

The sensitivity of tropical leaf litter decomposition to temperature: results from a large-scale leaf translocation experiment along an elevation gradient in Peruvian forests

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Summary

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- We present the results from a litter translocation experiment along a 2800-m elevation gradient in Peruvian tropical forests. The understanding of the environmental factors controlling litter decomposition is important in the description of the carbon and nutrient cycles of tropical ecosystems, and in predicting their response to long-term increases in temperature.
- Samples of litter from 15 species were transplanted across all five sites in the study, and decomposition was tracked over 448 d.
- Species' type had a large influence on the decomposition rate (k), most probably through its influence on leaf quality and morphology. When samples were pooled across species and elevations, soil temperature explained 95% of the variation in the decomposition rate, but no direct relationship was observed with either soil moisture or rainfall. The sensitivity of the decay rate to temperature (k_T) varied seven-fold across species, between 0.024 and 0.169°C^{-1} , with a mean value of $0.118 \pm 0.009^\circ\text{C}^{-1}$ (SE). This is equivalent to a temperature sensitivity parameter (Q_{10}) for litter decay of 3.06 ± 0.28 , higher than that frequently assumed for heterotrophic processes.
- Our results suggest that the warming of approx. 0.9°C experienced in the region in recent decades may have increased decomposition and nutrient mineralization rates by c. 10%.

Introduction

The decomposition of dead organic material is a fundamental global biogeochemical process, both through its role in the global carbon (C) cycle and, perhaps more importantly, through its role in the recycling to nutrients to soil and plant communities. Hence, changes in the rates of decomposition can have profound effects on ecosystem functioning and productivity, particularly in ecosystems, such as tropical forests, where nutrient supply for ecosystem productivity is predominantly through the decay and mineralization of plant material.

Global climate change is likely to increase the decomposition rates when long-term warming occurs in the absence of

moisture constraints, but few studies have explored the influence of environmental conditions on the decay rate in natural field conditions across multiple species (Gholz *et al.*, 2000; Santiago *et al.*, 2005; Cornelissen *et al.*, 2007; Zhou *et al.*, 2008; Cusack *et al.*, 2009; Powers *et al.*, 2009; Wieder *et al.*, 2009). In particular, with the exception of studies on unusual lava soils in Hawaii (Scowcroft *et al.*, 2000), there have been no investigations exploring the temperature sensitivity of decomposition *within* the tropics by exploiting elevation gradients in temperature. Any changes in decomposition processes can have profound impacts on the rate and pattern of nutrient cycling, and hence on forest plant and faunal community dynamics. To understand the responses of tropical rainforests to future

climate change, in terms of both shifts in biodiversity and biogeochemical cycling, it is crucial to understand and quantify the underlying controls on organic matter decomposition.

Environmental gradient studies have been recognized as powerful tools with which to explore and quantify the influence of environmental conditions on ecosystem processes (Dunne *et al.*, 2004; Malhi *et al.*, 2010). In particular, elevation studies have the potential to provide information on the sensitivity of ecosystem processes to temperature, although the covariance of temperature with other elevation-dependent variables necessitates caution in interpretation (Körner, 2002). Furthermore, reciprocal transplant experiments along environmental gradients can enable discrimination between direct environmental factors and other site-dependent factors, such as species' traits and composition (van de Weg *et al.*, 2009).

In this article, we report the results from a large-scale leaf material reciprocal transplant experiment along a 2800-m elevation gradient in the tropical Andes and adjacent Amazon lowlands. A moist tropical forest elevation gradient presents a number of logistical challenges, but also many scientific advantages, in particular the absence of substantial seasonality in temperature and of a dormant season (winter or strong dry season) that confounds the interpretation of latitudinal gradients. Furthermore, annual rainfall is consistently high, enabling a focus on temperature effects as the predominant control on ecosystem functioning.

The overall objective of this experiment was to examine biotic (litter quality) and abiotic (temperature, moisture) effects on fine litter decomposition. In this article, we focus

on temperature and moisture controls, and the influence of some leaf traits on decay rates.

We address the following research questions:

- How do the decomposition rate and mean residence time of leaf litter material vary with the elevation of the decomposition site?
- How much of the variation in the decomposition rate can be explained by temperature, and what is the sensitivity of leaf decomposition to temperature?
- How much do other environmental factors and leaf traits (e.g. soil moisture, variation in species of the source material) influence the decomposition rate?

Materials and Methods

Study site

We installed a 1.5-yr-long (448 d) reciprocal transplant and decomposition study in five tropical forest plots along a *c.* 2800-m elevation transect in Peru (Fig. 1). The study was carried out between 2007 and 2009 in five 1-ha plots of mature tropical rainforest (Table 1). The lowest site (elevation, 210 m) is in the Tambopata–Candamo National Reserve, in the lowland Amazon basin. The four upper sites are located in or close to the Manu National Park, centered on the Kosñipata Valley on the eastern flank of the Andes. Each site along the altitudinal gradient has unique vegetative features and climate. There is little seasonal variation in temperature at all sites and, although there is substantial seasonal variation in rainfall (Girardin *et al.*, 2010), there is little seasonal variation in soil moisture status.

