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Quantifying the factors affecting leaf litter decomposition across a tropical forest disturbance gradient

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Abstract. Deforestation and forest degradation are driving unprecedented declines in biodiversity across the tropics, and understanding the consequences of these changes for ecosystem functioning is essential for human well-being. Forest degradation and loss alter ecosystem functioning through changes in species composition and abiotic conditions. However, the consequences of these changes for heterospecific processes are often poorly understood. Leaf litter decomposition is a major source of atmospheric carbon and critical for carbon and nutrient cycling. Through a highly replicated litter-bag experiment (3360 bags), we quantified the effects of litter quality, decomposer functional diversity and seasonal precipitation regime on litter decomposition along a tropical disturbance gradient in SW China. In addition, using soil and litter from sites selected from across the disturbance gradient, we established replicated litter-bed treatments and exposed these to a gradient of simulated canopy cover in a shade-house. Across the landscape, mass loss from litter-bags after 12 months varied from 7% to 98%. Even after 12 months, litter-bags installed at the beginning of the dry season had much lower mass loss than those installed at the beginning of the wet season. As expected, litter quality and faunal exclusion had substantial effects on decomposition rates. Decomposition rates declined along the disturbance gradient from mature forest, through regenerating forest to open land, although the effect size was strongly dependent on installation season. The effect of excluding meso- and macro-invertebrates increased with increasing forest degradation, whereas the effect of litter quality declined. Results from the shade-house experiment strongly suggested that forest degradation effects were driven predominantly by changes in micro-climatic conditions resulting from increased canopy openness. To better model the impacts of anthropogenic global change on litter decomposition rates, it will be important to consider landscape scale processes, such as forest degradation.

Key words: carbon cycle; decomposition; disturbance gradient; landscape; leaf litter; litter-bags; litter fauna; mass loss; mesocosm; seasonality; soil properties; tropical forest.

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INTRODUCTION

Deforestation and forest degradation are driving unprecedented declines in biodiversity across the tropics and understanding the consequences of these changes for ecosystem functioning is essential for human well-being. Plant litter decomposition is a critical ecosystem process. It is the principle pathway for nutrient cycling and transfers of above-ground carbon to soil, by providing the primary resources for the micro-organisms and detritivores involved in the process (Parton et al. 2007, Berg and McClaugherty 2014). It is also a major component of the global carbon cycle, producing over three times more CO_2 than the fossil fuel combustion (Coûteaux et al. 1995, Gholz et al. 2000, IPCC 2007). Forest degradation alters species composition, and hence the collective functional attributes of the biotic community, and the abiotic conditions of the habitat. Thus, the consequences for heterospecific processes are often complex and understanding of the effects of forest degradation on plant litter decomposition remains poor.

At global and regional scales, climate and leaf traits are important factors in determining litter decomposition rates (Meentemeyer 1978, Aerts 1997, Gholz et al. 2000, Cornwell et al. 2008, Zhang et al. 2008, Currie et al. 2010, Bakker et al. 2011, García-Palacios et al. 2013). For example, Powers et al. (2009) found a strong correlation between decomposition rates and mean annual precipitation among different tropical forests. The relationship between litter chemistry and decomposition has also been widely studied (Meentemeyer 1978, Taylor et al. 1989, Vitousek et al. 1994, Aerts 1997, Valachovic et al. 2004, Bakker et al. 2011) and a meta-analysis by Cornwell et al. (2008) found that within biomes the effects of leaf traits on litter decomposition were stronger than climatic controls. Chemical characteristics that enhance decomposition rates include low C:N, low lignin:N, a high concentration of non-structural carbon (C6-sugars and starch), high concentrations of total phenolics, and low polyphenols concentrations, especially tannins (Meentemeyer 1978, Melillo et al. 1982, Bakker et al. 2011, Coq et al. 2011, Hättenschwiler et al. 2011). In addition, Handa et al. (2014) found that, across a broad range of biomes, litter species richness had a small positive effect on the rates of C and N cycling in both terrestrial and aquatic systems.

Although decomposition is predominantly a microbial process, soil and leaf litter invertebrates enhance leaf litter decomposition by physically breaking up the organic material and stimulating microbial activity (Anderson et al. 1983, Berg and McClaugherty 2014). Globally, the relative importance of this faunal effect is known to increase with increasing total precipitation and minimum temperature (García-Palacios et al. 2013). Locally, the faunal effect is determined by the composition, abundance, and activity of the soil fauna, which in turn are partially dependent on the abiotic micro-environment, in particular the temperature and moisture content of the litter (González and Seastedt 2001). However, the contribution of invertebrates to decomposition also varies with litter quality, with a larger effect reported for more rapidly decomposing litter (Yang and Chen 2009, Handa et al. 2014). Abundance of the soil and litter invertebrate fauna also varies seasonally and may be partially responsible for seasonal dynamics in litter decomposition rates (Seastedt and Crossley 1980).

Decomposition rates also vary seasonally, as a consequence of changes in litter temperature and moisture (Rozema et al. 1999, Rigobelo and Nahas 2004, Eviner et al. 2006), resulting in higher wet season mass loss across a range of forest types (Bernhard-Reversat 1982, Seastedt et al. 1983, Torres et al. 2005). Low precipitation can limit leaching of the dissolved organic material from the litter, as well as reducing the activity of decomposers (Rigobelo and Nahas 2004). Decomposer activity may also be affected by the seasonal differences in substrate supply and quality (Schmidt et al. 2007). In addition, microbial communities are specific to the different stages of decomposition, because the chemical composition and physical properties of litter changes over the course of decomposition (Griffith and Boddy 1990, Berg and McClaugherty 2014). Hence seasonal variation in temperature and moisture may differentially affect different stages in the decomposition process. Thus, changes in decomposition rates linked to seasonal climate may interact with the effects of variation in litter fall, litter quality and the phase of decomposition of the substrate. At landscape scales litter decomposition depends on plant community composition and the composition of litter fauna (Vitousek et al. 1994, González and Seastedt 2001, Berg and McClaugherty 2014), both factors that may be altered when forests are degraded or lost. Forest disturbance also alters the abiotic conditions on the forest floor. Increased canopy openness results in higher day-time temperatures and a more rapid drying out of leaf litter (Zhang and Zak 1995), which is likely to influence the biological processes involved in litter decomposition and results in reduced decomposition rates. Nevertheless, the effect of forest degradation on plant litter decomposition has not been well studied and, in particular, researchers have not previously attempted to partition the relative contribution of changes in biotic and abiotic conditions.

The goal of our study was to quantify the effects of forest degradation on leaf litter decomposition. We considered both the direct effects of forest degradation and interactions with important known determinants of decomposition rates, including litter quality, decomposer functional diversity and seasonal precipitation regime. To this end, we conducted a highly replicated leaf-litter decomposition experiment along a disturbance gradient from mature forest to impoverished grassland. In addition, we repeated our measurements of litter decomposition in a novel mesocosm experiment designed to partition the abiotic and biotic effects of forest degradation. Researchers have previously used litter-bed mesocosms as a common-garden approach to examine the effects of plant functional traits, nutrient addition and invertebrate functional diversity on leaf litter decomposition (Seastedt and Crossley 1983, Cornelissen 1996, González and Seastedt 2001). We extended this approach by establishing replicated litter-bed treatments, using soil and leaf litter from selected sites across the disturbance gradient, and exposed these to different levels of simulated canopy cover in a shade-house.

Through these experiments, we examined the over-arching hypothesis that litter decomposition rates decline along the disturbance gradient from mature forest to open land. And, as microbial decomposition is likely to be strongly affected by reduced water availability in habitats with higher canopy openness (Zhang and Zak 1995, Rigobelo and Nahas 2004), we predicted that (1) the effect of litter quality would be greater in more degraded habitats and that (2) the contribution of invertebrate decomposers would be greater in more disturbed sites. Also, because decomposition is a successional process with particularly rapid decomposition during the initial stages, we predicted that (3) litter installed at the beginning of the wet season would decompose faster than litter installed at the beginning of the dry season. Finally, through our mesocosm experiment we examined the hypothesis that these habitat effects are primarily driven through the impact of forest degradation on the abiotic microclimate, rather than through differences in biotic conditions on the forest floor.

MATERIALS AND METHODS

Study site

Our research was conducted in Mengsong, Xishuangbanna, China (UTM/WGS84: 47 Q 656355 E, 2377646 N, 1100–1900 m asl; Appendix A: Fig. A1). The climate is strongly seasonal with 80% of the rainfall occurring over six months from May to October. Annual mean precipitation varies from 1600 to 1800 mm (Xu et al. 2009). Forest in the area has been classified as seasonal tropical montane rain forest, which grades into seasonal evergreen broad-leaved forest on hill slopes and ridges (Zhu et al. 2005). The rain forest contains many floristic elements in common with rain forests throughout SE Asia, although Dipterocarps are absent. The evergreen broadleaf forest is floristically similar to more seasonal forests to the north, with many species of Fagaceae and Lauraceae in the canopy.

