

Altitude and species identity drive leaf litter decomposition rates of ten species on a 2950 m altitudinal gradient in Neotropical rain forests



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Abstract

Identifying the environmental factors controlling litter decomposition is key to understanding the magnitude and rates of nutrient cycling in tropical forests, and how they may be influenced by climate variability and environmental change. We carried out a leaf litter translocation experiment in mature rain forest over a 2,520 m altitudinal gradient in Costa Rica. Leaf litter decomposition rates (k) of ten tree species, two dominant species from each ecosystem, plus two standard species, were calculated over 540 days in four life zones. k was lowest in montane with 0.83 per year and lower montane forests with 2.21 per year. k did not differ between lowland and premontane forests at 3.12 per year, in spite of the 3°C difference of mean annual temperature between these life zones. k varied fourfold among species. Species decomposition rates ranked as follows, and were predictably related to leaf economic spectrum traits of the species: *Acalypha communis* (standard, fast decomposer) » *Hyeronima oblonga* » *Alchornea latifolia*, *Quercus bumelioides*, *Jarava ichu* (standard, slow decomposer) » *Minuartia guianensis* » *Magnolia sororum* » *Vochysia allenii* » *Pourouma bicolor*, *Carapa guianensis*. These two slowest-decomposing species were native premontane and lowland forest dominants, respectively, with tough, low-nutrient leaves. The ranking of species by k varied very little among life zones suggesting that decomposer organisms in very different ecosystems and environments react in similar ways to the litter quality in general. We conclude that while k decreases with temperature in rain forests on tropical mountains, bioclimatic zones defined as premontane may be “functionally lowland.” The effects of species identity on decomposition rates on tropical mountains are consistent and independent of environment for both standard and native species. Under climate change on these mountains, if moisture regimes do not change, decomposition rates will increase due to rising temperatures. Soil carbon storage may therefore decrease. Changes in the altitudinal distributions of currently dominant species will also affect this critically important biogeochemical process.

KEYWORDS

Acalypha communis, carbon and nutrient cycling, climate change, home effect, *Jarava ichu*, leaf traits, simple exponential decay model, tropical forest

1 | INTRODUCTION

Globally, degradation of natural habitats and the changing climate are altering forest function (Hooper et al., 2012). Nutrient cycling, through litter decomposition, is one of the most important forest ecosystem functions and is a key process in the carbon cycle and in the provision of ecosystem services like maintenance of productivity (Díaz, Hector, & Wardle, 2009). Spatial and temporal variation in litter decomposition rates can have major implications for ecosystem functioning of tropical forests (Salinas et al., 2011). Anthropogenic increases in atmospheric CO₂ are projected to drive significant changes in means and extremes of temperature and precipitation patterns (IPCC, 2014), which in turn will affect ecological systems and processes like litter decomposition (Grimm et al., 2013). Central America, where our study was carried out, is one of the world's regions most threatened, environmentally and socially, by these processes (Hannah et al., 2017). Rising temperatures, in the absence of moisture limitation, are expected to bring increases in decomposition rates and the ecosystem processes they are part of (Salinas et al., 2011). Increasing decomposition rates may bring about reductions in C storage in the soil, especially in montane forests (Veintimilla et al., 2019).

Natural forest ecosystems in tropical mountains are of global importance due to their high alpha and beta diversity, their high number of endemic species, their key role in the provision of ecosystem services, and the serious threat posed to them by climate change (Kappelle, 2001; Malhi et al., 2010). They also provide a valuable observatory for study of the response of ecosystem properties and processes to climatic factors, especially in places where the marked temperature gradients over short distances are found under constant moisture regimes (Dunne, Saleska, Fisher, & Harte, 2004; Malhi et al., 2010; Salinas et al., 2011). Knowledge of the variation of rain forest ecosystem properties and productivity in relation to temperature on tropical altitudinal gradients is increasing (Goldsmith et al., 2016; Malhi et al., 2016; Veintimilla et al., 2019), but is not matched by understanding of decomposition (Salinas et al., 2011).

Decomposition rates increased exponentially with temperature in an experiment on a 2,800 m elevational gradient in the Peruvian Andes and may also be affected by rainfall, soil moisture, and forest species composition (Bothwell, Selmants, Giardina, & Litton, 2014; Salinas et al., 2011). Species identity indeed has a very strong effect on litter decomposition (Pérez-Harguindeguy et al., 2013). For example, Makkonen et al. (2012) found, in a reciprocal translocation experiment, that rankings of 16 woody species by decomposition rates were maintained across a tropical-subarctic latitudinal gradient. They suggest that constant rankings occur because over a wide range of environmental conditions, different communities of decomposer organisms respond to litter traits in the same way.

Multiple-species translocation experiments under natural field conditions are powerful tools for understanding factors affecting decomposition rates (e.g., Powers et al., 2009), but we are aware of only one study that has used this approach to explore the temperature sensitivity of decomposition within the tropics in forest on a lowland to montane altitudinal gradient (Salinas et al., 2011). Key information is still missing from comparative, large-scale, and long-term decomposition

experiments in order to estimate future changes in response to climate change at global, regional, or ecosystem levels (Adair et al., 2008; Parton et al., 2007; Serna-Chavez, Fierer, & van Bodegom, 2013). The study of litter decomposition over altitudinal gradients, taking into account differences between species and sites, will contribute to understanding of the variability of carbon and nutrient cycling in response to future climate scenarios for tropical forest (Handa et al., 2014; Salinas et al., 2011; Saxe, Cannell, Johnsen, Ryan, & Vourlitis, 2001).

