Tropical forest above-ground productivity is maintained by nutrients cycled in litter

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RESEARCH ARTICLE

Tropical forest above-ground productivity is maintained by nutrients cycled in litter

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Abstract

1. Tropical forest productivity represents an important global carbon sink, but many tropical forests grow on infertile soils. Efficient nutrient cycling by litterfall has long been assumed to maintain tropical tree growth, but there is no direct evidence that the nutrients cycled in litterfall are essential for tropical forest productivity.

2. To test whether nutrient cycling by litterfall maintains tropical forest above-ground productivity, we established large-scale long-term litter removal (L−) and litter addition (L+) treatments in a mature lowland tropical forest. We hypothesised that the removal of nutrients in litter would reduce tree growth, survival and litter production in L− plots. By contrast, the addition of nutrients in litter would enhance tree growth, survival and litter production in L+ plots. To test our hypotheses, we recorded tree growth and survival every 2 years, and measured litterfall monthly during 17 years of treatments.

3. Tree growth and litterfall declined over time in L− plots, with consistently lower growth rates compared to controls after 8 years, and lower litter production after 4 years of treatments. By contrast, although litterfall was higher in the L+ plots relative to the controls, there was only a minor transient increase in tree growth immediately after the start of treatments. Tree survival declined over time in all treatments but was not affected by litter manipulation.

4. The long-term decline in tree growth and litterfall in the L− plots provides the first empirical evidence that nutrient cycling by litterfall plays a key role in maintaining above-ground productivity in this tropical forest. By contrast, the transient increase in growth in the L+ plots can be attributed to the large inputs of nutrients with the addition of the entire litter standing crop at the start of treatments. The addition of nutrients in litter over the long term was nonetheless sufficient to enhance litter production, possibly by accelerating leaf turnover.

5. *Synthesis*: Efficient nutrient cycling by litterfall makes an important contribution to the annual nutrient requirements of mature tropical forest trees, compensating for infertile soils. Disturbances that disrupt this finely balanced cycle could therefore reduce biomass carbon sequestration in tropical forests.

1 | INTRODUCTION

Tropical forest productivity represents a major sink for atmospheric CO_2 and yet most tropical forests occur on strongly weathered, nutrient-poor soils (Bruijnzeel, 1991; Vitousek & Sanford Jr., 1986). The maintenance of highly productive lowland tropical forests on infertile soils is often attributed to 'tight' or 'efficient' nutrient cycling via litterfall (Cuevas & Medina, 1988; Vitousek, 1984). Many tropical soils have low concentrations of plant-available phosphorus (P) and cations, but the annual nutrient return in litterfall could still meet a large proportion of plant nutrient requirements (Herrera et al., 1978; Richards, 1996). In this respect, leaf litter acts as a complete fertiliser because it contains all the nutrients trees require for growth in approximately balanced concentrations (Sayer et al., 2012). The stoichiometric balance of nutrients in plant litter is important because tropical forest productivity is limited by multiple nutrients (Kaspari et al., 2008; Wright et al., 2011), and the relative oversupply of one or few nutrients can create nutrient imbalances that limit important processes underpinning plant growth and nutrient availability (Vitousek et al., 1997). Besides acting as a major source of nutrients in tropical forests, plant litter also plays a crucial role in conserving scarce nutrients and maintaining tight nutrient cycling through the plant–soil system (Attiwill & Adams, 1993; Vitousek, 1984). The nutrients contained in litter are released gradually during decomposition, and thus, the layer of decomposing organic matter that forms the forest floor also helps retain mobile nutrients that would otherwise be rapidly lost from the system via leaching (e.g. Qualls et al., 1991; Tobón et al., 2004). Thus, efficient cycling of the substantial nutrient inputs with litterfall and the nutrient retention capacity of the forest floor offer a plausible explanation for the maintenance of high tropical forest productivity on infertile soils. However, despite decades of research into nutrient cycling and retention by tropical forest litterfall, there is no direct, conclusive evidence that the nutrients cycled in litterfall maintain tropical forest productivity.

Experimental litter manipulation is the only way to conclusively establish whether nutrients cycled in litterfall are crucial for tropical tree growth, but the limited temporal or spatial scale of most litter manipulation studies to date precludes the assessment of tree growth (but see Sayer, 2006). If a large proportion of the annual nutrient requirement for plant growth is cycled in litterfall,

then continuous, long-term litter removal would deplete soil nutrient reserves and remove a major source of nutrients for trees, resulting in declining productivity over time. By removing or adding leaf litter to experimental plots, several litter manipulation studies have demonstrated substantial changes in soil nutrients (e.g. Huang & Spohn, 2015; Kalbitz et al., 2007; Sayer et al., 2020; Sayer & Tanner, 2010; Wieder et al., 2011; Wood et al., 2009), microbial communities (Nemergut et al., 2010; Prevost-Boure et al., 2011; Sheldrake et al., 2017; Wang et al., 2014) and soil organic matter (Lajtha et al., 2018; Pisani et al., 2016; Sayer et al., 2019, 2021; Tanner et al., 2016; Wang et al., 2014), but as tree growth has not been measured in most litter manipulation studies, it is still unclear how these changes might affect overall forest productivity.