This landscape has been occupied by Akha people for at least two centuries and until the Chinese government logging ban in 1998, the Akha practiced slash-and-burn agriculture (Xu et al. 2009, Kai et al. 2014). Since 1998, Akha have

Fig. 1. Illustrations of the study site and methods. The landscape in Mengsong: (a) mature forest in background with a tea plantation in the foreground; (b) mature forest behind with regenerating forest in the foreground; (c) *Imperata cylindrica* grasslands. Methods: (d) litter-bags on the forest floor; (e) mixing litter at the plot level before distributing to the litter-bed treatments; (f) construction of the litter-beds; (g) one set of litter-bed treatments; (h) close view of litter-bed treatments with litter-bags installed; (i) overview of shade-house illustrating the different levels of simulated canopy cover.

increased production of monoculture cash crops, in particular tea. The landscape is thus a complex mosaic of mature forest, younger forest regenerating following cultivation and open habitats, including terraced tea fields and *Imperata cylindrica* (L.) Raeusch. dominated grasslands (Fig. 1a–c).

In 2010 and 2011, 28 sample plots were established using a stratified random approach that resulted in 10 mature forest plots, 12 regenerating forest plots and six open land plots interspersed across the landscape (Appendix A: Table A1 and Fig. A1). Each plot comprised nine sub-plots arranged on a 3 × 3 grid with 50-m spacing between sub-plots.

Vegetation sampling

Vegetation (trees, shrubs, lianas, and herbs) data were collected from all 28 plots at a sub-plot level during 2010 and 2011. The diameter at breast height (dbh) was measured at 1.3 m. Trees, lianas and bamboos with >10 cm dbh were sampled from a 10 m radius circular plot centered on the sub-plot center. Trees, lianas and bamboos with 2–10 cm dbh were sampled from within a 5 m radius circle. The abundance of all herbs and woody seedlings with diameter <2 cm dbh was assessed for a 1 m radius circle using the Braun-Blanquet scale. Vouchers were identified at the Xishuangbanna Tropical Botanical Garden (XTBG) herbarium and subsequently deposited at the herbarium of the Kunming Institute of Botany.

To calculate canopy openness, hemispherical photographs were taken above each sub-plot center and processed using ImageJ (Schneider et al. 2012, Beckschäfer et al. 2014).

Soil and topographic data

We sampled soil from all the 28 plots at sub-plot level. The top soil (0–0.15 m) was collected from 2 m away from the center point of the sub-plot in each of four directions (north, east, south and west) using a Dutch auger; and the four samples were mixed thoroughly to make a common pool. We analyzed these soil samples for total carbon (C), nitrogen (N), phosphorus (P), potassium (K), Calcium (Ca), Iron (Fe), and Manganese (Mn) concentrations, soil pH and soil texture. Prior to analyses, the soil samples were air dried (5 days) and sieved (<2 mm). Total carbon and nitrogen concentrations were measured by dry combustion using a CNS Elemental analyzer (ElementarVario EL, Hanau, Germany). Soil pH(H_2O) was measured on air dried soil in a 1:2.5 soil-to-water ratio. Soil texture was determined using the pipette method to distinguish the fractions clay (<0.002 mm), silt (0.002–0.063 mm), and sand (0.063–0.002 mm; König and Fortmann 1996).

Topographic parameters were measured at a sub-plot level for all 28 plots. Slope was measured using a clinometer measured over 5 m across the sub-plot center point. Elevation was measured using a daily calibrated barometric altimeter on the GPS (Garmin 60csx) to 1-m accuracy.

Plot land-use histories

We interviewed local residents about the recent land-use history for each plot. We asked interviewees to describe the land-use at different junctures in recent Chinese history, which were easily identifiable to them. If the historical land-use was different from the current land-use, we asked them to estimate when the land-use had changed.

Litter-bags

To assay litter decomposition rates, we used freshly senescent leaves of two non-native Dipterocarp species: *Dipterocarpus retusus* Blume was selected for its relatively recalcitrant litter as compared to *Parashorea chinensis* Hsie Wang. Litter substrates that were non-native to the site were used for two reasons. First, to separate the effects of habitat disturbance and litter quality on decomposition rates we needed standard substrates. Second, we wished to avoid any possible effects of local adaptation of the decomposer community to the litter substrate (Gholz et al. 2000, Ayres et al. 2009).

Leaves were collected from Xishuangbanna Tropical Botanical Garden, located approximately 50 km from the study site, in September–October 2011 and April–May 2012 for the dry and wet season installations, respectively. Collected leaf litter was air dried and then defaunated by oven-drying for 24 hours at +80°C, freezing for 24 hours at −80°C, and re-drying for 24 hours at +80°C (Bardgett et al. 1998, Laganière et al. 2010). Initial mass was recorded to 0.01 g (JA1200, NAPCO Electronic Balance, NAPCO Precision, Shenzhen, China).

Litter-bags with a mesh size of 0.068 mm were used to exclude meso- and macro-invertebrate fauna. For the faunal-access treatment, we used bags with a mesh size of 0.5 mm and cut 12 ~1-cm^2 perforations in the upper side of each bag to facilitate access by larger invertebrates (Vasconcelos and Laurance 2005).

Immediately following the placement of litter-bags in the field, a sample of 72 litter-bags (2 species × 2 bag types × 2 seasons × 9 replicates) were collected and returned to the laboratory to establish mass loss during handling, dry mass relations, and for analysis of leaf chemistry (C, N, P, cellulose, hemicellulose and lignin; Hättenschwiler et al. 2008). Following incubation in the field, litter-bags were collected and remaining litter was oven-dried at 60°C to constant mass. The mass was measured after removing any fine roots, litter fauna and their frass, and mud.

Landscape experiment

We established decomposition trials across all 28 sample plots. For five sub-plots in each plot (4 corners and center sub-plots), we established an experimental area ~5 m north of the center point

Table 1. Mean (±SD) daily maximum air temperature (Temp.), soil water content (Soil water), relative humidity (RH) and median photosynthetically active radiation (PAR) for 3 months in the middle of the wet (June–August) season in 2012 and dry (February–April) season in 2013. Data were recorded in the understory at three sites along a forest-disturbance gradient representing mature forest, regenerating forest and open land, and in a shade-house under three levels of simulated canopy cover (full canopy, half canopy and open canopy). For PAR, readings 1 h either side of the solar noon were used.

Season	Treatment level	Temp. (°C)	Soil water ($m^3\ m^{-3}$)	RH (%)	PAR (µE)
Forest disturbance gradient					
Wet	mature forest	20.6 (1.5)	0.124 (0.042)	98.0 (2.1)	9.8 (4.5)
	regenerating forest	21.5 (1.7)	0.297 (0.010)	98.5 (1.7)	31.1 (14.1)
	open land	23.0 (3.0)	0.222 (0.058)	96.7 (2.7)	668.2 (498.5)
Dry	mature forest	22.3 (2.4)	0.036 (0.046)	64.6 (18.6)	20.4 (12.7)
	regenerating forest	25.6 (3.0)	0.048 (0.020)	72.2 (16.1)	20.5 (6.2)
	open land	29.2 (3.0)	0.063 (0.038)	66.6 (14.7)	1419.0 (391.2)
Shade-house					
Wet	full canopy	24.9 (3.0)	0.169 (0.017)	95.4 (3.1)	108.9 (61.8)
	half canopy	28.2 (4.3)	0.131 (0.014)	91.1 (4.2)	297.0 (158.3)
	open canopy	30.5 (5.1)	0.140 (0.031)	89.9 (4.8)	770.4 (387.4)
Dry	full canopy	26.8 (2.3)	0.108 (0.033)	67.0 (16.5)	161.5 (39.6)
	half canopy	29.5 (3.0)	0.073 (0.033)	63.2 (15.4)	513.3 (122.4)
	open canopy	34.4 (3.1)	0.032 (0.033)	63.6 (15.7)	1460.5 (341.7)

of the sub-plot and 12 litter-bags (2 species × 2 mesh sizes × 3 collections) were installed (Fig. 1d). Each litter-bag was filled with 5 g of dry, defaunated leaves. All bags were fixed to the ground with nails to prevent movement of bags. We installed litter-bags at the beginning of the dry (October–November 2011) and wet (May–June 2012) seasons, respectively. Thus, altogether 3360 bags were installed.

Collections were made at 3, 6 and 12 months after installation. Among the 3360 litter-bags installed, data from 243 bags were not recovered: 147 bags were destroyed by fire, 72 fine mesh bags were rejected after small holes were discovered in the bags, and 24 bags were damaged by cattle trampling.

In a parallel study in the same landscape, we monitored litter fall and seasonal variation in litter quality (Paudel et al. 2015).

Mesocosm experiment

To partition the effects of litter-bed conditions and canopy cover, we conducted a mesocosm experiment (Fig. 1e–i).

A shade-house (20 × 20 m) was built, using bamboo poles and polyethylene shade-cloth (mesh size = ∼0.3 cm, strand thickness = 0.14 cm; Sinong Zheyang Wang, Kunming, China) approximately 1 km from Mengsong village (Fig. 1i). The shade-house was divided into nine equal-sized blocks in a 3 × 3 grid. We establish three levels of simulated canopy cover by using different amounts of shade-cloth in the roof of each block: no shade-cloth (open-canopy), one layer (half-canopy), and two layers (full-canopy; Fig. 1i). The range of micro-climatic conditions under the different levels of simulated canopy cover was approximately equivalent to those occurring across the landscape disturbance gradient (Table 1; Appendix B: Figs. B1–B8).

In the center of each block a 4.5 × 3 × 0.35 m deep pit was excavated and leveled. The pit was filled to a depth of 25 cm with compacted sand to separate the litter-beds from the soil by an inert but free draining barrier (Fig. 1f). Each pit was divided into six 1.5 × 1.5 m litter-beds with vertical aluminum sheets. These extended from 0.5 m above to 0.15 m below the surface of the sand to minimize movement of soil and litter fauna among litter-beds (Fig. 1f). Within each block, the positions of the litter-bed treatments were randomly assigned.