We performed a litter translocation decomposition experiment across a 2,520 m altitudinal gradient in Costa Rican rain forest, working between 430 masl and 2,950 masl at sites in four different forest life zones: lowland wet (430–620 masl), premontane (1,000–1,120 m), lower montane (1,400–1,660 m), and montane rain forest (2,150–2,950 m). We used litter from two dominant tree species from each of the four life zones, as well as standard litter from two species of central Argentina: one, *Acalypha communis* (Euphorbiaceae), characterized as having high decomposition rates (Cuchietti, Marcotti, Gurvich, Cingolani, & Harguindeguy, 2014; Vaieretti, Perez-Harguindeguy, Gurvich, Cingolani, & Cabido, 2005) and the other, *Jarava ichu* (Poaceae), having slow decomposition (Vaieretti et al., 2005). The standard species were effectively baselines in our experiment, whose well-known decomposition rates we were able to compare with those of tree species of a little-known tropical flora. The experiment was continued for 540 days. Our overall goal was to increase understanding of how litter decomposition rates might be affected by changing environmental conditions in tropical wet and rain forests on altitudinal gradients, and how this process might be affected by future climate change. We predicted that because of the decrease of temperature across the gradient between lowland, premontane, lower montane and montane wet and rain forests, decomposition rates would decrease across the life zones in that order. The execution of this study in wet and rain forest environments controls for any possible effect of rainfall variation on decomposition. We also predicted that the rankings of species by decomposition rates would remain constant across the four forest types. Constant rankings occur because although species assemblages of decomposer organisms change over the altitudinal gradient, they react in the same way to species litter quality. This prediction lines up with the principle that plant leaf litter has a characteristic decomposability due to its physical and chemical characteristics (Pérez-Harguindeguy et al., 2013). Finally, we tested the hypothesis that overall decomposition rates for species would be positively correlated with values of leaf economic spectrum traits for green leaves, and negatively with values of traits that measure leaf structural material and toughness (Pérez-Harguindeguy et al., 2013).

2 | METHODS

2.1 | Study site

A reciprocal translocation decomposition experiment was carried out over 540 d in a permanent forest sample plot (PSP) network covering an altitudinal range of 2,520 m on Costa Rica's Caribbean

slope (Figure S1). The 27 0.25 ha PSPs (50 × 50 m; see Veintimilla et al., 2019) were established in mature forest without evidence of recent human disturbance in four Holdridge Life Zones—lowland wet forest, premontane rain forest, lower montane rain forest, and montane rain forest (ITCR, 2008). On WorldClim climate surfaces (approximately 1 km² spatial resolution in our area: Hijmans et al., 2011, www.worldclim.org), mean annual temperature of the grid cells within which plots were located are 24°C, 20°C, 15°C, and 11°C for each life zone, respectively (Table 1). From the same source, mean annual precipitation ranges from a maximum > 4,000 mm at the lower montane rain forest site, to ca. 2,500 mm at the montane forest site. It should be noted that values of precipitation metrics from Worldclim are undoubtedly less accurate than for temperature (Hijmans et al., 2011). Species density in 0.25 ha declines linearly with altitude in these plots, from c. 70 in lowland wet forest to < 20 in montane rain forest (trees, palms, and tree ferns ≥ 10 cm dbh; Veintimilla et al., 2019). Soils are acid (overall mean pH in the plots 4.4, at 0–30 cm depth). Soil C: N, organic matter and C (%) all increase with altitude, and pH and cation exchange capacity decrease (Veintimilla et al., 2019). Clay content shows a negative quadratic relationship with altitude. It is highest in the lowland wet forest, declining in the premontane rain forest and lower montane rain forest where sandy loams and sandy clay loams predominate, and increasing again in montane rain forest (Veintimilla et al., 2019). ITCR (2008) classifies these soils as Inceptisols and Ultisols.

Twelve of the PSPs were selected for the experiment, three in each of the four forest types (lowland wet forest, premontane rain forest, lower montane rain forest, and montane rain forest). The

minimum distance between these plots within the forest types is 300 m. The two dominant tree species by forest type, identified as those with the highest basal area in the PSPs, were selected for the experiment, for a total of eight native species (Table 1). Fresh litter (senescent leaves released from the tree) was collected in and around the plots over a period of one year, oven dried at 65°C and stored. Litter of the two standard species, *A. communis* and *J. ichu*, was imported to Costa Rica from collection sites in Central Argentina (Cuchietti et al., 2017; Vaieretti et al., 2005).

We used the litterbag method to evaluate decomposition (Bocock et al., 1960). Plastic mesh bags (20 × 25 cm, 2 mm mesh size) were used to enclose 12 g of litter from each species, without petioles; we did not mix litter of different species in this experiment. The 2-mm mesh allows access to litterbags by soil mesofauna, but not macrofauna such as most earthworms and insects (Swift, Heal, & Anderson, 1979). Before filling the litterbags, stored litter was gently mixed to homogenize it. The experiment was established in December 2013, and litterbags were incubated in the field until July 2015. We placed litterbags on the soil surface, covered them with the natural litter layer, and exposed them to natural weather conditions.

