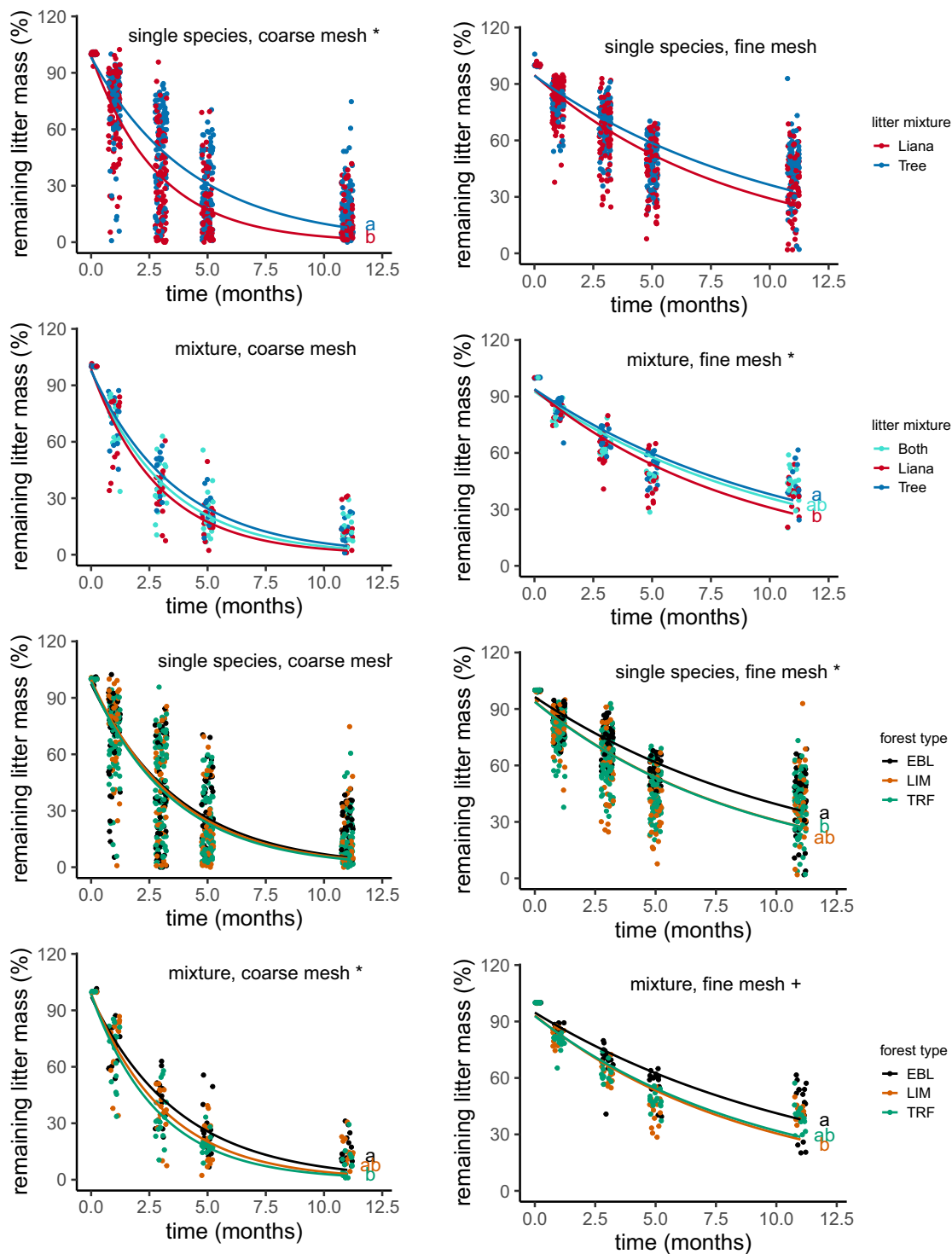


FIGURE 4 Influence of forest type and litter mixtures/growth form on the decomposition of litter in fine- and coarse-mesh bags over time. Bags included litter of single species or litter mixtures of up to nine species. Instead of mass loss we present remaining mass over time for easier visual understanding. Statistical models were done on mass loss over time, significant differences are indicated here with * ($p < 0.05$), + ($p < 0.1$) and small letters, details are given in Table 2.