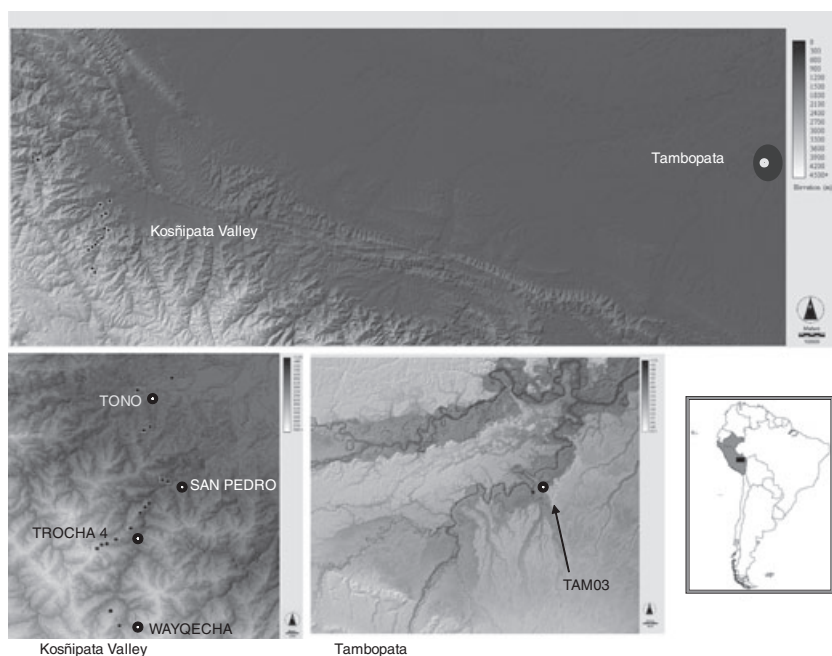


Fig. 1 Site map of the study region in the southern Peruvian Andes: Kosñipata valley, Manu National Park, and Tambopata–Candamo National Reserve, Peru.

Table 1 Summary of site characteristics; the soil nutrient data are for the organic layer

Study site	Lat (S)	Long (W)	Elevation (masl)	Temp. (°C)	Rainfall (mm yr ⁻¹)	Mean annual soil moisture (%)	Soil nutrient data (organic layer)		
							Total N (g kg ⁻¹)	Total P (g kg ⁻¹)	N : P
Tambopata	12°50'11"	69°16'45"	210	23.9	2730	21.3	16.4	1.4	11.7
Tono	12°57'33"	71°33'57"	1000	20.7	3087	39.8	14.7	0.9	16.3
San Pedro	13°2'56"	71°32'13"	1500	19.1	2631	28.5	12.2	1.1	11.0
Trocha Unión	13°6'30"	71°35'21"	2720	11.9	2318	37.3	17.0	0.6	26.5
Wayqecha	13°11'24"	71°35'13"	3025	11.1	1706	12.1	18.6	1.1	16.9

Experimental design

Leaves are the most important component of Amazon forest litterfall (Chave *et al.*, 2010). Leaves from the three dominant tree species in each plot were selected for translocation (summarized in Table 2). For the analysis presented here, we concentrate on senescent leaves from litterfall; in another paper, we will explore the differences between fresh and senescent leaves.

The study was conducted from December 2007 to May 2009. Leaf decomposition was evaluated through the litter bag technique (Swift & Anderson, 1989; Alvarez *et al.*, 1992). This is a useful technique to analyze and delineate differences in decomposition rate (Coleman & Crossley, 1996). Batches of approx. 3 g of senescent leaves were placed separately by species in 30 × 25-cm plastic mesh litter bags (2-mm netting). Each sample was weighed separately. The 2-mm mesh size was sufficiently small to prevent losses of litter caused by breakage, but not sufficiently large to permit the access of macrofaunal decomposers, such as worms and coleoptera. Therefore, we needed to add six small holes to ensure little restriction to macrofaunal access.

The litter bags from the 15 species were placed on the soil surface, on the five different plots, and exposed to natural

weather conditions and soil-borne decomposers by placement just under the natural litter layer in each forest plot.

Experiment layout

The same experimental layout was used for all 15 species; 21 samples from each species were placed in each plot in three clusters (replicates) of seven sample bags situated at distinct locations within the plots. One sample bag from each cluster was collected at every sample time (see the third paragraph in this section). Hence, in total, 105 sample bags (3 replicates × 7 sample bags × 5 plots) were installed for each species.

The same set-up was repeated for three dominant species from each plot (3 species × 5 plots = 15 sample species in total). The experiment was comprehensively symmetrical with every sample species distributed to every sample plot in the transect. Hence, in total, 1575 sample bags were installed (105 bags per species × 15 species) in the experiment reported here (a further 3150 bags of fresh leaf material samples were also installed for an analysis of fine vs coarse mesh decomposition rates to be reported in a separate paper). This was a substantial logistical undertaking in a transect stretching across challenging and remote terrain.

Table 2 List of species sampled at each source elevation, and their representativeness of the trees of > 10 cm diameter at breast height in the plot at that elevation, as a percentage of individuals and of basal area (BA)

Site	Elevation (masl)	Family	Species	% individuals	% BA
Tambopata	210	Clusiaceae	<i>Calophyllum brasiliense</i>	1.86	0.59
		Bixaceae	<i>Bixa arborea</i>	3.36	0.55
		Urticaceae	<i>Pourouma minor</i>	8.22	1.41
Tono	1000	Clusiaceae	<i>Symphonia globulifera</i>	0.83	0.17
		Moraceae	<i>Perebea guianensis</i>	8.92	0.86
		Myristicaceae	<i>Virola sebifera</i>	8.50	2.87
San Pedro	1500	Clusiaceae	<i>Vismia</i> sp.	0.93	0.45
		Euphorbiaceae	<i>Alchornea latifolia</i>	3.62	1.85
		Fabaceae	<i>Tachigali setifera</i> cf.	6.42	1.58
Trocha Union	2720	Clusiaceae	<i>Clusia alata</i> cf.	2.64	0.92
		Cunoniaceae	<i>Weinmannia bangii</i>	5.88	2.83
		Lauraceae	<i>Nectandra longifolia</i>	6.60	3.11
Wayqecha	3025	Clusiaceae	<i>Clusia alata</i> cf.	10.43	3.36
		Cunoniaceae	<i>Weinmannia crassifolia</i>	32.77	7.68
		Rosaceae	<i>Hesperomeles ferruginea</i>	3.04	1.18

After placement of the bags, one bag for the three replicated clusters was retrieved after 7, 14, 28, 56, 112, 224 and 448 d in each plot (each time interval being measured from initial installation). This made seven time sample points in total, separated logarithmically in time, over the period December 2007 to May 2009. Immediately after retrieval, the temperature in the surface soil beneath the removed bag was recorded using a TESTO 926 thermometer with a TESTO penetration probe T260 (Testo Ltd, Alton, Hampshire, UK). After this, all organic material was removed from the bag, carefully cleaned of roots and inorganic debris, dried at 80°C until constant mass and weighed.

