

Litter decomposition rates across tropical montane and lowland forests are controlled foremost by climate

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Funding information

National Science Foundation, Grant/
Award Number: (DEB)-1146446

Associate Editor: Ferry Slik

Handling Editor: Ann Russell

Abstract

The “hierarchy of factors” hypothesis states that decomposition rates are controlled primarily by climatic, followed by biological and soil variables. Tropical montane forests (TMF) are globally important ecosystems, yet there have been limited efforts to provide a biome-scale characterization of litter decomposition. We designed a common litter decomposition experiment replicated in 23 tropical montane sites across the Americas, Asia, and Africa and combined these results with a previous study of 23 sites in tropical lowland forests (TLF). Specifically, we investigated (1) spatial heterogeneity in decomposition, (2) the relative importance of biological factors that affect leaf and wood decomposition in TMF, and (3) the role of climate in determining leaf litter decomposition rates within and across the TMF and TLF biomes. Litterbags of two mesh sizes containing *Laurus nobilis* leaves or birchwood popsicle sticks were spatially dispersed and incubated in TMF sites, for 3 and 7 months on the soil surface and at 10–15 cm depth. The within-site replication demonstrated spatial variability in mass loss. Within TMF, litter type was the predominant biological factor influencing decomposition (leaves > wood), with mesh and burial effects playing a minor role. When comparing across TMF and TLF, climate was the predominant control over decomposition, but the Yasso07 global model (based on mean annual temperature and precipitation) only modestly predicted decomposition rate. Differences in controlling factors between biomes suggest that TMF, with their high rates of carbon storage, must be explicitly considered when developing theory and models to elucidate carbon cycling rates in the tropics.

Abstract in Spanish is available with online material.

KEYWORDS

Climate, common litter experiment, decomposition coefficient, leaves, litter arthropods, soil depth, wood

1 | INTRODUCTION

Litter decomposition plays a central role in carbon and nutrient cycling, influencing ecosystem productivity, soil physiochemical properties, the structure of soil organism communities, and the dynamics of food webs (Cornejo et al., 1994; Swift et al., 1979; Wieder et al., 2013). Given the global importance of decomposition, there have been a number of studies aimed at elucidating the role of abiotic and biotic controls over rates, both within (Bradford et al., 2014; Cornelissen et al., 2007; Powers et al., 2009) and across biomes (Aerts, 1997; Cornwell et al., 2008; Djukic et al., 2018; García-Palacios et al., 2013; Gholz et al., 2000; González et al., 2008; González & Seastedt, 2001; Wall et al., 2008; Zhang et al., 2008). These studies, to a great extent, support the “hierarchy of factors” hypothesis that states that decomposition rates are controlled primarily by climate, followed by edaphic conditions and biological variables (Lavelle et al., 1993; Tenney & Waksman, 1929). Recent research suggests that this hierarchy is not absolute, however, and challenges the primacy of climate as the overarching control on

decomposition (Bradford et al., 2014; Cornwell et al., 2008), but to date there have been few global comparative efforts that examine climate and other factors across biomes.

In global studies, there are a number of limitations that constrain our understanding of the “hierarchy of factors” hypothesis. First, many studies have measured litter decomposition in one small area and without within-site replication, or if replication exists, these studies differed in the statistical handling of replicates (Bradford et al., 2014, 2016). In both instances, this can potentially obscure underlying spatial variability, with important biological implications. Second, most studies only examine a few climate variables and there is no standardization for which climate variables are measured, limiting cross-study comparisons. Lastly, the geographic or spatial scale of the studies will influence the range of environmental conditions captured, and ultimately the form and strength of the relationship between climatic variables and decomposition, including interactions with other regulating factors. These limitations are sufficiently pervasive that a recent call was issued to rethink regional and global decomposition studies, not only to gain a better understanding of

the process in general, but to provide better support for global carbon modeling efforts (Bradford et al., 2016).

A review of global decomposition studies reveals sparse sampling in tropical montane forests (Djukic et al., 2018). This scarcity is problematic, because tropical mountains are important to a number of processes with regional to global impacts (Milliman et al., 2017; Peters et al., 2019; Rahbek et al., 2019), including water (Messlerli et al., 2004) and carbon cycling (de la Cruz-Amo et al., 2020; Nottingham et al., 2015; Ramos Scharrón et al., 2012; Sherman et al., 2012; Spracklen & Righelato, 2014). It has long been known that tropical montane forests (TMF), compared to their lowland (TLF) counterparts, exhibit very high soil C stocks per unit area, lower decomposition rates, and have higher soil organic matter and C:N ratios in litter and soils (Cavelier, 1996; Vitousek & Sanford, 1986). In addition to a reduction in air and soil temperature with elevation, the slower rates of decomposition in TMF may occur due to increased humidity (e.g., Martin & Fahey, 2014), frequent cloud cover affecting UV radiation, high soil water content, low nitrogen availability, poor litter quality, and shifts in microbial community diversity and composition (Benner et al., 2011; Cavelier, 1996; Dalling et al., 2015; Huang et al., 2020; Looby & Martin, 2020; Marian et al., 2017; Salinas et al., 2011; Vitousek & Sanford, 1986). Yet, not all TMF studies support these general observations because in reality, TMF are diverse in environmental conditions (González et al., 2014; Martin & Fahey, 2014), species associations (Sherman et al., 2005), disturbance regime (Crausbay & Martin, 2016), climate history (Crausbay et al., 2015), and biogeographic settings, making them difficult to define and delineate (Martin & Bellingham, 2016; Tanner et al., 1998).

As part of the Research Coordination Network *CloudNet* (Martin & Bellingham, 2016), we designed a large-scale decomposition experiment in TMF with two goals relating to the “hierarchy of factors” hypothesis. First, we investigate the role of climatic and biological factors in determining litter decomposition rates across a broad range of environmental conditions. Second, we address some of the methodological limitations of decomposition experiments. The large-scale litter decomposition experiment focused on TMF and mirrored to a large extent the work of Powers et al. (2009) in TLF in an effort to combine both studies to characterize variation in decomposition rates within TMF, between TMF and TLF, and among tropical sites. Both the TMF (RCN *CloudNet*) and the TLF (Powers et al., 2009) studies were replicated at 23 sites distributed in the Americas, Asia, Africa, and Oceania. Within-site replication allowed us to address questions related to spatial heterogeneity because of the edaphic conditions where litter lands are variable in tropical forests (Andersen et al., 2010). In addition, site comparisons allowed us to ask questions regarding the role of abiotic and biotic conditions on decomposition. To examine the role of climate on litter decomposition rates in a comprehensive way, we compiled 21 climate variables from a global data base. To examine the contribution of biotic conditions, we followed the work of Powers et al. (2009) and included litter type, faunal access to litter (mesh size), and litter placement (soil depth). Litter type addresses litter quality, mesh size influences access of roots and soil fauna to the litter, and burial depth provides

information about how the soil environment influences decomposition rates.

Based on the TMF (RCN *CloudNet*) and TLF (Powers et al., 2009) studies, we were able to address three questions.