2.2 | Experimental design

In each of the twelve PSPs, we prepared two separate decomposition beds in an area of 10 × 10 m under closed canopies, for a total of 24 decomposition beds. The beds were located in opposite quadrants of each PSP, with a minimal and maximum distance of 10 m to 17 m among them. A total of 100 litterbags (ten bags of each of the

TABLE 1 Plot locations, WorldClim climatic data and species selected for the litter translocation experiment in Costa Rica. Tree species native to the four wet and rain forest types studied (Holdridge Life Zones) were those of the highest basal area in permanent sample plots placed along the altitudinal gradient

Rain forest types	Locality	Altitude (masl)	Latitude (S)	Longitude (W)	Temperature (°C)	Rainfall (mm/year)	Litter species and family
Lowland wet (LWF)	Barbilla National Park	430–620	562,359.8	1,101,522.4	23.4–24.4	3500–3800	<i>Minuartia guianensis</i> (Olacaceae) <i>Carapa guianensis</i> (Meliaceae)
Premontane (PREMONTANE RAIN FOREST)	Esperanza/Copal Private Reserves	1000–1120	538,539.0	1,082,938.5	20.0–21.4	2700–3450	<i>Vochysia allenii</i> (Vochysiaceae) <i>Pourouma bicolor</i> (Cecropiaceae)
Low montane (LMRF)	Tapanti National Park	1400–1660	522,590.5	1,078,630.8	17.6–19.2	3686–4146	<i>Alchornea latifolia</i> (Euphorbiaceae) <i>Hieronyma oblonga</i> (Phyllanthaceae)
Montane (MRF)	Rio Macho Forest Reserve	2150–2950	533,289.7	1,058,038.5	10.0–13.5	2340–3000	<i>Quercus bumelioides</i> (Fagaceae) <i>Magnolia sororum</i> (Magnoliaceae)
Standard litter	Semi-arid Chaco (Argentina)	900–1000					<i>Acalypha communis</i> (Euphorbiaceae) <i>Jarava ichu</i> (Poaceae)

ten species) were placed in each decomposition bed, for a total of 200 bags by permanent plot and 600 litterbags by forest type. We laid litterbags out in ten by ten grids, with species randomly assigned to rows and with harvesting time randomized within the species row. A minimum distance of 50–100 cm was maintained between bags of different species and a 10–20 cm distance between bags of the same species. The overall total of litterbags was 2,400 (four forest types \times three permanent plots in each forest type \times two decomposition beds in each plot \times ten species in each decomposition bed \times ten harvesting times).

We collected one litterbag per species from each decomposition bed at each of ten harvesting times measured in days after the initiation of the experiment (30, 60, 90, 120, 180, 240, 300, 360, 450, 540 days). The percentage of dry matter remaining inside each litterbag (DM, %) was measured at each harvesting time. Thus, the main factor of the design was forest type (four categories), the second factor was species (ten categories), and the third factor was time (defined by ten different harvesting times).

2.3 | Data analysis

Analysis was carried out using InfoStat 2016 software (Di Rienzo et al., 2016). % dry matter remaining DM was ArcSin square root transformed to meet normality and homoscedasticity criteria for the comparison of main factors and their interaction using ANOVA (unpublished data). We used general linear mixed models for analysis (GLMM) to take into consideration the autocorrelation in repeated measures over time and the hierarchy of the plot structure, as well as the remaining heteroscedasticity. We set forest, species, time, and their interactions as fixed factors. Main plots, decomposition beds within them, and rows of litterbags within decomposition beds were all set as random factors.

We estimated litter decomposition rate coefficients (k) using a simple negative exponential model (Jenny, Gessel, & Bingham, 1949; Olson, 1963). A total of 240 k values were obtained fitting this model to eleven dry matter remaining values obtained for each of the six sampling units (three replicates by two plots by replicates) available for the 40 forest \times species treatments over the ten harvesting times. In addition, all the 240 decay curves were fitted to a double exponential model (Wieder & Lang, 1982). We compared double exponential models with the simple exponential model by means of AIC and BIC criteria. Single exponential models were used because of their superior fit in the great majority of cases. The 240 k values describing the decay rates of treatments were compared using GLMM ANOVA as described for DM.

Finally, we used principal components analysis (PCA) of standardized variables and linear regression to determine relationships between traits of green leaves of each species and their k values. We measured leaf nitrogen and phosphorous concentration (mg/g), specific leaf area (SLA, mm^2 per mg), leaf dry matter content (LDMC, mg/g), and force to tear (F_t , N/mm), for fresh leaves of each species following Pérez-Harguindeguy et al. (2013).

3 | RESULTS

A total of 2,399 of 2,400 litter bags were recovered from field incubation and 2,307 (96%) still contained dry matter on collection. We recovered the first empty litterbags after 180 days of litter incubation, with the highest number found at 540 days, the end of the experiment. The species that most frequently showed complete litter decomposition were *A. communis* and *Hieronyma oblonga*, followed by *J. ichu* and *Alchornea latifolia*. We found a higher number of empty bags in lowland wet forest, premontane rain forest, and lower montane rain forest than in montane rain forest. The DM assumed for empty bags was 0%.

3.1 | Litter decomposition rate

k values differed significantly among forest types ($F_{3; 20} = 69.57$; $p < .0001$) and species ($F_{9; 180} = 115.00$; $p < .0001$), and the forest \times species interaction was highly significant ($F_{27; 180} = 10.80$; $p < .0001$). The respective percentages of variance explained were 7.8% for forest type, 75.2% for species, and 14.1% for their interaction. Litter decomposition rates were lower in montane rain forest than in lower montane rain forest, with both upland forests having lower rates than the two lowland forests, which did not differ from each other (Figure 1a). At the species level, the standard, fast-decomposing *A. communis* had the highest k . It was followed by *H. oblonga* (native, lower montane rain forest dominant), *J. ichu* (standard, slow-decomposing), *Q. bumelioides* (montane rain forest), and *A. latifolia* (lower montane rain forest) had lower litter decay rates than these two species, but did not differ from each other. k was lower for *M. guianensis* (lowland wet forest), *M. sororum* (montane rain forest), and *V. allenii* (premontane rain forest), and the lowest values were observed for *P. bicolor* and *C. guianensis*. These two species, the slowest decomposers, are, respectively, premontane rain forest and lowland wet forest dominants (Figure 1b).