The initial mean specific leaf area (SLA) of the litter was calculated from the area estimated using punched lamina disks of known diameter: 5.54 mm. A total of 30 leaf disks from a minimum subsample of three leaves per litter bag was oven-dried to constant mass to derive SLA. Immediately after drying, the leaf discs were weighed and the SLA was derived as the leaf area per unit leaf dry weight ($\text{cm}^2 \text{g}^{-1}$).

Data analysis

The decomposition rate of any one cluster of seven samples per bag was estimated from the rate of mass loss over time. The decay rate was characterized by fitting a single exponential decay function first proposed by Jenny *et al.* (1949) and discussed in considerable detail by Olson (1963):

$$M_t = M_0 e^{-kt},$$

M_0 , initial mass; M_t , residual leaf mass after time t expressed as a proportion of the initial dry mass; k , decay constant expressed in units d^{-1} ; hence, k can be derived for any sample set as the slope of a linear regression of $\log_e(M_t/M_0)$ against time.

The appeal of this exponential model arises from the fact that a single constant k characterizes the loss of mass, thereby facilitating comparisons with other datasets and simplifying attempts to model the accumulation of organic C in soils (Olson, 1963; Oohara *et al.*, 1971). The assumption underlying this single-exponential model is that either the absolute decomposition rate decreases linearly with decreasing mass or, alternatively, the relative decomposition rate remains a constant fraction of the remaining litter mass (Hyvönen *et al.*, 2005):

$$\frac{dM}{dt} = -kM$$

Analysis of the temperature sensitivity of decay

We also exploited the elevation gradient to explore the sensitivity of the decay rate to temperature (assuming that

temperature was the main driver, direct or indirect, of differences seen between samples of common origin translocated to different sites).

We fitted an exponential model:

$$k = k_{15} \exp(-\kappa_T(T - 15)),$$

k , decay constant of samples from a particular species at a site with a measured mean temperature T (°C); k_{15} , reference decay constant at an arbitrary reference temperature of 15°C (a temperature within the range encompassed by the transect); κ_T , temperature sensitivity coefficient (unit: $^{\circ}\text{C}^{-1}$).

In ecophysiological literature, this temperature sensitivity is often expressed as a Q_{10} coefficient, where Q_{10} is the change in the decay constant associated with a 10°C change in temperature:

$$Q_{10} = \exp(10\kappa_T)$$

Results

The variation of climate (temperature, rainfall, mean soil moisture) with elevation is given in Table 1. These data were collected over the period 2006–08. As would be expected, the soil temperature (top 10 cm) decreases steadily with elevation, at a lapse rate of 4.79°C per 1000 m. Rainfall reaches a maximum near the base of the mountains at 1000 m and declines steadily up the Kosñipata valley, and also declines away from the mountains into the Amazonian lowlands. The decline of transpiration at high elevations (through cloudiness, high atmospheric humidity and low temperatures) maintains high and largely aseasonal soil moisture values throughout the montane transect.

How do the decomposition rate and the mean residence time of dead leaf organic material vary with elevation of the decomposition site?

The variation of the decay rate, averaged across all samples at each site, is illustrated in Fig. 2(a). This is the mean across the leaf samples from all 15 species deposited at each site, that is the same compiled set of 15 species decomposing at every site. The mean value of k declines from $(4.80 \pm 0.55) \times 10^{-3} \text{d}^{-1}$ at 210-m elevation to $(1.16 \pm 0.16) \times 10^{-3} \text{d}^{-1}$ at 3025 m. As would be expected, there is a general tendency for decay rates to increase with decreasing elevation (increasing temperature), but with evidence of substantial interspecific variability. All species tend to show a decline in k with elevation. In subsequent sections, we explore the interspecific variation of the decay rate.

When we consider the mean decay rates of all species in their original locations (i.e. considering only leaves from the three species sampled in each plot), there appears to be a

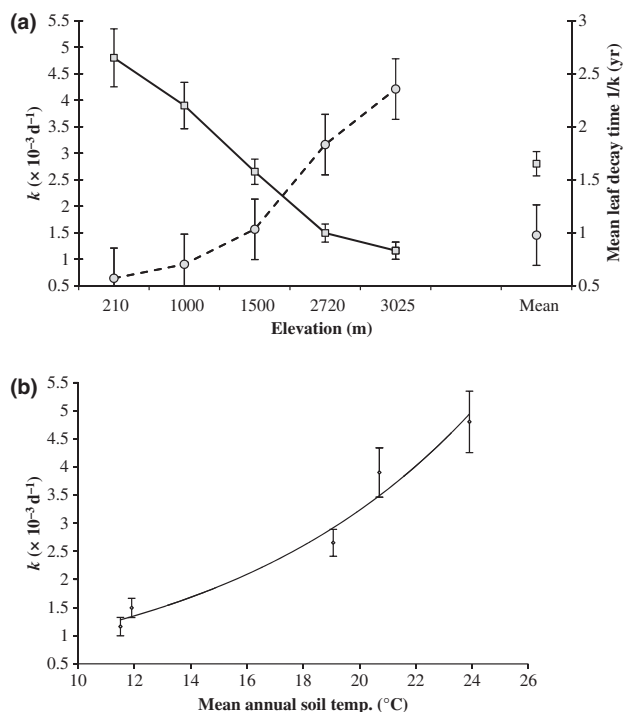


Fig. 2 (a) The mean measured decay rate parameter k along the altitudinal gradient and the residence time, inversely related to the decomposition rate, averaged across all 15 sampled species decaying at each elevation (the same compiled set of 15 species decomposing at every site). (b) The relationship between the mean decay rate (k , averaged across all 15 species) and temperature. The line indicates an exponential fit ($r^2 = 0.97$, $P = 0.002$, slope = $1.09\text{E}-01$).

step-like pattern, with the three lowest plots showing high decomposition rates and the two highest plots showing low decomposition rates (Fig. 3a). This is indicative of some interaction between species' composition and source elevation.