1. How does spatial variability within a given site influence decomposition rates vs. between-site level of variation in TMF? Our expectation was that there would be within-site variability in mass loss, because it is known that nutrient supply, soil moisture, or faunal species composition vary at small spatial scales, all of which can influence decomposition rates (Bradford et al., 2014).
2. What is the relative contribution of biological (litter type, mesh size, and burial depth) and climatic factors to litter decomposition rates within and between TMF and TLF? In the TMF, we compared decomposition rates of leaf vs. wood litterbags, whereas in the TMF vs. TLF, we compared leaf litterbags because the Powers et al. (2009) study did not include wood. In the Powers et al. (2009) TLF experiment, mesh size followed by mean annual precipitation had the largest influence on mass loss. Within TMF, we predicted a reduced role for mesofauna, as macroarthropods are less abundant at higher elevations (Maraun et al., 2008), and expected that climate and the soil environment would have greater influence on decomposition rates.
3. How do modeled global decomposition rates based on climate compare to observed rates measured in TMF and TLF? If biotic factors play a smaller role in TMF, we expected that climate-based global decomposition models would better fit observed decay rates in TMF than in TLF. The global model chosen was the Yasso07 model because in its simplest form it makes predictions on litter decomposition using only the well-studied climate variables: mean annual temperature (MAT) and precipitation (MAP) (Hernández et al., 2017; Tuomi et al., 2009). If Yasso07 does not predict decomposition well in our study sites with only these two variables, then this would support the hypothesis that additional climate variables or other biological and edaphic variables are important predictors at a global scale.

2 | METHODS

2.1 | Study sites

We conducted a large-scale field experiment across 23 TMF sites located in 14 countries in the Americas, Asia, Africa, and several islands in the Caribbean and the Pacific (Figure 1a; Table S1). These sites spanned a wide range of elevations (600–3202 m), mean annual temperatures (MAT, 3.0–23.0°C), mean annual precipitations (MAP, 335–5010 mm), and dry season length (0–6 months) (Table S1). Two sites, namely Kinabalu-ultramafic (KIU) and Kinabalu-sedimentary (KIS), deserve a special mention, because they are located very close to each other and at almost same elevation (Table S1) but they are underlain by different parent material that ultimately translate into

vegetation and soil differences (Aiba & Kitayama, 1999; Kitayama & Aiba, 2002; Kitayama et al., 2000). We augmented our study by including a previously published TLF dataset (Powers et al., 2009) that comprised of 23 tropical sites in 14 countries in Asia, Latin America, and Oceania, spanning a wide range of elevations (5–1200 m), mean annual temperatures (MAT, 18.5–26.5°C), mean annual precipitations (MAP, 760–5797 mm), and dry season length (0–10 months) (Figure 1a; Table S1). We excluded two sites from the TLF data set for our analysis: San Cayetano, Colombia (COL), because at 2800 m it is a TMF site, and Barito Ulu, Kalimantan (ULU), due to missing temperature and belowground decomposition data (Powers et al., 2009).

To examine climatic control over decomposition, we used three homogenized global datasets (1-km resolution) to characterize each site based on 21 variables (Table S2). WorldClim (Hijmans et al., 2005; <https://www.worldclim.org/data/v1.4/worldclim14.html>) provided 19 bioclimatic variables describing annual trends, seasonality, and extreme conditions and CGIAR CSI provided potential evapotranspiration (Zomer et al., 2007, 2008; <https://cgiarcsi.community/data/global-aridity-and-pet-database/>). Due to the

importance of clouds in TMF, we used mean annual cloud frequency (MODCF mean annual; % cloudy days) derived from MODIS (Wilson & Jetz, 2016; <http://www.earthenv.org/cloud>). In some instances, total annual precipitation from field sites did not match WorldClim's values (Table S1). This led us to examine Chelsa data (<https://chelsa-a-climate.org/>) and rerun analysis (see below). Because the results were similar and the TLF study had used WorldClim 1, we decided to continue to use WorldClim data.

2.2 | Experimental design

The *CloudNet* study followed the general design of the Powers et al. (2009) study to allow a combined analysis, with two exceptions: litter type and sampling intervals. Following the TLF study, we used bay leaves, but instead of using raffia leaves we used wood as a second substrate (Powers et al., 2009). Wood has been understudied (but see Pietsch et al., 2019) and in many tropical forests can be found as fine twigs on the forest floor and as coarse woody debris (Yang et al., 2021). In contrast to Powers et al. (2009) that incubated

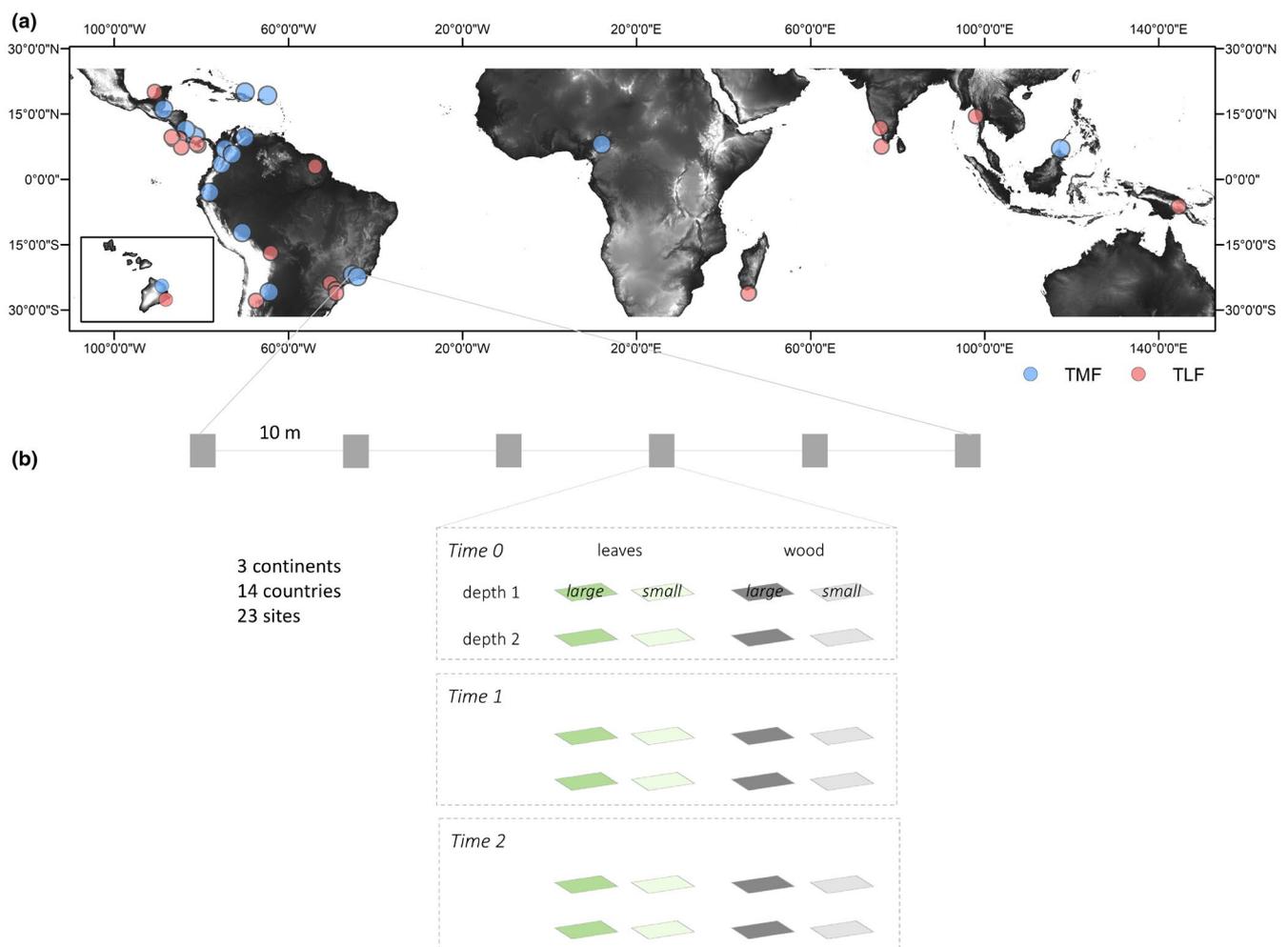


FIGURE 1 (a) Map showing TMF (RCN CloudNet) and TLF (Powers et al., 2009) sites. Some sites participated in both the TMF and TLF studies, thus overlap in this map. (b) Experimental setup for each of the TMF sites. At each site, six sampling stations were set up along a 50-m transect. At each station, there were 16 litterbags, with 2 litter types × 2 depths × 2 mesh sizes × 2 time points for bag collection