3.4 | Nutrient release from decomposing litter

The release rates of all nutrients were positively correlated to the decomposition rates of litter mass ($R^2 > 0.6$, $p < 0.001$) (Figure 6). All release rates were lower in fine- than in coarse-mesh bags. The

release rate of calcium was significantly higher in liana than in tree litter ($SS = 3.36$, $F_{1,62} = 4.64$, $p = 0.035$), release rates of Mg were higher in lianas and were almost significant ($SS = 1.27$, $F_{1,69} = 3.95$, $p = 0.051$) (Appendix S10.1). Release rate of potassium (K) was lower in EBL than in other forest types (Appendix S10).

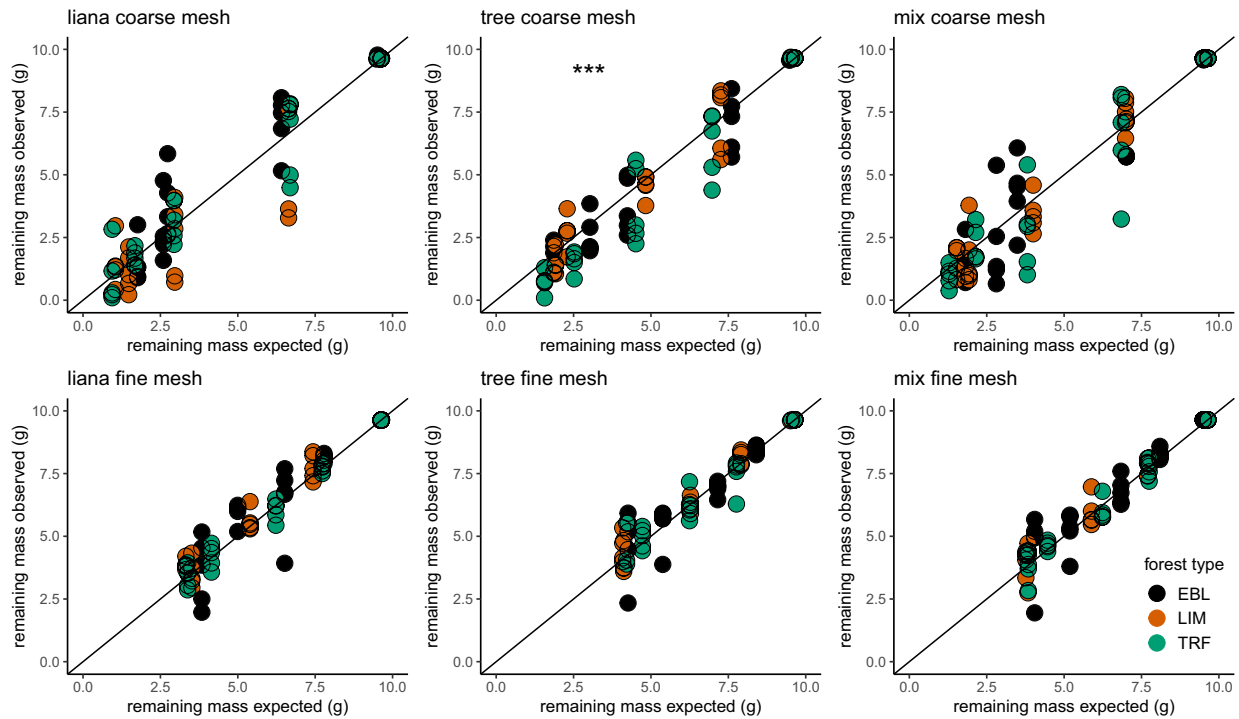


FIGURE 5 Expected and observed biomass remaining in mixed litter bags. Predicted values were calculated from mass remaining in single species bags (mean of 5 locations) per harvest time and forest type and summed up the fractions to match species proportion in the mixed bags. Colours indicate three forest types: Evergreen broadleaved forest (EBL) = brown, limestone forest (LIM) = yellow, tropical rain forest (TRF) = green. *** = *t*-test between predicted and observed biomass significant. The black line represents 1:1 line.