Continuous decreases in k were observed for almost all species from lowland to upland forests, with some exceptions observed at low and middle elevations (Table 2, Figure 2). All species had lowest k in montane rain forest and the highest k in lowland wet forest and premontane rain forest, again without clear differences between these two forest types. For five species (*C. guianensis*, *P. bicolor*, *J. ichu*, *A. latifolia*, and *H. oblonga*), k did not differ between lowland wet forest and premontane rain forest (Table 2). On the other hand, k was higher in lowland wet forest than premontane rain forest for *M. sororum*, *M. guianensis*, *Q. bumelioides*, and *A. communis*. Finally, one species, *V. allenii*, showed a faster decomposition rate in premontane rain forest than in lowland wet forest, possibly a home-field advantage (Table 2).

The effect of litter species identity on decomposition rates was largely consistent across the four life zones (Figure 2). The standard *A. communis* was the fastest decomposer in all four forest types. In lowland wet forest, *H. oblonga*, *A. latifolia*, and *Q. bumelioides* were the fastest decomposers among the native species. The standard

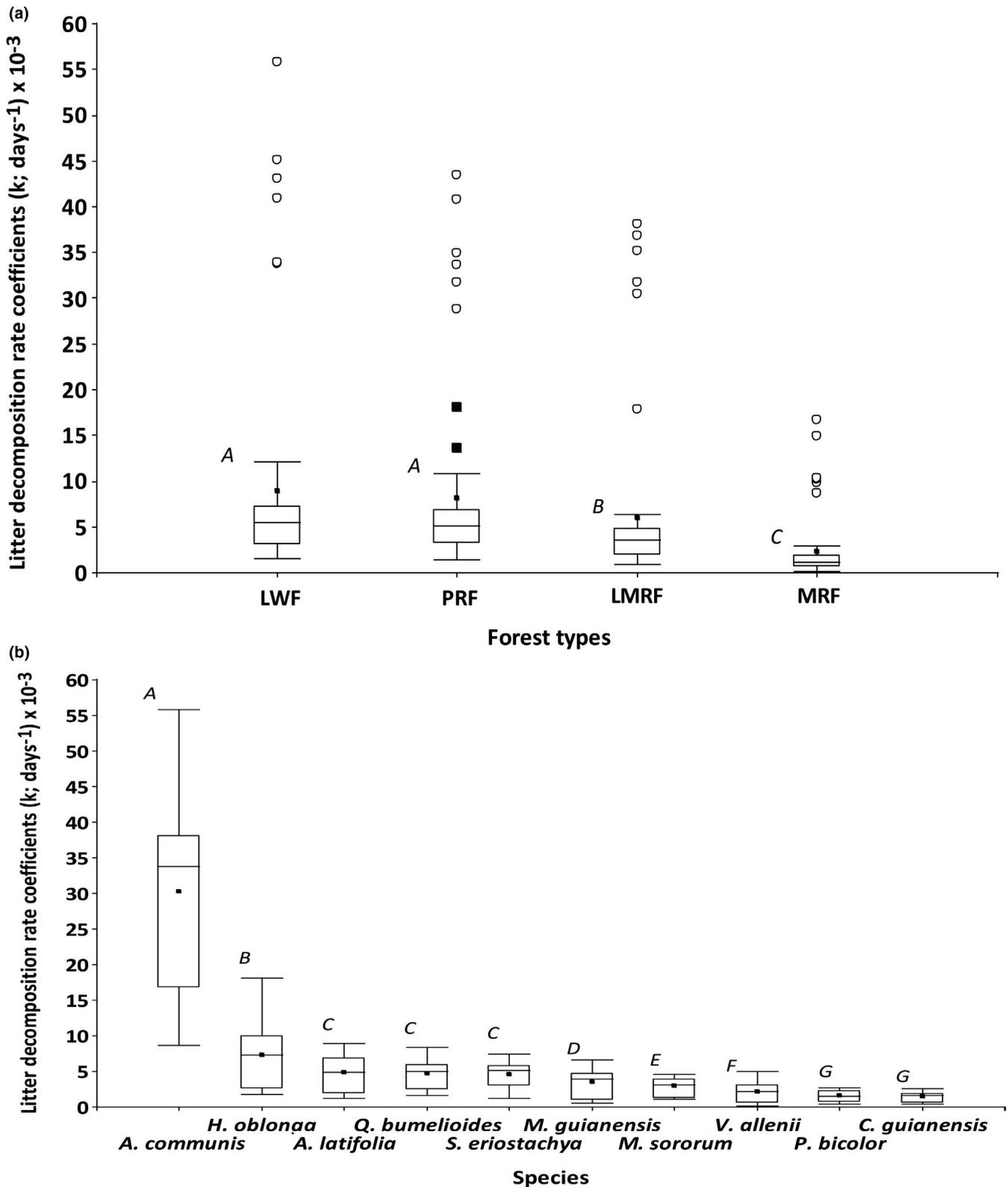


FIGURE 1 Litter decomposition rates coefficients (k) estimated using a single exponential decay model for ten litter species located along an altitudinal forest gradient: lowland wet (LWF), premontane (PREMONTANE RAIN FOREST), lower montane (LMRF), and montane (MRF). Different letters imply significant statistical differences ($p \leq .05$). Box plots depicting median (center lines), upper (Q3) and lower (Q1) quartile ranges (edges of boxes), mean (small black squares), quartile (Q1 and Q3) minus/plus 3 times the half of interquartile range (upper and lower whiskers), extremes values (big black squares), and highly extreme values (open circles) of decay rates (k) for different a) forest types and b) tree litter species

J. ichu and natives *M. guianensis* and *M. sororum* showed intermediate decomposition rates. Finally, *V. allenii*, *P. bicolor*, and *C. guianensis* showed the slowest rates. This overall ranking was largely maintained in premontane rain forest, lower montane rain forest, and montane rain forest (Figure 2).