the litterbags for 1, 3, 5, 7, and 9 months, we only incubated the bags for 3 and 7 months, times selected based on the observed decomposition rate for bay leaves in the Powers et al. (2009) dataset. Bay leaf (*Laurus nobilis*) (Frontier Co-op, www.frontiercoop.com) was the common leaf material in the TMF and TLF studies, and white birch (*Betula papyrifera*) wooden popsicle sticks (1 cm × 11.5 cm; Ben Franklin) the common wood material for the TMF sites. To determine initial mass of the litter types for the litterbags, the bay leaves (with absent or very short petioles) were oven-dried at 70°C for at least 48 h and subsequently weighed and placed into mesh litter bags (Figure 1b); the wood was initially dried at 120°C to release volatiles following the standardizing wood pre-treatment protocol (Cheesman et al., 2018) and then dried in the oven at 70°C for 48 h.

Mesh bags (10 × 15 cm) contained either 1.00 ± 0.01 g (mean ± 1 SD) dry mass of whole bay leaves or one popsicle stick (1.34 ± 0.12 g). Two nylon mesh sizes were used (52- μ m mesh and 1920- μ m mesh; Component Supply Company) to selectively exclude mesofauna (defined as 100 μ m to 2 mm) and fine roots. Litterbags were assembled in Hawai'i and mailed to all participants.

The experiment started at each of the 23 TMF sites between May and Dec 2017 and concluded between Dec 2017 and July 2018 (Table S1). At each site, we incorporated within-site replication by having litterbags deployed along a 50-m transect, subdivided into six stations 10 m apart (Figure 1b). At each station, we deployed 16 bags: 2 litter types, 2 burial depths, 2 mesh size treatments, and 2 collection times for a total of 2208 bags (Figure 1b). The burial depths were on top of the litter layer at the soil surface and 10–15 cm depth. We used a knife or machete to cut into the soil at a 45° angle, inserted the bag, and filled the hole. At each station, bags were anchored to a central stake using fishing line to facilitate retrieval. The initial bag placement occurred right before or at the beginning of the wet season (May–Dec 2017) for all sites with the exception of the Ngel Nyaki site, where the start of the experiment occurred in Nov 2017 at the beginning of the November–March dry season (Table 1; Chapman & Chapman, 2001). After retrieval at each harvesting time, the bags were cut open, the contents removed, and gently washed with tap water. Any soil or root material attached to the litter type was removed using tweezers. Samples were dried at 70°C and weighed to ± 0.01 g.

To compare decomposition rates between tropical montane and lowland forest, we subsampled the TLF dataset to include only bay leaves and match the 3- and 7-month sampling times. In the TMF dataset, the 3- and 7-month harvests occurred after 95 ± 8 days (mean ± 1 SD) and 226 ± 23 days, respectively; in TLF, those harvest times were 106 ± 22 days and 218 ± 15 days. This resulted in a subset of 483 bags (3 bags × 2 burial depths × 2 mesh treatments × 2 times) in the TLF dataset.

2.3 | Data analysis

We conducted extensive exploratory data analyses to clean the dataset, identify outliers and investigate the source of their distinctiveness, and examine collinearity among variables to be used in the main

analyses (Zuur & Ieno, 2016). We received information for 2200 out of the 2208 TMF bags that were deployed out in the field. After careful examination of the data, we retained 2162 for the analysis. For quality control, we subtracted the final weights of the litterbags from the initial weights with the expectation that differences should be positive; if the reported final weight of the litterbag was $\geq 10\%$ greater than the initial weight, the point was discarded. In some instances, we contacted the relevant co-author to clarify problematic data points that could not be resolved by the lead authors (e.g., mislabeled samples). Thus, 11 bags were discarded due to larger final versus original weights, and another 27 were discarded due to other reasons (e.g., lost, ruptured, unearthed bags). We used R version 4.0.3 (2020–10–10) to perform all subsequent analyses (R Core Team, 2018).

Climatic variables often exhibit a high degree of collinearity (Dormann et al., 2013; Veronika et al., 2013). We first ran a principal component analysis using the package *FactoMineR* (Lê et al., 2008) on the 21 climatic variables to explore which variables were highly correlated. Then, we used the *vif* function in the *car* package (Fox & Weisberg, 2019) to run two sets of variance inflation factor (VIF) analyses (TMF study and TMF & TLF studies combined) using a threshold >10 (Dormann et al., 2013), through each iteration variables with a VIF >10 were eliminated to produce a reduced model for further analyses. The VIF analyses eliminated mean annual temperature (MAT; bio_1) and total annual precipitation (MAP; bio_12), two variables that have been shown to predict global rates of decomposition (e.g., Gholz et al., 2000). Thus, we decided to run a second set of VIF analysis, retaining MAT and MAP through the various iterations.

We performed three broad sets of analyses to examine mass loss of leaves and wood in the TMF dataset, decay rates (*k* values) of leaves in the TMF and TLF datasets, and finally observed TMF and TLF *k* values with those predicted by the Yasso07 global decomposition model. The first analysis examined the relationship between proportion of mass remaining as the dependent variable and litter type, burial depth, mesh size, and study as fixed, independent variables. Site and station were included as random variables (see below). Because our response variable is a continuous proportion bounded by (0–1), we followed the recommendation of Douma and Weedon (2019) and Aguilar-Cruz et al. (2020) and used a beta errors general linear mixed effects model (GLMM). The models were fitted using maximum likelihood estimation via 'TMB' (Template Model Builder) using the *glmmTMB* function with family set to *beta_family* in the *glmmTMB* v1.1.2.2 R package (Brooks et al., 2017; Magnusson et al., 2017). In an effort to address the effects of spatial variability within sites on decomposition studies (i.e., Bradford et al., 2014, 2016), we ran the GLMMs both on the within-site (non-aggregated) and site averages (aggregated data). For the non-aggregated data, the six stations were considered nested within the transect at each site, and site and station were included as random effects (proportion mass remaining \sim litter × mesh × depth + 1|Site/Station). For the aggregated data, we averaged the values of the six stations and site was included as a random effect (proportion of mass lost \sim litter × depth × mesh + 1|Site). We also evaluated proportion mass remaining by averaging across the 3- and 7-month intervals, or only the final 7-month interval. In order to specifically contrast the

TABLE 1 Results of GLMM analysis on fraction of litter mass remaining as a response variable for the TMF litterbag experiment. Experimental variables were litter type (bay leaf or popsicle stick), depth (surface or buried), and mesh size (small and large). Analysis presented for both unaggregated data (all stations within sites represented) and aggregated data (site means). Mass remaining averaged between 3- and 7-month litter pickups, and only the final 7-month pickup is provided here for comparison. Significance is * $p < .05$, ** $< .01$, *** $< .001$, and $.05 < p < .10$ in italics

Source	Unaggregated data (replication within sites)									
	Average mass loss					7 month mass loss				
	Estimate	SE	z value	p value	Signif.	Estimate	SE	z value	p value	Signif.
Intercept	0.01	0.09	0.15	.88		-3.99	0.12	-3.36	7.67E-04	**
Litter Type	1.29	0.06	21.04	<2E-16	***	1.27	0.07	17.69		***
Depth	0.01	0.06	0.24	.81		-0.02	0.07	-0.33	.74438	
Mesh	0.15	0.06	2.61	.01	**	0.18	0.07	2.71	.01	**
Litter Type * Depth	0.22	0.09	2.50	.01	*	0.25	0.10	2.38	1.71E-02	*
Litter Type * Mesh	-0.21	0.09	2.50	.01	*	-0.32	0.10	-3.16	1.57E-03	**
Depth * Mesh	-0.15	0.08	-1.91	.06		-0.09	0.10	-0.91	.36	
Litter Type * Depth * Mesh	0.15	0.12	1.22	.22		0.21	0.14	1.43	.15	
<i>Random Effects</i>										
	Variance	SD				Variance	SD			
Station (site)	1.9E-10	1.4E-05				0.00117	0.1057			
Site	0.1321	0.3634				0.25793	0.5079			
	$n = 2162$; AIC = -2570.0					$n = 1088$; AIC = -1369.2				

two sites at Kinabalu, Malaysia underlain by different soil types, we ran a separate analysis but here mesh and burial depth were treated as fixed effects and station as a random effect.