Within each elevation, there is substantial interspecific variation of the decay rate for the three 'local' species (Fig. 3a). This is k for each species decomposing at its source location. The mean value of k shows a four-fold range from $(4.34 \pm 0.79) \times 10^{-3} \text{ d}^{-1}$ in *Pourouma minor* at 210-m elevation to $(1.03 \pm 0.24) \times 10^{-3} \text{ d}^{-1}$ in *Nectandra longifolia* sp. at 2720-m elevation.

The residence time of leaf litter, $1/k$, is shown in Table 3. Fig. 2(a) (by site) and Fig. 3(a) (by species) plot the estimated mean leaf decay time (in years) for leaf litter at each plot, across all species, and for only species originating from the same plot. Averages were calculated from the decay rate parameter k , annualized by multiplying by 365 (days), and then converted into a mean residence time in years by taking the reciprocal. This was calculated from averaged k , rather than averaging the residence times for each species, to maintain linearity. Across all 15 species, the mean residence time varies from 0.570 ± 0.064 yr

(= 7 ± 1 month) at 210 m to 2.35 ± 0.33 yr at 3025 m. Across samples, the longest residence times are found for *Nectandra longifolia* from 2720 m (at 2.6 yr), and the shortest times for leaves from *Pourouma minor* from 210 m (at 0.63 yr).

What does the variation in decomposition rate with elevation indicate about the sensitivity of leaf decomposition to temperature?

For each species, the mean decay rate of that species along the altitudinal gradient was regressed against site mean soil temperature using an exponential fit. On average, $83 \pm 4\%$ of the variance of the decay rate within each species across elevation (range across species, 38–99%) can be explained by an exponential regression of the mean decay rate over the temperature (see Table 3). When the decay rates of all samples at each site are averaged together (Fig. 2b), an exponential regression against temperature explains 97% of the variance of the decay rate with elevation. Hence, the variation in (across-sample averaged) decay rate along the transect is almost entirely explained by temperature.

The coefficient of the exponential regression is the temperature sensitivity parameter κ_T from which the Q_{10} parameter can also be derived. Fig. 3(c) plots the value of κ_T against sample species. The mean value of κ_T across the study (all 15 species) is $0.118 \pm 0.009^\circ\text{C}^{-1}$, from which we calculate a mean Q_{10} value of 3.06 ± 0.28 across the whole decomposition experiment. Across species (Table 3), κ_T varies by a factor of seven from 0.024°C^{-1} to 0.169°C^{-1} (corresponding to a Q_{10} variation from 1.28 to 5.43). When considering the source *site* of the leaf material, the highest temperature sensitivity of decay is found in leaf material from Tono (1000 m; $Q_{10} = 4.32$), and the lowest in San Pedro (1500 m) and Tambopata (210 m): $Q_{10} = 2.24$ and 2.50. The only two distinct samples from the same species at different elevations (*Clusia alata*: 2720 m and 3025 m) showed significantly different values of κ_T ($0.095 \pm 0.032^\circ\text{C}^{-1}$ and $0.141 \pm 0.014^\circ\text{C}^{-1}$, respectively), indicating that intraspecific variation may also be substantial.

How much do other environmental factors apart from temperature (e.g. soil moisture, rainfall) influence the decomposition rate?

From the exponential relationship with temperature, the species-specific temperature sensitivity κ_T and a temperature-adjusted decay rate (k_{15} , an estimate of the decomposition rate at a mean soil temperature of 15°C) were derived for each sample (Fig. 3b).

As expected from the high r^2 value of our exponential regression against temperature, for any particular species, there is a generally flat relationship between k_{15} and source