To facilitate direct comparison of our results with those from other studies, in Table 3 we present annual decay rates ($k \times 365$, per year) and residence times (RT) calculated as $1/k$ (year) following Salinas et al. (2011). Mean annual decay rates for the eight native species varied between 1.85 in lowland wet forest, 1.83 in premontane rain forest, 1.11 in lower montane forest, and 0.42 in montane rain forest. The corresponding residence times were 0.54, 0.54, 0.90, and 2.39 years (Table 3). Annual decay rates for species in their home life zones ranged from 0.41 for *M. sororum* in montane rain forest to 1.95 for *H. oblonga* in lower montane rain forest and were 0.76 and 1.9 for the two lowland wet forest species, similar to the ranges found for lowland tropical tree species found in other studies (Makkonen et al., 2012; Wieder, Cleveland, & Townsend, 2009). The only species common between our study and that of Salinas et al. (2011), *Alchornea latifolia*, showed very similar annual decay rates in Costa Rica and Perú at the same home elevation, 1,500 m (1.47 and 1.52, respectively).

3.2 | Leaf traits are related to litter decomposition rate

To explore potential relationships between traits of green leaves and decomposition in our species, in Figure 3a we show a principal components analysis ordination of our native species in space defined by leaf N, P, specific leaf area (SLA), leaf dry matter content (LDMC), force

to tear (F_t), and overall k values. The first axis of the PCA can be interpreted as a leaf economics spectrum, with the two fastest-decomposing species, *A. latifolia* and *H. oblonga*, having negative eigenvalues strongly associated with SLA and k . Both these species are lower montane rain forest dominants. Overall k values are strongly associated with SLA on PC 1. The slowest-decomposing species, the lowland wet forest dominant *C. guianensis* and the premontane rain forest dominants *P. bicolor* and *V. allenii*, all with positive eigenvalues on PC 1, have the most conservative leaves by the criterion of this set of leaf traits. There is a clear linear relationship between overall k , ln-transformed, and species eigenvalues on PC 1 (omitting k from the PCA ordination; $R^2 = 0.57$, $p = .0304$, Figure 3b). This result suggests that this set of leaf traits contributes at least indirectly to the determination of litter decomposition rates and therefore to the large variation among species.

4 | DISCUSSION

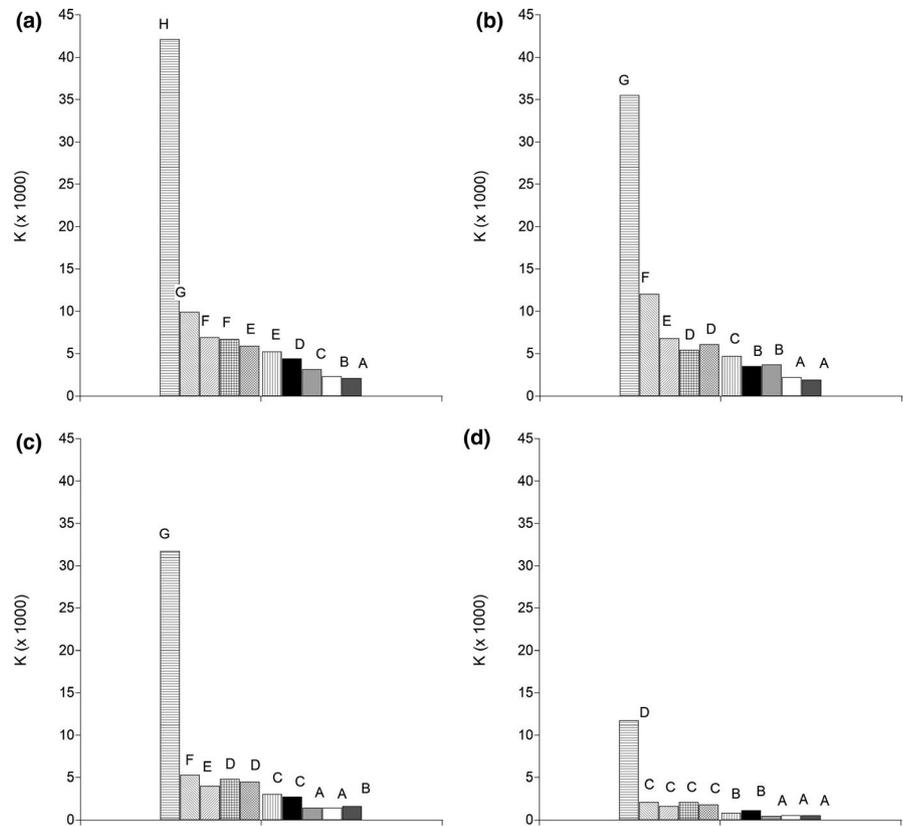
Our leaf litter translocation experiment over a 430–2950 masl altitudinal gradient in tropical wet and rain forests was implemented over a 540-day period. We used litter from two standard species, one of fast and one of slow decomposition, and from eight native species—two dominants from each of four forest life zones covering the altitudinal gradient. As far as we are aware, this is one of only two experiments of this nature and magnitude implemented in rain forests on tropical mountains, the other being that of Salinas et al. (2011).