The second set of analyses was aimed at establishing relationships between decomposition rates (k), climatic (21 variables), and biotic (litter type, mesh, depth) variables for the TMF and TLF individually and then combined (leaves) (Table S2). Analysis of the original TLF dataset containing five harvest periods indicated that the leaf data were best fit using a first-order exponential decay function (Powers et al., 2009). We estimated the coefficient k (units year⁻¹) (Wieder & Lang, 1982) for each of the TMF and TLF sites based on the initial, 3- and 7-month harvests using both the *nls* function (negative exponential model) in the stats package and the *litterFitter* package (Cornwell & Weedon, 2014; Cornwell et al., 2020). We then proceeded to model the relationship between k and the already reduced set of climatic variables using the *dredge* function in the MUMIn package (Bartoń, 2020) and chose the models with the lowest AIC to run stepwise multiple regressions using the *stepAIC* function in MASS (Venables & Ripley, 2002). We compared the models with and without forcing the retention of MAT and MAP and found that the former had lower or equal AIC values. Thus, we only present the models without forcing. Finally, we used generalized linear models in which we included the biotic and reduced set of climatic variables to explain variation in decomposition using the *glm* function with the *stepAIC* function. We compared those models with the lowest AIC values to ones that included both climatic and biotic variables to see how AIC changed. We also examined the relationship between leaf and wood k values in TMF using a linear model on log-transformed data.

The last set of analyses involved the prediction of litter decay rates, k , from the Yasso07 model (Steidinger et al., 2019; Tuomi et al., 2009) and comparisons with the observed values for the TMF and TLF sites. The Yasso07 model describes a climate dependence of mass loss based on temperature and precipitation. The full model also quantifies litter chemistry into fractions soluble in ethanol, water, acid, or insoluble (Tuomi et al., 2009), but we did not have those data. Instead, we calculated relative mass loss rather than absolute loss using modifications in Steidinger et al. (2019) that eliminates the litter quality term α . After dividing out α , k is related to temperature and precipitation at the global scale according to the following equation:

$$k = \exp(\beta_1 T_i + \beta_2 T_i^2) (1 - \exp[\gamma P_i]), \quad (1)$$

where T and P are MAT and MAP. The values for the parameters are $\beta_1 = 0.076$; $\beta_2 = -0.00089$; $\gamma = -1.27$ (Tuomi et al., 2009, 2011). Predicted and observed k values were compared using linear models to determine slopes, intercepts, and proportion of variance explained.

3 | RESULTS

3.1 | Spatial heterogeneity and the fraction of mass lost in TMF and TLF

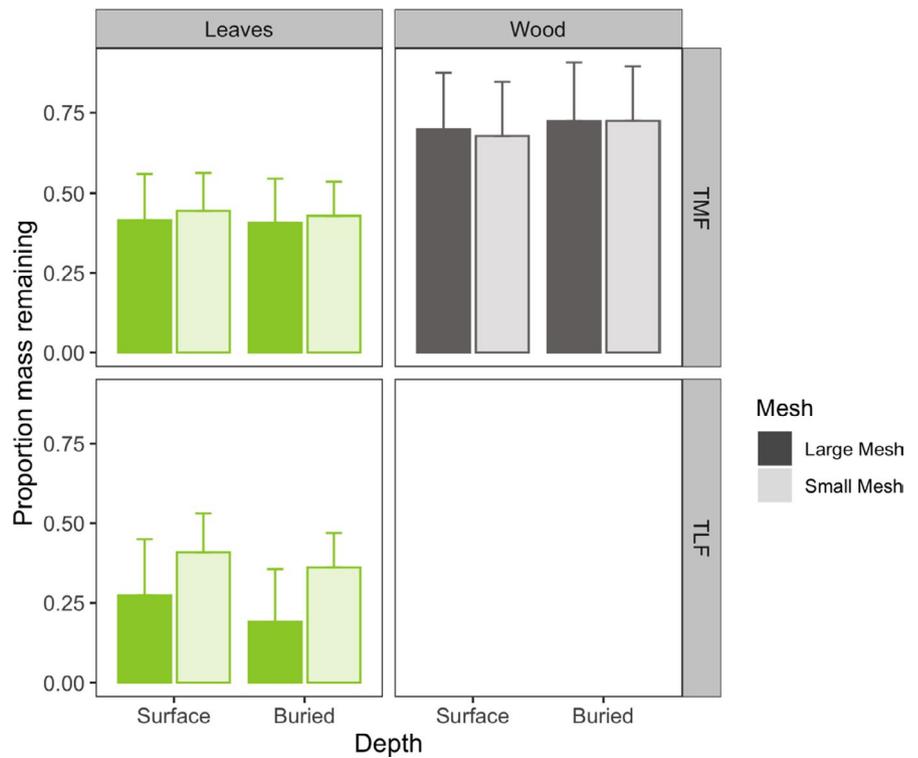
Spatial heterogeneity influenced the fraction of mass lost in both forest types. A greater number of factors were significant at the unaggregated than the aggregated levels (Tables 1 and 2). As an

Aggregated data (site means)									
Average mass loss					7 month mass loss				
Estimate	SE	z value	p value	Signif.	Estimate	SE	z value	p value	Signif.
0.01	0.10	0.13	.90		-0.40	0.12	-3.27	1.08E-03	**
1.32	0.12	11.15	<2E-16	***	1.28	0.10	12.44	<2E-16	***
0.01	0.11	0.08	.94		0.02	0.10	0.17	.87	
0.11	0.11	0.99	.33		0.15	0.10	1.47	.14	
0.09	0.17	0.52	.60		0.11	0.15	0.74	.46	
-2.35	0.17	-1.42	.16		-0.27	0.14	-1.84	.07	
-0.09	0.15	-0.61	.54		-0.08	0.14	-0.56	.58	
0.24	0.24	1.03	.30		0.18	0.21	0.89	.37	

Variance	SD	Variance	SD
0.1117	0.3342	0.223	0.4722

n = 366; AIC = -522.9

FIGURE 2 Fraction of mass remaining (mean and standard deviation) after 7 months at the TMF (top row) and TLF sites (bottom row), shown for each factor combination. Litter type was either bay leaves (green bars, left column) or wooden popsicle sticks (gray bars, right column). Soil fauna access was either large mesh (darker filled bars) or small mesh (larger filled bars). The x-axis shows the soil depth factor (surface vs. buried). Each bar represents a mean of the individual stations where litterbags were placed, to encompass spatial variation within a site. Note that the TLF experiment did not include wood



example, in the TMF, mesh was significant at the 7-month time point for unaggregated data, with small mesh bags losing slightly more mass, but that was not significant when replicates within sites were aggregated (Table 1; Figure 2). In addition, there were a number of

interactions in the unaggregated analysis that are significant, but only the main effect of litter type was significant in the aggregated analysis (Table 1). In the analysis that included both forest types, more of the biological factors were significant at the unaggregated

TABLE 2 Results of GLMM analysis on fraction of litter mass remaining as a response variable in both biomes. Experimental variables were study (TMF or TLF), depth (surface or buried), and mesh size (small and large). Analysis presented for both unaggregated data (all stations within sites represented) and aggregated data (site means). Mass remaining averaged between 3- and 7-month litter pickups, and only the final 7-month pickup is provided here for comparison. Significance is * $p < .05$, ** $< .01$, *** $< .001$, and $.05 < p < .10$ in italics.

