Forest Ecology and Management 353 (2015) 97–106

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Litterfall and nutrient return along a disturbance gradient in a tropical montane forest

Ekananda Paudel [a,b,c,d], Gbadamassi G.O. Dossa [b,c,d], Jianchu Xu [a,c,e], Rhett D. Harrison [a,c,e,*]

[a] Key Laboratory for Plant Diversity and Biogeography of East Asia (KLPB), Kunming Institute of Botany, Heilongtan, Kunming 650201, China
[b] University of Chinese Academy of Sciences, Beijing, China
[c] Centre for Mountain Ecosystem Studies, Kunming Institute of Botany, Kunming 650201, Yunnan, China
[d] Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan 666303, China
[e] World Agroforestry Centre, East and Central Asia Regional Office, Kunming 650201, Yunnan, China

ARTICLE INFO

Article history:
Received 4 January 2015
Received in revised form 21 May 2015
Accepted 21 May 2015
Available online 1 June 2015

Keywords:
Disturbance
Litterfall
Litter nutrient
Seasonality
Species composition
Tropical montane forest

ABSTRACT

Litterfall plays an important role in nutrient cycling and maintenance of soil fertility in terrestrial ecosystems. Annual and seasonal variation in litterfall have been investigated in various habitats, however, seasonality in nutrient supply is less well documented. We studied litterfall over two years and seasonal litter nutrient input over one year across a tropical disturbance gradient from mature forest to monoculture tea plantation. Total litter production in the mature forests and regenerating forests was not significantly different. However, tea plantations had significantly lower litter production. Total litterfall in forest habitats showed a clear seasonal pattern with a peak during the dry season (Mar.–May), as has been reported for other tropical seasonal forests. Contrary to expectations, there was no significant difference in litter nutrient concentrations across the disturbance gradient, although there was a substantial change in plant species composition. Litter nutrient concentrations also did not vary significantly across seasons, again contrary to our expectations. Thus, nutrient input was driven solely by the seasonal litterfall pattern. Our results suggest that at a landscape scale turnover in species composition linked to anthropogenic disturbance may not always lead to changes in litter quality, presumably because a similar spectra of leaf types may exist across communities. Seasonal litterfall patterns, which have been more commonly studied, may prove a reasonable proxy for nutrient input in forests.

1. Introduction

Litterfall and litter decomposition are the most important pathways for the transfer of nutrients from aboveground vegetation to soil (Berg and McClaugherty, 2014; Vitousek, 1982; Vitousek and Sanford, 1986) and are essential processes in maintaining the long-term forest nutrient status (Sayer and Tanner, 2010; Sayer et al., 2012; Tang et al., 2010; Vitousek and Sanford, 1986). For example, an experimental litterfall manipulation in a tropical forest drove rapid and substantial changes in the surface soil C pool (Leff et al., 2012), a doubling of litter input increased soil C by 31%, while removing surface litter decreased soil C by 26%. Litter turnover in terrestrial ecosystems is also a major carbon flux, and seasonal variation in litterfall and decomposition contributes to seasonal differences in the carbon cycle (De Weirdt et al., 2012). In addition, the leaf litter layer provides shelter to a wide range of organisms from microbes to small mammals.

Numerous studies have demonstrated that litterfall in forest ecosystems is dependent on seasonality, forest type or species composition, forest age, soil–water retention, and soil fertility (Facelli and Pickett, 1991; Vitousek and Sanford, 1986; Zhang et al., 2014). After reviewing a substantial number of articles, Zhang et al. (2014) reported that peaks of litterfall in tropical forests often occur during the dry season, suggesting that precipitation and radiation are controlling factors. In addition, litterfall seasonality in tropical forests also depends on plant composition, because plant phenological responses to environmental variation vary among species (Cuevas and Lugo, 1998; Duke, 1988; Harrison, 2008; Singh and Kushwaha, 2006; Zalamea and González, 2008). Inter-annual climatic variation is often substantial in the tropics and subtropics, and affects the phenology of the trees leading to irregular production of flowers and fruits, and ultimately drives inter-annual variation in total leaf litterfall (Liu et al., 2002; Sakai et al., 2006; Wright et al., 1999).

---

* Corresponding author at: World Agroforestry Centre, East and Central Asia Regional Office, Kunming 650201, Yunnan, China.

E-mail address: r.harrison@cgiar.org (R.D. Harrison).

http://dx.doi.org/10.1016/j.foreco.2015.05.028
0378-1127/

Similarly, litter nutrient concentrations may be dependent on climate, plant species composition, and soil properties (Berg and McClaugherty, 2014; Dent et al., 2006; Liu et al., 2006). For example, across Puerto Rico litter nitrogen (N) concentration was found to be positively correlated with the basal area of N-fixing trees (Erickson et al., 2014). Leaf litter N concentration for different plant functional groups, as well as species overall, had a linear relationship with precipitation and temperature across the Eurasian continent (Liu et al., 2006). Litter chemistry is a critical factor in determining litter decomposition rates at global, regional, and landscape scales (Berg and McClaugherty, 2014; Cornwell et al., 2008; Gholz et al., 2000; Paudel et al., in press). While a number of studies in the tropics have demonstrated a clear pattern of litterfall seasonality, temporal variation in leaf litter nutrient concentrations and total nutrient supply is less well documented (Edwards and Grubb, 1982; Liu et al., 2002; Pande et al., 2002; Wood et al., 2005), although these may be critical for understanding variation in rates of litter decomposition and nutrient availability in forests (Vitousek and Sanford, 1986).

Tropical forests are the most diverse terrestrial systems on Earth. Anthropogenic activities are the main drivers of deforestation and forest degradation, resulting in high levels of biodiversity loss (Barlow et al., 2007a; Gibson et al., 2011; Morris, 2010; Wright, 2005). Forest disturbance generates local variation in the micro-environment, including soil surface temperature and soil moisture, among habitats (Zhang and Zak, 1995) and affects species composition (Estes et al., 2011). These changes in turn alter ecosystem processes, including nutrient cycling and productivity. A number of studies have investigated the effects of disturbance on litterfall, but these have mostly focused on the effects of catastrophic natural disturbances, such as typhoons (Barlow et al., 2007b; Cizungu et al., 2014; Dezzeo and Chacón, 2006; Gairola et al., 2009; Shure and Phillips, 1987; Vendrami et al., 2012). The effects of anthropogenic forest disturbance on litter nutrient quality and nutrient inputs is less well understood.

Our aim was to understand seasonal variation in litter nutrient concentrations and input, including carbon, nitrogen, phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg), across a disturbance gradient in a tropical seasonal rain forest in SW China. To this end, we examined the following hypotheses. (i) Annual leaf-litter flux decreases with increasing disturbance (mature forest > regenerating forest > open tea fields). (ii) Litter nutrient quality decreases with increasing disturbance (mature forest > regenerating forest > open tea fields). (iii) Litter quality varies seasonally, with lower nutrient concentrations in the dry season (wet season > dry season).

2. Methods

2.1. Description of study site

This research was conducted in Mengsong, Xishuangbanna, Yunnan, SW China (UTM/WGS84: 47 N 656355 E, 2377646 N, Fig. 1). Elevation ranges between 1500 and 1900 m asl. The climate is strongly seasonal with 80% of the precipitation occurring during the wet season (May–Oct., Fig. 2). Mean annual precipitation ranges 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 classification of the forest as a rain forest is based on floristic similarities and forest physiognomy, although the seasonality and total rainfall might suggest otherwise. In this region the colder season coincides with the dry season, creating fogs which reduce the water deficit that would be expected otherwise, enabling rain forest to persist. The 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.

The landscape has been occupied by Akha people for at least two centuries. Until the Chinese government logging ban in 1998, the Akha practiced slash-and-burn agriculture and depended to a large degree on forests for their livelihoods (Kai et al., 2014; Xu et al., 2009). Since 1998, Akha have increased production of perennial crops, in particular tea, in monocultures, but still depend on the forest for various items, including firewood and mushrooms. In some areas, rough grasslands are maintained for grazing cattle by regular burning. The entire landscape is thus a complex mosaic of mature forest, younger forest regenerating following cultivation or other disturbances, and open habitats including terraced tea fields and degraded, *Imperata* dominated grasslands.