Litter removal treatments tend to have a more immediate and substantial influence on soil nutrients than litter addition treatments (Xu et al., 2021), with particularly marked declines in soil nitrogen (N) concentrations and soil organic matter in response to repeated litter removal (Sayer, 2006; Sayer et al., 2020; Xu et al., 2013), which should eventually affect tree growth. Changes in multiple soil properties and processes with litter removal are likely to exacerbate nutrient limitation of tree growth. For example, reduced soil microbial activity delays the mineralisation and release of nutrients during decomposition (Chen et al., 2014; Sayer et al., 2006), while the lack of a litter layer on the soil surface promotes leaching (Mo et al., 1995). In addition, changes in soil pH with litter removal can alter nutrient availability to plants (Sayer et al., 2020; Tóth et al., 2011) and lower inputs of certain organic compounds promote sorption of P, which is already in short supply in many tropical soils (Vitousek, 1984), to soil minerals (Schreeg et al., 2013). Thus, we would expect long-term litter removal to induce nutrient limitation and reduce tree growth and survival. Higher mortality, slower growth and reduced recruitment of trees into larger size classes would ultimately diminish above-ground biomass and forest carbon sequestration capacity.

Although there is now a global network of long-term litter manipulation experiments in forest ecosystems, most of these were designed to assess how plant litter contributes to soil organic matter dynamics (Lajtha et al., 2018; Nadelhoffer et al., 2004). Few other studies have evaluated how litter removal or addition affects forest productivity and only two of eight forestry studies investigating the effects of litter removal in young or thinned pine plantations in the United States found evidence of reduced growth

over a period of up to 7 years (Dickens et al., 2020). Litter manipulation experiments in tropical systems have also produced mixed or inconclusive results: 4 years of litter removal had no influence on litter production in a secondary tropical forest (Vasconcelos et al., 2008) or a neotropical savanna, but litter addition increased growth in one of six savanna tree species (Villalobos-Vega et al., 2011). By contrast, litter production almost doubled over a 6-month period following a single fourfold increase in litter inputs in tropical forest in Costa Rica, but there was no effect of litter removal, and no effect of either treatment on tree growth in the following year (Wood et al., 2009). Given the long lifespan of trees, it is perhaps unsurprising that experiments lasting only a few years have revealed little effect of litter manipulation on tree growth, especially in old-growth forest. In addition, trees can also adapt to changes in nutrient availability by adjusting foliar nutrient ratios (Ostertag & DiManno, 2016; Sardans et al., 2012), leaf lifespan (Harrington et al., 2001) and the allocation of resources to above-ground versus root growth (Bloom et al., 1985). Thus, large-scale studies of historical litter removal as a management practice in Central European forests showed marked declines in tree growth with litter removal only after around 15 years, although most of these studies were unreplicated (Sayer, 2006). Nonetheless, numerous litter manipulation experiments in forests around the world have now demonstrated declines in soil nutrient concentrations with litter removal (Hofmeister et al., 2008; Mo et al., 1995; Sayer et al., 2020; Tan et al., 2005; Tóth et al., 2011), and thus, litter removal is likely to influence tree growth, survival and forest productivity over the longer term.

The Gigante Litter Manipulation Project (GLiMP), situated in lowland tropical forest in Panama, is currently the only experiment in which long-term litter removal and addition treatments have been applied on a sufficiently large scale to assess the importance of litterfall for sustaining tropical forest productivity. Although no changes in tree growth or annual litterfall were apparent during the first 5–7 years of treatments (Sayer & Tanner, 2010), recent work demonstrated that 17 years of experimental litter manipulation have substantially altered soil nutrient concentrations and nutrient use efficiency (Sayer et al., 2020). Overall, litter removal has had a much greater impact on nutrient cycling and availability than litter addition, resulting in substantially reduced soil concentrations of N, potassium (K), calcium (Ca), magnesium (Mg), zinc (Zn; Sayer et al., 2020), organic P (Sheldrake et al., 2017; Vincent et al., 2010) and a moderate decline in extractable P (Sayer et al., 2020). Fine root production and survival has declined in the litter removal plots (Rodtassana & Tanner, 2018) and the removal of nutrients recycled in litter has also reduced foliar concentrations of N and P (Sayer & Tanner, 2010; Tanner et al., 2024), which could be a first indication that tree growth will start to slow as nutrients become increasingly limiting. Thus, we hypothesise that litterfall is essential for maintaining growth in lowland tropical forests, and we assess the impact of 17 years of continuous litter removal and litter addition treatments on tropical forest above-ground productivity. We used data from monthly litter collections (2003–2019)

and biennial censuses of tree growth (2001–2017) to test the following hypotheses:

Hypothesis 1. Tree growth, tree survival and fine litter production will decline over time with litter removal if litter removal induces nutrient limitation.