Source	Unaggregated data (replication within sites)									
	Average mass loss					7 month mass loss				
	Estimate	SE	z value	p value	Signif.	Estimate	SE	z value	p value	Signif.
Intercept	0.02	0.09	0.18	.86		-0.38	0.12	-3.12	1.79E-03	***
Study (TMF vs. TLF)	-0.81	0.14	-5.65	1.59E-08	***	-0.82	0.19	-4.41	1.02E-05	**
Mesh	0.14	0.05	2.56	.01	*	0.18	0.06	2.81	.00495	***
Depth	3.69E-03	0.05	0.07	.94		-0.18	0.07	-0.28	.78	
Study * Mesh	0.42	0.10	4.32	1.53E-05	***	-0.53	0.13	-4.06	4.89E-05	***
Study * Depth	-0.41	0.10	-4.06	4.83E-05	***	0.52	0.12	4.24	2.20E-05	***
Mesh * Depth	-0.13	0.08	-1.18	.09		-0.09	0.09	-0.99	.32	
Study * Mesh * Depth	0.37	0.14	2.59	.01	**	0.48	0.18	2.64	.01	**
<i>Random Effects</i>										
	Variance	SD				Variance	SD			
Station (site)	1.48E-10	1.22E-05				0.01068	0.1034			
Site	0.1734	0.1416				0.29368	0.5419			
	$n = 1564$; AIC = -1506.8					$n = 786$; AIC = -1017.3				

TABLE 3 Final models with the lowest AIC values. The three models predict the decomposition coefficient, k , as the response variable, for leaves only in TMF, wood only in the TMF, and for bay leaves in both TMF and TLF biomes. For comparison, the AIC values of including the biological variables of mesh size and depth are also included. Significance is * $p < .05$, ** $< .01$, *** $< .001$, and $.05 < p < .10$ in italics

Source	TMF leaves					TMF wood	
	Estimate	SE	t value	p value	Signif.	Estimate	SE
Intercept	0.539	0.189	2.857	.010	*	0.782	0.464
Bio2: Mean Diurnal Range (Mean of monthly (max temp - min temp))						0.068	0.026
Bio3: Isothermality (BIO2/BIO7) ($\times 100$)							
Bio8: Mean Temperature of Wettest Quarter	0.104	0.024	4.227	4.57E-04	***		
Bio9: Mean Temperature of Driest Quarter	-0.057	0.032	-1.763	.094			
Bio19: Precipitation of Coldest Quarter	6.40E-04	2.61E-04	2.453	.024	*	6.68E-04	1.59E-04
MODCF: MODIS Satellite-derived Cloud Frequency						-0.014	0.004
	AIC = -68.327					AIC = -70.737	
	AIC including mesh and depth = 41.64					AIC including mesh and depth = 8.31	

level than at the aggregated level (Table 2). These significance patterns suggest that the greater spatial coverage afforded by dispersing litterbags to achieve within-site replication better captures variation in decomposition rates.

In TMF, litter type had the strongest influence on mass loss, whereas mesh size had only a minor influence, and depth had no significant influence (Table 1; Figure 2). Bay leaves consistently had greater mass loss than the wood popsicle sticks, losing on average 39.74 ± 0.50 and 58.76 ± 0.64 percent of initial mass (mean \pm SE) after 3 and 7 months, respectively, while wood 13.67 ± 0.50 and

31.56 ± 0.91 after 3 and 7 months. After 7 months, there was 49.45 ± 19.2 percent of initial mass (mean \pm SE) loss at the surface and 49.78 ± 1.31 for buried bags. When comparing mass loss of leaves across studies, mass loss was faster in TLF than the TMF. On average, bay leaves in the TMF lost 58.76 ± 0.63 percent of initial mass, compared to 69.21 ± 1.07 in TLF after 7 months. The main effects of mesh and depth were not significant when data were aggregated together, but were significant when interacting with forest type, suggesting different controls over decomposition in the two tropical forest biomes (Table 2; Figure 2).

Aggregated data (site means)									
Average mass loss					7 month mass loss				
Estimate	SE	z value	p value	Signif.	Estimate	SE	z value	p value	Signif.
0.02	0.01	0.18	.86		-0.38	0.12	-3.08	2.09E-03	**
-0.74	0.15	-5.00	5.71E-07	***	-0.75	0.19	-4.17	3.01E-05	***
0.10	0.11	0.96	.34		0.14	0.13	1.26	.21	
3.39E-03	0.11	0.03	.97		0.02	0.11	0.15	.88	
0.43	0.16	2.74	.01	**	0.56	0.17	3.23	1.23E-03	**
-0.36	0.16	-2.21	.03	*	-0.53	0.18	-2.87	4.07E-03	**
-0.09	0.15	-0.56	.57		-0.08	0.16	-0.51	.61	
0.30	0.23	1.31	.19		0.42	0.25	1.69	.09	
Variance	SD				Variance	SD			
0.1045	0.3246				0.1946	0.4412			
n = 345; AIC = -403.4				n = 173; AIC = -273.7					

			TMF and TLF leaves				
t value	p value	Signif.	Estimate	SE	t value	p value	Signif.
1.684	.109		-2.656	0.905	-2.934	5.59E-03	**
2.603	.017	*					
			0.031	0.010	3.089	3.70E-03	**
			0.231	0.042	5.510	2.48E-06	***
			-0.144	0.039	-3.726	6.16E-04	***
4.192	4.94E-04	***	0.001	2.77E-04	3.865	4.10E-04	***
-3.261	.004	**					
AIC = -65.364							
AIC including mesh and depth = 451.68							

3.2 | Environmental correlates of decay rates

Decomposition coefficients (k) varied substantially among sites and overlapped between the biomes (Figure 3). Averaged over all mesh and burial treatments in TMF, k of bay leaves varied between 1.12 year^{-1} ($t_{1/2} = 0.89 \text{ year}$) and 2.52 year^{-1} ($t_{1/2} = 0.40 \text{ year}$) whereas k of wood between 0.18 year^{-1} ($t_{1/2} = 5.55 \text{ year}$) and 1.45 year^{-1} ($t_{1/2} = 0.69 \text{ year}$), (Table S2). In TLF, decomposition rates of bay leaves ranged between 1.28 year^{-1} ($t_{1/2} = 0.78 \text{ year}$) and 4.23 year^{-1} ($t_{1/2} = 0.24 \text{ year}$) (Table S2). We observed a strong

relationship between leaf and wood decomposition rates in TMF (linear model; $\log k_{\text{wood}} = 1.62 \times \log k_{\text{leaves}} - 0.61$; $R^2 = .54$, $F_{1,21} = 24.77$, $p < .0001$).