To establish the litter-bed treatments, we selected six plots from the landscape experiment; two each from mature forest, regenerating forest and open land. In each, we established nine 1.5 × 1.5 m quadrats. Litter and top soil to a depth of 10 cm were collected from each quadrat. The soil and leaf litter were each mixed thoroughly at the plot level and then distributed equally to the nine litter-beds assigned to that treatment (Fig. 1e, g, and h). To maintain the appropriate litter dynamics, a 1.5 × 1.5 m piece of shade-cloth was placed on the ground over each quadrat and every month the litter falling on these clothes was collected, mixed at the plot level, and divided among the appropriate litter-beds. This litter will have included any litter fauna that had colonized the litter prior to collection and hence this process will also have contributed to maintaining the abundance and composition of litter fauna. However, it should be noted that, as a consequence of varying litter decomposition rates under the different levels of simulated canopy cover, the condition of the litter-beds may have changed over time. Any such effect is incorporated into the simulated canopy cover treatment in our design.

For the mesocosm experiment, litter-bags were filled with 10 g of dried leaves and only the coarse-mesh bags (faunal access) were used (Fig. 1g and h). Altogether 648 bags were installed (3 simulated canopy cover treatments × 6 litter-bed treatments × 2 litter species × 2 seasons × 3 replicates × 3 collections). Collections were made at 3, 6 and 12 months after installation.

Microclimate monitoring

We compared micro-climatic conditions across forest disturbance categories and simulated canopy cover treatments over 3 months in the wet season (June–August) and 3 months in the dry season (February–April). We used Hobo Microstation Loggers (Version 5.0.0, Onset Computer, Cape Cod, Massachusetts, USA) to monitor air temperature and relative humidity (Smart sensor S-THB-M00x), surface soil moisture (0–5 cm, Smart sensor S-SMx-M005-EC-5), and photosynthetic active radiation (PAR; Smart sensor S-LIA-M003). Three loggers were installed across the disturbance gradient, one each in mature forest, regenerating forest and open land (September 2012–September 2013), and three loggers were installed in the shade-house, one for each level of simulated canopy cover (November 2012–September 2013). These data were compared with data from a government meteorological station in Mengsong, which has been in operation since 2012 (UTM/WGS84: 47 Q 653164 E, 2375685 N, 1718 m asl).

Data analysis

We performed all the analyses in R version 3.1.1 (R Core Team 2014).

To analyze the effects of independent variables and their interactions on leaf litter decomposition rates, we implemented linear mixed-effects models in the package lme4 (Bates et al. 2013). Our response variable was the percent mass loss (log transformed). For the landscape experiment, fixed effects included installment season (dry season/wet season), forest type (mature forest, regenerating forest, open land), litter-type (*Dipterocarpus*/*Parashorea*) and bag type (faunal access/faunal exclusion), and all two-way interactions. Our experimental design was equivalent to a split plot with repeated measures. Incubation time (days) was included as the fixed-time effect (modeled as a second-order polynomial) and we included an interaction with installment season. Because we found a substantial difference in variance among installation seasons, the plot and subject level random intercepts were modeled separately for each season. The model for the mesocosm experiment was similar, except that the independent effects were litter type (*Dipterocarpus*/*Parashorea*), simulated canopy cover (full-canopy, half-canopy and open-canopy) and litter-bed forest type (mature forest, regenerating forest and open land) and their two-way interactions. Hence, there were two replicates for litter-bed forest type within each replicate of simulated canopy cover. We included random effects for plot nested within shade-house position (ROW:COL) and for shade-house position. Again we estimated the plot level random intercept separately for each installment season.

In addition, for the landscape experiment we attempted to nuance the effect of forest disturbance by modeling the effects of plant-community composition (trees, herbs and lianas) and soil/topographic parameters (sand, silt and clay content, total C, N, K, P, Mn, Ca and Fe, C:N ratio, pH(H_2O), slope and elevation). Ordinations were carried out to reduce the number of explanatory variables. For plant species composition, we used non-metric multidimensional scaling (NMDS, Jaccard's distance) implemented in the package vegan (Oksanen et al. 2013) based on presence/absence data. All the species that occurred in only one plot were removed, as these do not contribute any information to community assemble patterns. We conducted a principal component analysis (PCA) of the soil/topographic parameters, after standardizing parameters to a mean of zero and standard deviation of one. Using the same model structure as above, we replaced the forest type term with the first two principle axes for plant composition or soil/topography, respectively. We then compared the marginal r^2 of these models with the original model and examined differences in responses.

We examined model fit by plotting the square-root of the absolute residuals against the fitted values, and checked the normality of the residuals and the random effects. To estimate the 95% confidence envelope of parameter estimates we used parametric bootstrapping (function *confint*, $n = 999$). We consider effects to be significant if the 95% confidence interval (CI) of the estimate did not overlap with zero. Relative effect size was assessed by comparing the absolute values of the estimates.

RESULTS

Plot characteristics

An overview of plot characteristics is presented in Table A1 (Appendix A). As expected, tree basal area declines and canopy openness increases along the disturbance gradient from mature forest to open land. In addition, the plot histories based on local knowledge corroborated our land-cover classification based on satellite imagery. Most plots classified as mature forest had been forest for >50 yrs, although the youngest was ~36 yrs old. In comparison, the forest age of regenerating forest plots varied from 15 to 46 yrs, although most were <30 yrs old. Nevertheless, in many of the regenerating forest plots people extracted timber, grazed cattle or cultivated tea or *Amomum* in the understory until more recently and hence a single, absolute measure of disturbance is not feasible.

Microclimate

Trends in microclimatic conditions were as anticipated (Table 1; Appendix B: Figs. B1–B8).

Daily maximum temperature was always lowest in the mature forest and highest in the open land, although the differences were less during the wet season (Table 1; Appendix B: Fig. B1). During the dry season, daily maximum temperature in the regenerating forest was comparable to that recorded at the climate station, whereas during the wet season daily maximum temperature at the climate station was more similar to the conditions recorded in open land (Appendix B: Fig. B1). In the shade-house daily maximum temperature was always lowest in the full-canopy and highest in the open-canopy treatments (Table 1; Appendix B: Fig. B2). However, mean conditions in the shade-house were 4–5 degrees higher than in the field and the variance was also higher.

During the wet season, surface soil moisture (0–5 cm depth) was always highest in the regenerating forest and lowest in the mature forest (Table 1). In the dry season the pattern was highly dependent on rare rainfall events (Appendix B: Fig. B3). During and immediately after rainfall events, soil moisture in open land and mature forest was similar and higher than in regenerating forest. However, surface soil moisture declined rapidly to baseline levels in the mature forest and more slowly in open land. In the shade-house, soil surface moisture in the wet season was always higher under the full-canopy than the half-canopy treatments, and soil moisture under the open-canopy treatment increased as the season progressed (Table 1; Appendix B: Fig. B4). During the dry season, soil moisture was always highest under the full-canopy treatment, intermediated under the half-canopy treatment and lowest under the open-canopy treatment (Table 1; Appendix B: Fig. B4).

In both seasons, photosynthetically active radiation (PAR) was always highest in the open land and lowest in the mature forest, and always highest under open-canopy treatment and lowest under the full-canopy treatment in the shade-house (Table 1; Appendix B: Figs. B5 and B6). PAR in the mature and regenerating forest was substantially lower than in the half-shade and full-shade treatments in the shade-house.

In both seasons, relative humidity was more or less similar across forest disturbance categories and among different levels of simulated canopy in the shade-house (Table 1; Appendix B: Figs. B7 and B8).

Initial leaf chemistry

Initial concentrations of carbon, nitrogen, phosphorus, potassium, cellulose and hemicellulose were higher in *Parashorea* litter than in

Table 2. Initial chemical concentrations of *Dipterocarpus retusus* and *Parashorea chinensis* leaf litter for dry season and wet season installations. For the dry and wet season installations, litter was collected in September–October 2011 and April–May 2012, respectively.

	Dry season		Wet season	
Property	*Dipterocarpus*	*Parashorea*	*Dipterocarpus*	*Parashorea*
Carbon (%)	41.85	45.86	41.61	46.94
Nitrogen (%)	0.76	1.21	0.80	1.04
Phosphorus (%)	0.03	0.08	0.03	0.07
Potassium (%)	0.23	0.64	0.20	0.48
Cellulose (%)	31.85	46.91	37.39	37.28
Hemicellulose (%)	26.68	41.89	27.05	42.28
Lignin (%)	15.87	7.54	22.88	5.82
C/N	55.12	37.96	51.84	45.31
Lignin/N	20.90	6.24	28.50	5.62

Dipterocarpus litter (Table 2). Whereas, lignin concentration and C:N and lignin:N ratios were much higher in *Dipterocarpus* litter. In addition, in *Dipterocarpus* litter lignin and cellulose concentrations were higher for the wet season installation, but the opposite was true for *Parashorea* litter.

Decomposition along a disturbance gradient

Across the Mengsong landscape, after one year mass loss from litter-bags varied from 7% to 98% and across treatments mean mass loss varied from 21% (95% CI: 18–25) to 78% (CI: 65–94; Fig. 2).