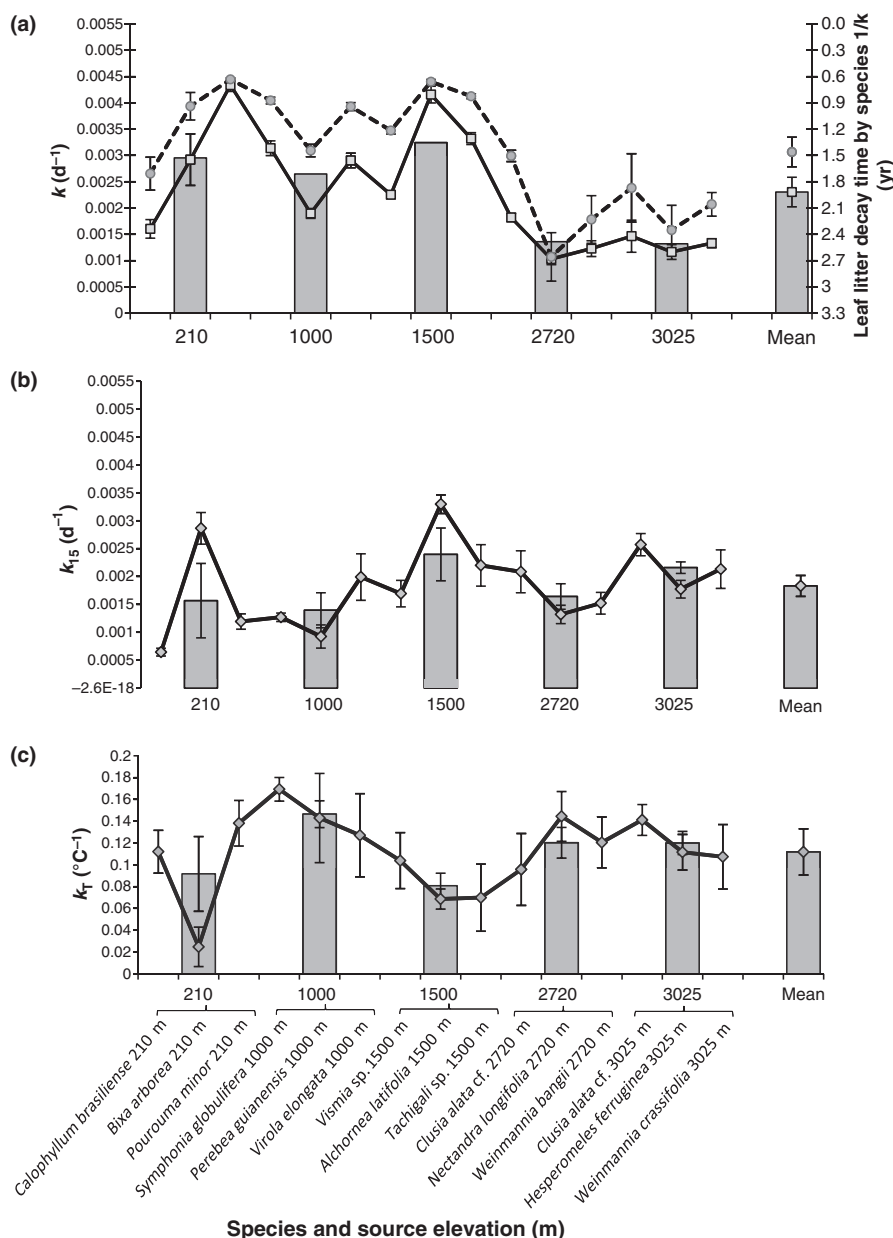


Fig. 3 (a) The measured decomposition rate parameter k (d^{-1}) along the altitudinal gradient and the residence time, inversely related to the decomposition rate, considering only the three species sampled and decay from the local site. The x-axis also indicates the source elevation of each species. The solid line with squares indicates the value for each species; bars indicate the mean averaged across the three species at each site. Error bars indicate the standard error of the mean ($n = 3$ for each species, $n = 9$ for each source elevation). Dashed line with circles, residence time. (b) Mean decomposition rate corrected to a standardized temperature of 15°C using an exponential fit against mean soil temperature. The x-axis also indicates the source elevation of each species. The solid line with diamonds indicates the adjusted decay rate k_{15} (d^{-1}) for each species; bars indicate the mean k_{15} value averaged across the three species at each site. Error bars indicate the standard error of the mean ($n = 3$ for each species, $n = 9$ for each source elevation). (c) Plots against sample species of the temperature sensitivity parameter κ_T ($^{\circ}\text{C}^{-1}$). The x-axis also indicates the source elevation of each species. The solid line and diamond indicate the mean value for each species; bars indicate the mean averaged across the three species derived from each elevation. Error bars indicate the standard error of the mean ($n = 3$ for each species, $n = 9$ for each source elevation).

elevation. The mean value of k_{15} is $(1.83 \pm 0.18) \times 10^{-3} \text{ d}^{-1}$; interspecific variation in k_{15} is very high (and explains more of the overall variance than temperature), with k_{15} showing more than a five-fold variation, ranging from

$(0.64 \pm 0.069) \times 10^{-3} \text{ d}^{-1}$ for *Calophyllum brasiliense* to $(3.30 \pm 0.16) \times 10^{-3} \text{ d}^{-1}$ for *Alchornea latifolia* (1500 m). A linear regression between the temperature-adjusted decay rate k_{15} and other climatic variables (mean rainfall, mean

Table 3 Values of the decay rate k (yr^{-1}) by site (mean k of all 15 species decaying at each site) and species, temperature-adjusted decay rate k_{15} (d^{-1}), temperature sensitivity parameters κ_T ($^{\circ}\text{C}^{-1}$) and Q_{10} for each species, with associated standard errors, and leaf litter residence time (RT, $1/k$) in years¹

