Elevated litterfall phosphorus reduces litter and soil organic matter pools in exotic-dominated novel forests in Singapore

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Abstract

The estimation of leaf litter turnover is often limited to early-stage decomposition using unrepresentative models and litter types. In tropical secondary forests, particularly exotic-dominated novel forests, the characterisation of litter turnover remains poor. This study estimated the annual turnover of *in-situ* leaf litter across four forest successional types in Singapore using a Weibull residence time model. Litter turnover and nutrient dynamics diverged between young secondary and old-growth forests. In particular, within novel forests, annual phosphorus return via leaf litterfall was three times that of primary forests, while the mass loss of *in-situ* leaf litter was highest among all forest successional types, estimated at 92.8% annually with a mean residence time of 176 days, resulting in a litter pool size a third that of primary forests. Our findings suggest that tree species composition and species-specific effects shaped the observed variations in litter turnover and nutrient dynamics across forest successional types and forest stands, whereas tree species richness, canopy structure, soil nutrient levels, and microclimate were found to be non-predictors. Taken together, our study provides an insight into litter turnover in human-modified tropical landscapes increasingly characterised by novel forests, potentially leading to a reduction in surface litter and soil organic carbon pools.

CAMBRIDGE UNIVERSITY PRESS

Introduction

The widespread abandonment of cultivated land and plantations in the tropics (Aide and Grau 2004; Cramer *et al.* 2008) is leading to a growing prevalence of tropical secondary forests (Gardner *et al.* 2010). Tree species composition in tropical secondary forests is altered and distinct from primary forests (Barlow *et al.* 2007a; Chazdon 2003; DeWalt *et al.* 2003). In some regenerating forests, the dominance of exotic tree species leads to novel species compositions (Cramer *et al.* 2008; Hobbs *et al.* 2006), creating 'novel forests' (Lugo 2009; Lugo and Helmer 2004). Understanding the functional implications of modified biodiversity in tropical secondary forests is crucial (Erickson *et al.* 2014; Guariguata and Ostertag 2001), particularly for key ecosystem processes such as litterfall production and decomposition (Naeem and Wright 2003).

The production and decomposition of plant litter is a major driver of carbon and nutrient cycling in terrestrial ecosystems (Meentemeyer *et al.* 1982; Vitousek 1984) and is especially important in nutrient-depleted tropical forests (Jordan and Herrera 1981; Tiessen *et al.* 1994). The quantity and quality (i.e. nutrient concentrations) of litterfall controls the return of nutrients to the forest floor (Vitousek 1984), and litterfall characteristics are shaped by the identity and composition of tree species within a forest stand (Vitousek *et al.* 1989; Ehrenfeld, 2003). Litter quality, which is typically represented by C:N and C:P ratios, in turn regulates decomposition rates (Aerts 1997; Swift *et al.* 1979). Nutrient concentrations in leaf litterfall also provide an indication of nutrient-use efficiency (Vitousek 1982) – a forest stand that produces more litterfall per unit of nutrient absorbed has higher nutrient-use efficiency (Birk and Vitousek 1986). Additionally, the stoichiometry of nutrients in leaf litterfall can reflect the relative availability of soil nutrients (Reich and Oleksyn 2004; Silver 1994) – particularly nitrogen and phosphorus, which are considered to be the most limiting nutrients in terrestrial ecosystems (Vitousek 1984).

However, despite the ubiquity of tropical secondary forests, most ecological studies remain focused on their structural and compositional attributes, while empirical data on their processes and functional characteristics, such as nutrient cycling (Guariguata and Ostertag 2001), are comparatively lacking (Bihn *et al.* 2010). This could be attributed to the bias towards understanding litterfall and decomposition in intact forests, while regenerating tropical forests are less-studied (Barlow *et al.* 2007b), especially those older than 10 years (Chazdon *et al.* 2009). Similarly, ecosystem processes in exotic-dominated tropical novel forests are usually poorly studied (Silva 2015), with studies largely limited to examples from Puerto Rico

(Erickson *et al.* 2014; Silva 2015) and Hawaii (Hughes and Denslow 2005; Hughes and Uowolo 2006). This possibly reflects the Neotropical bias in ecological studies on the functioning of tropical secondary forests (Guariguata and Ostertag 2001), with similar research being poorly replicated in tropical Southeast Asia, despite its expanding area of secondary forests (Miettinen *et al.* 2011).

Most decomposition studies focus narrowly on estimating early-stage decomposition rates, instead of estimating the total input of litterfall and the maximum extent of litter decomposed annually to derive litter turnover, which gives deeper insights into ecosystem functioning and carbon turnover (Prescott 2005). Litter turnover modulates the size of the surface leaf litter pool (Kaspari and Yanoviak 2008) – an important parameter to estimate in decomposition studies (Cornwell and Weedon 2014). The leaf litter pool also stores carbon, buffers against soil erosion and nutrient leaching, and provides habitats for the brown food web (Kaspari and Yanoviak 2008). However, it is often difficult to quantify litter turnover, given that decomposition studies frequently employ non-native common litter or single-species litterbags, which are not representative of actual decomposition patterns of diverse *in-situ* leaf litter assemblages in tropical forests (Hättenschwiler *et al.* 2011).

The accurate estimation of litter turnover is also compromised by the prevalent use of single-litter pool negative exponential decomposition models, which tend to overestimate litter mass loss and unjustifiably assume leaf litter to be of a single chemically homogenous pool (Cornwell and Weedon 2014). Instead, decomposition models that incorporate chemical heterogeneities by modelling a continuous distribution of litter quality should be adopted more widely, as they improve the balance between accuracy and parsimony (Manzoni *et al.* 2012). An example of a continuous litter quality model is the Weibull residence time model (Cornwell and Weedon 2014). Although used infrequently in decomposition studies, the Weibull residence model provided robust fits to a wide array of decomposition data and permitted decomposition rates to increase or decrease over time to account for the relative proportions of labile and recalcitrant material in litter (Cornwell and Weedon 2014; Olson 1963).

This study was conducted in Singapore, which offers a 'natural experiment' due to widespread historical forest clearance for agriculture and the chronologically staggered abandonments subsequently (Corlett 1992). The forest cover is dominated by secondary forests across a gradient of successional ages exceeding 100 years (Corlett 1997; Turner *et al.* 1996), and of varying land-use histories, habitat properties, and tree species compositions, offering a spatial mosaic of forest successional types as 'treatments' for comparison (Yee *et al.* 2016; Yee *et al.* 2011). Some of the young secondary forests form canopies that are dominated by exotic species (Corlett 2011; Kee 2012; Tan *et al.* 2010) and so can be viewed as novel forests (Hobbs *et al.* 2006). In contrast, the remnant fragments of primary and old secondary forests are generally resistant to species invasion (Teo *et al.* 2003).

Although the compositional shifts and decline of tree diversity in Singapore's secondary forests are well characterised (Corlett 1997; Kee 2012; Neo 2012; Turner *et al.* 1997), there remains a paucity of research on their ecosystem functioning, particularly in key processes such as litterfall and decomposition. This mosaic of forest fragments in Singapore also provides an excellent opportunity to predict the fate of ecosystem processes in similar human-modified landscapes, which increasingly defines the tropics (Gardner *et al.* 2009). Moreover, the presence of 100-year-old secondary forests

provides a rare opportunity to investigate the long-term recovery of litter and nutrient cycling processes, as similar studies are typically limited to young secondary forests (Chazdon *et al.* 2009). Furthermore, the high floristic richness and complex stand structure across the forest types used in this study permit a more robust inference of the linkage between species richness and litterfall production – this linkage has more often been assessed in species-poor and structurally simple monoculture plantations or controlled experimental plots (Huang *et al.* 2017; Scherer-Lorenzen *et al.* 2007).