Even after one year, mass loss from litter-bags installed at the beginning of the wet season was substantially greater than for litter-bags installed at the beginning of the dry season (Figs. 2 and 3a). As anticipated, *Parashorea* litter decomposed faster than *Dipterocarpus* litter (Figs. 2 and 3a; Appendix D: Table D1; $\beta = 0.473 \pm 0.02$, $t = 26.69$) and faunal exclusion (fine mesh litter bags) slowed decomposition relative to faunal access (coarse mesh litter bags; $\beta = -0.136 \pm 0.02$, $t = -7.65$), although the effect size was small compared to that for litter-type (Figs. 2 and 3a). Interactions between installment season and litter-type and between installment season and faunal exclusion were not significant (95% confidence interval overlapped zero).

As predicted, decomposition rates declined as the intensity of disturbance increased, but the effect size was strongly dependent on installment season (Figs. 2 and 3a). For bags installed at the start of the dry season the effect was small and non-significant. Whereas, for the wet season installation decomposition rates were substantially reduced in the open land, compared to forest plots ($\beta = -0.625 \pm 0.09$, $t = -6.81$). In addition, the effect of faunal exclusion increased with increasing disturbance (Fig. 3a; $\beta = 0.182 \pm 0.02$, $t = 7.75$). Whereas, the effect of litter-type was reduced in open land compared to forest plots (Fig. 3a; $\beta = -0.092 \pm 0.02$, $t = -3.92$).

Mesocosm experiment

In the mesocosm experiment, mass loss from litter-bags after one year varied from 15% to 82% and mean mass loss across treatments varied from 18% (95% CI: 16–21) to 78% (95% CI: 67–89; Fig. 4). Results broadly mirrored those from the landscape-disturbance gradient (Figs. 3b and 4). *Parashorea* litter decomposed faster than *Dipterocarpus* litter (Figs. 3b and 4; Appendix D: Table D2; $\beta = 0.576 \pm 0.05$, $t = 10.75$). The effect of simulated canopy cover was strongly dependent on installment season (Figs. 3b and 4). For the dry season installation, litter in the open-canopy treatment actually decomposed slightly faster than litter under the full or half-canopy treatments (Fig. 4; $\beta = 0.253 \pm 0.05$, $t = 5.41$). However, for the wet season installation, litter under the full-canopy treatment decomposed faster than litter under the half-canopy treatment ($\beta = 0.448 \pm 0.06$, $t = 7.96$), which decomposed faster than litter under the open-canopy treatment ($\beta = 0.948 \pm 0.06$, $t = 16.85$; Figs. 3b and 4). The litter-type effect was also reduced under more open conditions, especially the open-canopy treatment ($\beta = -0.207 \pm 0.05$, $t = -3.87$; Fig. 3b). In contrast to the results for simulated canopy cover, the effect of litter-bed forest type

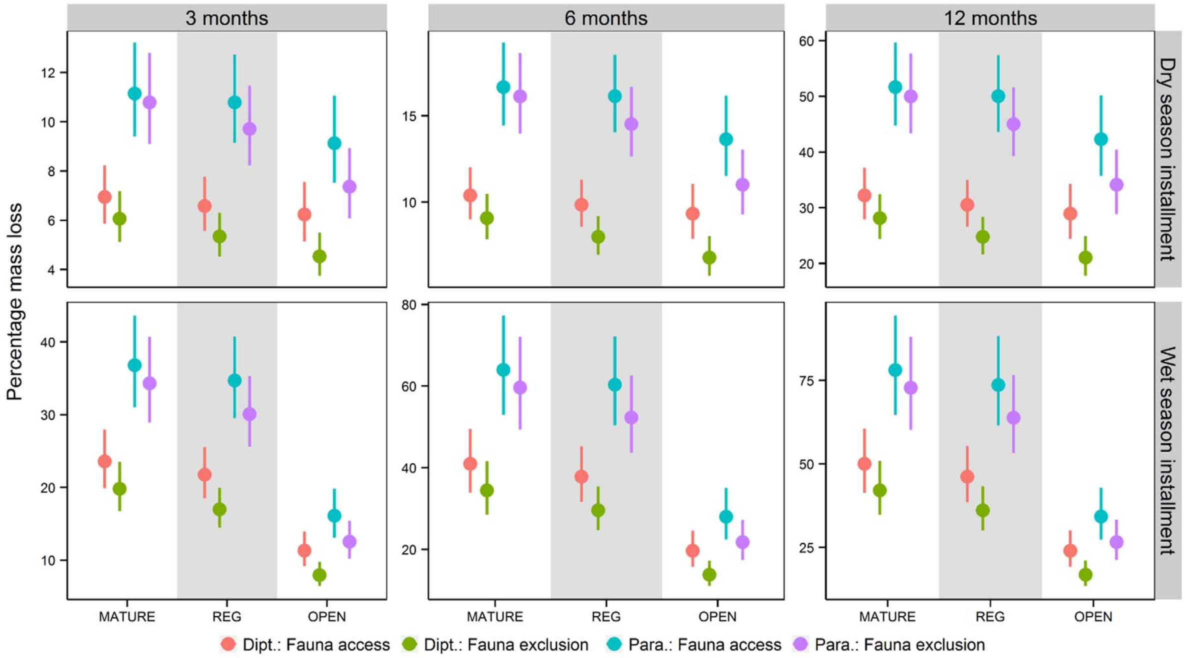

Fig. 2. Percentage mass loss from litter-bags installed across 28 plots in the Mengsong landscape after 3 month, 6 month and 12 month incubation. The experiment was run twice with litter-bags installed at the beginning of the dry (top row) and wet (bottom row) seasons, respectively. Points represent predicted mean values (±95% confidence interval) for two litter species (*Dipterocarpus retusus* and *Parashorea chinensis*) with respect to faunal exclusion (mesh size = 0.068 mm)/access and forest disturbance category (mature forest, regenerating forest and open land). At our study site, the dry and wet-seasons each last approximately six months.

(mature forest, regenerating forest, and open land) was not significant (Figs. 3b and 4).

Effects of plant species composition and soil/topography on litter decomposition

We re-analyzed the data from the landscape decomposition experiment replacing forest type with data on plant species composition and soil/topography. The first axis of our NMDS ordination of plant species composition was closely aligned with the disturbance gradient from mature forest (positive) to open land (negative), which can also be seen from the close correlation of axis values with basal area (Fig. 5). The second axis (NMDS2) reflected plant compositional differences between rain forest (negative) and broadleaf evergreen forest (positive) sites and between terraced tea (negative) and grassland (positive; Fig. 5). When these ordination axes were substituted into the leaf litter decomposition model in place of forest disturbance category, the model explained fractionally more variance in the response (marginal $r^2 = 0.84$ vs. 0.83; note the marginal r^2 is the variance explained by the fixed effects after removing the variance accounted for by the random effects). Interestingly, for the dry season installation there was a small but significant positive effect for NMDS1 (Appendix D: Table D3; $\beta = 0.146 \pm 0.07$, $t = 2.13$) and a stronger negative effect for NMDS2 ($\beta = -0.291 \pm 0.11$, $t = -2.60$; Fig. 6a), but for the wet season installation both axes had a strong positive effect (Appendix D: Table D3; NMDS1: $\beta = 0.584 \pm 0.08$, $t = 6.99$; NMDS2: $\beta = 0.368 \pm 0.14$, $t = 2.70$). Thus, more disturbed plots had lower decomposition rates for both installations. However, for the dry season installation broadleaf evergreen forest plots and grassland plots had lower decomposition rates compared to rain forest and terraced tea plots, respectively, but this pattern was reversed for the wet season installation. In addition, both axes had small but significant interactions with litter type, indicating that the

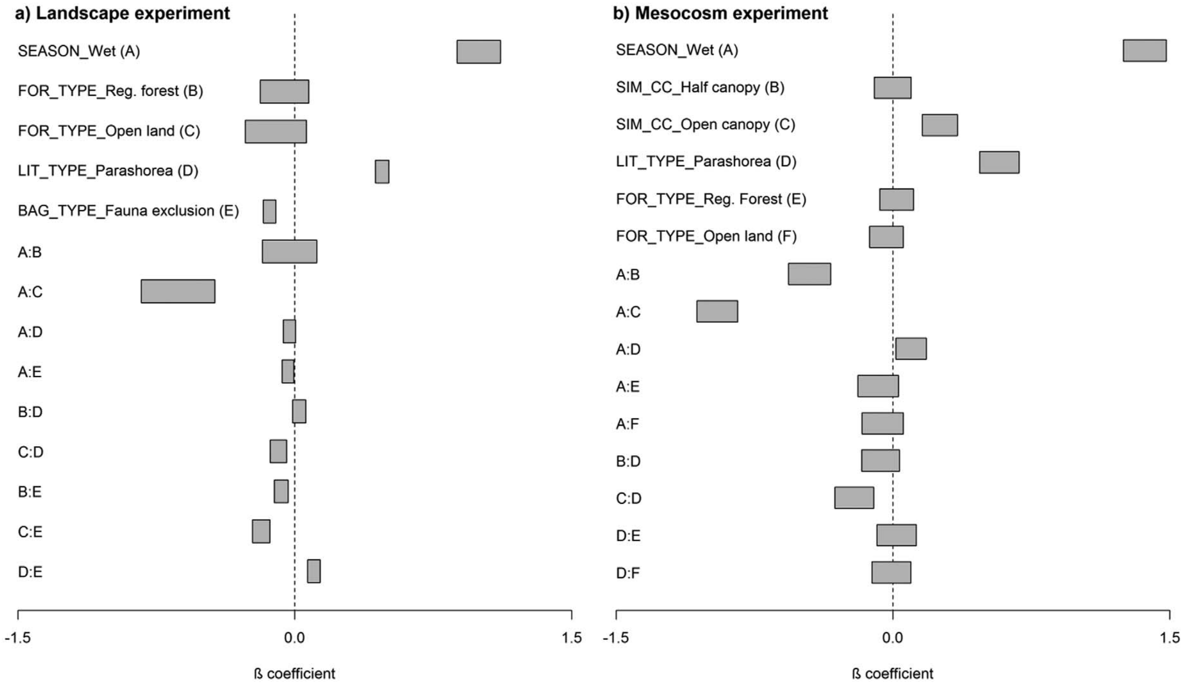

Fig. 3. Model results for the (a) landscape experiment, and (b) mesocosm experiment. Bars represent the 95% confidence intervals for the estimates of the beta-coefficients and were obtained from parametric bootstrapping ($n = 999$). Models estimated the effect of variables on log percent mass loss from litter-bags. Independent variables included installment season (SEASON; dry vs wet), forest type (FOR_TYPE; mature forest, regenerating forest, and open land), litter type (LIT_TYPE; *Dipterocarpus* vs *Parashorea*), and simulated canopy cover (SIM_CC; full-canopy, half-canopy and open-canopy).