Place/species/elevation	k (yr^{-1})	k_{15} (d^{-1})	Δk_{15}	κ_T ($^{\circ}\text{C}^{-1}$)	$\Delta \kappa_T$ $^{\circ}\text{C}^{-1}$	r^2	P	Q_{10}	ΔQ_{10}	RT 1/ k (yr)
Tambopata 210 m	1.753									0.571
<i>Calophyllum brasiliense</i> 210 m	0.586	6.45E-04	6.93E-05	0.1121	0.0196	0.9158	0.0106	3.0673	0.6017	1.707
<i>Bixa arborea</i> 210 m	1.066	2.86E-03	2.84E-04	0.0248	0.0181	0.3852	0.2639	1.2814	0.2317	0.938
<i>Pourouma minor</i> 210 m	1.582	1.19E-03	1.37E-04	0.1382	0.0209	0.9356	0.0071	3.9826	0.8335	0.632
Tono 1000 m	1.424									0.702
<i>Symphonia globulifera</i> 1000 m	1.145	1.27E-03	7.53E-05	0.1693	0.0108	0.9879	0.0006	5.4376	0.5882	0.873
<i>Perebea quianensis</i> 1000 m	0.692	9.25E-04	2.07E-04	0.1430	0.0409	0.8027	0.0396	4.1778	1.7095	1.444
<i>Virola sebifera</i> 1000 m	1.060	1.99E-03	4.16E-04	0.1271	0.0382	0.7871	0.0447	3.5652	1.3609	0.943
San Pedro 1500 m	0.968									1.033
<i>Vismia</i> sp. 1500 m	0.822	1.69E-03	2.38E-04	0.1039	0.0257	0.8450	0.0272	2.8262	0.7259	1.216
<i>Alchornea latifolia</i> 1500 m	1.518	3.30E-03	1.66E-04	0.0687	0.0092	0.9488	0.0050	1.9875	0.1831	0.659
<i>Tachigali setifera</i> cf. 1500 m	1.212	2.20E-03	3.71E-04	0.0699	0.0308	0.6318	0.1081	2.0124	0.6203	0.825
Trocha Union 2720 m	0.546									1.832
<i>Clusia alata</i> cf. 2720 m	0.665	2.09E-03	3.77E-04	0.0958	0.0330	0.7378	0.0622	2.6060	0.8592	1.505
<i>Nectandra longifolia</i> 2720 m	0.376	1.32E-03	1.65E-04	0.1445	0.0228	0.9304	0.0080	4.2409	0.9673	2.656
<i>Weinmannia bangii</i> 2720 m	0.448	1.52E-03	1.95E-04	0.1205	0.0234	0.8988	0.0141	3.3382	0.7797	2.230
Wayquecha 3025 m	0.424									2.356
<i>Clusia alata</i> cf. 3025 m	0.535	2.57E-03	1.99E-04	0.1412	0.0141	0.9708	0.0021	4.1041	0.5801	1.870
<i>Hesperomeles ferruginea</i> 3025 m	0.425	1.77E-03	1.59E-04	0.1116	0.0163	0.9397	0.0064	3.0534	0.4983	2.351
<i>Weinmannia crassifolia</i> 3025 m	0.486	2.13E-03	3.45E-04	0.1074	0.0295	0.8150	0.0358	2.9280	0.8652	2.057
Mean across all species		1.83E-03	1.88E-04	0.1119	0.0094					
Q_{10} mean derived from mean κ_T								3.06	0.29	

¹The coefficient of determination r^2 gives the fraction of variance in decay rate within a species that is explained by an exponential regression against temperature; the P value is the significance of the regression fit. Bold values indicate the mean k of all species decaying at each site.

soil moisture) suggested no significant linear relationship with either soil moisture ($r^2 = 0.27$, $P = 0.37$) or annual rainfall ($r^2 = 0.28$, $P = 0.35$). In summary, 97% of the variation of (across-species' mean) decay rate with elevation can be explained by the mean annual temperature, and moisture/rainfall explains only an additional 1–2% the variance.

Is there a relationship between the source elevation of the material and the decay rate?

Fig. 3(b) (bars) shows the variation in the temperature-adjusted decay rate (k_{15}) for each source elevation across the altitudinal gradient. There is no overall trend in k_{15} against source elevation, but significantly higher values in material from 1500- and 3025-m elevation. The 1500-m result is caused by high values for a single species, *Alchornea latifolia*, and, to a lesser extent, at 3025 m, *Clusia alata* shows high k_{15} . Hence, there may be some site-to-site variation in the temperature-adjusted decay rates, although, with only three species sampled per site, this result is tentative, as such an analysis is probably dominated by the decay characteristics of the particular species that happen to be sampled.

When we examine the single species sampled at more than one site, *Clusia alata*, the samples from two different

elevations (3025 and 2720 m) present no significantly different temperature-adjusted rates of decomposition k_{15} (from 3025 m, $k_{15} = (2.57 \pm 0.19) \times 10^{-3} \text{ d}^{-1}$; from 2720 m, $k_{15} = (2.09 \pm 0.37) \times 10^{-3} \text{ d}^{-1}$).

How much do the properties of the source leaf material (e.g. SLA) influence the decomposition rate?

As already pointed out, there is a five-fold variation in the temperature-adjusted decay rate k_{15} between species. This difference may be caused by the morphological characteristics of the leaves (e.g. epidermis with thick cuticle), or the content of nutrients or specific structural compounds (e.g. lignin or phenols). In order to explore these different traits in the leaves, we quantified SLA, nitrogen (N), C, C : N ratio and morphological data for each species (Table 4). We did not have access to data on structural compounds such as lignins. There was no significant relationship in the linear regression of k_{15} vs SLA ($r = 0.02$, $P = 0.55$), N ($r = 0.01$, $P = 0.70$), C ($r = 0.03$, $P = 0.50$) or C : N ($r = 0.01$, $P = 0.70$). Therefore, the across-species' variation in k_{15} cannot be explained by these simple composition indicators; more detailed chemical or structural analysis is probably required to identify the species-specific controls on the decomposition rate.

Table 4 Correlation analyses between the decay rate corrected to a standardized temperature of 15°C using an exponential fit against mean soil temperature (k_{15}), temperature sensitivity coefficient (κ_T) and leaf traits