Therefore, this study aims to investigate the following across the primary and secondary forests of Singapore: (1) quantify annual litterfall production; (2) determine leaf litter quality and quantify the annual return of nitrogen and phosphorus via the leaf litterfall fraction (and hence infer nutrient-use efficiencies and relative nutrient limitations); (3) estimate the annual turnover of *in-situ* leaf litter from the soil surface and its contribution to the accumulation of soil organic matter by fitting a Weibull residence time model; and (4) evaluate the roles of forest successional type, soil nutrient concentrations, and leaf litter quality in shaping the observed patterns of leaf litter production and turnover. We hypothesise that litterfall and litter turnover is positively associated with forest successional age, i.e. primary forest stands producing the most litterfall and with the fastest turnover.

Materials and methods

Study sites and forest types

This study was conducted in Singapore, a highly urbanised island-state located in Southeast Asia. The climate is equatorial and aseasonal, with an average mean daily temperature of 27.0°C and an annual rainfall of 2331 mm, with no months receiving less than 100 mm of rain on average (National Environment Agency 2016).

Eighteen study sites, classified into four forest successional types, were selected (Figure S1). The classification of forest types followed Corlett (2011) and Yee *et al.* (2011). *Primary forests* refer to lowland dipterocarp forests, which was historically the dominant dryland vegetation of Singapore (Corlett 1991b). Today, only 0.25% of Singapore's land area or approximately 192 ha is covered by primary lowland dipterocarp forests (Corlett 1997), forming remnant primary forest fragments surrounded by larger tracts of old secondary forests (Turner and Corlett 1996). *Old secondary forests* in Singapore are tall secondary forests of approximately 100 years of age or more (Corlett 1997; Turner *et al.* 1996), having regenerated on abandoned plantations, mainly of gambier (*Uncaria gambir*) and pepper (*Piper nigrum*) crops (Corlett 1992). Old secondary forests are dominated by late-successional native plant species (Yee *et al.* 2016) and harbour about 60% of the tree species found in primary forests (Turner *et al.* 1997). Today, the total area of old secondary forest fragments is approximately 1000 ha – less than 1.4% of Singapore's land area (Yee *et al.* 2011). Primary and old-secondary forests are collectively referred to as old-growth forests in this study.

Two categories of young secondary forests – *abandoned rubber plantations* and *waste woodlands* – were selected for this study. At its peak, Pará rubber (*Hevea brasiliensis*) plantations occupied up to 40% of Singapore's land area (Corlett 1991b). Subsequently, rubber plantations were abandoned between the 1940s and late 1950s (Shepherd and Shepherd 1968). Although the canopy in abandoned rubber plantations remains dominated by rubber trees, the mid- and understorey layers harbour mostly native species

(Neo 2012; Yee *et al.* 2016). Approximately three-quarters of the overall vascular flora recorded from abandoned rubber plantations are native species (Neo 2012).

Waste woodlands represent the youngest secondary forests in this study with a successional age well under 50 years, having regenerated from abandoned villages and farmland cleared after the 1960s (Yee *et al.* 2016). Land clearance involved bulldozers (Corlett 2011), resulting in the removal or perturbation of topsoil (Yee *et al.* 2016). The degraded land in the absence of a canopy cover (Corlett 1991a) enabled a spontaneous regeneration dominated by easily dispersed exotic tree species (Kee 2012), many of which are invasive (Corlett 2011; Tan *et al.* 2010) – notably Albizia (*Falcataria falcata*) and Earleaf Acacia (*Acacia auriculiformis*). Waste woodlands in Singapore are hence also viewed as novel forest ecosystems (Yee *et al.* 2016). Overall, across the forest successional types evaluated in this study, the relative dominance of exotic plants generally increases as forest successional age decreases, while species richness decreases, hence providing a 'natural experiment' to assess the influence of species composition and species richness on litter turnover dynamics.

Study design

Above-ground fine litterfall was estimated following a tropical forest protocol by Muller-Landau and Wright (2010). In each study site, six above-ground litterfall traps were installed in a rectangular grid layout spaced 30 m apart. In total, 108 litterfall traps were installed. Litterfall traps had openings of 70.7 cm by 70.7 cm, representing a sampling area of 0.5 m^2 each, and were placed at a standardised height of 90 cm above the forest floor.

Fine litterfall was collected monthly between February 2014 and January 2015 and dried at 60°C until it reached constant mass. It was subsequently separated into its constituent fractions – leaves, fine wood, reproductive litter, and debris. Fine wood included woody material such as bark and branches ≤20 mm in diameter. Reproductive litter was defined as flowers, fruits, and seeds, as well as their accessory structures. Debris referred to fine litter fragments and dust that passed through a 2 mm sieve. Non-plant material, e.g. invertebrates and feathers, were omitted. The dry mass of each litterfall fraction was recorded to the nearest 0.01 g. Using each litterfall trap as a replicate, mean annual litterfall production (Mg/ha/yr) was estimated for each study site and forest type.

The returns of carbon and nutrients to the forest floor via leaf litterfall were estimated by quantifying the concentrations of carbon and nutrients within leaf litterfall bulked and homogenised per study site per month. Carbon concentration was sampled using leaf litterfall collected in February 2014, while the concentrations of nitrogen and phosphorus were sampled and averaged using leaf litterfall collected in August 2014 and January 2015. Total carbon was determined with an elemental analyser (Vario EL, Elementar, Germany), while total nitrogen was determined with the Kjeldahl method (Kjeldahl 1883), and total phosphorus was determined by an inductively coupled plasma (ICP) emission spectroscopic method following dry ashing and acid digestion. Nitrogen and phosphorus nutrient-use efficiencies (NUE and PUE, respectively) were calculated as the ratio of leaf litterfall produced to the amount of nutrient returned through leaf litterfall, following Vitousek (1982). Leaf litterfall C:N, C:P, and N:P ratios were also calculated.

In-situ leaf litter mass loss was estimated using nylon litterbags with a coarse mesh aperture of 2 mm, which permitted the entry of all microfauna and mesofauna, as well as most macrofauna (Swift *et al.* 1979). Leaf litterfall collected over 2 months (February and

March 2014) was bulked and homogenised per study site, from which a subsample of 15–20 g (dry mass) was placed into individual litterbags. The litterbag contents thus form a stand-level sample of the *in-situ* leaf litter assemblage produced within each study site.

Nine litterbags were deployed per study site. Litterbags were secured to stakes and placed in direct contact with the forest topsoil by temporarily shifting the litter layer aside and returning it thereafter to maintain a representative decomposition micro-environment. All 162 litterbags were deployed in April 2014 and subsequently retrieved following a destructive sampling approach. Litterbags were retrieved after deployment lengths of *ca.* 60 and 210 days at all sites, and after *ca.* 330 days in abandoned rubber plantations and waste woodlands, or after *ca.* 390 days in primary and old secondary forests; the longer periods were used to account for the slower mass loss and to improve model fitting. Retrieved litterbags were dried until they reached constant mass at 60°C. The litter mass remaining was weighed after removing foreign material such as soil particles, roots, and invertebrates.

Characterisation of habitat properties

Air temperature and relative humidity in each study site were recorded using data loggers (iButton Hygrochron DS1923, Dallas Semiconductor, TX, USA). Soil volumetric water content was recorded using sensor probes buried 10 cm deep and connected to a HOBO Micro Station data logger (Onset Computer Corporation, MA, USA). Canopy openness directly above each litterfall trap was measured indirectly using canopy hemispherical photography; canopy photographs were analysed using the CIMES software package (Gonsamo *et al.* 2011) (Table S1).