litter type effect diminished in more disturbed sites ($\beta = 0.066 \pm 0.02$, $t = 2.98$), but was enhanced in broadleaf evergreen and grassland sites compared to rain forest and terraced tea fields, respectively ($\beta = 0.095 \pm 0.04$, $t = 2.70$). Furthermore, there was a positive interactive effect between faunal exclusion and NMDS1 ($\beta = 0.174 \pm 0.02$, $t = 7.89$), but the sign was reversed for NMDS2 ($\beta = -0.082 \pm 0.04$, $t = -2.34$). Thus, as observed in the first model, the effect of faunal exclusion increased along the disturbance gradient, but was also slightly greater for evergreen broadleaf plots and grassland plots compared to rain forest and terraced tea plots, respectively.

Principal component analysis (PCA) showed that 56% of the total variance in the data was explained by first two components, 30.6% and 25.3% for PC1 and PC2, respectively. The first component (PC1) was positively correlated with C:N, C, N, and sand; and negatively correlated with pH(H_2O), Mn, Fe, P, and Ca (Fig. 7). While, the second component (PC2) was positively correlated with K, sand, and pH(H_2O); and negatively correlated with N, C, Fe, P, and elevation (Fig. 7). The model using soil/topography data had a substantially lower marginal r^2 than the original model (marginal $r^2 = 0.75$ vs. 0.83) and effects sizes were mostly non-significant (Fig. 6b; Appendix D: Table D4). An overview of soil properties by forest disturbance category is presented in Table C1 (Appendix C).

DISCUSSION

Forest degradation is a major global change process, especially in the tropics, and hence it is essential to understand the consequences for ecosystem function. However, from a biological perspective forest degradation is a complex process that simultaneously alters various attributes of the biotic and abiotic environment. The goal of our study was to quantify the effects of

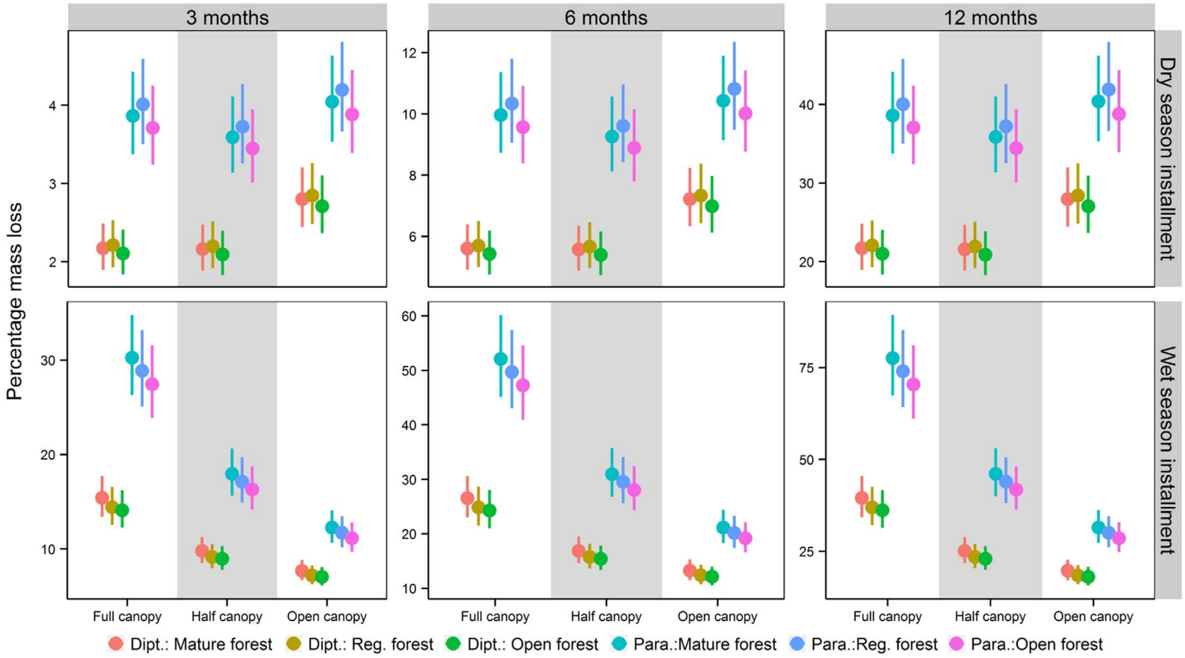

Fig. 4. Percentage mass loss from litter-bags installed in a litter-bed mesocosm experiment after 3 month, 6 month and 12 month incubation. The experiment was run twice with litter-bags installed at the beginning of the dry (top row) and wet (bottom row) seasons, respectively. Points represent predicted mean values (±95% confidence interval) for two litter species (*Dipterocarpus retusus* and *Parashorea chinensis*) with respect to simulated canopy cover and litter-bed treatment (mature forest, regenerating forest and open land). At our study site, the dry and wet-seasons each last approximately six months.

forest degradation on leaf litter decomposition, and disentangle the interactions with other known determinants of litter decomposition. Specifically, our aim was to quantify the effects of forest degradation with respect to leaf litter quality, decomposer functional diversity and seasonal precipitation regime. In addition, we attempted to experimentally partition the effects of changes in the litter-bed conditions on the forest floor from the effects of changes in the micro-climatic conditions caused by increased canopy openness.

As hypothesized, we found that litter decomposition rates declined along the forest degradation gradient from mature forest to open land (Fig. 2). However, when forest disturbance was specified using our initial categories (based on interpretation of satellite images) this effect was only significant for litter that was installed at the beginning of the wet season. Moreover, there were no significant differences between mature and regenerating forests. However, when we used data on plant species composition, results indicated that the degree of disturbance had a significant effect in both seasons, but was still substantially larger for the wet-season installation. We also found that the effect of litter quality declined with increasing disturbance, whereas the effect of excluding meso- and macro-invertebrates increased. The results from our mesocosm experiment supported the hypothesis that these effects of forest degradation were driven primarily by the changes in micro-climate resulting from increased canopy openness, rather than changes in the biotic conditions of the forest floor environment.

Earlier studies have reported mixed results concerning the effects of forest disturbance on litter decomposition, including increasing, decreasing and no change in decomposition rates with increasing disturbance (removal of canopy cover). For example, in temperate forests more rapid litter mass loss was reported in clear-cut (open canopy) sites than in sites with higher

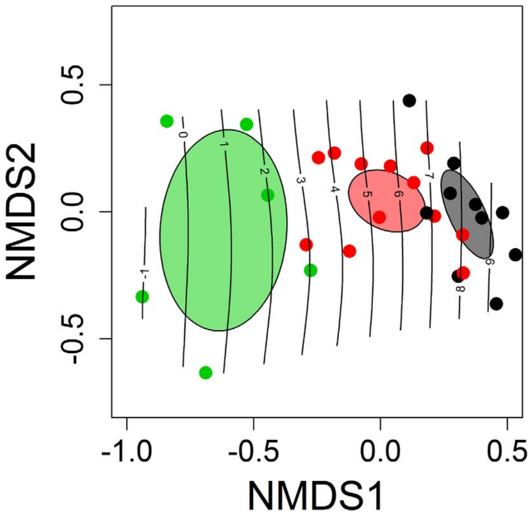

Fig. 5. A non-metric multidimensional scaling (NMDS) ordination of plant species composition, including trees, herbs and lianas, based on presence-absence data (Jaccard's distance). Points and ellipses represent the sampling plots ($n = 28$) and 95% confidence interval of group centroids for each forest type, respectively (black = mature forest, red = regenerating forest, green = open land).

canopy cover (Edmonds 1990, Kim et al. 1996, Kim 2000). Conversely, in subtropical forests mass loss from litter-bags placed under closed canopy or within small gaps was faster than those placed in large gaps created from tree-falls or in open canopy sites (Yin et al. 1989, Zhang and Zak 1995). However, these studies did not separate the effects of forest degradation from other important drivers of decomposition, such as seasonality, decomposer functional diversity or litter quality. At our site, we found a consistent decline in decomposition rates along the disturbance gradient from mature forest to open land, after controlling for these factors.