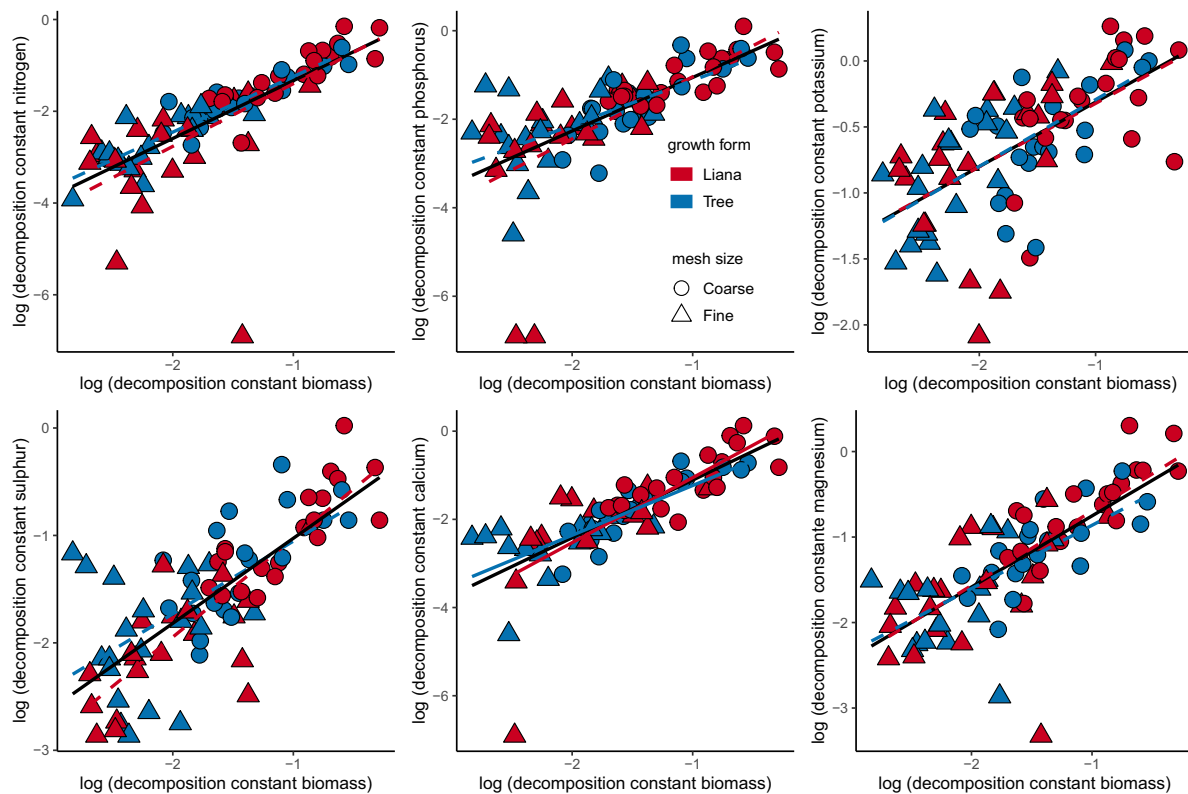


FIGURE 6 Decomposition rates of litter mass in relation to decomposition rate of nutrients in lianas (red) and tree species (blue), in fine-mesh (triangle) and coarse-mesh bags (circles). All correlations were $R^2 > 0.6$, $p < 0.001$. Calcium decayed significantly faster in liana species than tree species ($p < 0.05$). Dashed lines represent non-significant differences and solid lines significant differences in liana and trees in the linear models (Appendix S10).

4 | DISCUSSION

Recent literature reports on the proliferation of lianas in forests (Marshall et al., 2020; Schnitzer & Bongers, 2011) and their effects on ecosystem structure. Given previously established differences in the nutrient contents and other functional traits of living lianas versus trees (Asner & Martin, 2012), it is probable that these differences in ecosystem structure will have knock-on effects on food webs and nutrient biogeochemical cycling. Due to our study design, which employed many representative species in several forest types and which accounted for litter interactions and invertebrate contributions, we were able to do a comprehensive analysis and uncover noticeable trends of the influence of lianas.