We found that litter decomposition rates depend strongly on forest life zone and species identity. Variation among life zones fits our prediction of decreasing temperature with increasing altitude

TABLE 2 Litter decomposition rates coefficients (k mean ($d^{-1} \times 10^{-3}$) \pm 1SE) estimated by a single exponential model for eight native species and two standard species (*) across four different wet and rain forest types located along an altitudinal gradient: lowland wet¹ (LWF), premontane² (PREMONTANE RAIN FOREST), lower montane³ (LMRF), and montane rain forest⁴ (MRF) in Costa Rica. Values for home species (species that were dominants in each forest type) in bold. Different letters imply statistical significant differences among species ($p \leq .05$)

Species (n = 240)	Forest types (n = 60)				
	LWF	Premontane Rain Forest	LMRF	MRF	
<i>Carapa guianensis</i> ¹	1.5 ± 0.1A	2.1 ± 0.1C	1.9 ± 0.1C	1.6 ± 0.2C	0.5 ± 0.04A
<i>Pourouma bicolor</i> ²	1.6 ± 0.2A	2.3 ± 0.2C	2.2 ± 0.2C	1.4 ± 0.3B	0.5 ± 0.10A
<i>Vochysia allenii</i> ²	2.2 ± 0.3B	3.1 ± 0.2D	3.7 ± 0.4E	1.4 ± 0.2B	0.4 ± 0.05A
<i>Magnolia sororum</i> ⁴	2.9 ± 0.3C	4.4 ± 0.1F	3.5 ± 0.2E	2.7 ± 0.2D	1.1 ± 0.03B
<i>Minuartia guianensis</i> ¹	3.5 ± 0.4D	5.2 ± 0.3G	4.7 ± 0.4F	3.0 ± 0.3D	0.8 ± 0.10A
<i>Jarava ichu</i> *	4.6 ± 0.4E	5.9 ± 0.4G	6.1 ± 0.3G	4.5 ± 0.3F	1.8 ± 0.20C
<i>Quercus bumelioides</i> ⁴	4.7 ± 0.4E	6.7 ± 0.4H	5.4 ± 0.3G	4.8 ± 0.3F	2.1 ± 0.10C
<i>Alchornea latifolia</i> ³	4.8 ± 0.5E	6.9 ± 0.4H	6.8 ± 0.3H	4.0 ± 0.2E	1.6 ± 0.10C
<i>Hyeronima oblonga</i> ³	7.3 ± 0.9F	9.9 ± 0.6I	12.0 ± 1.3I	5.3 ± 0.2G	2.1 ± 0.10C
<i>Acalypha communis</i> *	30.3 ± 2.7G	42.1 ± 3.4K	35.5 ± 2.3J	31.7 ± 3.0J	11.7 ± 1.30I
All species		8.9 ± 1.5A	8.2 ± 1.3A	6.0 ± 1.2B	2.3 ± 0.40C
Natives only		5.1 ± 0.4	5.1 ± 0.5	3.1 ± 0.2	1.2 ± 0.10

FIGURE 2 Rankings of species by decay rates within each forest type. a), lowland wet forest, b), premontane rain forest, c), lower montane rain forest, and d), montane rain forest. In all graphs, species are ordered on the basis of the ranking for the lowland wet forest. From left to right, *Acalypha communis*, *Hyeronima oblonga*, *Alchornea latifolia*, *Quercus bumelioides*, *Jarava ichu*, *Minquartia guianensis*, *Magnolia sororum*, *Vochysia allenii*, *Pourouma bicolor*, and *Carapa guianensis*. Different letters imply significant statistical differences ($p \leq .05$)



and therefore temperature, though the lowland wet forest and premontane rain forests did not differ in overall rates, or in the rates for some individual species. The variation of decomposition rates among species was markedly greater than the variation among life zones. Although the standard *A. communis* was always the fastest decomposer, the standard *J. ichu*, considered a slow decomposer in the flora of Central Argentina where it originates (Vaieretti et al., 2005), had faster decomposition rates than five native species, including species from each of the four life zones.

4.1 | Decomposition rates decline with temperature

While rainfall controls decomposition rates in tropical forests with similar temperature regimes (Powers et al., 2009), temperature controls decomposition rates in tropical forests with similar rainfall regimes (Powers et al., 2009; Salinas et al., 2011). Including only native species, variation of overall mean decomposition rates was fourfold across our 2,520 masl rain forest gradient, as on the 2,800 masl Andean gradient studied by Salinas et al. (2011). As the climatic moisture regime over this gradient is uniformly wet, temperature, measured by its surrogate altitude, is very likely to be the main control over this variation of decomposition rates. Overall k values were lowest in montane rain forest (WorldClim MAT 11°C), higher in lower montane rain forest (WorldClim MAT 18.5°C), and highest in lowland wet forest and premontane rain forest (WorldClim MAT 20.5°C and 24.0°C, respectively) with

no difference of mean k between the latter two life zones. Our montane rain forest sites do not have either a winter or a strong dry season, as emphasized by Salinas et al. (2011) for their Andes–Amazon transect, but they are subject to frost (Herrera, 2005). The effects of occasional frost on decomposition in tropical montane rain forest sites are not known and require further more detailed research.

The lack of a difference of overall decomposition rates between lowland wet forest (mean annual temperature 24°C) and premontane rain forest (mean annual temperature 21°C) suggests that although life zones and other bioclimatic vegetation classifications are based by their developers on functional and forest ecological criteria, they do not necessarily differ in rates of ecological processes. Similarly, the floristic differences between the forests of these two life zones are relatively small in the context of the overall change of forest composition over the whole gradient (Veintimilla et al., 2019). Simple statistical models can explain the variation of decomposition rates across long climatic gradients in the tropics—the linear relationship of decomposition rate to rainfall demonstrated by Powers et al. (2009) and the exponential relationship to temperature of Salinas et al. (2011)—but our results suggest that important patterns may occur within such gradients. In the same way as for our lowland wet forest and premontane rain forest sites, mean overall k does not appear to differ between the Salinas et al. (2011) study sites at 210 m asl and 1,000 m asl (their Figure 2). If adjacent bioclimatic zones do not differ in the rates of ecological processes, the consequences of such a pattern for regional and global models of climate change should be explored.