Hypothesis 2. Tree growth, tree survival and fine litter production will increase over time with litter addition if the forest is limited by nutrients primarily cycled in litterfall.

2 | METHODS

2.1 | Study site and experimental design

The fieldwork was carried out with the permission and support of the Smithsonian Tropical Research Institute. The Gigante Litter Manipulation Project (GLiMP) is located in old-growth lowland semi-evergreen tropical forest on Gigante Peninsula, within the Barro Colorado Nature Monument, Panama, Central America (9°06′31″ N, 79°50′37″ W). Mean annual rainfall is *c.* 2600 mm with a strong dry season from January to April, and the mean annual temperature is *c.* 26°C (Leigh, 1999; Paton, 2020). The soil is an Oxisol with pH *c.* 5.5; litter nutrient concentrations indicate high N and moderate P availability (Sayer et al., 2020), but previous work in the study forest indicated that different components of forest productivity may be limited by N, P or K (Kaspari et al., 2008; Wright et al., 2011, 2018). Between 2000 and 2002, we established 15 experimental plots (45 m × 45 m each), which were trenched to *c.* 0.5-m depth to limit nutrient transfer between plots via roots and mycorrhizas; the walls of the trenches were double-lined with construction plastic and backfilled. Starting in 2003, the litter in five litter removal (L−) plots was raked up every 1–2 months and spread as evenly as possible on five litter addition (L+) plots, leaving five plots with natural litter inputs as controls (CT). Previous studies within the experimental plots have demonstrated that the L+ treatments effectively increase the mass and depth of the litter standing crop relative to the controls (Ashford et al., 2013; Sayer et al., 2006). The treatments were initially assigned to the plots in a stratified random design, whereby plots were ranked by annual litterfall in 2002, divided into blocks of three and then each plot within a block was randomly assigned one of the treatments. However, given that litter was always moved between pairs of L− and L+ plots, each replicate block used for analysis comprises paired L− and L+ plots and the closest control plot (Figure S1; see Sayer et al., 2006; Sayer & Tanner, 2010 for further details).

2.2 | Tree growth and survival

All trees with a diameter at breast height (DBH) >10 cm were initially identified, tagged, mapped and measured in 2000–2001, and a line

indicating the point of measurement (POM) for each tree was painted around the circumference of the trunk. We remeasured the girth of all trees annually using a tape measure aligned with the top of the POM from 2002 to 2018, except for 2006 and 2008 when no measurements were made. During each census from 2003 to 2017, we recorded measurement accuracy using a three-point scale, where 1 is repeatable with high accuracy, 2 is repeatable with good accuracy and 3 is an inaccurate measurement due to obstructions (e.g. large lianas, tree falls) or irregularities (e.g. buttress roots, deeply creviced stems or stems with large spines). Deviations of the POM from the standard height of 1.3 m were recorded and any change in the POM due to growing buttresses or obstructions was noted with the year in which a new POM was designated. New recruits that had attained 10 cm DBH were identified, tagged, mapped, marked with paint and included in subsequent censuses. Dead trees were recorded during each census and revisited in the subsequent year to confirm mortality. During the 2018 census, we confirmed trees recorded as dead in 2017, checked the species identification and estimated the height and canopy exposure of all live, measured individuals. In total, we measured 1388 individual trees, of which 93% (1293) were identified to species, 2% (28) to genus and 5% (67) were unidentified. As our hypotheses relate to the effects of treatments over time, we only include trees in our analyses that were recorded during at least two census intervals.

2.3 | Litterfall

Fine litter (leaves and woody debris <2 cm diameter) was collected on the last Thursday of every month from February 2002 to December 2019. Litter samples were collected from 10 litter traps (0.76 m × 0.76 m) per plot from 2003 to 2007 and from five litter traps per plot in 2002 and from 2008 to 2019. The litter samples were weighed after oven-drying to constant weight at 60°C and monthly litterfall rates were expressed as $g\,m^{-2}\,day^{-1}$ to account for differences in collection intervals (28 or 35 days). Pretreatment litterfall measured in 2002 was used to assign treatments but was not included in further analyses. Annual litterfall rates for 2002–2008 and 2003–2009 have been previously reported in Sayer and Tanner (2010) and Sayer et al. (2012), respectively.

2.4 | Calculations

To assess whether litter manipulation has affected tree growth over time, we calculated mean annual DBH growth ($mm\,year^{-1}$) for eight 2-year census intervals (2001–2003, 2003–2005, 2005–2007, 2009–2011, 2011–2013, 2013–2015 and 2015–2017) as:

$$mm.\,growth = (DBH_{t2} - DBH_{t1}) / t_2 - t_1 \qquad (1)$$

where DBH_{t1} and DBH_{t2} are the measured values during the first (t_1) and last (t_2) year of each measurement interval, respectively. For each 2-year interval, we only calculated growth rates for trees