Species and elevation	SLA (cm ² g ⁻¹)	N (%)	C (%)	C : N	k_{15}	κ_T
<i>Calophyllum brasiliense</i> 210 m	111.4	1.19	53.61	45.05	0.001	0.112
<i>Bixa arborea</i> 210 m	250.0	2.46	49.99	20.32	0.003	0.025
<i>Pourouma minor</i> 210 m	111.4	2.04	49.75	24.39	0.001	0.138
<i>Symphonia globulifera</i> 1000 m	122.5	2.33	51.51	22.11	0.001	0.169
<i>Perebea guianensis</i> 1000 m	81.7	2.09	45.00	21.53	0.001	0.143
<i>Virola elongata</i> 1000 m	53.3	1.95	53.80	27.59	0.002	0.127
<i>Vismia</i> sp. 1500 m	94.2	1.34	51.68	38.57	0.002	0.104
<i>Alchornea latifolia</i> 1500 m	81.7	1.70	48.01	28.24	0.003	0.069
<i>Tachigali</i> sp. 1500 m	87.5	2.48	50.65	20.42	0.002	0.070
<i>Clusia alata</i> cf. 2720 m	49.0	1.44	50.58	35.13	0.002	0.096
<i>Nectandra longifolia</i> 2720 m	40.8	1.27	52.06	40.99	0.001	0.144
<i>Weinmannia bangii</i> 2720 m	72.1	1.18	50.18	42.53	0.002	0.121
<i>Clusia alata</i> cf. 3025 m	61.3	1.47	50.53	34.37	0.003	0.141
<i>Hesperomeles ferruginea</i> 3025 m	55.7	0.63	51.06	81.05	0.002	0.112
<i>Weinmannia crassifolia</i> 3025 m	55.7	0.46	45.51	98.93	0.002	0.107
Correlation with k_{15}	$r = 0.17$ $P = 0.55$	$r = 0.11$ $P = 0.70$	$r = 0.19$ $P = 0.50$	$r = 0.31$ $P = 0.91$		

r and P values are given. The values suggest no significant relationship. SLA, specific leaf area.

Is there a relationship between the (temperature-corrected) decay rate and the sensitivity of the decay rate to temperature?

Fig. 4 plots κ_T against k_{15} . There is a significant negative relationship ($\kappa_T = (-33.1 \pm 10.5) \times k_{15} + (0.17 \pm 0.02)$, $P < 0.01$, adj. $r^2 = 0.43$). Hence, leaves that have intrinsically slow decomposition rates tend to have a higher sensitivity of the decay rate to temperature. The two parameters κ_T and k_{15} are quite independent: κ_T is the slope of the linear regression of $\log(k)$ against temperature, and k_{15} is the intercept of that regression at $T = 15^\circ\text{C}$. As $T = 15^\circ\text{C}$ is fairly central in the dataset, there is little *a priori* relationship to be expected between κ_T and k_{15} .

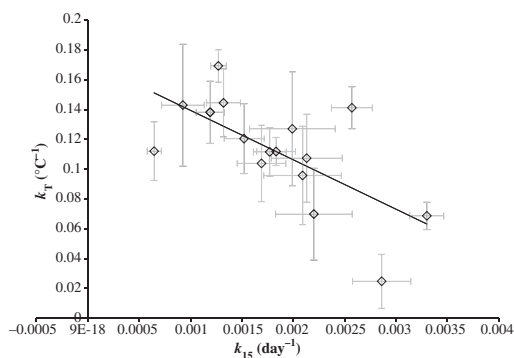


Fig. 4 A plot of κ_T against k_{15} , showing the relationship between the (temperature-corrected) decay rate and the sensitivity of the decay rate to temperature. Species with a high intrinsic decay rate have decay rates that are less sensitive to temperature. The linear fit is $\kappa_T = -33.133k_{15} + 0.1725$ ($r^2 = 0.43$, $P = 0.01$).

Discussion

Elevation and leaf decomposition rates

To some extent, this transect represents near-ideal conditions for a translocation experiment of this sort, with fairly constant year-round temperatures, no evidence of substantive soil moisture restrictions and no dormant winter season. Hence, it is very likely that the primary abiotic factor affecting the decomposition rate across sites is temperature. Overall, the rate of decomposition declined steadily with elevation. At the species' level, there was a substantial (four-fold) variation in the decay rate among species; however, once we averaged across species and examined only the environmental drivers of decay, we found that an exponential response to the annual mean soil temperature could account for 97% of the variance in the decay rate, and soil moisture/rainfall could account for only a further 1–2%. The dominant role of temperature in our data may appear surprising, given the importance of moisture content for decomposition (Howard & Howard, 1979), but it appears that the annual timescale of our analysis means that any short-term effects of low moisture availability on leaf litter decomposition (e.g. as observed for soil respiration; Zimmermann *et al.*, 2009a,b) are slight.

Similarly, some differences among sites and species may have reflected differences by site in the availability of litter-consuming macrofauna. Our data did not suggest a large explanatory role for this, except where the macrofauna were themselves correlated with temperature (e.g. termite abundance and activity increases with temperature). The strong relationship with temperature, and the extensive nature of

this translocation experiment, led us to speculate that our results may be used as a generalized estimate of the sensitivity of the decomposition of tropical forest leaf material to temperature (Fig. 2b), although we also note the large inter-species' variation in our data (Fig. 3c). We found that the temperature coefficient κ_T , when averaged across the study (all 15 species), was $0.111 \pm 0.009^\circ\text{C}^{-1}$, which corresponds to a mean Q_{10} value of 3.06 ($\text{CI}_{95} = \pm 0.56$), very similar to the value reported by Scowcroft *et al.* (2000) ($Q_{10} = 2.96$; $\text{CI}_{95} = 1.2$) from a single-species' litter transplant experiment along an elevation transect in Hawaii. Similarly, Gholz *et al.* (2000) reported a Q_{10} value of 2.70 for leaves from two contrasting tree species transplanted over a large latitudinal gradient from Arctic tundra to the tropics, although the interpretation of latitudinal gradients is complex because of the variation in seasonality. The value of Q_{10} is higher than that found for some heterotrophic processes, and is substantially higher than assumed in many ecosystem models (where Q_{10} is typically assumed to be *c.* 2; Hyvönen *et al.*, 2005).