Forest types	Species	n	K (year)	RT (year)
LWF	All species	60	3.23 ± 0.55	0.31
	8 native species	48	1.85 ± 0.14	0.54
	<i>Carapa guianensis</i>	6	0.76 ± 0.06	1.32
	<i>Minquartia guianensis</i>	6	1.90 ± 0.09	0.52
PRF	All species	60	2.99 ± 0.46	0.34
	8 native species	48	1.83 ± 0.17	0.54
	<i>Pourouma bicolor</i>	6	0.79 ± 0.07	1.26
	<i>Vochysia allenii</i>	6	1.36 ± 0.14	0.73
LMRF	All species	60	2.21 ± 0.42	0.45
	8 native species	48	1.11 ± 0.08	0.90
	<i>Alchornea latifolia</i>	6	1.47 ± 0.05	0.68
	<i>Hyeronima oblonga</i>	6	1.95 ± 0.09	0.51
MRF	All species	60	0.83 ± 0.16	1.20
	8 native species	48	0.42 ± 0.04	2.39
	<i>Magnolia sororum</i>	6	0.41 ± 0.01	2.43
	<i>Quercus bumelioides</i>	6	0.76 ± 0.04	1.31
Total mean/species	All species	10	2.31 ± 0.99	0.43
	8 native species	8	1.30 ± 0.26	0.77
Total mean/forest types	All species	4	2.31 ± 0.54	0.43
Total mean	All species	240	2.31 ± 0.22	0.43

TABLE 3 Decay rates (k mean (year) ± 1 SE) and leaf litter residence time (RT, $/k$) estimated in years for all litter species, the native species only, and the home litter species across four different wet and rain forest types located along an altitudinal gradient: lowland wet (LWF), premontane (PREMONTANE RAIN FOREST), lower montane (LMRF), and montane rain forest (MRF) in Costa Rica

4.2 | Species identity is the main source of variation in decomposition rates

As species identity is the main source of variation in decomposition experiments like ours, the choice of species may clearly affect the results of these experiments. Patterns in overall decomposition rates are influenced by the patterns shown by the individual species. In our experiment, for example, k for the fast-decomposing standard species *A. communis* and the slow-decomposing *C. guianensis* did not differ among lower montane rain forest, premontane rain forest, and lowland wet forest, but was lowest in montane rain forest. The lack of a difference of overall k between lowland wet forest and premontane rain forest in our experiment might therefore be due partially to species choice, though like Salinas et al. (2011) we selected dominant native species because of their likely importance to ecosystem processes. In line with our prediction, k was lower in premontane rain forest than in lowland wet forest for four species. However, it did not differ between these life zones for five species and for *V. allenii*, k was higher in premontane rain forest than in lowland wet forest. Therefore, the overall relationship of mean k to temperature may depend on between-species differences in the temperature sensitivity of k (Salinas et al., 2011) and in our case, a possible home-field advantage in *V. allenii*, discussed below.

The wide variation of decomposition rates among species in our results is expected and is the principle that underlies the use of reciprocal translocation experiments (Salinas et al., 2011; Wieder et

al., 2009). The chemistry of litter (i.e., litter traits) has been shown by Cusack et al. (2009) to strongly affect decomposition rates in Neotropical forests—they measured initial litter N, lignin, lignin:N and C:N as well as tannins and polyphenols, for standard species and species native to their sites. We have measured leaf traits for all the dominant tree species of the long-term research plots in which our decomposition experiment was carried out (Veintimilla et al., 2019, Finegan et al., in revision). Leaf traits are sometimes related to decomposition rates, and sometimes not (Cornelissen et al., 1999, Jackson et al., 2012, Hättenschwiler et al., 2011). Our results suggest that overall, for this set of species, the leaf economic spectrum traits (SLA, N, P) and traits reflecting leaf structural material, longevity, and toughness (LDMC, F_t), contribute to predicting the decomposition rates of their litter. In relation to leaf traits, a number of studies have suggested that overall, their values become more conservative with altitude in tropical mountain gradients like ours (e.g., Salinas et al., 2011). This is not the case for the dominant species selected for our study. The montane rain forest dominants *M. sororum* and *Q. bumelioides* have intermediate values of leaf traits (Figure 3a) for example. The slowest-decomposing species, *C. guianensis*, *P. bicolor*, and *V. allenii*, are lowland wet forest and premontane rain forest dominants associated with high LTS and LDMC on the traits PCA. On comparison with other biomes, the lowland wet tropics are not necessarily associated with fast-decomposing acquisitive leaves. *A. communis*, whose leaves have high SLA, N, and P and low LDMC and LTS (Vaieretti et al., 2005), had the highest k in our experiment by a considerable margin. On the