that were recorded as present and alive during the whole interval, and which were measured at the same POM throughout the interval. Trees growing within c. 2 m of the trenches (226), and those with a mean accuracy score >2 (86), or that were only measured in a single census interval (39) were excluded entirely. Thus, tree growth was calculated for 987 individuals. For trees with multiple stems, we only included the main stem in analyses of growth rates. Given that negative diameter growth can be the result of changes in tree water status or an early indication of mortality (e.g. Baker et al., 2002; Preisler et al., 2021; van den Berg et al., 2012), we retained negative growth rates in our analyses. However, we excluded growth increments (both negative and positive) when the recorded DBH measurements indicated measurement error (i.e. when the DBH was recorded as >2% higher or lower in a single year compared to both previous and subsequent years; <1% of all observations). We used the data collected in 2018 to identify and exclude measurement errors during the final census interval (2015–2017). As the tree growth data were strongly right-skewed, we transformed the annual growth rates for each individual before analysis to meet modelling assumptions. To reduce skewness, we used a modulus transformation (John & Draper, 1980) with a power <1 ($\lambda = 0.55$) following Condit et al. (2017):

$$mm.\,growth_{trans} = mm.\,growth^{0.55} \text{ for positive growth rates} \quad (2)$$

and

$$mm.\,growth_{trans} = - \left\{ (-mm.\,growth)^{0.55} \right\} \text{ for negative growth rates} \tag{2a}$$

where $mm.growth_{trans}$ is the transformed value of absolute annual growth rates (mm.growth) for each census interval. This transformation constrained both positive and negative outliers to the same extent and provided a range of transformed growth rates with low skewness and similar mean and median values (Condit et al., 2017).

Litterfall data were summarised per plot as monthly and annual mean mass per unit area ($g\,m^{-2}\,day^{-1}$ and $g\,m^{-2}\,year^{-1}$, respectively). As the trap-level litter mass data were log-normally distributed, we log-transformed the data before calculating plot means (Limpert et al., 2001). All figures for tree growth and litterfall rates show untransformed values.

2.5 | Statistical analyses

Data analyses were conducted using the lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2017) packages in R version 4.3.1 (R Development Core Team, 2023), using ggplot2 for visualisation (Wickham, 2016).

We evaluated the effects of litter manipulation on tree growth using linear mixed effects models (*lmer* function) to model mm.growth$_{trans}$ as a function of litter manipulation treatment, time and their interaction as fixed effects, with initial tree size (DBH_{t1}) as a covariate. We accounted for the experimental

design by including replicate block as a random effect, and for variance among individuals and species by including individual nested within species as a random effect. As arithmetic means do not back-transform, but medians back-transform exactly (Condit et al., 2017), figures for tree growth show median annual growth rates. We assessed whether litter manipulation treatments affected litter production using linear mixed effects models (*lmer* function) to model annual litterfall rates as a function of treatment, year and their interaction (fixed effects), with replicate block included as a random effect.

We assessed whether litter manipulation treatments affected tree survival using generalised linear mixed models (*glmm* function) with a binomial error distribution, modelling the survival of individual trees per census interval (1 or 0) as a function of treatment, time and their interaction (fixed effects), including species and replicate block as random effects.

For all mixed effects models, the best model fit was determined by successively excluding terms and comparing models using the Akaike information criterion (AIC) and *p*-values to check for model improvement, and diagnostic plots to assess model residuals (Pinheiro & Bates, 2000). The final models were compared to appropriate null models using likelihood ratio tests; for tree growth, the null model retained initial DBH as a random effect, whereas the null models for tree survival and litterfall were intercept only (Table S1). Two models for tree survival were an equally good fit to the data and we therefore averaged the models (*model.avg* function in the MuMin package; Barton, 2023) and report full model-averaged coefficients. For linear mixed effects models, we used the Satterthwaite method to generate *p*-values and *F*- or *t*-statistics for fixed effect terms (treatment or year); for generalised mixed effects models, we used a Wald *z*-distribution approximation to compute 95% confidence intervals (CIs) and *p*-values (*anova* and *summary* functions in the lmerTest package). We report fixed effects estimates (*β*-values) for significant results at $p < 0.05$ and we give non-significant results at $p < 0.1$ as trends.

3 | RESULTS

3.1 | Tree growth

Tree growth diverged among treatments over time (time×treatment interaction: $F = 11.0$, $p < 0.001$; Figure 1; Table S1a). Tree growth was unaffected by litter addition, although it is noteworthy that tree growth was *c.* 14% higher in the L+ plots compared to the controls during the first census interval after the start of treatments (2003–2005; Figure 1; Table S2). Tree growth declined with litter removal over time ($β = -0.053$, $p < 0.001$; Figure 1; Tables S1a and S2). Thus, despite higher pretreatment growth rates in the L− plots (Table S2), median growth rates were consistently lower in L− plots compared to controls from 2011 to 2013 onwards (Figure 1; Table S2).