Climate variables had greater importance in GLM models predicting k values than the biotic variables as suggested by the lower AIC values resulting from the elimination of mesh and depth (Table 3). Importantly, significant predictor variables differed for leaf and wood decomposition in the TMF and for the analysis including both biomes. In the TMF, the best model to predict k in leaves included biol_8 (mean temperature in wettest quarter), bio_9 (mean

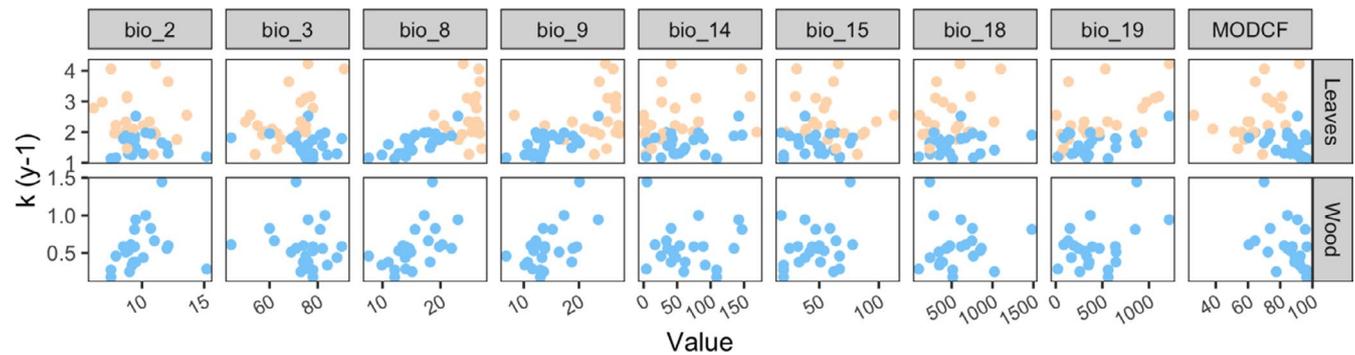


FIGURE 3 Scatterplots for the climate variables that turned up as potentially important in analysis without forcing of any climate variables. Decomposition rate constants (k) are shown in TLF forest (beige dots) and TMF (blue dots). Climate variables are bio_2 (mean annual temperature range), bio_3 (isothermality), bio_8 (mean temperature in wettest quarter), bio_9 (mean temperature in driest quarter), bio_14 (precipitation of driest month), bio_15 [precipitation seasonality (coefficient of variation)], bio_18 (precipitation of warmest quarter), bio_19 (precipitation in coldest quarter), and MODCF (MODIS satellite-derived cloud frequency). For significant variables in the models, see Table 3

temperature in driest quarter), and bio_19 (precipitation in coldest quarter). For wood, the best predictors were BIO2 (mean annual temperature range) and MODCF (MODIS satellite-derived cloud frequency) (Table 3). Across biomes, the best model to predict k in leaves included BIO3 (isothermality), bio_8, bio_9, and bio_19 (Table 3). The climatic variables included in these models are not the typical MAT and MAP, but suggest interactions between temperature and precipitation.

3.3 | Global model comparison

When both biomes were considered, observed leaf k values were positively related to the Yasso07 global decomposition model predictions ($F_{1,42} = 27.51$, $R^2 = .396$, $p < .0001$). This relationship was much stronger for the TMF ($F_{1,21} = 26.19$, $R^2 = .555$, $p < .0001$) than for the TLF sites ($F_{1,19} = 0.63$, $R^2 = .03$, $p = .436$) (Figure 4).

4 | DISCUSSION

A common litter experiment across sites allows for the teasing apart of the “hierarchy of factors” in litter decomposition (Lavelle et al., 1993; Tenney & Waksman, 1929). In understudied tropical montane sites, this study showed the importance of spatial variability in litterbag studies, given that there were some significant differences between the aggregated and unaggregated data sets. It was also determined that litter type (leaves vs. wood) and climate were extremely important, greatly outweighing effects of litter fauna or burial depth.

When comparing across biomes, climate was the factor that most influenced k values, yet GLM models and comparison to a global model, showed that the two most commonly measured climate variables, MAT and MAP, were not the best predictors. In sum, the results suggest that litter decomposition in TMF and TLF experience enough differences in the relative importance of controlling

factors that they should not be lumped together as generic tropical forest.

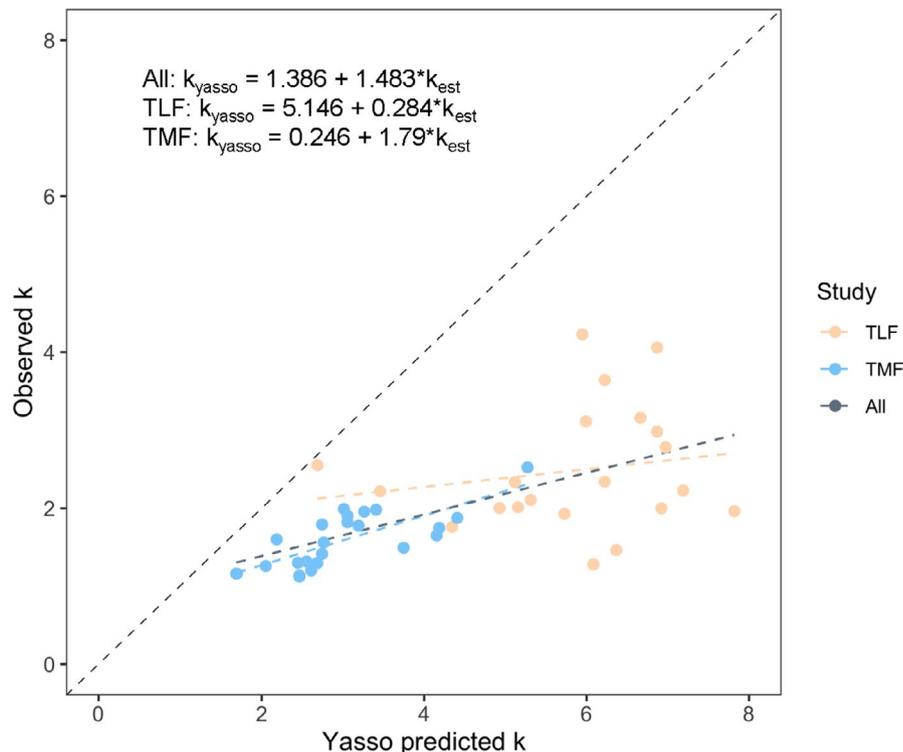
4.1 | Spatial heterogeneity in decomposition studies

A sampling design with within-site environmental heterogeneity is not often seen in other decomposition studies, but tropical forests can have variation in microtopography, microclimate, and edaphic conditions that could influence litter decomposition. The TMF design had higher within-site spatial spread (50-m long transects) and replication ($n = 6$ locations per site) than the TLF study (13-m transects; Powers et al., 2009) and replication (2 locations per site). When the within-site unaggregated data were considered, we found a significant mesh effect in TMF (Table 1), and we noted significant interactions in TMF-TLF comparison (Table 2). These results conform with Bradford et al. (2016), who demonstrated within-site variability can be high in their reanalysis of data from Prescott (2010), and with a reciprocal transplant field study that showed the slope position where the litterbags are placed influences decomposition (Werner & Homeier, 2015). Patterns of variability with our TMF unaggregated data suggest that environmental heterogeneity in bag placement may help reveal the role of other factors on decomposition rates. We therefore agree with the recommendations that future decomposition studies incorporate high within-site replication in their design and collect environmental measurements at the scale of individual litterbags (Bradford et al., 2016).