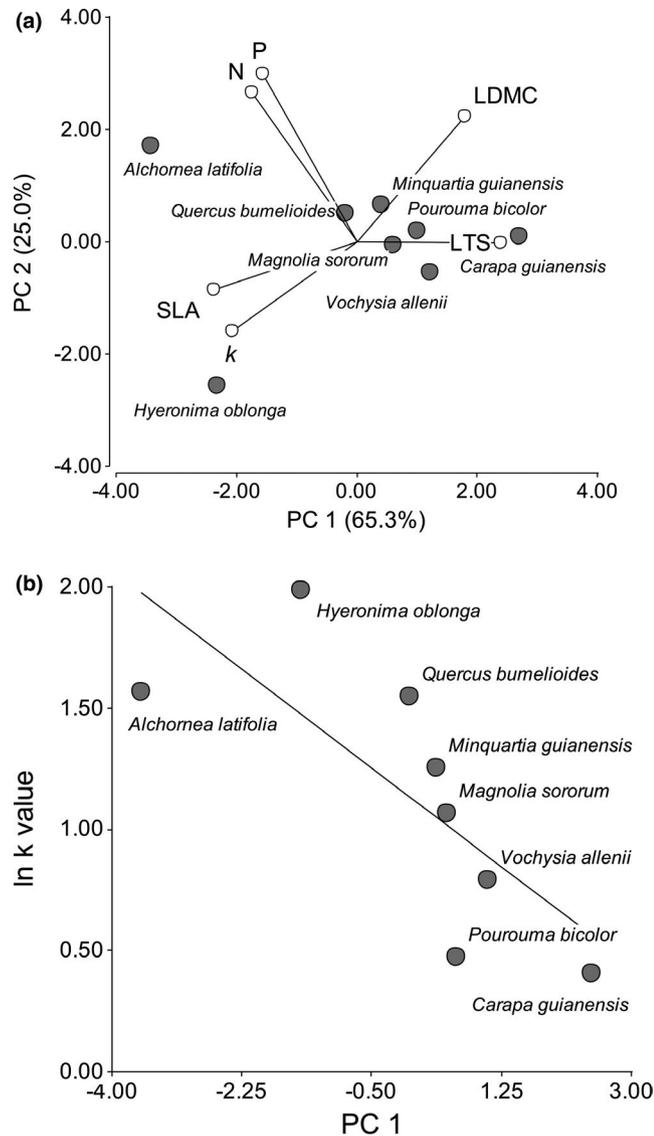


FIGURE 3 (a) Principal components analysis of native litter species in space defined by their leaf traits and k values. Trait abbreviations: SLA, specific leaf area, $\text{mm}^2 \text{mg}^{-1}$; LDMC, leaf dry matter content, mg/g ; F_p , force to tear, N/mm ; N, leaf nitrogen, mg/g ; P, leaf phosphorus, mg/g . b) Linear regression showing the relationship between k and species value on PC 1 of a principal components analysis without k ; $R^2 = 0.57$, $p = .0304$

other hand, five of our native tree species decomposed slower than the slow-decomposing standard species, *J. ichu*. This grass has high LTS, cellulose, and hemicellulose (Vairetti et al., 2005, who use the name *Stipa eriostachya* for this species). Similarly, in a reciprocal translocation experiment with twelve species from across a subarctic to tropical gradient, Makkonen et al. (2012) found that three tropical tree species had the lowest overall k values. Their tropical species had especially low P and high lignin and hemicellulose contents in their litter.

Soil factors may also contribute to the lack of a difference of decomposition rates between lowland wet forest and premontane rain forest. Compared to lowland wet forest, premontane rain forest

soils have higher pH, N, Ca, and Mg, lower mean clay contents (50% of that of lowland wet forest), and much lower acidity and acid saturation (40% of that of lowland wet forest) (Veintimilla et al., 2019). These soils differences may have positive effects on decomposition rates in premontane rain forest. However, the soils of the two life zones do not differ in extractable P, which is the better indicator of decomposition rates in the tropics (Wieder et al., 2009). We nevertheless suggest that through effects on the activity of decomposer organisms, the greater fertility of premontane rain forest soils may compensate for the potential reduction of decomposition rates due to the temperature difference between the life zones. Such an effect could be exacerbated by high Al^{3+} in the soil solution associated with low pH and high acid saturation in lowland wet forest soils, which may reduce decomposition rates in these soils (Takahashi & Dahlgren, 2016).

As we predicted, species rankings by decomposition rates remained broadly the same across all four life zones. We suggest that decomposer organisms in tropical rain forest ecosystems spanning a 10–24°C gradient of mean annual temperature respond to litter quality in the same way (cf. Makkonen et al., 2012). Our study shows that interspecific rankings by decomposition rates can be consistent across altitudinal gradients within the wet tropics.

Vochysia allenii was the only species that showed a potential home-field effect, decomposing faster in its “home” premontane rain forest than in lowland wet forest and contributing variation to species rankings across life zones. Our experiment was not designed to test for home-field effects, which are defined in relation to faster decomposition rates in the vicinity of the plant of origin of the litter (e.g., Veen, Freschet, Ordóñez, & Wardle, 2015). We nevertheless suggest that like *V. ferruginea* (Herrera & Finegan, 1997) and probably all other species of the Vochysiaceae family (de Andrade et al., 2011), *V. allenii* is a hyper-accumulator of foliar Al. If this is the case, then the high Al may be interacting with decomposer organisms or soil characteristics to increase the decomposition rate of this species at its home site. Given the dominance of this species throughout premontane rain forest of Costa Rica's Caribbean slope (Heaney & Proctor, 1989; Veintimilla et al., 2019), the potential effect of Al hyper-accumulation on carbon cycling is of great interest.

4.3 | Final comment

The expected effects of global change drivers on ecological processes in rain forest on tropical mountains will have consequences not only on those mountains but also throughout their drainage basins. The decomposition of leaf litter is a fundamentally important biogeochemical process, at scales from that of the drainage basin to the global. Our study has focused on the effects of altitude and therefore temperature, as well as species identity, on decomposition rates. The overall decline of rates with increasing altitude suggests that in the absence of changes in moisture regime in our study area, decomposition rates will increase as a

direct effect of increasing temperatures. Such an increase may potentially bring about reductions in soil carbon storage, which is especially high in the montane rain forests (Veintimilla et al., 2019). On the other hand, the lowland wet and premontane rain forest life zones in our area did not differ strongly in their decomposition rates, suggesting that at least the premontane zone may not change greatly under warming in the premontane zone. Finally, species identity is a major factor affecting decomposition rates. If warming of the study area brings about changes in the potential altitudinal distributions and abundances of currently dominant species, then these changes will likely affect this critically important biogeochemical process.

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.1jwstqjqt> (Esquivel et al., 2019).

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SUPPORTING INFORMATION

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