4.1 | Liana litter decomposes faster than tree litter

While a few previous studies reported a trend that liana leaf litter decomposes faster than tree litter, our study shows this comprehensively across several tropical forest communities. This trend was found in all our four litter treatment combinations (single or mixed bags in fine or coarse mesh) and was significant in two cases. Even though mesofauna generally accelerated the decomposition process, it did not change the pattern already present in bags excluding mesofauna (i.e. no interaction growth form \times mesh size).

Differences in decomposition are determined by differences in litter traits (Cornwell et al., 2008; Dias et al., 2017). Liana litter had greater nitrogen content and SLA compared to tree litter (beside other physical trait differences) across our three forest types. This agrees with trait data from live leaf material (Asner & Martin, 2012; Medina-Vega et al., 2021; Mello et al., 2020), demonstrating that lianas generally invest less in structural defence than trees, and more in leaf traits that support carbon-efficient light capture and fast growth. Additionally, we found that leaf dry matter content (LDMC) and toughness of trees spanned a wide range of trait values, whereas values for lianas were more restricted to the lower values of these traits, meaning that lianas in general were missing tough dry leaves and on average were decomposed more rapidly (see next section). We covered most of the trait range of woody species in the study region, so we are confident that these trait differences between lianas and trees are not biased by species selection. Our study with native liana-tree assemblages provides additional insights compared to studies on invasive lianas or climbers, which are likely biased towards fast life-history traits typical of invasive species such as high SLA, high nutrient contents and fast growth potential (Van Kleunen et al., 2010). While lianas often already have 'fast' life-history traits *sensu* Reich (2014), the subset of invasive lianas could be expected to have even faster life-history traits. Comparing native trees and invasive lianas might therefore lead to exaggerated trait differences.

4.2 | Influence of traits and nutrients on decomposition

Generally, litter decomposition is related to the leaf economic spectrum, which includes many traits and spans from slow to fast return on resource investment (Cornwell et al., 2008; Santiago, 2009). Our results followed roughly this pattern: tough litter of high dry matter content decomposed slowly, whereas litter with high nutrient content and SLA decomposed faster (see PCA and bivariate analyses). Litter decomposition with mesofauna present was significantly (negatively) related to the physical trait LDMC but not to nutrients, whereas litter decomposition excluding mesofauna was negatively related to LDMC, but also positively related to Ca, K and tannin content. This suggests that mesofauna may prefer more 'juicy', physically less tough litter irrespective of its nutrient content. In a global study, Makkonen et al. (2012) found that water saturation capacity of litter (a trait reciprocal to LDMC) was consistently related to decomposition in the presence of mesofauna. LDMC is also found to be a good predictor for fresh leaf herbivory (Loranger et al., 2013). For micro-organisms, K and Ca played an important role. They are dominant base cations (together with Mg), water soluble and found to be related to mass loss driven by micro-organisms (e.g. Cornelissen & Thompson, 1997). One possible explanation is that mechanical deconstruction (e.g. chewing, grazing) is less important for micro-organisms, so they are more responsive to chemical litter properties than mesofauna. The positive influence of tannin content on decomposition may be due to our extraction method that mainly captured soluble tannins. Condensed tannins are known to slow down decomposition (e.g. Makkonen et al., 2012), whereas soluble tannins degrade quite fast or are quickly leached (in our chemical analysis almost nothing was detected after 3 months).

Lianas tended to release some key nutrients for plant growth (Mg, Ca, N, P) faster to the environment over time than trees, but the trend was only significant for Ca. Calcium is an important component for the invertebrate exoskeleton, and therefore could be a target nutrient for mesofauna decomposers. We identified the mesofauna for all mixed litter bags and found a broad range of decomposer orders (mainly arthropods) in all litter mixture types (trees/liana/both) and forest types and a clear relation of fauna abundance as well as fauna richness to remaining litter mass (detailed data not shown here).