Effects of installment season and forest degradation

In our study, the installment season was not replicated, as the experiment was run only once from the beginning of the dry and wet seasons, respectively. Hence, it should be considered a block effect and caution is, therefore, warranted in interpreting its effects in our experiments. Nevertheless, a substantial amount is known concerning the effects of climate on leaf litter decomposition and hence some reflection of our observations in the light of this knowledge is possible. For both installments, as anticipated, dry season decomposition was much reduced compared to wet season decomposition (Figs. 2 and 4). The initial stages of decomposition are often rapid, because of removal of soluble organic material by leaching (Berg and McClaugherty 2014), but this process is precipitation dependent (Bernhard-Reversat 1982, Seastedt et al. 1983, Torres et al. 2005). In our experiments, even after 12 months, mass loss from litter-bags installed at the beginning of the dry season was substantially lower in mature forest (28–52%) and regenerating forest (25–50%) than from bags installed at the beginning of the wet season (mature forest: 42–78%, regenerating forest: 36–74%). This suggests there may be a marked legacy effect of slow initial decomposition rates. For open land there was no significant difference between installation seasons (dry season 21–42%; wet season: 17–34%).

The initial chemical properties of the litter were generally similar between seasons, but the C:N ratio and lignin:N ratio of *Dipterocarpus* litter was higher for the litter used in the wet season installation, while the opposite was true for *Parashorea* litter (Table 2). This suggests we might have expected the effect of litter-type to be larger for the wet-season installation, but this was not the case. We also did not detect any significant interaction between faunal exclusion and installment season.

For the wet season installation, litter in open land decomposed substantially slower than in the forest. However, these effects were reduced for the dry season installation. This suggests that we can expect the effects of forest degradation on litter decomposition to be greater in more humid environments and those with lower rainfall seasonality.

Litter-quality and forest degradation

Leaf litter from different plant species decomposes at different rates within a common environment, because of variation in leaf traits (Cornelissen 1996, Cornelissen et al. 1999, Hättenschwiler 2005, Hättenschwiler et al. 2008, Bakker et al. 2011, Salinas et al. 2011). Moreover, it was previously found that, through changes in plant species composition, litter quality increased along a tropical forest disturbance gradient

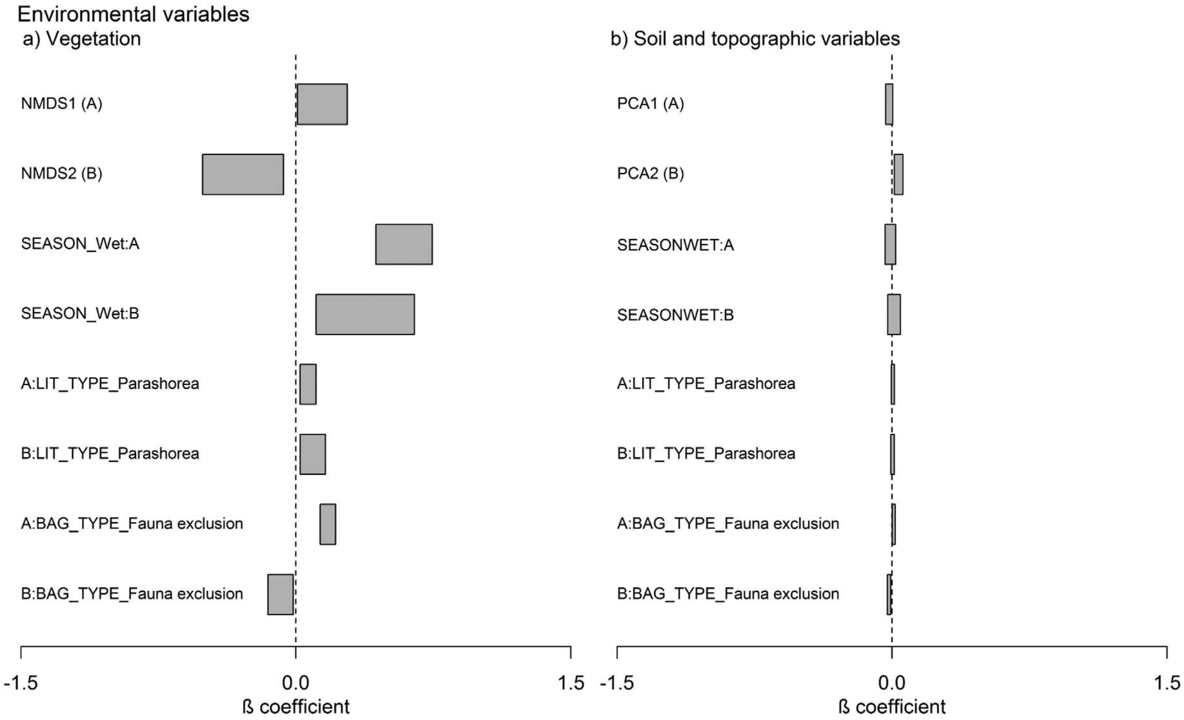

Fig. 6. Model results for the landscape experiment using (a) plant composition data and (b) soil/topographic data. Bars represent the 95% confidence intervals for the estimates of the beta-coefficients obtained through parametric bootstrapping ($n = 999$). Models estimated the effect of variables on log percent mass loss from litter-bags. NMDS1 and NMDS2 represent the first and second axes of a non-metric multiple dimensional scaling ordination (Jaccard's distance) for plant species composition (Fig. 5). PCA1 and PCA2 represent the first and second axes for a principle component analysis of soil/topographic parameters (Fig. 7; other parameters were not shown for clarity, but were similar to Fig. 3a).

(Bakker et al. 2011). This relationship between initial litter chemistry and decomposition rate is commonly explained through differences in the initial N concentration or C:N or Lignin:N ratios. As expected, we observed much higher mass-loss rates from bags with *Parashorea* litter, which has lower C:N and lignin:N ratios, compared to bags with *Dipterocarpus* litter. However, this difference was reduced in open land as compared with forest and, likewise, in the open-canopy treatment of the mesocosm experiment compared to the half-canopy and full-canopy treatments. Hence, contrary to our prediction, increased forest degradation or canopy openness resulted in a decline in the effect of litter quality on decomposition.

A reduced effect of litter quality in more open habitats would tend to dampen any effect of differences in litter quality along a disturbance gradient (Bakker et al. 2011). However, in a separate study in Mengsong we monitored litter fall and litter quality and found that although there was a marked decline in the amount of litter in open habitats, litter quality did not vary significantly (Paudel et al. 2015).

Decomposer functional diversity and forest degradation

The role of soil and litter fauna in leaf litter decomposition has been widely studied (Heneghan et al. 1999, González and Seastedt 2001, Powers et al. 2009, García-Palacios et al. 2013, Handa et al. 2014). Our landscape experiments showed clear evidence that exclusion of meso- and macro-fauna decreased leaf litter decomposition rates, irrespective of installment season or litter-type. However, consistent with our predictions, the magnitude of this effect increased along

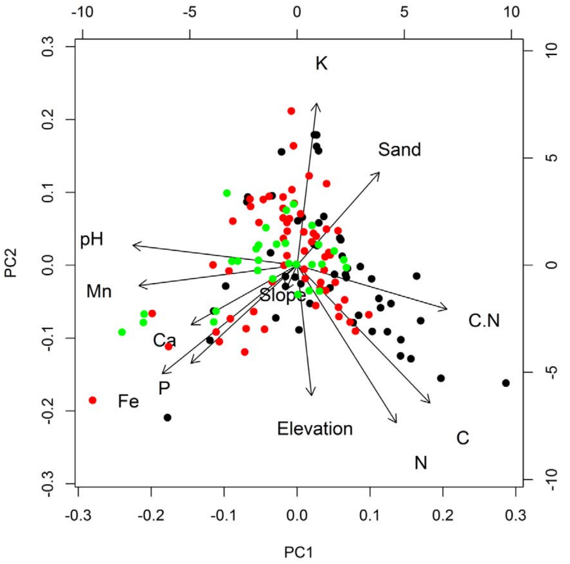

Fig. 7. Principle components analysis (PCA) of soil chemical properties and topography. Points indicate the individual sampling points (28 plots × 5 sub-plots) and arrows represent the coefficients of each parameter. Black, red and green points represent mature forest, regenerating forest and open land, respectively.

the disturbance gradient. Previous studies have suggested that the faunal effect is greater in the warmer and wetter habitats (González and Seastedt 2001, Wall et al. 2008, García-Palacios et al. 2013), possibly reflecting high invertebrate decomposer abundance (González and Seastedt 2001). However, microbial decomposition is also expected to decline with increasing canopy openness, because of the rapid drying out of litter in direct sun (Zhang and Zak 1995, Rigobelo and Nahas 2004). At our site the increased effect of invertebrate decomposers in more degraded sites may reflect an increased role of termites, in particular, as these appeared more prevalent in our litter-bags in the more disturbed sites. Nevertheless, this result could also represent an experimental artifact, as litter bags possibly represented a resource windfall for decomposers in the most disturbed habitats.

The effect of faunal exclusion was also greater in *Dipterocarpus*, the more recalcitrant litter which is contrary to the patterns reported in most studies. Previous researchers have either reported a larger effect of faunal exclusion for higher quality litter (Spain and Le Feuvre 1987, Coq et al. 2010, Handa et al. 2014) or no significant difference between litter of different quality (González and Seastedt 2001, Powers et al. 2009). However, Yang and Chen (2009) reported that the effect of faunal exclusion was greater for lower quality litter in rain forest. The interactive effect between faunal exclusion and litter quality may be strongly dependent on the composition of the decomposer community. At our site, termites are an important element of the decomposer community and play an especially significant role in the decomposition of recalcitrant substrates, which might explain the greater role of invertebrates on decomposition in this system. This would also be consistent with Yang and Chen (2009)'s results, as termites are more abundant in rain forest than in broad-leaf evergreen forest.