To determine soil organic matter and nutrient content (Table S1), 15-cm deep soil cores were obtained. A pair of soil cores was obtained from opposite sides of each litterfall trap. The topsoil samples were pooled and homogenised for each study site for analysis. Total soil nitrogen was determined by the Kjeldahl method (Bremner 1960; Kjeldahl 1883). Soil phosphorus, potassium, calcium, and magnesium were extracted using Mehlich-3 extract (Mehlich 1984) and quantified using ICP spectroscopy. Soil organic matter was determined by the loss on ignition method (Ball 1964). Soil organic matter was not determined for two study sites (IK and PU) as they were cleared for developments prior to soil sampling.

Data analysis and modelling
Annual litterfall production
Annual total and leaf litterfall production were fitted using multivariate linear mixed-effects models; the fine wood, reproductive, and debris litterfall fractions were not modelled given their minor contributions. Forest type, soil nitrogen content, and soil phosphorus content were included in the models as fixed effect predictors, while study site was included as a random effect. To investigate if litterfall production is influenced by canopy structure and density, the canopy openness (%) directly above each litterfall trap, as estimated by hemispherical photography, was also included as a fixed-effect predictor in the linear mixed-effects models. The models were fitted by maximising the restricted log-likelihood using the 'nlme' package (lme function) (Pinheiro *et al.* 2017) in R (R Core Team 2016). Model residuals were visually checked against assumptions of homoscedasticity and normality. For pairwise comparisons of litterfall production between forest types, a Tukey's post-hoc test at a significance level of 0.05 was

performed using the R package 'multcomp' (glht function) (Hothorn *et al.* 2008).

Leaf litter mass loss and annual turnover

The mass loss of leaf litter was modelled using the Weibull residence time model, following Cornwell and Weedon (2014):

$$W(t) = e^{-\left(\frac{t}{\beta}\right)^{\alpha}} \tag{1}$$

where $W(t)$ is the relative weight of litter remaining, t is the deployment period (days), and α and β are the shape and scale parameters of the mass loss trajectory, respectively. The temporal trajectory of litter mass loss was fitted to equation (1) using a non-linear least square approach (Gauss–Newton algorithm). Models were fitted separately for each forest type and for each study site. The model-predicted proportion of leaf litter loss annually was then used to estimate the dry mass of leaf litterfall that is loss and accumulated annually on a stand-level for each study site. Additionally, leaf litter half-life and mean residence time were calculated, following Cornwell and Weedon (2014) (see Supplementary Material Note 1).

Evaluating predictors of leaf litter production, nutrient dynamics, and mass loss

Annual leaf litter mass loss, soil nutrient and organic matter content, NUE, and PUE (as derived from leaf litter nutrient concentrations) were modelled using multivariate linear regression models (candidate models are shown in Table S5) due to the absence of a random effect (study site), as leaf litter turnover, leaf litter nutrient, and soil nutrient data were pooled at the site level. To fulfil linear modelling assumptions where the dependent variable is a proportion (annual leaf litter mass loss) or percentage (soil organic matter content), the dependent variable was transformed using a logit transformation, following Warton and Hui (2011) (see Supplementary Material Note 2 for the interpretation of model coefficients with logit-transformed dependent variables).

All multivariate linear mixed-effects and regression models were checked for multicollinearity by using the R package 'car' (function variance inflation factor (VIF)) (Fox and Weisberg 2011) and following Zuur *et al.* (2010), where explanatory variables with a VIF greater than three had to be omitted – the predictors of soil potassium, magnesium, and calcium content exhibited evidence of multicollinearity and were omitted from the linear mixed-effects models of total and leaf litter production. Subsequently, candidate models were assembled using the remaining explanatory variables in all combinations (see Table S3 and Table S5), and the best (most parsimonious) model was selected using Akaike's information criterion corrected for small sample sizes (AICc) with the R package 'AICcmodavg' (Mazerolle 2016). The model with the lowest AICc was taken to have the strongest support, since it represents the best balance between accuracy and parsimony (Burnham and Anderson 2002). For the most parsimonious models with multiple explanatory variables, the relative importance of each explanatory variable was calculated using the R package 'relaimpo' (Gromping 2006), and adopting the LMG method described by Lindeman *et al.* (1980), which decomposes overall R^2 by calculating the contribution of each predictor (the squared semi-partial) at all possible points of entry into the model and taking the average.

Results

Annual litterfall production

Annual litterfall production generally declined with decreasing forest successional age, with waste woodlands being an exception. Despite being the youngest forest successional type, waste woodlands produced the most total litterfall annually (Figure 1), averaging 12.78 ± 0.96 Mg ha^{-1} yr^{-1}, which was 16% higher than the mean of 10.98 ± 0.65 Mg ha^{-1} yr^{-1} recorded in primary forests. Leaf litter formed the dominant fraction ($\geq$70%) of total litterfall, hence the pattern of leaf litterfall production across forest types closely mirrored that of total litterfall production (Figure 1).

However, the large heterogeneity in litterfall production between study sites meant that the increase in total and leaf litterfall production in waste woodlands compared to primary forests was not statistically significant (Figure 1; Table 1, site-specific details in Table S2). The large variance in litterfall production between study sites was also reflected by the >50% improvement in model fits (as interpreted by the coefficients of determination) when study site was accounted for as a random effect in linear mixed-effects models (Table 1). Other litterfall fractions – fine wood, reproductives, and debris – showed no statistically significant differences in annual production between forest types, with the sole exception being the significantly higher production of debris litterfall recorded in waste woodlands (Figure 1).

Forest type was a predictor of total and leaf litterfall production in the most parsimonious linear mixed-effects models, while soil nitrogen content was also a predictor for total litterfall production (Table 1). Soil phosphorus content and canopy openness above each litterfall trap were excluded as model predictors during the AIC-based model selection process (Table S3). Overall, forest successional type was the predictor that exhibited the largest effect size and thus explained most of the variation in litterfall production.

Leaf litterfall quality and annual nitrogen and phosphorus return

Leaf litterfall quality as measured by C:N and C:P ratios reduced with increasing forest successional age – leaf litterfall C:N and C:P ratios were higher in younger secondary forests compared to old-growth forests (Figure 2a). The variations of leaf litterfall C:N and C:P ratios largely reflected the variations in leaf litterfall nitrogen and phosphorus concentrations, given that leaf litterfall carbon content was relatively uniform across study sites, at approximately 50% (Table S2). Across forest types, leaf litterfall C:P ratios exhibited a larger divergence relative to C:N ratios, while N:P ratios increased with increasing forest successional age (Figure 2a, site-specific details in Table S2). Taken together, leaf litterfall nutrient stoichiometry showed that phosphorus was the primary contributor to elevated leaf litterfall quality in young secondary forest types.