In 2010 and 2011, 28 sampling plots were established throughout the landscape with the aim of obtaining a representative sample of biodiversity across the disturbance gradient (Beckschäfer et al., 2014, 2013; Paudel et al., in press). For biodiversity sampling, plots were divided into a 3 × 3 grid of nine subplots, with 50 m between subplot centers (Fig. 1).

To obtain an unbiased selection with sample plots of different degradation status distributed across the landscape, we derived plot locations by applying double sampling with stratification. A 500 × 500 m grid of points was placed over a remotely sensed image (SPOT 5 acquired in Oct. 2009) of the landscape and each point was classified by eye as mature forest, regenerating forest, or open-land. Approximately 10% of the points were ground-truthed to verify our classification and adjustments were made accordingly. Points were accepted as being mature forest if the site was dominated by large (>30 cm dbh) trees with no evidence of recent disturbance (stumps or visible char on trunks). Forests dominated by smaller trees or with signs of recent disturbance were classified as regenerating forest. Most of these were young successional seres re-growing from slash-and-burn, although some were older forests that were highly disturbed, for example, through cultivation of tea in the understory. Open-land points included grasslands and terraced tea fields, with few or no trees. Points landing on water bodies, within villages and within a small area of paddy field next to the largest village were removed from the selection. In addition, we removed points that fell on the boundary between land-cover categories, so that our sample plots could be unambiguously assigned to a single category. Next, we divided the landscape into 16 compact equal-area units from which 12 were randomly selected for sampling, and we selected points within these units using a random number generator. We selected a mature and regenerating forest point in each of the 12 units, although two of the units did not have any mature forest. Open-land points were selected from every second unit, because it was expected that these would be more self-similar and hence require a lower level of replication for our biodiversity studies. Thus, the process resulted in a final selection of ten mature forest points, twelve regenerating forest points and six open-land points.

Vegetation (trees, shrubs, lianas, and herbs) data were collected from all the 28 plots in 2010 and 2011. For each subplot, trees, lianas and bamboos with (dbh) > 10 cm were sampled with a 10 m radius circle and trees, lianas and bamboos with dbh 2–10 cm were sampled from 5 m radius circle. The coverage of herbs and woody plants <2 cm dbh were surveyed within a 1 m radius circle.

2.2. Monthly litterfall collections

For monitoring litterfall, we selected 12 out of the 28 plots based on accessibility. Five were located in mature forest, four in

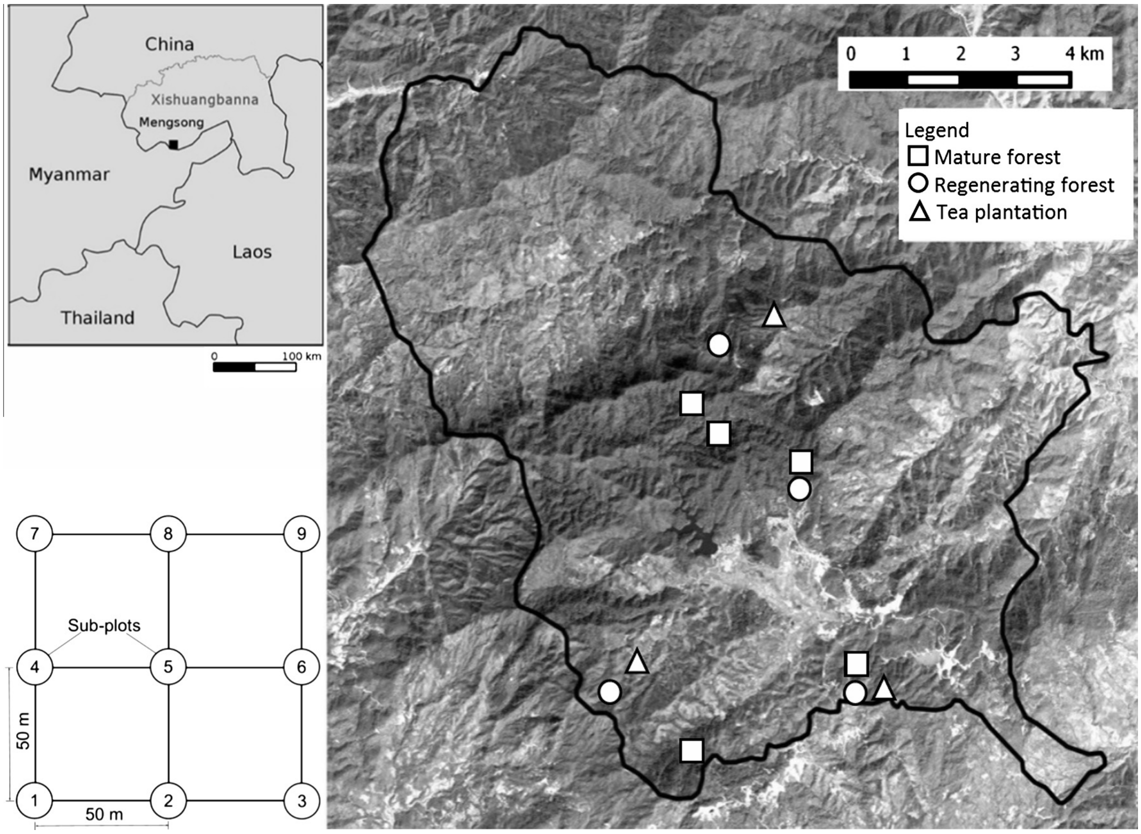

Fig. 1. Study site location: Mengsong, Xishuangbanna, southern Yunnan, China (top left). Distribution of plots in the Mengsong landscape (squares = mature forest plots, circles = regenerating forest plots, and triangles = tea plantation plots) (right). The plot design of a 3 × 3 grid of nine circular subplots (bottom left).

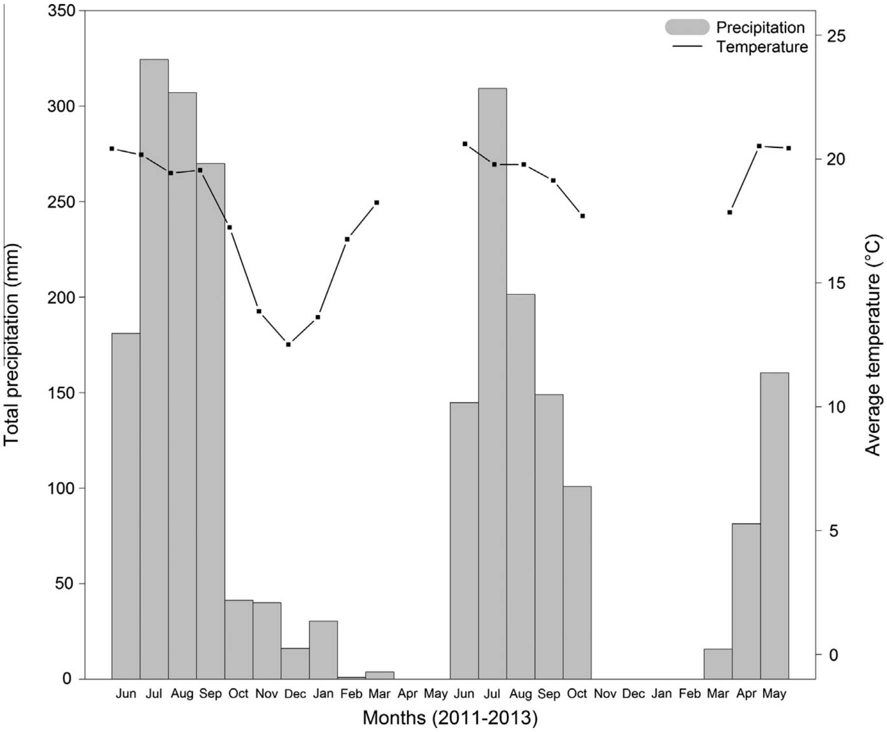

Fig. 2. Monthly average temperature and total precipitation of the study area during study period from a government weather station in Mengsong, Xishuangbanna, China (UTM/WGS84: 47 N 653164 E, 2375685 N, 1718 m asl.). Gaps (Apr.–May, Nov.–Dec. 2012 and Jan.–Feb. 2013) represent the missing data.

regenerating forest and three in monoculture tea plantations. These tea plantations were located either at the forest edge or interspersed with other crop tree plantations.