Partitioning biotic and abiotic effects of forest degradation

Increased canopy openness has a direct effect on the micro-climate of the forest floor (Tian et al. 1993, Zhang and Zak 1995). Litter fauna abundance and diversity is dependent on litter composition and specially litter depth on the forest floor (Migge-Kleian et al. 2007) and a decrease in soil and litter macro-faunal abundance with increasing disturbance has been reported from tropical forest and agroforestry systems (Migge-Kleian et al. 2007, Kone et al. 2010, Bartz et al. 2014). Meanwhile, microbial activity is dependent on temperature and moisture content of the litter layer. While, the temperature of the forest floor increases with increasing canopy openness (see Table 1), this is also associated with a decrease in litter moisture content (Zhang and Zak 1995). Thus, increased canopy openness is predicted to slow microbial activity and lead to a decline in decomposition rates.

Our use of litter-beds as an experimental treatment was novel and, in combination with our simulated canopy cover treatments, enabled us to partition the effects of canopy openness and microclimate from the role of the biotic conditions of the forest floor. Despite very large differences in the quantity of litter and, therefore, the litter depth (Fig. 1h), the effect of litter-bed treatments was small and non-significant (Fig. 3b). In contrast, the effect of the simulated canopy cover was substantial and mirrored the effect of forest degradation status in the landscape experiment. These experimental results suggest that the effects of forest degradation on litter decomposition are predominantly driven by changes in micro-climatic conditions on the forest floor caused by increased canopy openness.

A few caveats are warranted here. First and most obviously, litter-beds do not perfectly replicate all the biotic elements of the forest floor environment. For example, the small spatial scale may affect invertebrate abundances, the soil structure has been disturbed and the soil lacks tree roots. We maintained litter input in the litter beds by adding fresh litter collected from the field on a monthly basis, and this litter will have contained any litter fauna that had colonized the litter in the field. Hence, these additions will also have served to help maintain the abundance and composition of the leaf litter fauna in the litter-beds. Perhaps more importantly, the different simulated canopy cover treatments resulted in different rates of decomposition of the litter-bed litter, and hence the litter-bed conditions will have changed to some degree as the experiment progressed. In our experimental design, if these changes had any effect on decomposition they would have been detected as an effect of the simulated canopy cover treatment. Finally, although the trends in microclimatic conditions recorded across the simulated canopy cover treatments in the shade-house and the disturbance gradient in the field were similar for most variables, conditions were not exactly the same (Table 1; Appendix B). Probably because it was located in a large gap, air temperature in the shade-house was on average 4–5°C higher. Also, soil moisture in mature forest was lower than for regenerating forest and open land, whereas it was always highest under full shade in the shade-house. This is presumably a consequence of high evapotranspiration in the mature forest. However, it should be noted that the relative humidity was similar in both sites and this likely to be a better reflection of litter moisture content. The degree to which the artificial conditions of the shade-house might have affected our results is an arguable point. Nonetheless, it is noteworthy that the effects of the simulated canopy cover treatment were very similar to those of the disturbance gradient measured in the field, both in terms of direction and magnitude.

Plant community composition and soil/topographic parameters

The use of plant composition data enabled us to improve the understanding of our results. NMDS1 was correlated with the disturbance gradient, and our results indicated a significant reduction in decomposition rates with increasing disturbance for both the dry and wet season installments. Meanwhile, NMDS2 reflected differences in vegetation type. Evergreen broadleaf forest and grasslands had lower decomposition rates in the dry season but higher decomposition rates in the wet season compared to rain forest and terraced tea fields, respectively. Hence, it seems likely that the reason we failed to detect an effect of forest disturbance for the dry season installation in our first analysis was because of the confounding effect of vegetation type. Rain forest tends to occur in the valleys and retains a higher level of humidity through the dry season, which may explain why litter decomposition rates were higher in this habitat.

Soil physical and chemical properties are important for soil-water dynamics, nutrient mobility and microbial community composition, and thus indirectly affect the decomposition process (Berg and McClaugherty 2014). Moreover, the impact of exogenous nutrients on decomposition is less well studied than the impact of litter nutrient inputs (Berg and McClaugherty 2014). However, we found that soil/topographic parameters were poor predictors of litter decomposition rates at our site. This may reflect the relatively large variance in soil parameters at our site that was unrelated to forest disturbance status (Appendix C: Table C1). However, it also suggests vegetation characteristics may be more important for litter decomposition at local scales, particularly in landscapes, such as ours, that incorporate a wide range of vegetation conditions.

Conclusions

We found forest degradation had a substantial effect on leaf litter decomposition rates at a landscape scale. As predicted, decomposition rates declined along the disturbance gradient. Moreover, the results of our mesocosm experiment strongly suggest this was predominantly driven by changes in micro-climatic conditions resulting from increased canopy openness.

The effect of forest disturbance was more pronounced for litter-bags that were installed at the beginning of the wet season, apparently because of more marked differences in decomposition rates across disturbance categories during the initial decomposition phase. The effect of litter quality was reduced in open land plots, compared to forest plots, while in contrast, effects of faunal exclusion increased with increasing disturbance. Both these observations may reflect a reduced role of microbial decomposition in open habitats, as a consequence of the rapid drying out of litter in direct sunlight (Meentemeyer 1978, Zhang and Zak 1995). For most effects, differences in litter decomposition rates between mature forest and regenerating forest were slight, as has been found elsewhere (Vasconcelos and Laurance 2005).

Nutrient-transfer rates are reduced when decomposition rates are lower. Our results suggest this may affect the abiotic resources available to biotic communities in disturbed environments. To better model the impacts of anthropogenic global change on litter decomposition rates, it will be important to consider the role of forest degradation and loss at landscape scales.

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LITERATURE CITED

Aerts, R. 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79:439–449.

Anderson, J. M., J. Proctor, and H. W. Vallack. 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak: III. Decomposition processes and nutrient losses from leaf litter. Journal of Ecology 71:503–527.

Ayres, E., H. Steltzer, B. L. Simmons, R. T. Simpson, J. M. Steinweg, M. D. Wallenstein, N. Mellor, W. J. Parton, J. C. Moore, and D. H. Wall. 2009. Home-field advantage accelerates leaf litter decomposition in forests. Soil Biology and Biochemistry 41:606–610.

Bakker, M. A., G. Carreño-Rocabado, and L. Poorter. 2011. Leaf economics traits predict litter decomposition of tropical plants and differ among land use types. Functional Ecology 25:473–483.

Bardgett, R. D., S. Keiller, R. Cook, and A. S. Gilburn. 1998. Dynamic interactions between soil animals and microorganisms in upland grassland soils amended with sheep dung: a microcosm experiment. Soil Biology and Biochemistry 30:531–539.

Bartz, M. L. C., G. G. Brown, R. Orso, Á. L. Mafra, and D. Baretta. 2014. The influence of land use systems on soil and surface litter fauna in the western region of Santa Catarina. Revista Ciência Agronômica 45:880–887.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2013. lme4: linear mixed-effects models using eigen and S4. R package version 1.0-4. http://CRAN.R-project.org/package=lme4

Beckschäfer, P., L. Fehrmann, R. D. Harrison, J. Xu, and C. Kleinn. 2014. Mapping leaf area index in subtropical upland ecosystems using RapidEye imagery and the randomForest algorithm. iForest 7:1–11.

Berg, B., and C. McClaugherty. 2014. Plant litter: decomposition, humus formation, carbon sequestration. Springer-Verlag, Berlin, Germany.

Bernhard-Reversat, F. 1982. Measuring litter decomposition in a tropical forest ecosystem: comparison of some methods. International Journal of Ecology and Environmental Sciences 8:63–71.

Coq, S., J. M. Souquet, E. Meudec, V. Cheynier, and S. Hättenschwiler. 2010. Interspecific variation in leaf litter tannins drives decomposition in a tropical rain forest of French Guiana. Ecology 91:2080–2091.

Coq, S., J. Weigel, O. Butenschoen, D. Bonal, and S. Hättenschwiler. 2011. Litter composition rather than plant presence affects decomposition of tropical litter mixtures. Plant and Soil 343:273–286.

Cornelissen, J. H. C. 1996. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. Journal of Ecology 84:573–582.

Cornelissen, J. H. C., N. Pérez-Harguindeguy, S. Díaz,

J. P. Grime, B. Marzano, M. Cabido, F. Vendramini, and B. Cerabolini. 1999. Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. New Phytologist 143:191–200.

Cornwell, W. K., et al. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters 11:1065–1071.

Coûteaux, M. M., P. Bottner, and B. Berg. 1995. Litter decomposition, climate and litter quality. Trends in Ecology and Evolution 10:63–66.

Currie, W. S., M. E. Harmon, I. C. Burke, S. C. Hart, W. J. Parton, and W. Silver. 2010. Cross-biome transplants of plant litter show decomposition models extend to a broader climatic range but lose predictability at the decadal time scale. Global Change Biology 16:1744–1761.

Edmonds, R. L. 1990. Organic matter decomposition in western United States forests. Pages 118–128 *in* A. E. Harvey and L. F. Neuenschwander, editors. Proceedings of Management and Productivity of Western-Montane Forest Soils. General Technical Report INT-280. USDA Forest Service Intermountain Research Station, Ogden, Utah, USA.