Consequently, waste woodlands returned the largest amounts of nutrients to the forest floor via leaf litterfall, particularly for phosphorus, given the combined effects of increased leaf litterfall quality and increased annual leaf litterfall production. Waste woodlands returned 4.57 kg ha^{-1} yr^{-1} of phosphorous to the forest floor, almost thrice the amount recorded in old-growth forests (Figure 2c). Furthermore, the amount of phosphorus return via leaf litterfall was found to be a significant determinant of soil phosphorus levels (Table 2), serving as a better predictor compared to forest type (Table S5). While nitrogen return was also higher in waste woodlands, the magnitude of increase was smaller – waste woodlands returned 175 kg ha^{-1} yr^{-1} of nitrogen via leaf litterfall

Table 1. Summary of the most parsimonious linear mixed-effects models to evaluate controls on annual total litterfall and annual leaf litterfall (a list of all candidate models evaluated are shown in Table S3). Study site was modelled as a random effect. The marginal R^2 considers only the variance of the fixed effects, while the conditional R^2 takes both the fixed and random effects into account

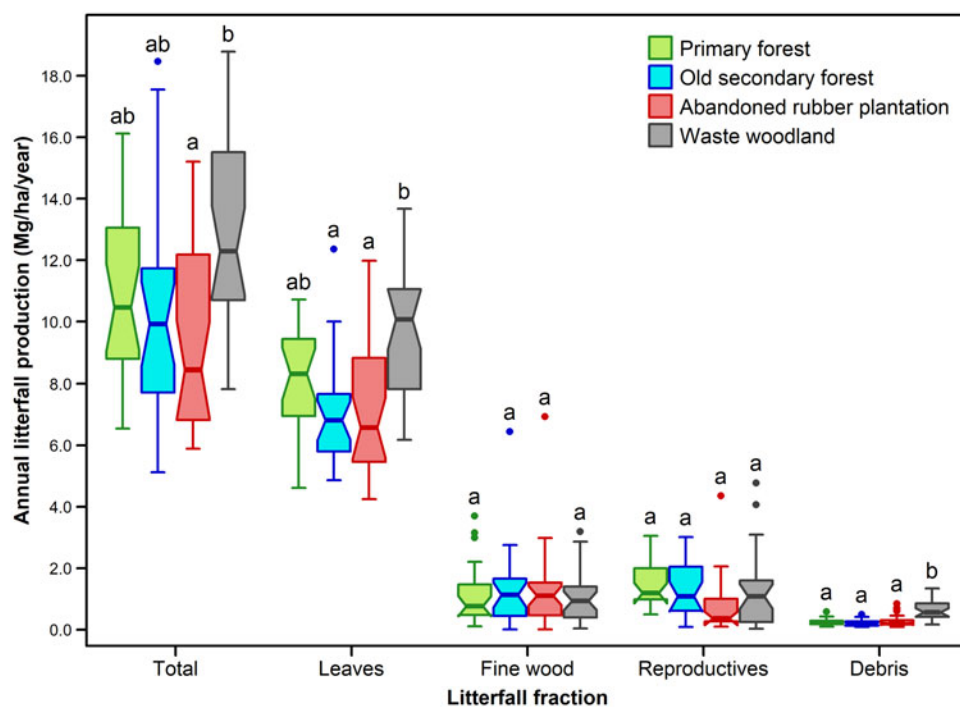|		Annual *total* litterfall production	Annual *leaf* litterfall production
Predictors (fixed effects)		Estimate	Estimate
Forest type:	Primary forest (intercept)	8.689	8.066
	Old secondary forest	−1.316	−0.864
	Abandoned rubber plantation	−1.872	−0.852
	Waste woodland	1.577	1.772
Soil nitrogen content (mg/kg)		0.001	−
Random effects			
Site (between-site variance)		7.176	3.038
Residual (within-site variance)		1.143	0.997
Marginal R^2, conditional R^2		0.205/0.315	0.235/0.424

Figure 1. Notched boxplots of annual litterfall production and its constituent fractions across different forest successional types. The notch approximates the 95% confidence interval of the median. For each litterfall fraction, forest successional types that do not share the same letter code exhibited statistically significant differences (Tukey's post-hoc test following a linear mixed-effects model, $p \leq 0.05$).

compared to 111 kg ha^{-1} yr^{-1} in primary forests (Figure 2b). Therefore, the amount of nitrogen returned via leaf litterfall was not found to be a predictor of soil nitrogen levels (Table 2).

Overall, soil nitrogen and soil phosphorus levels were not predictors of NUE and PUE, respectively, when analysed using linear regression models. Instead, PUE was predicted by forest type, which explained most of its variation (Table 2). Conversely, forest type was not a significant predictor of NUE, given the large overlaps in NUE across forest types (Table S2).

Annual turnover of leaf litterfall and its contribution to soil organic matter

Old-growth forest and young secondary forest successional types exhibited divergent patterns of *in-situ* leaf litter mass loss, with the latter supporting higher mass losses from litterbags (Figure 3).

Using a Weibull residence model, it was estimated that the *in-situ* leaf litter mass loss in waste woodlands was 92.8% annually, compared to 71.2% and 67.4% in primary forests and old secondary forests, respectively (Figures 3 and 5). However, stand-level analysis using linear regression models revealed that leaf litter C:N and C:P ratios explained more variation in annual leaf litter mass loss ($R^2 = 0.809$; Table 2) compared to forest type (Table S5) and were inversely associated with annual leaf litter mass loss (Table 2). Analysis of the relative importance of leaf litter C:N and C:P ratios in regulating mass loss revealed that approximately 60% of the explained variance in annual leaf litter mass loss was attributable to leaf litter C:N ratio, while the remaining 40% was attributable to leaf litter C:P ratio (Table 2). Soil moisture content was not found to be a predictor of annual leaf litter mass loss (Table S5).

The Weibull residence model predicted the mean residence time of leaf litter to be shorter than a year across all forest types, and
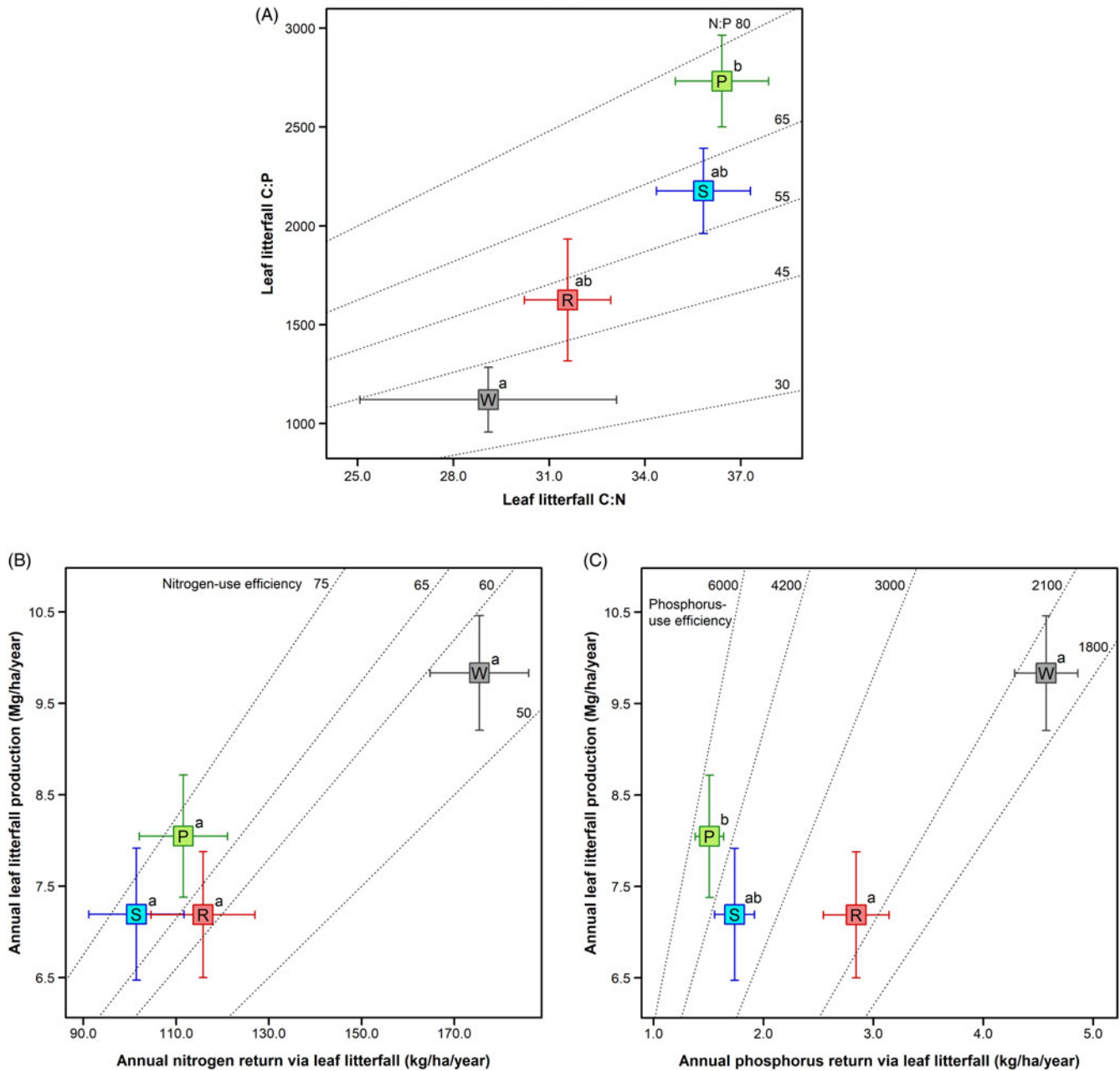
Figure 2. (**A**) Leaf litterfall chemical quality across forest successional types as represented by C:P and C:N ratios. The relationship between C:P and C:N provides N:P, which is indicative of the relative availability of nitrogen and phosphorus; dotted lines indicate constant N:P. (**B & C**) Nitrogen-use efficiency (NUE) and phosphorus-use efficiency (PUE) across forest types as represented by the relationship between annual leaf litterfall production and the annual return of nitrogen and phosphorus, respectively, through leaf litterfall; dotted lines indicate constant NUE or PUE values. Annual nutrient returns and nutrient-use efficiencies per study site are detailed in Table S2. Error bars represent standard errors of the mean. Letters to the top-right of symbols represent the results from a Tukey's post-hoc test following a linear model; forest types that do not share the same letter exhibited statistically significant differences ($p < 0.05$) in N:P, NUE, or PUE. P: primary forest; S: old secondary forest; R: abandoned rubber plantation; W: waste woodland.