3.2 | Litterfall

Annual litterfall diverged among treatments over time (treatment×year interaction: $F = 7.11$, $p < 0.001$; Table S1b, Figure 2). Annual litterfall was 12% higher in the L+ plots compared to the controls across all years ($β = 109.9$, $p = 0.047$; Tables S1b and S3), but there was no trend of increasing litterfall over time (Tables S1b and S3). By contrast, annual litterfall in the L− plots declined significantly over time ($β = -13.2$, $p = 0.015$), with lower litterfall than the controls in all years from 2007 onwards (mean 11.5%, range 5%–28%; Figure 2; Tables S1b and S3).

3.3 | Tree survival

Across all census intervals, mean annual tree survival rates did not differ among L+ plots (98.2%±0.03%), controls (97.80%±0.35%) or L− plots (97.90%±0.30%). The tree survival model including the time×treatment interaction and the model including time but not
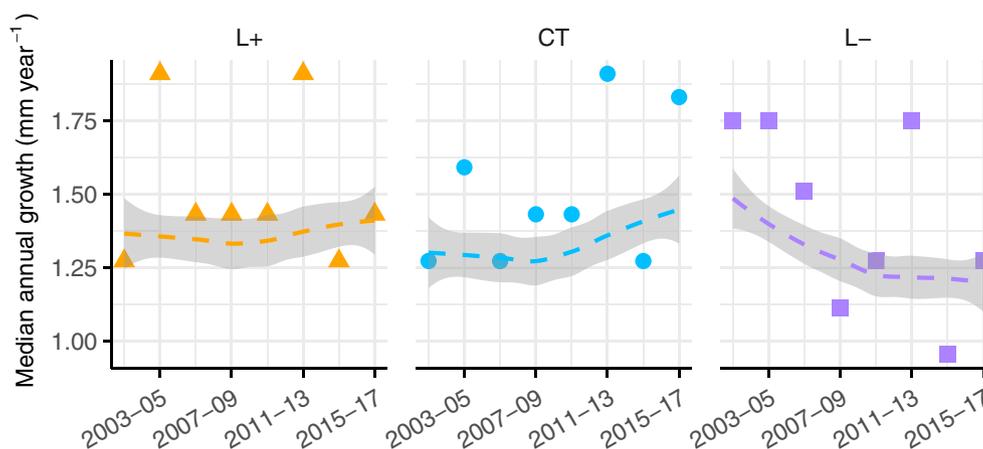
FIGURE 1 Stem diameter growth of lowland tropical forest trees with a diameter at breast height (DBH) > 10 cm in experimental litter addition (L+; orange triangles), control (CT; blue circles) and litter removal (L−; purple squares) plots over eight 2-year census intervals from 2001 to 2017; symbols denote medians for $n = 5$ plots per treatment, and dashed lines with shading denote model-predicted annual growth with 95% confidence intervals.
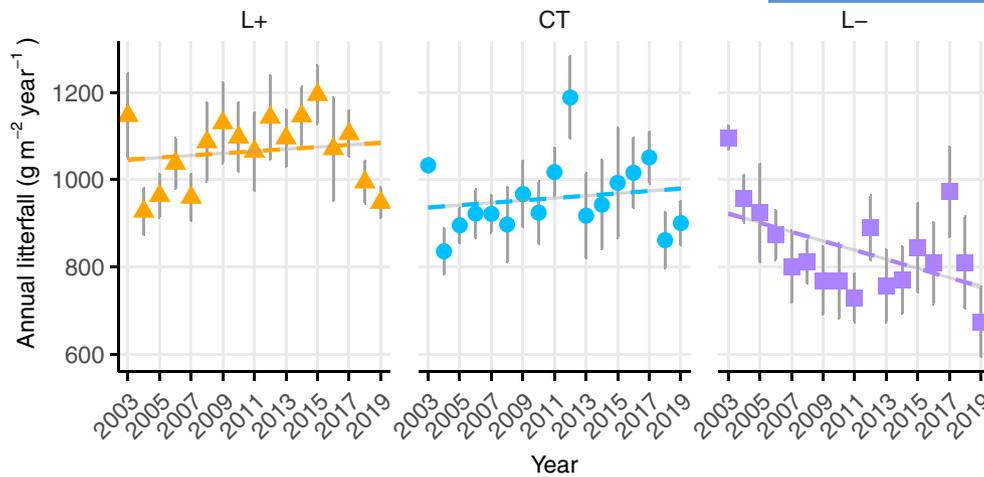
FIGURE 2 Annual litterfall rates in litter manipulation plots in lowland tropical forest in Panama, Central America from 2003 to 2019. L+ (orange triangles) is litter addition, CT (blue circles) is control and L− (purple squares) is litter removal; symbols and whiskers denote means ± S.E. for $n = 5$ plots per treatment, and dashed lines with shading denote model-predicted annual litterfall with 95% confidence intervals.
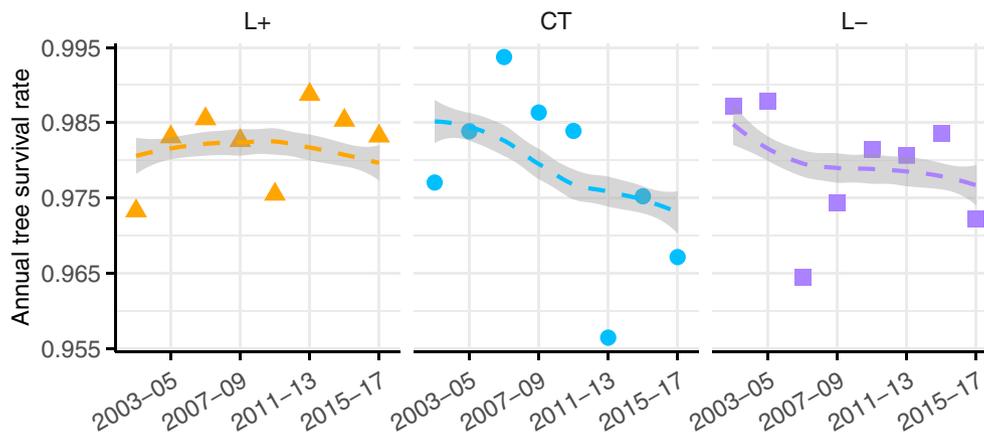
FIGURE 3 Relative annual survival rates of lowland tropical forest trees with a diameter at breast height (DBH) > 10 cm in experimental litter addition (L+; orange triangles), control (CT; blue circles) and litter removal (L−; purple squares) plots over eight 2-year census intervals from 2001 to 2017; symbols denote medians for $n = 5$ plots per treatment, and dashed lines with shading denote model-predicted annual survival rates with 95% confidence intervals.