Eviner, V. T., F. S. Chapin, III, and C. E. Vaughn. 2006. Seasonal variations in plant species effects on soil N and P dynamics. Ecology 87:974–86.

García-Palacios, P., F. T. Maestre, J. Kattge, and D. H. Wall. 2013. Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. Ecology Letters 16:1045–1053.

Gholz, H. L., D. A. Wedin, S. M. Smitherman, M. E. Harmon, and W. J. Parton. 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Global Change Biology 6:751–765.

González, G., and T. R. Seastedt. 2001. Soil fauna and plant litter decomposition in tropical and subalpine forests. Ecology 82:955–964.

Griffith, G. S., and L. Boddy. 1990. Fungal decomposition of attached angiosperm twigs. I. Decay community development in ash, beech and oak. New Phytologist 116:407–415.

Handa, I. T., et al. 2014. Consequences of biodiversity loss for litter decomposition across biomes. Nature 509:218–221.

Hättenschwiler, S. 2005. Effects of tree species diversity on litter quality and decomposition. Pages 149–164 *in* M. Scherer-Lorenzen, C. Korner, and E. D. Schulze, editors. Forest diversity and function: temperate and boreal systems. Springer-Verlag, Heidelberg, Germany.

Hättenschwiler, S., B. Aeschlimann, M. Coûteaux, J. Roy, and D. Bonal. 2008. High variation in foliage and leaf litter chemistry among 45 tree species of a neotropical rainforest community. New Phytologist 179:165–175.

Hättenschwiler, S., S. Coq, S. Barantal, and I. T. Handa. 2011. Leaf traits and decomposition in tropical rainforests: revisiting some commonly held views and towards a new hypothesis. New Phytologist 189:950–965.

Heneghan, L., D. C. Coleman, X. Zou, D. A. Crossley, and B. L. Haines. 1999. Soil microarthropod contributions to decomposition dynamics: tropical–temperate comparisons of a single substrate. Ecology 80:1873–1882.

IPCC [Intergovernmental Panel on Climate Change]. 2007. Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Kai, Z., T. S. Woan, L. Jie, E. Goodale, K. Kitajima, R. Bagchi, and R. D. Harrison. 2014. Shifting baselines on a tropical forest frontier: extirpations drive declines in local ecological knowledge. PLoS ONE 9:e86598.

Kim, C. 2000. Canopy cover effects on cellulose decomposition in Oak and Pine stands. Journal of Forest Research 5:145–149.

Kim, C., T. L. Sharik, and M. F. Jurgensen. 1996. Canopy cover effects on mass loss, and nitrogen and phosphorus dynamics from decomposing litter in oak and pine stands in northern Lower Michigan. Forest Ecology and Management 80:13–20.

Kone, M., S. Konate, K. Yeo, P. K. Kouassi, and K. E. Linsenmair. 2010. Diversity and abundance of terrestrial ants along a gradient of land use intensification in a transitional forest-savannah zone of Cote d'Ivoire. Journal of Applied Biosciences 29:1809–1827.

König, N., and H. Fortmann. 1996. Probenvorbereitungs-, untersuchungs- und elementbestimmungsmethoden des umweltanalytik-labor der niedersächsischen forstlichen versuchsanstalt und des zentrallabor II des forschungszentrums waldökosysteme.teil 1: elementbestimmungsmethoden A-M. Berichte des Forschungszentrums Waldökosysteme der Universität Göttingen.

Laganière, J., D. Paré, and R. L. Bradley. 2010. How does a tree species influence litter decomposition? Separating the relative contribution of litter quality, litter mixing, and forest floor conditions. Canadian Journal of Forest Research 40:465–475.

Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. Ecology 59:465–472.

Melillo, J. M., J. D. Aber, and J. F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621–626.

Migge-Kleian, S., L. Woltmann, I. Anas, W. Schulz, A.

Steingrebe, and M. Schaefer. 2007. Impact of forest disturbance and land use change on soil and litter arthropod assemblages in tropical rainforest margins. Pages 149–165 *in* T. Tscharntke, C. Leuschner, M. Zeller, E. Guhardja, and A. Bidin, editors. The stability of tropical rainforest margins, linking ecological, economic and social constraints of land use and conservation. Springer Verlag, Berlin, Germany.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens, and H. Wagner. 2013. vegan: community ecology package. http://cran.r-project.org/web/packages/vegan/index.html

Parton, W., et al. 2007. Global-scale similarities in nitrogen release patterns during long-term decomposition. Science 315:361–364.

Paudel, E., G. G. O. Dossa, J. Xu, and R. D. Harrison. 2015. Litterfall and nutrient return along a disturbance gradient in a tropical montane forest. Forest Ecology and Management 353:97–106.

Powers, J. S., et al. 2009. Decomposition in tropical forests: a pan-tropical study of the effects of litter type, litter placement and mesofaunal exclusion across a precipitation gradient. Journal of Ecology 97:801–811.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rigobelo, E. C., and E. Nahas. 2004. Seasonal fluctuations of bacterial population and microbial activity in soils cultivated with *Eucalyptus* and *Pinus*. Scientia Agricola 61:88–93.

Rozema, J., B. Kooi, R. Broekman, and L. Kuijper. 1999. Modelling direct (photodegradation) and indirect (litter quality) effects of enhanced UV-B on litter decomposition. Pages 135–157 *in* J. Rozema, editor. Stratospheric ozone depletion: the effect of enhanced UV-B radiation. Backhuys, Leiden, The Netherlands.

Salinas, N., Y. Malhi, P. Meir, M. Silman, R. R. Cuesta, J. Huaman, D. Salinas, V. Huaman, A. Gibaja, M. Mamani, and F. Farfan. 2011. The sensitivity of tropical leaf litter decomposition to temperature: results from a large-scale leaf translocation experiment along an elevation gradient in Peruvian forests. New Phytologist 189:967–977.

Schmidt, S. K., E. K. Costello, D. R. Nemergut, C. C. Cleveland, S. C. Reed, M. N. Weintraub, A. F. Meyer, and A. M. Martin. 2007. Biogeochemical consequences of rapid microbial turnover and seasonal succession in soil. Ecology 88:1379–1385.

Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature Methods 9:671–675.

Seastedt, T. R., and D. A. Crossley, Jr. 1983. Nutrients in forest litter treated with naphthalene and simulated throughfall: a field microcosm study. Soil Biology and Biochemistry 15:159–165.

Seastedt, T. R., and D. A. Crossley, Jr. 1980. Effects of microarthropods on the seasonal dynamics of nutrients in forest litter. Soil Biology and Biochemistry 12:337–342.

Seastedt, T. R., D. A. Crossley, Jr., V. Meentemeyer, and J. B. Waide. 1983. A two-year study of leaf litter decomposition as related to macroclimatic factors and microarthropod abundance in the southern Appalachians. Holarctic Ecology 6:11–16.

Spain, A. V., and R. P. Le Feuvre. 1987. Breakdown of four litters of contrasting quality in a tropical Australian rainforest. Journal of Applied Ecology 24:279–288.

Taylor, B. R., D. Parkinson, and W. F. J. Parsons. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. Ecology 70:97–104.

Tian, G., L. Brussaard, and B. T. Kang. 1993. Biological effects of plant residues with contrasting chemical compositions under humid tropical conditions: effects on soil fauna. Soil Biology and Biochemistry 25:731–737.

Torres, P. A., A. B. Abril, and E. H. Bucher. 2005. Microbial succession in litter decomposition in the semi-arid Chaco woodland. Soil Biology and Biochemistry 37:49–54.

Valachovic, Y. S., B. A. Caldwell, K. Cromack, Jr., and R. P. Griffiths. 2004. Leaf litter chemistry controls on decomposition of Pacific Northwest trees and woody shrubs. Canadian Journal of Forest Research 34:2131–2147.

Vasconcelos, H. L., and W. F. Laurance. 2005. Influence of habitat, litter type, and soil invertebrates on leaf-litter decomposition in a fragmented Amazonian landscape. Oecologia 144:456–462.

Vitousek, P. M., D. R. Turner, W. J. Parton, and R. L. Sanford. 1994. Litter decomposition on the Mauna Loa environmental matrix, Hawai'i: patterns, mechanisms, and models. Ecology 75:418–429.

Wall, D. H., et al. 2008. Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. Global Change Biology 14:2661–2667.

Xu, J., L. Lebel, and J. Sturgeon. 2009. Functional links between biodiversity, livelihoods, and culture in a Hani swidden landscape in southwest China. Ecology and Society 14:20.

Yang, X., and J. Chen. 2009. Plant litter quality influences the contribution of soil fauna to litter decomposition in humid tropical forests, southwestern China. Soil Biology and Biochemistry 41:910–918.

Yin, X., J. A. Perry, and R. K. Dixon. 1989. Influence of canopy removal on decomposition. Canadian Journal of Forest Research 19:204–214.

Zhang, D., D. Hui, Y. Luo, and G. Zhou. 2008. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. Journal of Plant Ecology 1:85–93.

Zhang, Q., and J. C. Zak. 1995. Effects of gap size on litter decomposition and microbial activity in a subtropical forest. Ecology 76:2196–2204.

Zhu, H., J. P. Shi, and C. J. Zhao. 2005. Species composition, physiognomy and plant diversity of the tropical montane evergreen broad-leaved forest in southern Yunnan. Biodiversity and Conservation 14:2855–2870.

SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

Appendices A–D are available online: http://dx.doi.org/10.1890/ES15-00112.1.sm

DATA AVAILABILITY

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.8h4v0