that leaf litter in waste woodlands exhibited the shortest mean residence time, at 176 days, compared to 317 days in old secondary forests (Figure 4). Consequently, it was estimated that waste woodlands accumulated the smallest leaf litter pool annually, despite supporting the highest annual leaf litterfall production. By contrast, old-growth forests accumulated three times more annual leaf litterfall into the litter pool – approximately 2.3 Mg ha^{-1} yr^{-1} (Figure 5). The estimated size of leaf litter pool accumulated annually was found to be a significant ($p = 0.0034$) and positive predictor of soil organic matter content (Figure 6), when analysed on a stand-level using a linear regression model (Table 2), while

forest type was excluded from the most parsimonious model (Table S5), reflecting the heterogeneity in soil organic matter content across forest types (Figure 6).

Discussion

Litterfall production

Contrary to the positive correlations between litterfall production and forest successional age observed in other tropical forests (Cole *et al.* 2020; Huang *et al.* 2017), our finding of the highest litterfall

Table 2. Summary of the most parsimonious linear regression models to evaluate controls on nutrient-use efficiencies, the estimated proportion of annual leaf litterfall mass loss annually, and soil phosphorus, nitrogen, and organic matter content (a list of all candidate models evaluated is shown in Table S5). For multivariate models, the relative importance (proportion of model R^2 explained) of each predictor variable is shown

| Response	Predictors		Estimate	Relative importance of predictors	Model R^2
Nitrogen-use efficiency (NUE)	Intercept		67.522	–	0
	Soil nitrogen content		-5.90×10^{-4}		
Phosphorus-use efficiency (PUE)	*Forest type:*	Primary forest (intercept)	5416.7	–	0.643
		Old secondary forest	−1083.3		
		Abandoned rubber plantation	−2188.1		
		Waste woodland	−3075.4		
Soil phosphorus content	Intercept		2.298	–	0.391
	Annual phosphorus return via leaf litterfall		1.422		
Soil nitrogen content	Intercept		1807.618	–	0.011
	Annual nitrogen return via leaf litterfall		1.116		
Proportion of leaf litterfall mass loss annually (logit-transformed)	Intercept		8.881	–	0.809
	Leaf litterfall C:N ratio		−0.172	0.604	
	Leaf litterfall C:P ratio		-6.77×10^{-4}	0.396	
Soil organic matter content (%) (logit-transformed)	Intercept		−3.19	–	0.470
	Estimated amount of leaf litterfall accumulated annually		0.306		
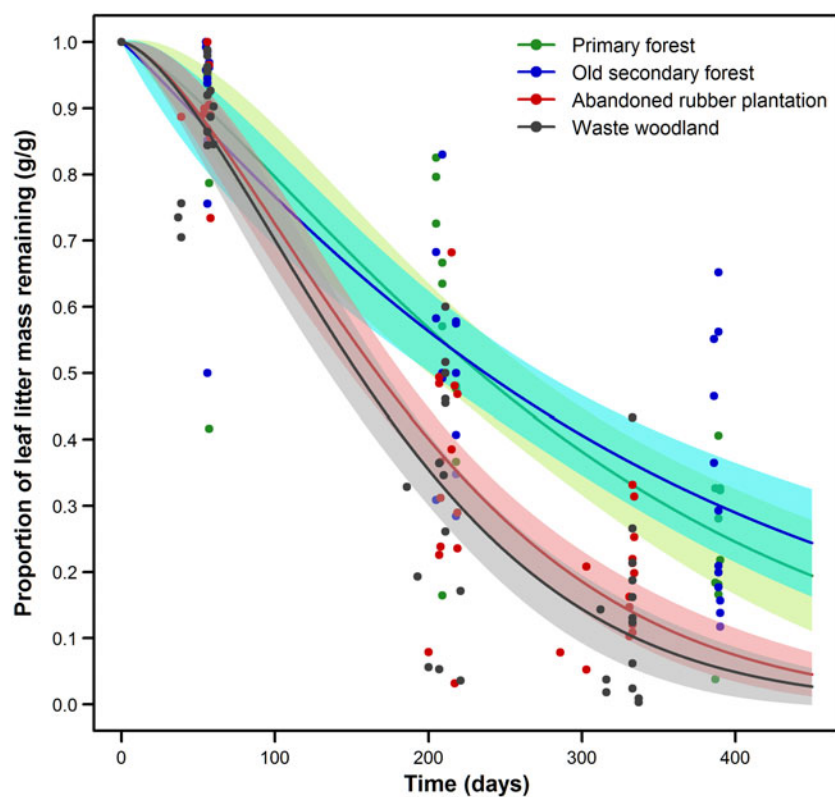
Figure 3. Estimated mass loss of *in-situ* leaf litter per forest successional type fitted with the Weibull residence model. Data points represent observations for each litterbag. Shaded region represents the 95% confidence interval of the model-predicted mean derived from bootstrapping ($n = 1000$).

production in the youngest and most depauperate forest successional type – waste woodlands – was unexpected and contrary to our hypothesis. The increased leaf litterfall in waste woodlands could be attributed to its dominance of exotic species, which typically exhibit increased growth rates, lower leaf construction costs, and reduced leaf strength (Baruch and Goldstein 1999; Daehler 2003; Reich *et al.* 1997). Reduced leaf strength was indeed evident in waste woodlands species here, as inferred by the increased debris fraction of litterfall recorded, presumably due to increased fragmentation of weaker leaf litter. The observed