Our litterfall collection protocol was based on the Center for Tropical Forest Science protocols (Muller-landau and Wright, 2010), with minor adaptations. Litter was collected from paired aboveground and ground level traps that were 0.5 m^2 (70.7 cm × 70.7 cm PVC frame) in each of the nine subplots in all 12 plots. In each subplot, the aboveground traps were positioned horizontally 15 cm above the forest floor approximately 2 m NE of the subplot center, while the ground level traps were installed approximately 2 m E of the aboveground trap. We used an aboveground trap height of 15 cm, so as to obtain better litter collections from our monoculture tea plantation sites, as the vegetation at these sites was typically only about 1.2 m high. The aboveground traps were constructed with strong and well-draining nylon mesh ($\sim 1 \times 1$ mm). The nylon mesh was suspended inside the square PVC frame, although care was taken that the nylon mesh did not touch the forest floor. Herbs under the traps were removed on a regular basis to avoid contact with the underside of the nylon mesh, which might have affected retention of litter in the traps. Trap contents were collected monthly for two consecutive years (Jun. 2011–May 2013). Occasional damage to traps was recorded during the monthly collections and damaged traps were repaired immediately. Data from any damaged traps were discarded for the period affected. Leaves longer than 50 cm and the branches longer than 50 cm or >2 cm in diameter were discarded from aboveground traps. For ground-level traps (placed directly on the ground), only the leaves longer than 50 cm and branches >50 cm in length and <2 cm diameter were collected. Large leaves (banana and some other tree leaves in our sites) and longer branches may easily slide down from aboveground traps (Muller-landau and Wright, 2010) and so the purpose of the ground-traps was to correct for this bias.

After collection, the contents from all the traps were dried in an oven at 65 °C till constant weight and sorted into four categories; leaves (including petioles and rachis; as well as non-woody tendrils); branches (including bark and woody tendrils); reproductive parts (flowers, fruits, seeds and their supporting structures); and miscellaneous materials (caterpillar frass, dust, dead insects, and any materials passing through 2 mm sieve e.g., fragmented leaves, flowers and fruits). Each of the separated samples was weighed to the nearest 0.01 g (JA1200, NAPCO Electronic Balance, NAPCO Precision instrument, Shenzhen, China).

2.3. Chemical analysis

The oven-dried monthly samples of each litter component were stored in air-tight zip-lock bags in a dry location. We analyzed litter chemistry of samples corresponding to a one year period (Mar. 2012–Feb. 2013). To reduce costs of analyses, the monthly litter samples were homogenized and 50 g subsamples were taken. These monthly subsamples were pooled to make composite 3 month samples viz. late dry season (Mar.–May), early wet season (Jun.–Aug.), late wet season (Sep.–Nov.) and early dry season (Dec.–Feb.). All the samples were analyzed at the Yunnan Agricultural Academy of Sciences laboratory, Kunming, Yunnan, China. The N and P contents were analyzed using the micro-Kjeldahl method. The Ca, Mg, and K were determined by atomic absorption spectrophotometry. The C content was determined by $K_2Cr_2O_7$ digestion (Institute of Soil Academia Sinica, 1978).

2.4. Data analysis

We performed all the analyses in R v3.1.1 (R Development Core Team, 2014).

To visualize the effect of disturbance on plant species composition, we used non-metric multidimensional scaling (function *metaMDS*) implemented in the package vegan (Oksanen et al., 2013), based on presence/absence data (Jaccard's distance). All species that occurred in only one plot were removed, as these do not contribute any information to community assembly patterns. The basal area of each plot was calculated based on all stems with >2 cm dbh and super-imposed on the ordination as a contour plot (function *ordisurf*).

We compared litterfall, litter chemistry and total nutrient input across the disturbance gradient (mature forest, regenerating forest, and tea plantations), and among the seasons. Litter quality was compared using two-way ANOVA (disturbance category, season). We used *a priori* contrasts to compare (i) regenerating forests with mature forests and (ii) tea fields with forest plots. Similarly, we used *a priori* contrasts to compare nutrient concentrations between (i) dry season and wet season, (ii) early dry season and late dry season, and (iii) early wet season and late wet season. To calculate the total nutrient input, the litter nutrient concentration measurements were multiplied by the litterfall mass by component, and calculated for each disturbance category and season. In the case of our analyses of litter chemistry and total nutrient input, because of the large number of the models run ($n = 4$ litter components × 6 nutrients = 24), we used Bonferroni corrections to adjust the probability of a Type I error.

3. Results

3.1. Plot characteristics

Average tree basal area of mature forest plots (28.3 ± 4.1 m^2 ha^{-1}) was higher but not significantly different from the regenerating forest plots (21.4 ± 6.2 m^2 ha^{-1}, Table 1). Similarly, tree density and average tree species richness were also higher in mature forest, whereas mean canopy openness was lower in mature forest, compared to regenerating forest (Table 1), but these differences were not significant. However, all of the above variables differed significantly different between tea plantation plots and forest plots (Tukey's HSD test, $p < 0.05$, Table 1).

The first axis of NMDS (NMDS1) ordination revealed that the plant species composition varied markedly across the disturbance gradient from mature forest (positive) to tea plantations (negative), which can be understood from the close correlation with basal area. The second axis (NMDS2) reflected plant compositional differences between rain forest (negative) and broadleaf evergreen forest (positive) sites, and also between terraced tea plantation

Table 1

Mean and standard deviation of plot characteristics. Basal area and tree density of plots were calculated based on all tree species with >2 cm dbh across all nine subplots (combined area = 0.28 ha). Species richness denotes all the species of trees, lianas, bamboos and bananas. Canopy openness was estimated from hemispherical photographs taken in the center of each subplot and averaged across all nine subplots (Beckschäfer et al., 2014). Forest ages were derived from interviews with knowledgeable local people and only information from people familiar with the actual plot sites were used.

	Mature forest	Regenerating forest	Tea plantation
Basal area (m^2 ha^{-1})	$28.3^a \pm 4.1$	$21.4^a \pm 6.2$	$3.6^b \pm 1.8$
Tree density (trees ha^{-1})	$2238^a \pm 396.4$	$1917^a \pm 296.5$	$457^b \pm 288.3$
Species richness	$79.8^a \pm 5.1$	$63^a \pm 26.8$	$19.3^b \pm 16.2$
Canopy openness (%)	$4.5^b \pm 0.7$	$7.6^b \pm 4.4$	$49.27^a \pm 8.0$
Forest age (yr)	>50	<30	0

Values with the same superscript letter within a row are not significantly different ($P < 0.05$; Tukey's HSD).

(negative) and the tea plantations containing some forest trees (positive) (Fig. 3).

3.2. Litterfall

Mean annual litterfall production ranged from 3.28 ± 1.49 Mg ha^{-1} yr^{-1} in open land to 11.26 ± 2.25 Mg ha^{-1} yr^{-1} in regenerating forest (Table 2). The mean total annual litterfall in regenerating forest was not significantly different from that in mature forest (Table 2). The results were similar when litterfall was divided into each of the four component categories. The contribution of different litter components to the total litterfall showed a consistent pattern: leaves > fine wood > reproductive parts > miscellaneous (Table 2). The proportional contribution from leaves was the highest in tea fields (~73%) and the lowest in regenerating forest (~63%). Meanwhile, the proportional contribution from fine wood decreased from mature forest (~25%) to tea field (~13%) (Table 2).