treatment were an equally good fit (Table S1c). However, based on the averaged model, tree survival rates only differed significantly over time, with a general trend towards declining tree survival (time effect: $\beta = -0.14$, $p = 0.016$; Table S1c; Figure 3).

4 | DISCUSSION

The declines in tree growth and litterfall after almost two decades of continuous litter removal treatments constitute the first conclusive empirical evidence that litterfall plays a key role in maintaining lowland tropical forest above-ground productivity. By contrast, litter addition over the same period only increased annual litterfall. Here, we discuss how our findings might be explained by changes in litter nutrient inputs, or other important functions of the litter layer.

4.1 | Productivity declines with decadal-scale litter removal

Slower tree growth and reduced litter production with long-term litter removal are consistent with our first hypothesis (H1). Given the widely assumed importance of nutrients from litterfall and year-round growth in tropical forests, we expected that litter removal would reduce productivity within only a few years. We estimate that the removal of litter withdrew 2246 kg N ha^{-1}, 77 kg P ha^{-1} and 710 kg K ha^{-1} between 2003 and 2017, which has resulted in notably lower soil concentrations of these nutrients in the L− plots (Sayer et al., 2020). Although continued withdrawal of nutrients by litter removal only reduced tree growth consistently after c. 8 years of treatments (Figure 1; Table S2), this is still much less time than it took for the effects of litter removal to curtail the growth of mature temperate trees in Central Europe (Sayer, 2006).

Previous work at the study site suggests that trees initially compensate for lower nutrient inputs to sustain stem growth via multiple mechanisms that increase nutrient use efficiency (Sayer et al., 2020). For example, the decline in litterfall after c. 4 years (Figure 2) likely indicates reduced investment in leaf production and possibly greater leaf longevity (Harrington et al., 2001), which was accompanied by lower concentrations of N, P, K and Zn in leaf litter (Sayer et al., 2020; Sayer & Tanner, 2010), suggesting reduced nutrient uptake or greater re-translocation (Harrington et al., 2001). Although greater allocation of resources to roots is also thought to support tree growth at nutrient-limited sites (Chapin III, 1980), litter removal also reduced fine root biomass, production or survival at our site (Rodtassana & Tanner, 2018; Sayer et al., 2006). Instead, greater N-use efficiency of plants in the L− plots (Sayer et al., 2020), combined with increased turnover of organic P (Vincent et al., 2010) and shifts in the communities of root-associated arbuscular mycorrhizal fungi (Sheldrake et al., 2017), could all have contributed to the maintenance of stem growth for several years after the start of litter removal treatments.

Interestingly, the lower growth rates in the L− plots were due to reduced growth of both small trees (10–20 cm DBH) and large trees (>30 cm DBH; Supplementary Methods and Results 1; Table S4; Figure S2). The high photosynthetic rates of canopy trees are related to leaf N content (Carswell et al., 2000), which could make them more susceptible to the removal of nutrients with litter, especially as soil inorganic N concentrations declined rapidly in the L− plots (Sayer et al., 2020; Sayer & Tanner, 2010). By contrast, smaller trees are likely to be primarily constrained by low-light conditions (Coomes & Allen, 2007), but the responsiveness of small trees to litter removal is consistent with the positive growth responses observed for deeply shaded, understorey seedlings in six nutrient addition experiments conducted in tropical forests (Wright, 2019). As competition for nutrients can limit the growth of trees of all sizes (Coomes & Allen, 2007), it is conceivable that increased competition with canopy trees for nutrients could make small trees susceptible to litter removal.