Figure 4. Mean residence time and mean half-life of *in-situ* leaf litter per forest successional type calculated using the Weibull residence model-estimated parameters of α and β, following Cornwell and Weedon (2014) (equations in Supplementary Material Note 1). Error bars represent standard errors of the mean. Numerical values indicate the ratio (mean residence time): (mean half-life) – an estimator of the relative proportions of recalcitrant and labile material in leaf litter (Cornwell and Weedon 2014).
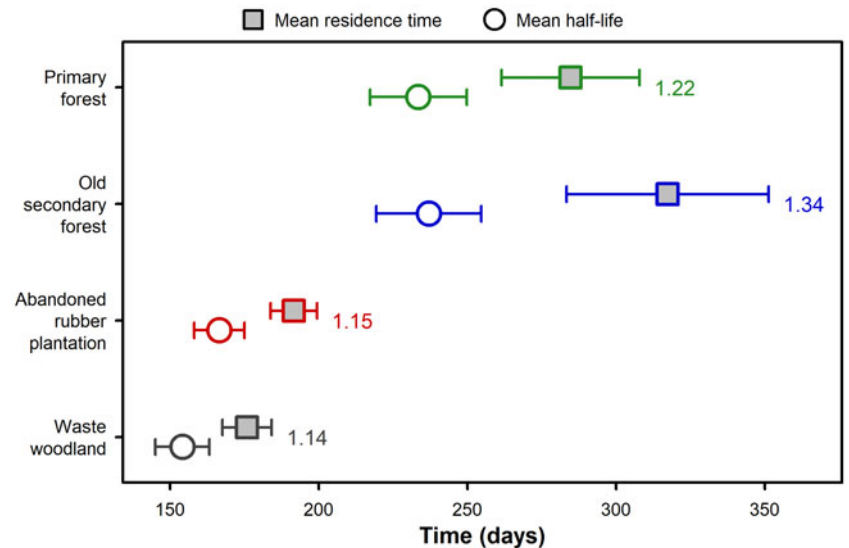

Figure 5. Amount of annual leaf litterfall loss and accumulated per forest successional type as estimated by the Weibull residence model. Error bars represent standard error of the mean for annual leaf litterfall production. Values within bars indicate the Weibull model-estimated percentages of leaf litter mass loss annually and the standard deviations per forest type. Letters within bars represent the results from a Tukey's post-hoc test following a linear model; forest successional types that do not share the same letter exhibited statistically significant differences ($p \leq 0.05$) in the estimated amount of leaf litterfall accumulated annually.
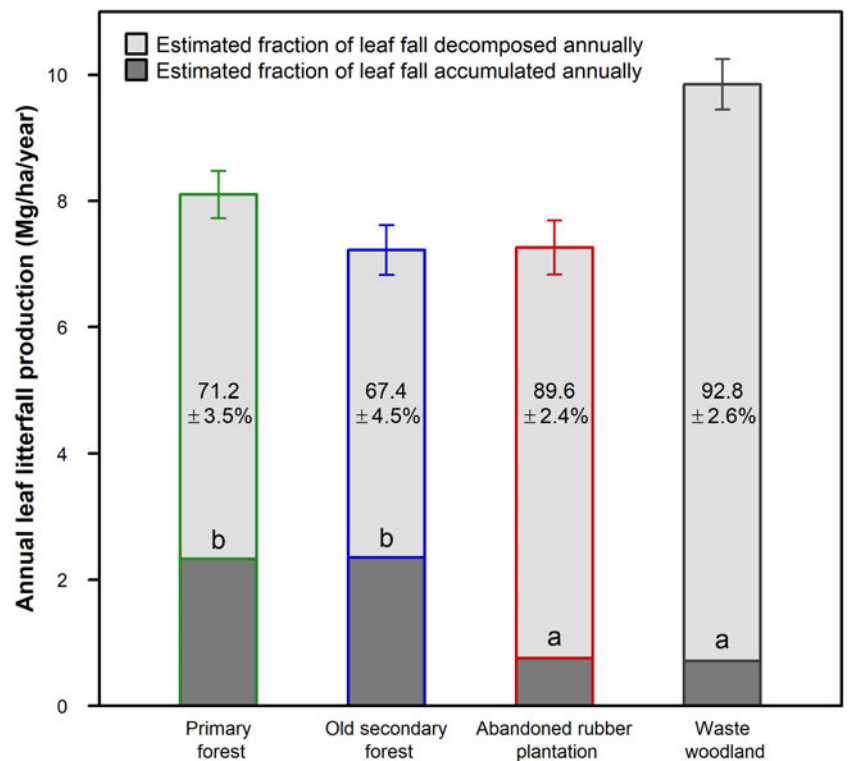
association of litterfall production with exotic species dominance in this study is consistent with observations from other tropical novel forests dominated by similar invasive trees such as *Acacia auriculiformis*, *Falcataria falcata*, and *Spathodea campanulata* (Abelleira Martinez 2011; Hughes and Denslow 2005; Milton 1981; Witkowski 1991).

Nonetheless, a key difference is that the increased litterfall observed in the aforementioned studies was also associated with a net increase in floristic richness driven by exotic species introductions, whereas the increased litterfall recorded in waste woodlands here occurred despite the introduction of exotic species resulting in depauperate floristic richness, while old-growth forests remain highly species-rich. This strongly suggests that the stand-

level composition of coexisting tree species is a stronger determinant of litterfall production than stand-level species richness (Kotowska *et al.* 2016; Tang *et al.* 2010). The absence of strong correlations between litterfall and overhead canopy openness in this study, as exemplified by waste woodlands producing the most litterfall despite supporting the lowest canopy cover, further reinforces the importance of canopy species identity and composition in influencing litterfall compared to forest structural attributes such as stand density and biomass, mirroring Tang *et al.* (2010) and Kotowska *et al.* (2016). However, this study did not explicitly investigate the influence of stand-level tree species composition on litterfall production. Further studies should quantify species-specific contribution of tree species
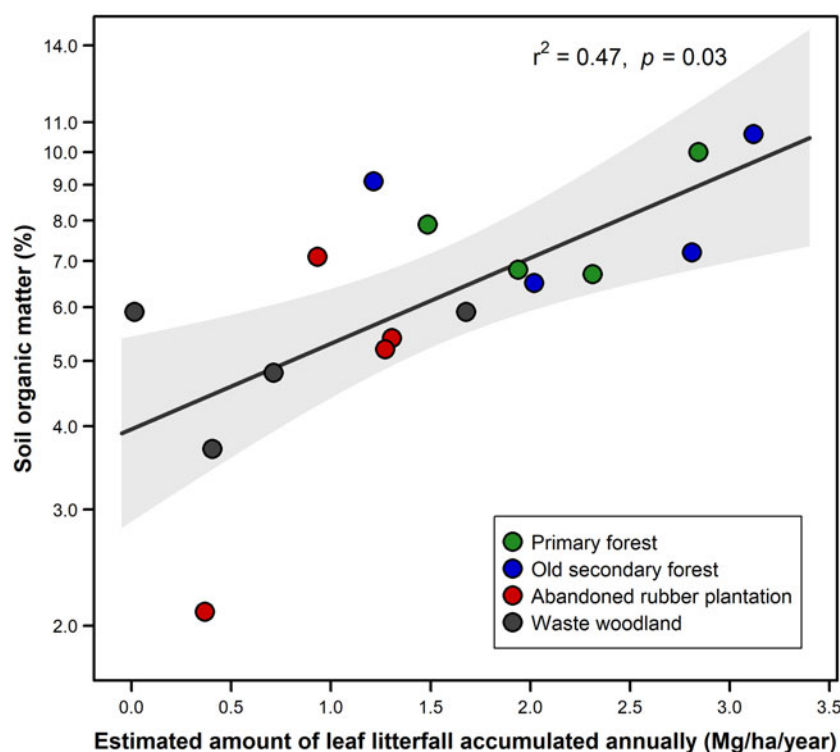
Figure 6. Soil organic matter content predicted by the estimated amount of leaf litterfall accumulated annually using a linear regression model. Model estimates are shown in Table 2. Shaded region represents the 95% CI of the model-predicted mean. Y-axis is displayed on a logit scale – percentage data of soil organic matter was converted to proportional data and logit transformed to fulfil linear modelling assumptions.