Total litterfall in mature forest and regenerating forest evidenced a clear seasonal pattern, with a major peak during the late dry season (Mar.–May). However, for tea plantations there was no clear seasonal pattern (Figs. 4 and 5). The seasonal pattern for leaves and miscellaneous materials in mature forest and regenerating forest was similar to the overall pattern, but there was no clear seasonal pattern for fine wood and reproductive parts (Fig. 4 and online supplementary materials Fig. S1).

Total annual litterfall in forests was slightly higher during the Year I, but the reverse was true for the tea plantations. The result followed similar pattern when the litter components were considered separately (Table 2).

3.3. Nutrient concentrations

Even though there was a clear separation of plant species composition from mature forest to tea plantation, the concentration of most of the elements did not significantly differ among forest disturbance categories for any of the litter components in any season (Fig. 6; online supplementary materials, Table S1). K concentrations in leaves, reproductive parts, and miscellaneous material were significantly higher ($p < 0.001$, adjusted p-value after Bonferroni correction) in the dry season (Fig. 6; online supplementary materials, Table S1). In miscellaneous material the C concentration was significantly higher in tea plantations ($p = 0.001$) and during the dry season ($p < 0.05$), and P was significantly higher ($p < 0.05$) during the dry season.

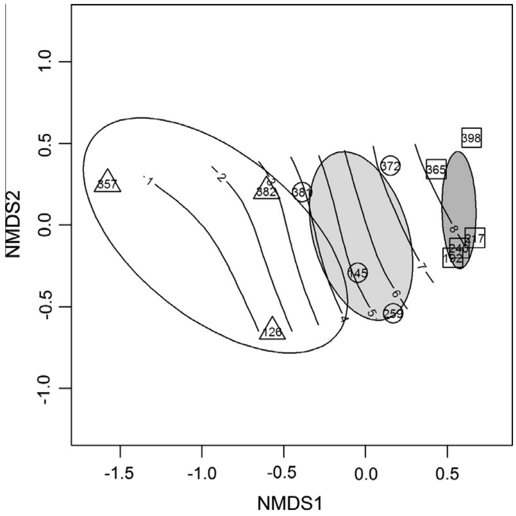

Fig. 3. A non-metric multidimensional scaling (NMDS) ordination of plant species composition, including trees, herbs and lianas, based on presence–absence data (Jaccard's distance). Points and ellipses represent the sampling plots ($n = 12$) and the 95% confidence interval around the group centroids for each disturbance category (dark gray ellipse with square points = mature forest, light gray ellipse with circular points = regenerating forest, white ellipse with triangular points = tea plantations). The numerals refer to the plot numbers.

3.4. Forest type, season and nutrient return to the forest floor

The total annual nutrient return in mature forest was slightly higher than in regenerating forest but not significantly so, while tea plantations had significantly lower nutrient return than the forest plots (Table 3). Because there was little seasonal variation in litter nutrient concentrations (Fig. 6), the seasonal pattern of total nutrient input was determined by the seasonal litterfall pattern. In forest habitats total nutrient return was the highest in late dry season (online supplementary materials Fig. S2). In open land, there was no significant seasonal pattern of nutrient input (online supplementary materials Fig. S2).

4. Discussion

4.1. Nutrient concentration variation along seasons and forest types

The nutrient concentration of leaf litter is affected by seasonal variation in the nutrient status of green leaves, which may be determined by soil nutrient and water availability when leaves are expanding, the ability of the plant to recover nutrients before leaf senescence, and factors such as herbivory (Wood et al., 2005). Higher nutrient concentrations in litter during the wet season is considered important, because the moist soil conditions make the nutrients available for plant uptake. In addition, nutrient leaching from litter that has built up during the dry season increases nutrient availability to plants in the early wet season. Moreover, if heavy rainfall is associated with strong winds this may mechanically remove the nutrient-rich green leaves and other immature plant parts, adding to the high nutrient concentrations of litter during the wet season (Cuevas and Lugo, 1998; Wood et al., 2005). Thus, green leaves that expand in wet season usually have higher nutrient concentrations than those that expand during the dry season. Although there are relatively few studies comparing litter nutrient concentrations among seasons, these have tended to find seasonal variation in nutrient concentrations (Andivia et al., 2009). For example, significantly higher P and lower N during wet season were reported from a Costa Rican rain forest (Wood et al., 2005). In a montane moist evergreen broad-leaved forest in China, higher concentrations of nutrient elements were recorded in the wet season, with the exception of K (Liu et al., 2002). Similarly, among all the nutrients measured (N, P, K, Ca, and Mg) concentrations were higher in wet season in a tropical dry deciduous teak forest of the Satpura plateau in central India (Pande et al., 2002). However, in contrast and contrary to our hypothesis, our study found that mean concentrations of most nutrients did not differ significantly among seasons, even when we considered the different litter components and forest types separately. Only K in leaves and reproductive parts was significantly higher in the dry season, which may result from reduced leaching (Edwards and Grubb, 1982; Liu et al., 2002). There was some variation in nutrient concentrations in miscellaneous material, but this is most likely because of the inconsistent composition of litter components incorporated in it.

Within the same climatic envelope, plant species composition is the most important factor in determining litter nutrient quality (Hättenschwiler et al., 2008). A number of researchers have reported differences in nutrient concentration among forests with different plant composition, successional age, and intensity of

Table 2
Annual dry mass (Mg ha^{-1} yr^{-1}) (±standard deviation) production from total litterfall and different litter components. The values inside the parenthesis are the percentage of total litter in that forest type. The litterfall was collected across the disturbance gradient (mature forest $n = 5$, regenerating forest $n = 4$ and tea plantation $n = 3$) over two years (Jun., 2011–May, 2013).

Litter components	Year	Mature forest	Regenerating forest	Tea plantation
Leaves	I	7.41 ± 0.15(64.38)	7.3 ± 1.29(62.45)	2.35 ± 1.33(72.31)
	II	6.98 ± 0.93(63.51)	6.79 ± 0.72(62.70)	2.44 ± 0.98(73.72)
	Average	7.19 ± 0.67(63.97)	7.05 ± 1.01(62.61)	2.4 ± 1.04(73.17)
Fine wood	I	2.86 ± 1.03(24.85)	2.49 ± 1.06(21.30)	0.41 ± 0.24(12.62)
	II	2.66 ± 0.81(24.20)	2.64 ± 1.63(24.38)	0.47 ± 0.3(14.20)
	Average	2.76 ± 0.88(24.56)	2.56 ± 1.27(22.74)	0.44 ± 0.25(13.41)
Repro. parts	I	0.68 ± 0.4(5.90)	1.24 ± 0.88(10.60)	0.22 ± 0.23(6.76)
	II	0.81 ± 0.63(7.37)	0.85 ± 0.38(7.84)	0.24 ± 0.19(7.25)
	Average	0.75 ± 0.5(6.67)	1.05 ± 0.66(9.33)	0.23 ± 0.19(7.01)
Miscellaneous	I	0.56 ± 0.1(4.87)	0.66 ± 0.09(5.65)	0.27 ± 0.09(8.31)
	II	0.54 ± 0.13(4.91)	0.55 ± 0.15(5.08)	0.16 ± 0.14(4.83)
	Average	0.55 ± 0.11(4.89)	0.6 ± 0.13(5.33)	0.21 ± 0.12(6.40)
Total	I	11.51 ± 1.09	11.69 ± 2.2	3.25 ± 1.75
	II	10.99 ± 1.63	10.83 ± 2.54	3.31 ± 1.57
	Average	11.14 ± 1.33	11.26 ± 2.25	3.28 ± 1.49