4.2 | Biological controls over decomposition

The leaf k coefficients from our study of TMF and TLF (1.12–4.23 range) match well to an elevation gradient study with common litter substrates from lowland to montane forest in Costa Rica (0.41–3.23 range), although they used different leaf species than this study

FIGURE 4 The relationship among decomposition rate (k coefficients) for bay leaf litter, estimated in this study for TMF and TLF sites and the Yasso7 global model. All points are below the 1:1 line. Equations and regression lines are shown for both biomes together and for TLF and TMF separately. The TLF regression was not significant (see text)



(Esquivel et al., 2019). The most significant of biological factors in our TMF study was litter type—leaves decomposed faster than wood. This result is not surprising, given known differences in C:N values and other litter quality measurements (Jackson et al., 2013). Wood has been shown to decompose more slowly than other plant parts (Pietsch et al., 2014, 2019), but in general wood decomposition has been poorly studied, especially in the tropics (but see Seibold et al., 2021). Estimated rates of wood decomposition can be highly variable due to a lack of standardization across studies (e.g., different bole sizes, wood densities, etc.) (Cheesman et al., 2018). The use of common wood material in our study addresses the standardization issue, but the popsicle sticks are more likely to represent fine wood such as small twigs, not coarse woody debris or bark. Our study found a relatively strong positive correlation ($R^2 = .54$) between leaf and wood decay. In a global meta-analysis, this relationship was much weaker ($R^2 = .22$) and was not significant when angiosperms and gymnosperms were considered separately (Pietsch et al., 2014); however, they used multiple species and our study used a common litter. Notably, one of our sites (Ngel Nyaki, Nigeria) had leaf and wood decomposition rates that were similar, but the reasons are not clear; no macro-arthropod damage was seen in the litterbags and there was no difference in mass remaining (28%) between large and small mesh bags.

Mesh size exerted a significant influence on decomposition in the TLF, but only a small one in TMF. In the TLF study, the small mesh bags had approximately half the rate of decomposition compared to the large mesh (Powers et al., 2009). Mesh size can influence access of fine roots, which can penetrate the litterbags. Fine roots can actively forage for nutrients in the litter layer (Cuevas & Medina, 1988), which could indirectly influence leaf decomposition. Furthermore,

soil fauna influence litter decomposition in a variety of forests, both as decomposers and as predators of decomposers (Gonzalez et al., 2001; Heneghan et al., 1999; McGlynn & Poirson, 2012; Meyer et al., 2011; Paudel et al., 2015; Powers et al., 2009). Along one elevation gradient in Ecuador, larger arthropod decomposers were less common in TMF (Maraun et al., 2008) and decreased in abundance (Illig et al., 2008) and species richness (Maraun & Scheu, 2000) with altitude. Similarly, in a study on Sarawak, there was a 17.8-fold difference in macrofaunal abundance from the bottom of an elevation transect at 130 m and the mountain summit at 2376 m (Collins, 1980). However, there are exceptions to this elevation pattern, such as the giant earthworms in Puerto Rico (Gonzalez et al., 2007). There are not many studies on mesofauna, but in Ethiopia there was a decrease in abundance with elevation, along an 1800–3200 m gradient (Striganova & Rybalov, 2008). Without as many of the larger fauna, the TMF is likely to be dominated by soil microfauna that may primarily influence decomposition not through the physical breakdown of the litter, but by feeding on fungi and other litter colonizing organisms (Illig et al., 2008; Schneider et al., 2004). However, when microarthropods were excluded in a study using very fine mesh sizes in two TMF elevations in Ecuador, their role in decomposition was small in comparison with microorganisms (Illig et al., 2008). In our study, we used two mesh sizes and the largest mesh only excluded fauna >2 mm and so results need to be interpreted in that context.

While Powers et al. (2009) detected a strong main effect of burial depth in TLF, our study found that it was not significant as a main effect in TMF and when significant as an interaction was due to its importance in TLF and not TMF. There could be several explanations for this pattern. TMF can experience frequent waterlogged conditions (Martin & Bellingham, 2016), concomitant with low soil redox

potentials (Kitayama et al., 1997; Santiago et al., 2000) and soil oxygen (Silver & Miya, 2001). The influence of slope inclination on soil water accumulation and the movement of litter could also be important, as there are much steeper slopes in many TMF sites compared with TLF. In flat areas, there is a greater chance of flooding, and aboveground litter might experience pulses of nutrient release that stimulate decomposition, but litter buried belowground is likely to be in mainly anoxic conditions that impede microbial activities. In a study of litter decomposition in seasonally flooded prairie marshes, litter was placed aboveground and belowground as in our study, with the leaf litter aboveground increasing in decomposition rate after flooding, while the belowground litter decomposition rate was impeded (Neckles & Neill, 1994). Another possibility is that burial buffers the litter from temperature or humidity conditions that might dry out the litter or affect the microbial community. A third explanation is that in the TLF study, they found that leaf litter decomposition rate was related to an interaction between mean annual rainfall and burial depth, with leaf litter decomposing faster belowground in drier forests (< 3000 mm MAP) but faster aboveground in wetter forests (> 3000 mm MAP) (Powers et al., 2009). While many of the TMF sites have MAP < 3000 m, they also tend to have shorter dry seasons than TLF, with some sites having no dry season at all (Table S1). More research is needed to explore how decomposition at different depths relates to seasonality, soil moisture and oxygen, rainfall, and slope inclination.

The two sites in Malaysia, Kinabalu-ultramafic (KIU) and Kinabalu-sedimentary (KIS), allowed us to examine the influence of soil type. Forests at KIU exhibit shorter trees, lower aboveground biomass, and lower total soil phosphorus than at KIS (Aiba & Kitayama, 1999; Aiba et al., 2015; Kitayama & Aiba, 2002; Kitayama et al., 2000). As expected, there was more mass remaining at the KIU site—only slightly for leaves and much more dramatically for wood (Table S3). Ultramafic sites have lower soil nutrient availability, and more research is needed to untangle the mechanisms behind the significant interaction between site and litter type (Table S3).

4.3 | Climate as the predominant control of decomposition

This study confirmed that climate was the predominant control on decomposition within TMF and indicated only marginal importance for burial depth. In contrast, Powers et al. (2009) found that mesh and burial depth were major influences on decomposition in TLF, perhaps because of differences climatic variability among biomes (Table 2). When both biomes were analyzed together, climate far outweighed biological factors, regardless of litter type.

In fact, because studies vary in which climate variables are measured, it is difficult to fully understand the role of climate on litter decay. Studies that focus on climate often analyze one of five main variables (e. g., MAT, MAP, annual evapotranspiration, dry season length, and a combined index of temperature and moisture seasonality) (Bradford et al., 2016). MAP and MAT are by far the most commonly reported in decomposition studies, either measured on

site or through interpolated spatial models like WorldClim (e.g., Djukic et al., 2018). By evaluating a broader array of climatic variables, however, our study found that less studied climate variables—temperature and precipitation seasonality, temperature range, and cloud cover—were the best predictors. In addition, only one variable (Bio19, precipitation in coldest quarter) was significant in all analyses (Table 3). Our study suggests that interactions between temperature and rainfall may be more influential than either factor alone. Six of the TMF sites could be considered subtropical (>15 degrees latitude), and one possible interaction is that during periods of cooler temperatures, rainfall is less likely to evaporate. The resultant higher soil moisture levels could influence decomposition rates (Castanha et al., 2018; Petraglia et al., 2019).

The importance of the less studied climate variables are highlighted by the broad range of tropical sites encompassed in our study, and these variables might be disproportionately important, but hitherto largely overlooked, in tropical ecosystems. Another issue is that global climate data bases may not always capture local climatic conditions in TMF, which can be steep and located in small watersheds. In addition, precipitation as conventionally measured may not be an appropriate metric of moisture in TMF because many forests therein get significant additional moisture from fog drip and wind-driven rain that is difficult to measure (Bruijnzeel, 2001). The frequent cloud cover in montane regions may also reduce the role of UV-B, which has been shown to be involved in the physical rather than chemical breakdown of litter (Austin & Vivanco, 2006; Marinho et al., 2020). To get a better handle on conditions in tropical forests now and with projected climate change, we suggest that future studies of decomposition and C-cycling incorporate a wider range of climate variables, including seasonality and interactions among climate variables.