(Scherer-Lorenzen et al. 2007) that represent the major contributors of stand-level litterfall.

This study is among a few that have examined litterfall production in tropical secondary forests with more than a century of relatively undisturbed regeneration. Our results revealed that despite only harbouring approximately 60% of the tree species richness in primary forests (Turner et al. 1997), old secondary forests almost matched the litterfall production in primary forests. The slight reduction in litterfall in old secondary forests is potentially explained by its compositional dissimilarity with primary forests here (Chua et al., 2013) – e.g. primary forest sites likely support a higher proportion of tree species with larger investments into herbivory defence (Eichenberg et al. 2014), hence resulting in reduced herbivory and higher net litterfall.

Nutrient return though leaf litterfall, with insights on nutrient-use efficiencies and nutrient limitations

The clear divergence in litter quality between waste woodlands and primary forests here provides evidence that a novel assemblage dominated by a small number of functionally distinct invasive tree species, compared to a speciose assemblage of primary forest species, can fundamentally alter stand-level litterfall nutrient dynamics. Exotic species are typically characterised by elevated leaf litter quality compared to co-occurring native species (Erickson et al. 2014; Mascaro et al. 2012), given their differences in functional and physiological traits, e.g. increased photosynthesis and growth rates that are associated with increased foliar nutrient content and litter quality (Baruch and Goldstein 1999; Ehrenfeld 2003; Reich et al. 1997). In novel forests in Hawaii and Puerto Rico, invasion by *Falcataria falcata*, a nitrogen-fixing tree also widespread in waste woodlands in Singapore (Tan et al. 2010; Yee et al. 2016), has also led to increases in litterfall nitrogen and phosphorus content (Erickson et al. 2014; Hughes and Denslow 2005; Hughes and Uowolo 2006). However, our study revealed high stand-level

variability in the elevated leaf litter quality within waste woodlands, implying a strong species-specific influence (Hector et al. 2000; Tang et al. 2010; Wardle et al. 2006), e.g. litterfall nitrogen content was higher in waste woodlands stands dominated by *Falcataria falcata* compared to stands dominated by *Acacia auriculiformis* (Table S2), despite both species being facultative nitrogen-fixers (Kirby 2020; Zheng et al. 2016). Nonetheless, the role of species composition in shaping litter quality was not explicitly investigated in this study. Specifically, species-specific contributions to stand-level litterfall quality and nutrient return warrant elucidation in future studies.

The change in litterfall nutrient dynamics within waste woodlands was most pronounced for phosphorus, concurring with findings that elevated nutrient return through litterfall in tropical secondary forests was contributed predominantly by phosphorus, not nitrogen (Brown and Lugo 1990). Our finding is aligned with ecological theory that tropical primary forests are highly phosphorus-limited ecosystems (Brookshire et al. 2012; Vitousek 1984), while nitrogen is less limiting given its efficient biological fixation and accumulation (Hedin et al. 2009). This was likely demonstrated by the marginal differences in leaf litterfall nitrogen content between primary forests and waste woodlands here, despite the latter being dominated by nitrogen-fixing invasive trees such as *Acacia auriculiformis* and *Falcataria falcata*, which would have generated larger increases in leaf litter nitrogen concentrations in nitrogen-limited novel ecosystems (Hughes and Denslow 2005; Witkowski 1991). The novel composition of invasive species in waste woodlands appeared to have lessened the degree of phosphorus limitation, as evidenced by the threefold increase in annual phosphorus return compared to primary forests, leading to elevated soil phosphorus levels. Notably, the degree of phosphorus limitation in the primary forests here appears to be in the higher range globally (Vitousek and Sanford Jr 1986), as inferred by the high leaf litter N:P ratio of 74.8, which surpasses the pantropical mean leaf litterfall N:P of 27.3 (Yuan and Chen 2009)

and the N:P of 44.0 recorded in dipterocarp primary forests in Sumatra (Kotowska et al. 2016). This is concurred by Grubb et al. (1994), who found that the concentrations of phosphorus in the soil and leaf litter of primary forests in Bukit Timah (where two of our study sites were located) were distinctly low and potentially represent an extreme example among non-peat swamp dipterocarp forests – mean leaf litter N:P recorded in that study was 62.2.

In-situ leaf litter mass loss

Our results suggest that the markedly elevated mass loss of in-situ leaf litter from the soil surface in young secondary forests, particularly waste woodlands, was largely driven by the elevated litter phosphorus content – in highly phosphorus-limited tropical ecosystems, litter decomposition rates have been shown to be strongly governed by litter phosphorus content (Wieder et al. 2009; Xuluc-Tolosa et al. 2003). Moreover, our study showed that soil phosphorus concentrations in young secondary forests were raised in response to elevated litter phosphorus content and return, which in turn further enhances leaf litter decomposition (Kaspari et al. 2008). Leaf litter rich in inorganic nutrients, particularly nitrogen and phosphorus, supports increased decomposition as the activity and biomass of microbial decomposers are maximised (Bardgett 2005; Manzoni et al. 2010). The dominance of invasive tree species in waste woodlands here likely resulted in the production of nutrient-rich litter and hence increased decomposition, mirroring observations from other tropical novel forests (Erickson et al. 2014; Hughes and Denslow 2005; Hughes and Uowolo 2006; Mascaro et al. 2012). Moreover, invasive plants often exhibit altered functional traits, which include increased growth rates, lowered leaf construction costs, and increased specific leaf area, resulting in thinner and softer leaves that are more accessible to the decomposer community (Baruch and Goldstein 1999; Ehrenfeld 2003; Reich et al. 1997).

In contrast, the slower litter mass loss in old-growth forests here was likely associated with the poorer in-situ leaf litter quality – carbon-rich but nutrient-poor leaf litter is less accessible by microbial decomposers, resulting in energy starvation and reduced decomposition rates (Hättenschwiler et al. 2011; Wieder et al. 2009). Moreover, plants growing on nutrient-poor soils in old-growth tropical forests tend to produce tough high-density leaves with chemical defences to minimise herbivory (Coley and Barone 1996; Coley et al. 1985), which increase the recalcitrance of leaf litter and retard decomposition (Bakker et al. 2011; Hättenschwiler et al. 2011; Kaspari et al. 2008). The increase in in-situ leaf litter recalcitrance within old-growth forests was indeed inferred from the higher ratio of estimated litter mean residence time to half-life from our results, indicating an increased proportion of recalcitrant compounds relative to labile compounds (Cornwell and Weedon 2014). Notably, litter recalcitrance was highest in old secondary forest – the only forest type with litterbags containing more than 50% of the initial litter mass even after a year-long incubation. This is potentially attributed to the abundance of tree species in Singapore's old secondary forests, such as Campnosperma auriculatum, which is a pioneer tree species that produces recalcitrant litter (Goldsmith et al. 2011; Turner et al. 1997). Nonetheless, our estimates of decomposition in old-growth forests here remain consistent with other decomposition studies in tropical forests, where native leaf litter lost an average mass of 67% after a 312 day period (Hättenschwiler et al. 2011) and exhibited mean residence times shorter than a year (Olson 1963).