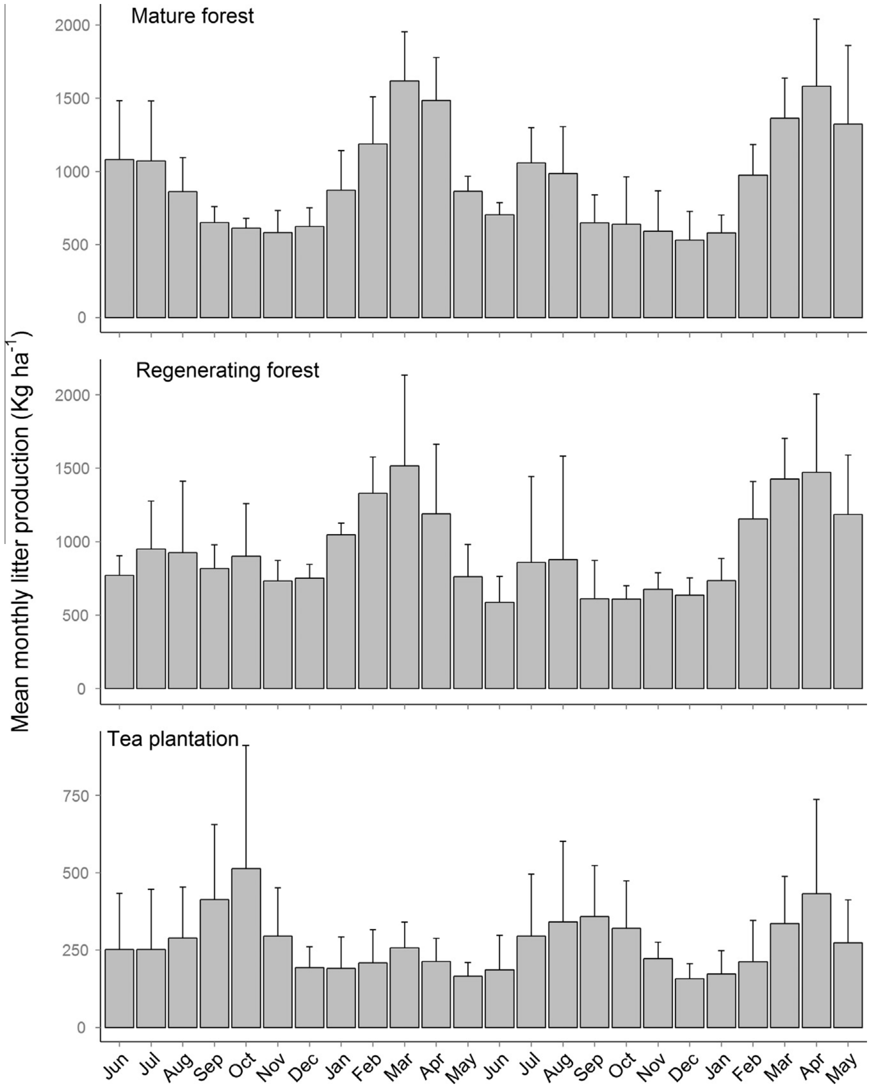

Fig. 4. Mean monthly litter production across the disturbance gradient (mature forest $n = 5$, regenerating forest $n = 4$ and tea plantation $n = 3$) over two years (Jun., 2011–May, 2013). The vertical lines represent the 95% confidence interval.

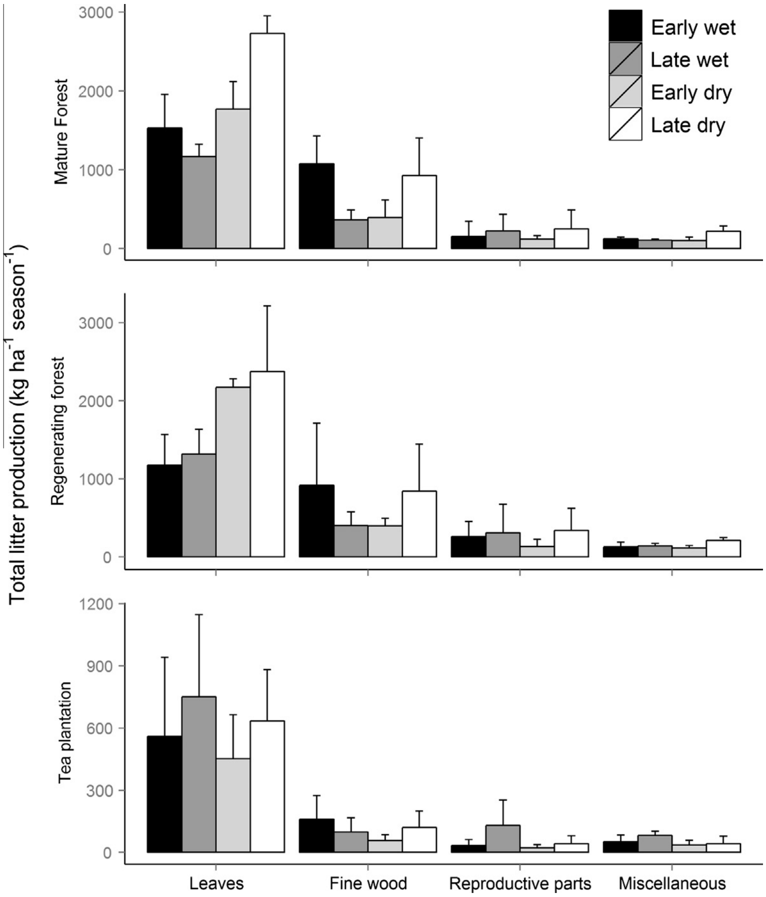

Fig. 5. Seasonal mean production (kg ha^{-1}) of different litter components across the disturbance gradient (mature forest $n = 5$, regenerating forest $n = 4$ and tea plantation $n = 3$). The vertical lines represent the 95% confidence interval.

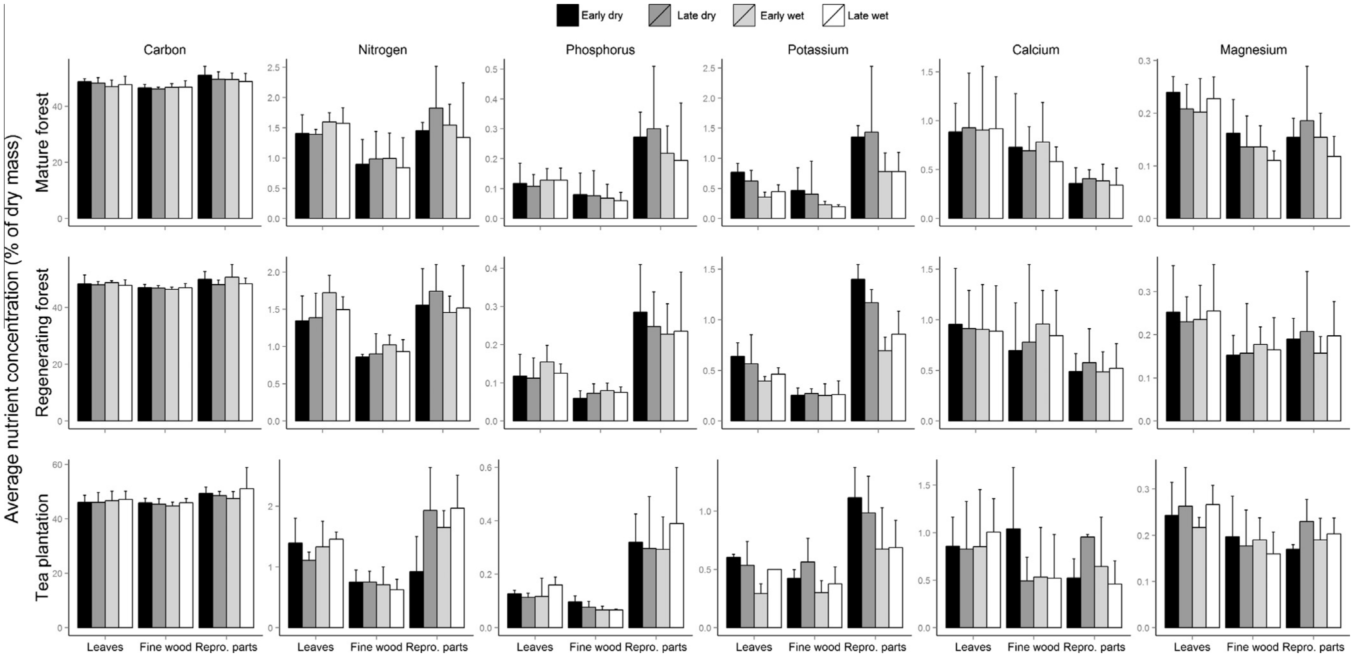

Fig. 6. Seasonal variation of average nutrient concentration from different litter components across the disturbance gradient (mature forest $n = 5$, regenerating forest $n = 4$ and tea plantation $n = 3$). The vertical lines represent the 95% confidence interval.