The decline in above-ground productivity with litter removal advances our understanding of tropical forest nutrition by demonstrating that the nutrients in litterfall compensate for low soil nutrient concentrations. It has long been hypothesised that efficient nutrient cycling might explain how tropical forests maintain such high productivity on nutrient-poor soils (Vitousek, 1984). However, our experiment provides the first empirical evidence that nutrients in litter make a major contribution to tree growth over decadal timescales. Importantly, the relatively short period of time within which we observed declining litter production in the L− plots (4 years) suggests that the forest nutrient cycle is finely balanced. Perturbations that disrupt this natural forest nutrient cycle could therefore affect site productivity.

4.2 | Only litterfall increases with decadal-scale litter addition

Our second hypothesis predicted that litter addition would boost above-ground productivity by enhancing nutrient inputs (H2).

Although litterfall was significantly higher in the L+ plots across all years, we found no indication that litterfall or tree growth was increasing over time with continued litter addition (Figures 1 and 2). As the treatments were assigned based on pretreatment (2002) litterfall, the overall higher litterfall in the L+ plots can be attributed to an immediate effect of litter addition during the first year of treatments that was then maintained over time. The transient increase in tree growth in the L+ plots after the start of treatments is also noteworthy (2003–2005; Figure 1; Table S2), because the entire litter standing crop from the L− plots was added to L+ plots during the first treatment cycle. Previous work reported higher wet season litterfall in the L+ plots during the first 5 years of treatments (Sayer & Tanner, 2010) and a similar short-lived (6 months) but substantial increase in litter production was observed in response to quadrupled litter inputs in a Costa Rican forest (Wood et al., 2009). Based on the nutrient concentrations of the litter standing crop measured in 2005, the first application of the litter addition treatment added $362 \, kg \, N \, ha^{-1}$, $11 \, kg \, P \, ha^{-1}$ and $21 \, kg \, K \, ha^{-1}$ within just a few weeks, which could have been sufficient to boost productivity. By contrast, greater nutrient use efficiency and declining nutrient return with litterfall in the L− plots (the source of litter added to the L+ plots; Sayer et al., 2020) could have weakened the effects of litter addition over time. During the first 5 years of the experiment, the litter removed from the L− plots added an estimated $143 \, kg \, N \, ha^{-1} \, year^{-1}$ and $5.8 \, kg \, P \, ha^{-1} \, year^{-1}$, respectively, to the L+ plots (Sayer & Tanner, 2010), but this had declined to $128 \, kg \, N \, ha^{-1} \, year^{-1}$ and $3.4 \, kg \, P \, ha^{-1} \, year^{-1}$ after 15 years of treatments (Sayer et al., 2020). It is therefore conceivable that the sudden substantial increase in nutrient inputs by doubling the litter standing crop temporarily boosted tree growth at the start of the litter addition treatment, but the declining monthly additions of nutrients in litter were only sufficient to maintain higher litter production, but not higher tree growth rates, in the L+ plots over the long term.

The growth response of trees to added nutrients is probably limited by other constraints, such as adaptation to low nutrient availability, pest pressure or insufficient experimental duration (Wright et al., 2018). The lack of tree growth response in the L+ plots, despite almost two decades of nutrients added with litter, mirrors the findings of a long-term fertilisation experiment in the same study area, which reported no increase in trunk growth after adding similar amounts of N and c. 10× greater amounts of P for 15 years (Wright et al., 2018). Our old growth forest site is dominated by shade-tolerant trees, but fast-growing species have greater capacity to respond to nutrient addition (Sayer & Banin, 2016). It is therefore notable that trees with a high light requirement grew faster in the L+ plots (Supplementary Methods and Results 2; Table S5). Faster growth by resource-acquisitive species in the L+ plots suggests that the ability of trees to benefit from added nutrients depends on their life-history strategy (Sayer & Banin, 2016) and differences among tree functional types could account for the lack of an overall growth response to litter addition.

The sustained increase in litterfall in the L+ plots might indicate increased leaf turnover in response to added nutrients (Zhang

et al., 2022), especially as the increase in litterfall in response to litter addition occurred primarily during the rainy season (Sayer et al., 2012; Figure S3). Overall, the relatively minor stimulation of above-ground productivity in response to litter addition and fertilisation treatments, compared to the notable decline in above-ground productivity with litter removal, suggests that nutrient cycling in litterfall is an important mechanism to compensate for infertile soils.