In contrast to the strong influence of litter quality on litter mass loss, the uniform microclimatic conditions across the study sites here meant that environmental factors such as soil moisture content were poor predictors of decomposition, mirroring findings from Waring (2012) and Xuluc-Tolosa et al. (2003). Nonetheless, to properly distinguish the relative roles of litter quality, microclimatic, and environmental factors in regulating decomposition, concurrent incubation of a common litter with native leaf litter (Xuluc-Tolosa et al. 2003) is required in further studies. Furthermore, a common and native litter study approach coupled with suitable soil fauna exclusion techniques (Teo et al. 2020) can help uncover the substantial contribution of soil fauna in driving litter mass loss and soil organic matter turnover relative to microbial decomposers (Frouz 2018) and achieve a more holistic understanding of decomposition determinants in tropical forest environments (Hättenschwiler et al. 2011).

Our results also revealed that the broad relationship between forest type, litter quality, and mass loss showed some overlap when assessed on a stand-level, e.g. in-situ leaf litter in some young secondary forest stands exhibited a larger mass loss extent than those in old-growth forest stands despite having lower litter quality. This implies that decomposition rates were not entirely governed by litter quality as represented by C:N and C:P ratios (Heal et al. 1997) but potentially also moderated by other indicators of litter quality, such as calcium content (Waring 2012) and lignin:P ratios (Wieder et al. 2009). Indeed, the ten-fold increase in soil calcium levels recorded in waste woodlands (Table S1) and its potential linkage with litter calcium content, soil invertebrates, microbes (Kaspari and Yanoviak 2009), and decomposition warrant further investigation but were not studied here. This distinct increase in soil calcium level in waste woodlands is potentially attributed to anthropogenic enrichment given its agricultural land-use legacy and/or historical perturbation of soil and bedrock – calcium is a rock-derived nutrient typically depleted in weathered tropical soils (Wardle et al. 2004). Additionally, the unexplained variation in litter mass loss here could also be shaped by the stand-level assemblage of tree species (Hector et al. 2000; Tang et al. 2010; Wardle et al. 2006) – a limitation of this study that should be addressed by further studies incorporating stand-level tree species data.

This study also validated the application of the Weibull residence time model (Cornwell and Weedon 2014) for decomposition studies in tropical forests, where it is rarely used – the model generally fitted well to the litter mass loss data, with goodness-of-fit measure (R^2) exceeding 0.9 for most study sites (Table S4). Notably, the estimated model parameter α, which controls the shape of the decomposition curve, i.e. early-stage decomposition trajectory (Cornwell and Weedon 2014), showed no noticeable pattern across forest types (Table S4). This reiterates the caveat of drawing inferences on long-term decomposition extent using decomposition rates estimated from the early stages of decomposition (Prescott 2005). Validation of the Weibull residence time model in more decomposition studies is recommended to gain additional insights into litter residence time and turnover dynamics.

Accumulation of litter pool and soil organic matter and implications on carbon balance

The marked decrease in accumulated litter pool in young secondary forests here has potential ramifications for carbon balance, given that the litter pool serves as an important carbon

sink in tropical forests and contributes to its soil carbon storage capacity (Kaspari and Yanoviak 2008). This was also supported by our finding that the size of the accumulated litter pool determines the amount of soil organic matter – a major carbon store in terrestrial ecosystems (Silver *et al.* 2000; Trumbore 2000). As inferred from our results, the reduced recalcitrance of leaf litter in young secondary forests and the shortened litter residence time will likely limit the build-up and stabilisation of soil organic carbon stocks (Dungait *et al.* 2012; Trumbore 1997).

Conversely, the slower litter mass loss in old-growth forests was predicted to result in an accumulated litter pool thrice that of young secondary forests. Notably, it was estimated that the accumulation of the litter pool in old secondary forests slightly exceeds that of primary forests, consistent with observations from an old secondary forest fragment in Singapore, where the increase in leaf litter depth relative to adjacent primary forests has been linked to the slow decomposition of poor quality litter (Chua and Potts 2018) produced by dominant tree species such as *Campnosperma auriculatum* (Goldsmith *et al.* 2011), thus reiterating the importance of species identity in shaping litter turnover.

Taken together, our study suggests that the conversion of tropical primary forests to secondary forests, particularly exotic-dominated novel forests, potentially accelerates decomposition and reduces the soil organic carbon pool (Chapin *et al.* 2011; Smith *et al.* 2008). Nonetheless, the estimate of litter pool accumulation in this study is limited by its short study duration – litterfall, unlike decomposition, can exhibit significant inter-annual variability (Parsons *et al.* 2014). Long-term monitoring of litterfall inputs should be conducted to obtain more robust estimates of litter pool accumulation.

Implications of forest successional trajectory on litter turnover and nutrient dynamics

Considering litterfall production, nutrient return, and litter turnover dynamics among the secondary forest types here, old secondary forests appeared to converge towards primary forests, strengthening the evidence that ecosystem functioning in secondary forests can recover long before floristic richness (Guariguata and Ostertag 2001). Indeed, the apparent recovery of ecosystem functioning in old secondary forests here occurred despite a 40% reduction in tree species richness compared to primary forests (Turner *et al.* 1997) and the associated floristic and structural distinctions (Chua *et al.* 2013). This apparent convergence in ecosystem functioning will likely strengthen further over time given the dispersal of native late-successional species into old secondary forests of Singapore from contiguous primary forest fragments (Yee *et al.* 2016).

In contrast, waste woodlands may persist in a state of arrested succession, given their isolation from native seed sources and the low diversity of seed dispersers (Shono *et al.* 2006). Furthermore, even if propagules arrive, the regeneration of primary forest species in waste woodlands in Singapore is hampered by the poor microclimatic and soil conditions (Shono *et al.* 2006). It is likely the exotic-dominated species assemblage in waste woodlands will persist and perpetuate the state of increased litter turnover, nutrient return, and soil nutrient levels, particularly for phosphorus. This creates a positive feedback loop, as the nutrient-rich soils in waste woodlands will continue to favour establishment of invasive plants over native species (Allison and Vitousek 2004; Ostertag and Verville 2002). Findings from waste woodlands in

this study therefore provide predictions of litter turnover dynamics in future novel forests in the region, given that the dominant non-native trees here, e.g. *Falcataria falcata* and *Acacia auriculiformis*, are also cultivated widely in plantations or land restoration projects in the region (Otsamo 2002; Turnbull *et al.* 1998).

Conclusion

The youngest forest successional type in this study – waste woodlands – exhibited the highest litterfall production and fastest litter turnover, despite supporting the lowest tree species richness, which was contrary to our hypothesis. Compositional differences in tree species and species-specific effects, instead of species richness and environmental factors, likely shaped the observed variations in litter turnover and nutrient dynamics. The dominance of invasive tree species in waste woodlands caused shifts in functional traits and elevated litter nutrient content, particularly phosphorus, resulting in the fastest turnover of leaf litter from the forest floor. Consequently, the accumulated leaf litter pool in waste woodlands was only a third that of old-growth forests and was found to be associated with reduced soil organic matter content. Taken together, our study suggests that the prevalent conversion of tropical primary forests to exotic-dominated novel forests potentially accelerates decomposition and reduces the soil organic carbon pool.

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