Table 3
Annual nutrient return (kg ha^{-1} yr^{-1}) (±standard deviation) to the forest floor from total litterfall (MF = mature forest, RF = regenerating forest and TP = tea plantation). The litterfall was collected across the disturbance gradient (mature forest $n = 5$, regenerating forest $n = 4$ and tea plantation $n = 3$) over two years (Jun., 2011–May, 2013).

Forest type	Nutrient	Leaves	Fine wood	Repro. Parts	Miscellaneous	Total
MF	C	3283.81 ± 286.80	1160.91 ± 325.97	374.58 ± 268.08	258.63 ± 73.58	5077.93
	N	100.64 ± 12.99	22.49 ± 3.29	11.13 ± 6.69	13.08 ± 4.31	147.34
	Ca	63.17 ± 29.6	16.96 ± 1.88	2.49 ± 1.48	5.07 ± 2.51	87.69
	K	39.25 ± 9.98	6.55 ± 0.5	8.23 ± 5.21	4.98 ± 1.82	59.01
	Mg	14.96 ± 2.67	3.22 ± 0.57	1.09 ± 0.7	1.44 ± 0.64	20.71
	P	8.11 ± 2.61	1.55 ± 0.14	1.76 ± 1.04	1.7 ± 0.7	13.12
RF	C	3162.29 ± 401.25	1054.77 ± 643.92	400.22 ± 185.08	242.64 ± 64.47	4859.92
	N	94.74 ± 15.30	21.13 ± 12.76	12.33 ± 5.62	12.51 ± 3.19	140.71
	Ca	61.89 ± 32.07	19.93 ± 13.84	4.16 ± 2.59	4.78 ± 2.45	90.76
	K	34.93 ± 8.33	6.52 ± 5.81	8.34 ± 3.9	4.01 ± 1.35	53.8
	Mg	16.28 ± 6.59	4.15 ± 3.49	1.57 ± 0.99	1.54 ± 0.74	23.54
	P	8.08 ± 2.43	1.57 ± 0.77	1.81 ± 0.92	1.7 ± 0.31	13.16
TP	C	1048.43 ± 424.35	159.69 ± 79.95	109.55 ± 90.97	58.43 ± 48.96	1376.1
	N	30.9 ± 17.37	2.54 ± 1.8	3.63 ± 3.42	2.76 ± 2.42	39.83
	Ca	22 ± 18.09	2.44 ± 2.58	0.94 ± 0.74	1.18 ± 1.27	26.56
	K	10.87 ± 5.49	1.31 ± 0.31	1.92 ± 1.6	1.07 ± 0.84	15.17
	Mg	5.56 ± 2.04	0.56 ± 0.09	0.39 ± 0.31	0.33 ± 0.25	6.84
	P	3.06 ± 1.85	0.25 ± 0.14	0.76 ± 0.89	0.42 ± 0.42	4.49

disturbance (Chandrashekara and Ramakrishnan, 1994; Erickson et al., 2014; Gairola et al., 2009; Herbohn and Congdon, 1998; Proctor et al., 1983; Tang et al., 2010). For example, changes in species composition following a disturbance event led to enhanced leaf litterfall nutrient concentrations in canopy thinned plots (Silver et al., 2014) and following a hurricane (Scatena et al., 1996). Based on these earlier results, we predicted that the more disturbed, species poor habitats would produce poorer quality litter. However, contrary to our expectations, nutrient concentrations did not vary significantly among disturbance categories, although species composition varied substantially. Leaf chemistry are also determined by plant strategies for defense, carbon gain and water acquisition and there may be substantial variation among plant strategies within habitats, according to factors such as plant life-history and canopy position (Cunningham et al., 1999; Van Dam et al., 1996). Our site supports high plant species richness and this may have contributed to a broad spectrum of litter types within habitats. Moreover, at our site soil fertility varied substantially among sites, reflecting variation in underlying soil conditions and complex land-use history. As litter nutrient concentrations are directly linked to soil fertility in forest stands, this may also have increased the variance in litter quality within disturbance categories (Dent et al., 2006; Herbohn and Congdon, 1998). Nevertheless, our results indicate that degraded habitats may not necessarily have poorer quality litter.

4.2. Annual litterfall and seasonal pattern

There was no significant difference in litterfall between mature forest and the regenerating forest, but the tea plantations had substantially lower litterfall than the forest plots. Thus, although litterfall declined in the most degraded habitats as hypothesized, we did not detect any trend in litterfall within increasing forest degradation within the forest habitat. Similar or even greater litter production in regenerating forests compared to mature forest has been reported elsewhere (Barlow et al., 2007b; Tang et al., 2010). The high litter production in secondary forests may be because the regenerating forest or early successional seres are often more productive (Facelli and Pickett, 1991).

The amount of litterfall in the mature and regenerating forests in Mengsong were somewhat higher than the mean annual litterfall (5.63–8.65 Mg ha^{-1} yr^{-1}) reported from tropical moist forests (Sundarapandian and Swamy, 1999) and in a montane moist evergreen broad-leaved forest (7.1 Mg ha^{-1} yr^{-1}) 250 km north of our site in Yunnan, China (Liu et al., 2002). Moreover, the proportion of leaf material in total litter in mature forest and regenerating forest from our study (range 62.5–64.5%, Table 2) is comparable to the other studies; globally (e.g., 64%; Meentemeyer et al., 1982) and close to the proportion recorded (65.4%) in an evergreen montane forest (Liu et al., 2002). The proportion of fine wood to total litter in forest habitats ranged from 21% to 25%, which is slightly higher than the reported by some previous studies (Caritat et al., 2006; Liu et al., 2002; Tang et al., 2010).

Most tropical and subtropical forests are characterized by a strong seasonality in leaf litterfall (Barlow et al., 2007b; Köhler et al., 2008; Liao et al., 2006; Liu et al., 2002; Sundarapandian and Swamy, 1999; Tang et al., 2010). Similar to these previous studies, our results demonstrated a clear seasonal litterfall pattern in mature and regenerating forest with a major peak during late dry season.

4.3. Nutrient return to the forest floor

Because there was no significant difference in nutrient concentrations among the forest types or seasons, the pattern of nutrient input mirrored that of litterfall. Total annual nutrient return was similar in mature and regenerating forests and substantially higher than in tea plantations. Similarly, in forest plots nutrient return peaked during late dry season, as a result of increased litterfall during that season.

5. Conclusions

Our results demonstrated that forest degradation had a substantial effect on nutrient input to the forest floor: monoculture tea plantations had substantially lower annual nutrient input than forest habitats. However, there was no significant difference between mature forest and regenerating forests. Low nutrient input has significant long-term consequences for soil fertility, which in turn affects plant growth and species composition. Contrary to previous reports, the nutrient concentration of leaf litter did not vary significantly across the disturbance gradient. There was also no significant seasonal variation in litter nutrient concentrations. Hence, patterns of nutrient input were driven solely by litterfall dynamics.