This strong sensitivity to temperature of the leaf decay rate will affect both the C cycle and the rates of mineralization and nutrient supply. In many tropical forests on infertile soils, the bulk of nutrient supply required for new production comes from the recycling of litter material (Vitousek, 1984), and hence productivity in tropical forests may be particularly sensitive to rates of leaf decay. This sensitivity of net primary production to temperature may be greatest in tropical montane systems, where nutrient supply may be more limited by mineralization rates than in lowland tropical forests (Schoor, 2003). On this elevation transect, we found increasing net primary production with increasing temperature (Girardin *et al.*, 2010), which may be explained, at least partially, by nutrient supply, although other factors, such as direct temperature effects on plant physiology, are also likely to be important.

Recently, Powers *et al.* (2009) reported a global litter decomposition experiment in which samples of two species were placed in litter bags in 23 tropical forest sites. They found that annual precipitation was the best predictor of decomposition rates in tropical forests ($r^2 = 0.6$, after excluding two outliers), and that temperature added little predictive value. This appears to contradict our results found here. One key feature is that there is little seasonal soil moisture limitation along our transect, except perhaps at the lowland site (Girardin *et al.*, 2010; this is probably driven as much by the reduction in transpiration and cloud interception in the high montane zones as by precipitation). Coupled with the size of our temperature contrasts, this enables us to detect a strong temperature effect, which may be difficult to distinguish in the multi-region analysis of Powers *et al.* (2009), where biogeographical variations and confounding climatic or edaphic variables may complicate a simple regression analysis, and most sites are at similar

warm temperatures. Hence, we suggest that temperature *does* have a strong impact on tropical decomposition rates, whilst recognizing that seasonal moisture limitation is also important in many tropical regions. At a time when tropical rainforest regions are showing a spatially consistent warming (Malhi & Wright, 2004), but spatial variability in directions of precipitation change, this distinction between temperature and moisture effects on decomposition rates is important.

Influence of source material

Although temperature is the overriding environmental influence on the decay rate along this transect, the nature of the source material probably also has a major influence on the rate of decay. Our leaf litter k -values ranged from 0.37 to 1.58 yr^{-1} across species (Table 3), a four-fold variation, greater than the range in the mean decomposition rate along the transect. Wieder *et al.* (2009) noted a similar four-fold range ($0.86 \pm 0.07 \text{ yr}^{-1}$ to $3.24 \pm 0.14 \text{ yr}^{-1}$) for the decomposition rate across 11 tropical species in Costa Rica, and the strong influence of leaf traits on the decomposition rate has been noted in a recent global analysis (Cornwell *et al.*, 2008). We found no correlation with obvious leaf chemical properties, No obvious relationship was found between (temperature-corrected) decomposition rates and leaf litter traits, such as SLA, initial N content or C content. This has also been found in other reported studies. Li *et al.* (2008) found no obvious correlation between SLA and leaf litter decomposition rate across 20 species in China, and also indicated that leaf litter decomposition was not affected by mature leaf N content. However, data were not available on lignin content in our study, which has been shown to be a good predictor of tropical leaf decomposition rates (Wieder *et al.*, 2009).

We explored whether there was any systematic relationship between the decay rate characteristics of the source material and its elevation. We found substantial site-to-site variation, but little evidence of an overall trend in either the temperature-adjusted decay rate (k_{15}) or the sensitivity to temperature (κ_T or Q_{10}). This variation between species is consistent with the work of Ewel (1976) and Songwe *et al.* (1995), who suggested that litter decay rates are strongly influenced by leaf characteristics (soft pubescent leaves decompose faster than leaves with prominent midribs and glabrous leathery cuticles), although we found limited evidence for this latter constraint. The relationship between the (temperature-adjusted) decay rate and the sensitivity to temperature (Fig. 4) is intriguing; species that are more resistant to decay appear to have a higher sensitivity to temperature. A high sensitivity to temperature indicates a high activation energy of the decomposition process in Arrhenius–Boltzmann kinetics (Gillooly *et al.*, 2002). Hence, a high mean activation energy of decomposition in some species (probably related to the content of lignin and other

breakdown-resistant compounds) appears to cause both a slow intrinsic decomposition rate (k_{15}) and a high sensitivity of decomposition to temperature (κ_T). Thus, it is possible that forests in which decomposition-resistant species predominate (i.e. forests on more infertile soils) may have a higher overall sensitivity of leaf decomposition to temperature than do forests with less protected leaves (usually fast-growing forests on more fertile soils).

Conclusions

We have presented results from what is, to our knowledge, the largest scale leaf decomposition study conducted in the tropics to date in terms of the number of samples. We have exploited a large elevation gradient to explore the environmental drivers of leaf decomposition along this 'ideal' transect with little constraint on water supply and little seasonality in temperature. Having found that temperature is overwhelmingly the most important driver, we have determined the sensitivity of the decay rate to temperature, resulting in an estimated Q_{10} value of 3.06 ($CI_{95} = \pm 0.56$), although we note that species' identity can strongly influence this value, and shifts in community leaf traits over time will influence the long-term temperature response of ecosystem decomposition rates to rising temperature and CO_2 .

An obvious final question that arises is whether this temperature sensitivity of leaf litter decay is maintained under higher temperatures than those currently experienced in the Amazonian lowlands. The lowland tropics have been warming at *c.* 0.3°C per decade since the 1970s (Malhi & Wright, 2004), and are projected to warm by 4°C under mid- to high-greenhouse gas emission scenarios for the 21st century. Applying a Q_{10} value of 3.06 for this whole period, and assuming no seasonal or climate change-related moisture constraint, this would imply that litter decay rates may have increased by up to 10% for a 0.9°C warming over the last three decades, and would increase by up to 53% from a 4°C warming. If lowland tropical forest productivity is limited to some extent by nutrient supply through litter decay, such an increase in temperature, coupled with increasing atmospheric CO_2 concentrations, may be part of an explanation of why forests in lowland Amazonia appear to have accelerated in growth and increased in biomass in recent decades (Phillips *et al.*, 1998; Malhi & Phillips, 2004).

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