Further research is needed to examine the importance of seasonality, where it would be useful to have data that fully encompasses the seasons of the study sites (i.e., longer than a 7-month period). Seasonality did influence decomposition in an earlier global common litter experiment, the Long-Term Intersite Decomposition Experiment (LIDET), in which leaves and fine roots of pine and a tropical hardwood were placed at sites across North and Central America. Decomposition was best explained by a combination of MAT, MAP, actual evapotranspiration, and DEFAC (a decomposition factor based on the interaction of temperature and moisture, that is part of the CENTURY model (Gholz et al., 2000). In addition, in a study in Peru and Ecuador, there is evidence of the importance of seasonality—areas with more seasonality in precipitation (upper elevations) were associated with less soil carbon and more carbon in biomass (above- and belowground) than in the lowlands (de la Cruz-Amo et al., 2020).

4.4 | Tropical forests and global model comparison

The Yasso07 model (Tuomi et al., 2009, 2011) was developed to use climatological variables to predict stocks and long-term dynamics of

dead organic matter in forests and can be used for leaf litter, soil, or wood (Didion et al., 2014). Originally based on mainly European litterbag data (Liski et al., 2005), only one species studied in five tropical sites in Central America was used in the parameterization of the model (Guendehou et al., 2013). Several studies have attempted to validate the model with field litter decomposition data from other locations and the results have been mixed. For example, in 18 upland Canadian forest sites, leaf decomposition rate in the model was often underestimated in relation to MAT (Palosuo et al., 2005). Didion et al. (2014)—comparing observed decomposition rates of leaves, fine roots, and dead trees in Swiss forests varying in climate—found that the decomposition of tree logs fit the model well, depending on the inventory date, but that the model underestimated leaf decomposition especially in sites with either low or high MAP. This lack of fit in high rainfall areas could be a problem when applying the Yasso07 model to tropical forests. We found only one other tropical study that used Yasso07, which found the model inadequate for the decomposition dynamics of the five leaf litter species tested in a TLF in southern Benin (Guendehou et al., 2013). Our current study points to additional limitations. First, Yasso07 strongly overestimates k for a given MAT or MAP in both forest types (see 1:1 line in Figure 4), suggesting possible interactions between these variables and the importance of non-climate variables in tropical decomposition dynamics. Second, the Yasso07 model was built on mean annual estimates but neither MAT nor MAP best predict the observed variation in our study. In addition, the Yasso07 model better fits the TMF than the TLF data, and one hypothesis justified by our study is that non-climatic variables may have greater relative importance on decomposition in lowland sites. Clearly, more study is needed to better parameterize the model for tropical forest ecosystems.

4.5 | Future Directions

The body of tropical work on productivity and carbon cycling has been dominated by lowland forest ecosystems (Malhi, 2012), and it is the same situation for litter decomposition. For example, in a global common litter experiment using tea bags at 570 sites, nine biomes were examined across a range of climates (MAT from -9 to 26°C , and MAP from 60 to 3113 mm); one biome was equivalent to climatic conditions of TLF, but there was no climatic equivalent of TMF (Djukic et al., 2018). Similar to our study, litter type was an important control over decomposition, but their litter type (green tea and rooibos tea) explained the largest variation in litter mass loss (65%), followed by biome (13%), within-site variation (11%), and climate ($<5\%$) (Djukic et al., 2018). The lack of a strong climate effect across biomes is intriguing, and one possible explanation may be the absence of other climatological variables in their analysis. Because we do not yet have a global common litter study that is comprehensive in both biome types and climate, the hierarchy of factors question is not fully answered. Yet, our study points out that including more biomes and climate variables can lead to more nuanced assessments of global decomposition patterns (Figure 4).

While carbon cycling in TMF is not as well understood, there is recent evidence from forest inventory plots and remote sensing that these forests store more carbon than previously acknowledged (Cuni-Sanchez et al., 2021; Spracklen & Righelato, 2014). Adding data from montane forests improves models of the relationship between climate and decomposition across tropical forest biomes, while elucidating that the importance of soil fauna, fine roots and burial depth are largely biome specific. TMF was not as different in decomposition rates between the buried and surface litter or between mesh sizes. In addition, TMF was more tightly correlated with MAP and MAT in the Yasso07 model than TLF. These differences lead to a new hypothesis that decomposition rates in the TMF may be more constrained or more easily predicted by climate than TLF, arguing for the need for additional work in the TMF biome. It should be noted, however, that one major factor, soil nutrient availability, was not part of this study and may greatly influence litter decomposition rates (Ge et al., 2013). Much remains to be understood about the partitioning of carbon among roots, aboveground parts, and soils in TMF ecosystems (de la Cruz-Amo et al., 2020; Girardin et al., 2010), and litter decomposition is a crucial process in elucidating those patterns. The carbon stores of these iconic montane forests of the tropics face threats from climate change (Nottingham et al., 2015) and deserve more attention in global ecosystem studies.

ACKNOWLEDGMENTS

This work was supported by National Science Foundation grant from the Division of Environmental Biology (DEB)-1146446 and the NSF-sponsored research coordination network *CloudNet* (<http://duclouclou.net.wpengine.com>). We thank William K. Cornwell for help with litterfitter. At individual sites, we would like to acknowledge the following: CEM: We thank Federico Valverde for granting permission to work at Cerro de la Muerte Field Station. The School for Field Studies Costa Rica provided logistical support for data collection at the Cerro de la Muerte site. Emily Blau and Anne Häger assisted with field and laboratory work. Meteorological data were provided by the Instituto Meteorológico de Costa Rica. CLB: We thank Cloudbridge Nature Reserve for their support of this project as well as Tim Carlson and Janina Harms for their assistance with fieldwork. EXT and VIR: We thank The Nature Conservancy (TNC) and the São Paulo Research Foundation—FAPESP (grant 2015/50682-6) for the fieldwork support. LAU: We thank Mikkel Gantzler and Oliver Andersen for field sampling support, and Christa Nicholas, Kaikea Blakemore, and Rebecca Carpenter for assembling the litter bags, and Tabetha Block for permitting help. MON: We thank to the Monteverde Cloud Forest Reserve for research permission and to the National Science Foundation for financial support (Gotsch IOS Award #1556289). MUC: We thank INPARQUES (Venezuela) for facilitating access to the plots and J.E. Torres and M. Fernandez for assistance during fieldwork. NGE: We thank the Nigerian Montane Forest Project field assistants. HON and QUE: We thank Evidelio García and Juliana Pardo for field assistance. SAN: We thank the Deutsche Forschungsgemeinschaft (DFG) for the fieldwork support

(grant Ho 3296/4-2). SLM: work in the SLM was possible through grant NSF-DEB 1556878 to CR.

AUTHOR CONTRIBUTIONS

The first four authors organized and lead the study, and the rest made equal contributions and are listed in alphabetical order.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.z8w9ghxdk> (Ostertag et al., 2021).

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How to cite this article: Ostertag, R., Restrepo, C., Dalling, J. W., Martin, P. H., Abiem, I., Aiba, S.-I., Alvarez-Dávila, E., Aragón, R., Ataroff, M., Chapman, H., Cueva-Agila, A. Y., Fadrique, B., Fernández, R. D., González, G., Gotsch, S. G., Häger, A., Homeier, J., Iñiguez-Armijos, C., Llambí, L. D., ... Williams, C. B. (2022). Litter decomposition rates across tropical montane and lowland forests are controlled foremost by climate. *Biotropica*, 54, 309–326. <https://doi.org/10.1111/btp.13044>