Acknowledgements

We would like to thank Atu and his family, and other local people from Mengsong for their assistance from the beginning of experimental set up to the completion of field work. We also thank Dr. Philip Beckschäfer and Sreekar Rachakonda for the study area map and aid during field work, respectively. We are also grateful to Bulong Nature Reserve for providing the permission to perform the experiments. Funding for this research was generously provided by GTZ/BMZ (Project No. 08.7860.3-001.00 and 13.1432.7-001.00) on behalf of the Government of the Federal Republic of Germany.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.05.028.

References

Andivia, E., Fernández, M., Vázquez-Piqué, J., González-Pérez, A., Tapias, R., 2009. Nutrients return from leaves and litterfall in a mediterranean cork oak (*Quercus suber* L.) forest in southwestern Spain. Eur. J. For. Res. 129, 5–12. http://dx.doi.org/10.1007/s10342-009-0274-6.

Barlow, J., Gardner, T.A., Araujo, I.S., Avila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santos, R., Nunes-Gutjahr, A.L., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Junior, M.A., da Silva, M.N.F., da Silva Motta, C., Peres, C.A., 2007a. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proc. Natl. Acad. Sci. USA 104, 18555–18560. http://dx.doi.org/10.1073/pnas.0703333104.

Barlow, J., Gardner, T.A., Ferreira, L.V., Peres, C.A., 2007b. Litter fall and decomposition in primary, secondary and plantation forests in the Brazilian Amazon. For. Ecol. Manage. 247, 91–97. http://dx.doi.org/10.1016/j.foreco.2007.04.017.

Beckschäfer, P., Mundhenk, P., Kleinn, C., Ji, Y., Yu, D.W., Harrison, R.D., 2013. Enhanced structural complexity index: an improved index for describing forest structural complexity. Open J. For. 03, 23–29. http://dx.doi.org/10.4236/ojf.2013.31005.

Beckschäfer, P., Fehrmann, L., Harrison, R.D., Xu, J., Kleinn, C., 2014. Mapping leaf area index in subtropical upland ecosystems using RapidEye imagery and the randomForest algorithm. iForest 7, 1–11. http://dx.doi.org/10.3832/ifor0968-006.

Berg, B., McClaugherty, C., 2014. Plant Litter: Decomposition, Humus Formation, Carbon Sequestration. Springer-Verlag, Berlin Heidelberg.

Caritat, A., Garcia-Berthou, E., Lapena, R., Vilar, L., 2006. Litter production in a *Quercus suber* forest of Montseny (NE Spain) and its relationship to meteorological conditions. Ann. For. Sci. 63, 791–800. http://dx.doi.org/10.1051/forest:2006061.

Chandrashekara, U.M., Ramakrishnan, P.S., 1994. Successional patterns and gap phase dynamics of a humid tropical forest of the Western Ghats of Kerala, India: ground vegetation, biomass, productivity and nutrient cycling. For. Ecol. Manage. 70, 23–40. http://dx.doi.org/10.1016/0378-1127(94)90072-8.

Cizungu, L., Staelens, J., Huygens, D., Walangululu, J., Muhindo, D., Van Cleemput, O., Boeckx, P., 2014. Litterfall and leaf litter decomposition in a central African tropical mountain forest and *Eucalyptus* plantation. For. Ecol. Manage. 326, 109–116. http://dx.doi.org/10.1016/j.foreco.2014.04.015.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H.M., Santiago, L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T.V., Díaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A., Vaieretti, M.V., Westoby, M., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecol. Lett. 11, 1065–1071. http://dx.doi.org/10.1111/j.1461-0248.2008.01219.x.

Cuevas, E., Lugo, A.E., 1998. Dynamics of organic matter and nutrient return from litterfall in stands of ten tropical tree plantation species. For. Ecol. Manage. 112, 263–279. http://dx.doi.org/10.1016/S0378-1127(98)00410-1.

Cunningham, S.A., Summerhayes, B., Westoby, M., 1999. Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. Ecol. Monogr. 69, 569–588.

De Weirdt, M., Verbeeck, H., Maignan, F., Peylin, P., Poulter, B., Bonal, D., Ciais, P., Steppe, K., 2012. Seasonal leaf dynamics for tropical evergreen forests in a process-based global ecosystem model. Geosci. Model Dev. 5, 1091–1108. http://dx.doi.org/10.5194/gmd-5-1091-2012.

Dent, D.H., Bagchi, R., Robinson, D., Majalap-Lee, N., Burslem, D.F.R.P., 2006. Nutrient fluxes via litterfall and leaf litter decomposition vary across a gradient of soil nutrient supply in a lowland tropical rain forest. Plant Soil 288, 197–215. http://dx.doi.org/10.1007/s11104-006-9108-1.

Dezzeo, N., Chacón, N., 2006. Litterfall and nutrient input in undisturbed and adjacent fire disturbed forests of the Gran Sabana, southern Venezuela. Interciencia 31, 894–899.

Duke, N.C., 1988. Phenologies and litter fall of two mangrove trees, *Sonneratia alba* Sm. and *S. caseolaris* (L.) Engl., and their putative hybrid, *S.* × *Gulngai* N.C. Duke. Aust. J. Bot. 36, 473–482. http://dx.doi.org/10.1071/BT9880473.

Edwards, P.J., Grubb, P.J., 1982. Studies of mineral cycling in a montane rain forest in New Guinea. IV. Soil characteristics and the division of mineral elements between vegetation and soil. J. Ecol. 65, 943–969.

Erickson, H.E., Helmer, E.H., Brandeis, T.J., Lugo, A.E., 2014. Controls on fallen leaf chemistry and forest floor element masses in native and novel forests across a tropical island. Ecosphere 5, 1–28. http://dx.doi.org/10.1890/ES13-00263.1.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D.A., 2011. Trophic downgrading of planet Earth. Science 333, 301–306. http://dx.doi.org/10.1126/science.1205106.

Facelli, J.M., Pickett, S.T.A., 1991. Plant litter: its dynamics and effects on plant community structure. Bot. Rev. 57, 1–32. http://dx.doi.org/10.1007/BF02858763.

Gairola, S., Rawal, R.S., Dhar, U., 2009. Patterns of litterfall and return of nutrients across anthropogenic disturbance gradients in three subalpine forests of west Himalaya, India. J. For. Res. 14, 73–80. http://dx.doi.org/10.1007/s10310-008-0104-6.

Gholz, H.L., Wedin, D.A., Smitherman, S.M., Harmon, M.E., Parton, W.J., 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Glob. Change Biol. 6, 751–765. http://dx.doi.org/10.1046/j.1365-2486.2000.00349.x.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478, 378–381. http://dx.doi.org/10.1038/nature10425.

Harrison, R.D., 2008. Adaptive significance of phenological variation among monoecious hemi-epiphytic figs in Borneo. Symbiosis 45, 83–90.

Hättenschwiler, S., Aeschlimann, B., Coûteaux, M., Roy, J., Bonal, D., 2008. High variation in foliage and leaf litter chemistry among 45 tree species of a neotropical rainforest community. New Phytol. 179, 165–175. http://dx.doi.org/10.1111/j.1469-8137.2008.02438.x.

Herbohn, J.L., Congdon, R.A., 1998. Ecosystem dynamics at disturbed and undisturbed sites in North Queensland wet tropical rain forest. III. Nutrient returns to the forest floor through litterfall. J. Trop. Ecol. 14, 217–229. http://dx.doi.org/10.1017/S0266467498000170.

Institute of Soil Academia Sinica, 1978. Analysis of Soil Physics and Chemistry. Science and Technology of Shanghai Publications, Shanghai (in Chinese).

Kai, Z., Woan, T.S., Jie, L., Goodale, E., Kitajima, K., Bagchi, R., Harrison, R.D., 2014. Shifting baselines on a tropical forest frontier: extirpations drive declines in local ecological knowledge. PLoS One 9, e86598. http://dx.doi.org/10.1371/journal.pone.0086598.