4.3 | Litter removal interacts with rainfall to reduce tree growth

The role of the litter standing crop in regulating soil water content (Walsh & Voigt, 1977) might contribute to interannual variation in the effects of litter manipulation on productivity in our study, especially as the forest experiences a strong dry season around January–April each year (Leigh, 1999). Litterfall follows a strong seasonal pattern in our study forest, with higher rates of leaf abscission during the dry season (Wright & Cornejo, 1990), and differences in litter production among treatments in our study were generally greater during the wet season (Sayer et al., 2012; Figure S3). Interactions between water deficit and litter removal can contribute to transient changes in productivity (Dickens et al., 2020). For example, short-term declines in tree growth after the start of litter removal in pine forests have been attributed to greater water stress with the removal of the forest floor (Ginter et al., 1979; Haywood et al., 1998; McLeod et al., 1979), which exacerbates evaporation and run-off from the soil surface (Sayer, 2006). The strong decline in growth in the 2007–2009 census interval (Figure 1; Table S2) also coincided with one of the driest years during the study period, when annual rainfall was 500 mm below the 2600 mm average (2008; Paton, 2020; Figure S4). Thus, we propose that long-term declines in forest productivity with litter removal can be attributed to the disruption of nutrient cycling by litterfall, but interannual variation in precipitation and changes in soil hydrology with litter removal contribute to transient or particularly strong changes in productivity.

4.4 | Tree survival

In contrast to our first hypothesis (H1), we cannot attribute declining tree survival rates to long-term litter removal, as tree survival declined over time in all three treatments (Figure 3). It is likely that tree survival is mostly affected by large treefalls, which frequently kill surrounding smaller trees (Lugo & Scatena, 1996). Although we also found little evidence that litter addition has enhanced tree survival (H2), it is noteworthy that survival rates in the L+ plots did not decline to the same extent as in CT or L− plots (Figure 3; Table S1c). However, given the low annual mortality of trees in our plots, we cannot yet conclude with certainty that 17 years of litter addition has enhanced tree survival.

Together, declining tree survival and the distinct tree growth responses to litter manipulation treatments had a substantial overall impact on above-ground woody biomass over the 17 years of litter manipulation treatments. Above-ground woody biomass in the L− plots declined by 8% from $325 \pm 63\,\mathrm{Mg\,ha^{-1}}$ before the start of treatments to $299 \pm 55\,\mathrm{Mg\,ha^{-1}}$, whereas above-ground woody biomass remained largely unchanged in the control plots (330 ± 38 and $327 \pm 39\,\mathrm{Mg\,ha^{-1}}$) and increased by 15% in the L+ plots (from 288 ± 33 to $331 \pm 45\,\mathrm{Mg\,ha^{-1}}$) over the same time period (Supplementary Methods and Results 3).

5 | CONCLUSIONS

Our long-term, large-scale litter removal treatments provide the first experimental evidence that the nutrients cycled in litterfall play a major role in maintaining tree growth and litter production in mature lowland tropical forest. Additional nutrient inputs with litter addition have enhanced litter production but not tree growth, despite higher soil nutrient concentrations. Nonetheless, declining productivity with litter removal can be largely attributed to the withdrawal of substantial amounts of nutrients over time, and changes in soil water status could have a knock-on effect for productivity. Our long-term experiment thus provides the first empirical evidence that the nutrients cycled in litterfall make a major contribution to maintaining tropical forest growth. The fine balance between nutrient inputs, uptake and losses suggests that disturbances that disrupt the natural forest cycle are likely to affect tropical forest biomass carbon storage.

AUTHOR CONTRIBUTIONS

E. V. J. Tanner, E. J. Sayer and S. J. Wright conceived the ideas and designed the methodology; E. J. Sayer, S. F. Leitman, C. Rodtassana, A. G. Vincent, L. M. Bréchet, B. Castro, O. Lopez and E. V. J. Tanner collected the data; A. Wallwork provided additional data and interpretation; E. J. Sayer and S. F. Leitman performed quality control checks on the data and analysed the data; E. J. Sayer led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for submission.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Comparison of models testing the effect of litter manipulation on (a) tree growth, (b) litterfall and (c) tree survival.

Table S2. Mean annual tree diameter growth in a litter manipulation experiment in tropical forest in Panama during eight 2-year census intervals from 2001 to 2017.

Table S3. Mean annual litterfall in a litter manipulation experiment in tropical forest in Panama during eight two-year census intervals from 2001 to 2017.

Table S4. Comparison of models testing the effect of litter manipulation the growth of trees in three different size classes.

Table S5. Comparison of models testing the effect of litter manipulation on the growth of trees depending on their light requirement index (LRI).

Figure S1. Map of the study site within the 48-ha area of lowland tropical forest on Gigante Peninsula, Barro Colorado Nature Monument, Panama, showing the location of the litter manipulation plots.

Figure S2. Median annual stem diameter growth of (a) small trees (10–20 cm diameter at breast height DBH), (b) medium trees (20–30 cm DBH) and (c) large trees (>30 cm DBH) in experimental litter manipulation plots in lowland tropical forest over eight 2-year census intervals from 2003 to 2017.

Figure S3. Monthly litterfall rates in litter manipulation plots in lowland tropical forest in Panama, Central America from 2003 to 2019, grouped by season.

Figure S4. Annual precipitation and dry season length recorded on Barro Colorado Island, Panama, Central America, during the study period, showing the long-term (1925–2019) average annual precipitation and dry season length.

Supplementary Methods and Results 1. Tree growth by size class.

Supplementary Methods and Results 2. Influence of growth strategy on tree responses to litter manipulation.

Supplementary Methods and Results 3. Calculation of aboveground woody biomass.