4.3 | Decomposition rate differences across forest types

Differences in decomposition between forest types are influenced by microclimate, soil, traits of community litter and decomposer composition (Paudel et al., 2015), components we could not disentangle in our experimental design since the forest types we studied differ with respect to all of these. We observed differences in decomposition rate across forest types, these effects were additive

and independent of growth form effects, suggesting forest liana litter decomposed consistently rapidly across forest types despite comprising different species identities and trait values. EBL forest litter showed lower decomposition rates than TRF and/or LIM forest and the same pattern was found for neutral filter paper, though not significantly so. Possible explanations are lower nutrient availability in EBL litter, low soil pH and fertility and reduced water availability at ridge positions. Water restriction is unlikely to be the main explanation because our first two harvests were taken during the rainy season, and LIM is also known as a water restricted habitat. Yang and Chen (2009) tested autochthonous unaltered litter mixes from the forest floor in two of our forest types (TRF, EBL) and showed that litter decomposed slower in EBL than in TRF with bags allowing mesofauna access, but the opposite occurred in fine-mesh bags. They inferred that faunal influence was more important in TRF. Despite using only a subset of species in these communities, we can at least partly confirm their results (slow decomposition in EBL). A main segregation of EBL forest from other forests was the very low content of K and Ca in the litter, which, in turn, reduced decomposition in fine-mesh bags (as discussed above). The litter of the selected species in our three forest types can be described as follows: litter in TRF was soft, nutrient rich and large; litter in EBL was small, tough, high in carbon and low in nutrients; and LIM forest litter was in between these but with high calcium contents. This span of high-quality litter (TRF) to low-quality litter (EBL) was also reflected in the speed of litter decomposition. These findings indicate that, when comparing decomposition and associated nutrient release processes of liana versus tree litter, it is important not to detach species from the local environmental context that determines overall decomposition rates, as this is the scale at which the combined litter dynamics of lianas and trees contribute to forest ecosystem functioning.

4.4 | No complementarity effect of lianas on tree litter decomposition

Several studies that focused on single liana species found mixture effects previously, however in our present multispecies study liana litter did not enhance decomposition in tree–liana litter mixtures. This contrasts with Chen et al. (2013) and Leicht-Young et al. (2009) who established that invasive liana species enhanced decomposition in mixed liana and tree litter, whereas Badre et al. (1998) found that ivy (evergreen) (*Hedera helix*) decomposed slower under oak compared to two other deciduous tree species. Scowcroft (1997), on the other hand, detected no acceleration of decomposition of native plants after mixing litter with an invasive liana species. A study testing varying litter mixtures of 3 lianas and 3 tree species in pairs, observed positive effects of lianas, but mainly at early decomposition stages and high liana litter ratios (Li et al., 2013). An obvious difference to the above-mentioned studies is the number of species we used, which also led to an overlap of traits between growth forms and this, in turn, might average out effects. If this pattern persists when even more realistic species numbers (best scenario: many species subsets of realistically

co-occurring litter on the floor) are used in mixtures, then this would suggest that the complementarity effect is driven by the dissimilarity of litter quality. This dissimilarity will likely be harder to observe, the more complex a system gets in terms of species and traits. Our results suggest that decomposition of mixed bags excluding mesofauna was purely additive, and possible effects of difference in food quality, microhabitat structure or potential nutrient transfers by leaching did not affect microbial activity. Litter bags that allowed mesofauna access were exposed to more stochastic processes, for example, visits by termites in one bag but no termite invasion in the neighbouring bag. This might explain the wide data scatter for observed and predicted values in our coarse mixed bags. Another possibility, not tested here, is that our tropical region influences the complementarity effect. A global meta-analysis suggests that mixture effects depend on latitude and change from negative in the temperate to zero in the subtropics, to positive in the tropics (Njoroge et al., 2022). Regardless of the complementarity effect, liana litter has a tendency for faster decomposition, which, in turn, means that changes in relative liana to tree abundance can alter biogeochemical cycling processes in forests.

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AUTHOR'S CONTRIBUTIONS

MR conceived the idea, organized the funding, designed the methodology, collected the data; AN and XY consulted the experimental set up, MR, GGOD, KT and JHCC analysed the data or provided ideas for analysis; all authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

PEER REVIEW

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Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.547d7wmbv> (Roeder, 2022).

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