Köhler, L., Hölscher, D., Leuschner, C., 2008. High litterfall in old-growth and secondary upper montane forest of Costa Rica. Plant Ecol. 199, 163–173. http://dx.doi.org/10.1007/s11258-008-9421-2.

Leff, J.W., Wieder, W.R., Taylor, P.G., Townsend, A.R., Nemergut, D.R., Grandy, A.S., Cleveland, C.C., 2012. Experimental litterfall manipulation drives large and rapid changes in soil carbon cycling in a wet tropical forest. Glob. Change Biol. 18, 2969–2979. http://dx.doi.org/10.1111/j.1365-2486.2012.02749.x.

Liao, J., Wang, H., Tsai, C., Hseu, Z., 2006. Litter production, decomposition and nutrient return of uplifted coral reef tropical forest. For. Ecol. Manage. 235, 174–185. http://dx.doi.org/10.1016/j.foreco.2006.08.010.

Liu, W., Fox, J.E.D., Xu, Z., 2002. Litterfall and nutrient dynamics in a montane moist evergreen broad-leaved forest in Ailao Mountains, SW China. Plant Ecol. 164, 157–170. http://dx.doi.org/10.1023/A:1021201012950.

Liu, C., Berg, B., Kutsch, W., Westman, C.J., Ilvesniemi, H., Shen, X., Shen, G., Chen, X., 2006. Leaf litter nitrogen concentration as related to climatic factors in Eurasian forests. Glob. Ecol. Biogeogr. 15, 438–444. http://dx.doi.org/10.1111/j.1466-822x.2006.00251.x.

Meentemeyer, V., Box, E.O., Thompson, R., 1982. World patterns and litter amounts of terrestrial plant production. Bioscience 32, 125–128. http://dx.doi.org/10.2307/1308565.

Morris, R.J., 2010. Anthropogenic impacts on tropical forest biodiversity: a network structure and ecosystem functioning perspective. Philos. Trans. R. Soc. B Biol. Sci. 365, 3709–3718. http://dx.doi.org/10.1098/rstb.2010.0273.

Muller-landau, H.C., Wright, S.J., 2010. Litterfall Monitoring Protocol: CTFS Global Forest Carbon Research Initiative.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Wagner, H., 2013. Vegan: community ecology package.

Pande, P.K., Meshram, P.B., Banerjee, S.K., 2002. Litter production and nutrient return in tropical dry deciduous teak forests of Satpura plateau in central India. Trop. Ecol. 43, 337–344.

Paudel, E., Dossa, G.G.O., Blécourt, M. de, Beckschäfer, P., Xu, J., Harrison, R.D., 2015. Quantifying the factors affecting leaf litter decomposition across a tropical forest disturbance gradient. Ecosphere (in press).

Proctor, J., Anderson, J.M., Fogden, S.C.L., Vallack, H.W., 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu national park, Sarawak: II. Litterfall, litter standing crop and preliminary observations on herbivory. J. Ecol. 71, 261–283.

R Development Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org/>.

Sakai, S., Harrison, R.D., Momose, K., Kuraji, K., Nagamasu, H., Yasunari, T., Chong, L., Nakashizuka, T., 2006. Irregular droughts trigger mass flowering in aseasonal tropical forests in Asia. Am. J. Bot. 93, 1134–1139. http://dx.doi.org/10.3732/ajb.93.8.1134.

Sayer, E.J., Tanner, E.V.J., 2010. Experimental investigation of the importance of litterfall in lowland semi-evergreen tropical forest nutrient cycling. J. Ecol. 98, 1052–1062. http://dx.doi.org/10.1111/j.1365-2745.2010.01680.x.

Sayer, E.J., Joseph Wright, S., Tanner, E.V.J., Yavitt, J.B., Harms, K.E., Powers, J.S., Kaspari, M., Garcia, M.N., Turner, B.L., 2012. Variable responses of lowland tropical forest nutrient status to fertilization and litter manipulation. Ecosystems 15, 387–400. http://dx.doi.org/10.1007/s10021-011-9516-9.

Scatena, F.N., Scatena, F.N., Moya, S., Moya, S., Estrada, C., Estrada, C., Chinea, J.D., Chinea, J.D., 1996. The first five years in the reorganization of aboveground biomass and nutrient use following Hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. Biotropica 28, 424–440.

Shure, D.J., Phillips, D.L., 1987. Litter fall patterns within different-sized disturbance patches in a southern Appalachian Mountain forest. Am. Midl. Nat. 118, 348–357.

Silver, W.L., Hall, S.J., González, G., 2014. Differential effects of canopy trimming and litter deposition on litterfall and nutrient dynamics in a wet subtropical forest. For. Ecol. Manage., 535–554 http://dx.doi.org/10.1016/j.foreco.2014.05.018.

Singh, K.P., Kushwaha, C.P., 2006. Diversity of flowering and fruiting phenology of trees in a tropical deciduous forest in India. Ann. Bot. 97, 265–276. http://dx.doi.org/10.1093/aob/mcj028.

Sundarapandian, S.M., Swamy, P.S., 1999. Litter production and leaf-litter decomposition of selected tree species in tropical forests at Kodayar in the Western Ghats, India. For. Ecol. Manage. 123, 231–244. http://dx.doi.org/10.1016/S0378-1127(99)00062-6.

Tang, J.-W., Cao, M., Zhang, J.-H., Li, M.-H., 2010. Litterfall production, decomposition and nutrient use efficiency varies with tropical forest types in Xishuangbanna, SW China: a 10-year study. Plant Soil 335, 271–288. http://dx.doi.org/10.1007/s11104-010-0414-2.

Van Dam, N.M., De Jong, T.J., Iwasa, Y., Kubo, T., 1996. Optimal distribution of defenses, are plants smart investors? Funct. Ecol. 10, 128–136.

Vendrami, J., Jurinitz, C., Castanho, C., 2012. Litterfall and leaf decomposition in forest fragments under different successional phases on the Atlantic Plateau of the state of Sao Paulo, Brazil. Biota Neotrop. 12, 134–141. http://dx.doi.org/10.1590/S1676-06032012000300016.

Vitousek, P., 1982. Nutrient cycling and nutrient use efficiency. Am. Nat. 119, 553–572.

Vitousek, P.M., Sanford Jr., R.L., 1986. Nutrient cycling in moist tropical forest. Annu. Rev. Ecol. Syst. 17, 137–167. http://dx.doi.org/10.1146/annurev.es.17.110186.001033.

Wood, T.E., Lawrence, D., Clark, D.A., 2005. Variation in leaf litter nutrients of a Costa Rican rain forest is related to precipitation. Biogeochemistry 73, 417–437. http://dx.doi.org/10.1007/s10533-004-0563-6.

Wright, S.J., 2005. Tropical forests in a changing environment. Trends Ecol. Evol. 20, 553–560. http://dx.doi.org/10.1016/j.tree.2005.07.009.

Wright, S.J., Carrasco, C., Calderón, O., Paton, S., 1999. The El Niño Southern Oscillation, variable fruit production, and famine in a tropical forest. Ecology 80, 1632–1647. http://dx.doi.org/10.1890/0012-9658(1999)080[1632:TENOSO]2.0.CO;2.

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

Zalamea, M., González, G., 2008. Leaffall phenology in a subtropical wet forest in Puerto Rico: from species to community patterns. Biotropica 40, 295–304. http://dx.doi.org/10.1111/j.1744-7429.2007.00389.x.

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

Zhang, H., Yuan, W., Dong, W., Liu, S., 2014. Seasonal patterns of litterfall in forest ecosystem worldwide. Ecol. Complex. 20, 240–247. http://dx.doi.org/10.1016/j.ecocom.2014.01.003.

Zhu, H., Shi, J.P., Zhao, C.J., 2005. Species composition, physiognomy and plant diversity of the tropical montane evergreen broad-leaved forest in southern Yunnan. Biodivers. Conserv. 14, 2855–2870. http://dx.doi.org/10.1007/s10531-004-8220-x.