Biotropica

WILEY

bioTROPICA ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION

ORIGINAL ARTICLE OPEN ACCESS

Leaf Litter Decomposition in the Tropics Dynamically Recovers Following Experimental Disturbance Across Temporal Scales

Arianna Tartara[1] | Karla Neira-Salamea[2,3,4] | María-José Endara[4] | Sebastián Escobar[4] | Genoveva Granda Albuja[4] | Juan E. Guevara-Andino[4] | Mark-Oliver Rödel[2] | Emma J. Sayer[5,6,7] | Eva Tamargo López[8] | Edith Villa-Galaviz[9] | Nico Blüthgen[9] | Michael Heethoff[1]

[1]Technische Universität Darmstadt, Animal Evolutionary Ecology, Darmstadt, Germany | [2]Museum für Naturkunde – Leibniz Institute for Evolution and Biodiversity Science, Berlin, Germany | [3]Humboldt-Universitat zu Berlin, Faculty of Life Sciences, Unter den Linden 6, Berlin, Germany | [4]Grupo de Investigación en Ecología y Evolución en los Trópicos-EETrop, Universidad de Las Américas, Quito, Ecuador | [5]Institute of Botany, Ulm University, Ulm, Germany | [6]Lancaster Environment Centre, Lancaster University, Lancaster, UK | [7]Smithsonian Tropical Research Institute, Panama City, Republic of Panama | [8]Conservation Ecology, Department of Biology, Philipps-Universität Marburg, Marburg, Germany | [9]Technische Universität Darmstadt, Ecological Networks, Schnittspahnstraße 3, Darmstadt, Germany

Correspondence: Arianna Tartara (ariannatartara@yahoo.com) | Michael Heethoff (heethoff@bio.tu-darmstadt.de)

Received: 13 June 2025 | **Revised:** 24 January 2026 | **Accepted:** 16 February 2026

Associate Editor: Rhett D. Harrison | **Handling Editor:** Jennifer Powers

Keywords: chronosequence | Ecuadorian Chocó | legacy | litterbags | tropical ecosystem processes | unassisted forest regeneration

ABSTRACT

Litter decomposition by arthropods and microbes is a key ecosystem process in tropical forests, yet its response to disturbance and forest regeneration remains poorly understood. To investigate decomposition dynamics across forest succession, we conducted a space-for-time study in the Ecuadorian lowland Chocó spanning active cacao plantations and pastures (year 0), regenerating secondary forests (1–38 years), and old-growth forest. We deployed litterbags in 32 plots, with aboveground litterbags accessible to arthropods and belowground ones allowing only microbial decomposition. Each litterbag contained standardized leaf litter from five common tree species. We modeled litter mass loss as a function of forest age and environmental variables associated with regeneration. To assess ecosystem resilience to new disturbances, we also tested how localized pulse perturbation (forest clearing) and fencing (large ground-dwelling animal exclusion) influenced decomposition. Aboveground decomposition was primarily driven by surface temperature, elevation, tree biomass, and forest age, with trajectories varying by land-use history. In sites recovering from cacao cultivation, decomposition followed a U-shaped pattern, with lower rates during mid-succession and again higher rates in old-growth forest. This suggests that faunal decomposers respond non-linearly to successional changes, likely reflecting shifts in habitat quality and resource availability. Belowground decomposition remained stable across forest ages and was shaped by soil moisture and soil carbon-to-nitrogen ratios, indicating strong environmental filtering on microbial communities. Perturbation reduced decomposition, especially aboveground, and the rates in fenced treatments did not reach undisturbed levels. Our findings highlight the effects of large- and small-scale disturbances on an essential process for successful tropical forest restoration.

1 | Introduction

Litter decomposition is a fundamental ecological process in forests, driving the breakdown of fallen leaves and organic material on the forest floor through the activity of bacteria, fungi, insects, and other invertebrates (Liu et al. 2005; Makkonen et al. 2012). Decomposition plays a pivotal role in nutrient cycling, thus supporting the fertility and productivity of forests (Long et al. 2021). Understanding decomposition dynamics is particularly relevant in regenerating secondary tropical forests, as they are expanding due to land abandonment (Heinrich et al. 2021) and now represent 70% of tropical forest area globally (Ngo Bieng et al. 2021). Secondary tropical forests have thus become critical for carbon storage and biodiversity conservation, yet their recovery trajectories vary depending on how the land was used in the past (land-use legacy), disturbance history, and environmental conditions (Poorter et al. 2016). To understand how nutrient cycling and forest productivity will develop during forest regrowth, it is imperative to ascertain the impact of disturbance and local environmental factors on litter decomposition.

In lowland tropical rainforests, variations in local climatic conditions and soil characteristics occur within regions, across landscapes and at the forest microhabitat level (Ostertag et al. 2022; Paudel et al. 2015). This is usually due to differences in land-use legacy (Foster et al. 2003; Kallenbach and Stuart Grandy 2015), disturbance level (Röder et al. 2024), or successional stage (Attignon et al. 2004; Stone et al. 2020). These factors, in turn, strongly drive tree species diversity, which largely determines litter quality (Sánchez-Silva et al. 2018) and shapes decomposer community structure (Ashford et al. 2013), thus influencing decomposition rates (Cornwell et al. 2008; García-Palacios et al. 2013).

Previous forest succession studies (Morffi-Mestre et al. 2023; Paudel et al. 2015; Powers et al. 2009; Sánchez-Silva et al. 2018) indicate that decomposition rates tend to increase along chronosequences (space-for-time experiments) of forest recovery. When forests become older and their vegetation more complex, decomposition rates increase proportionally with aboveground biomass accumulation (Lohbeck et al. 2015). This “vegetation quantity effect” suggests that the recovery of ecological processes as decomposition is closely tied to biomass accumulation. Mature forests have more constant microclimates which enhance microbial activity and promote a stable decomposer community (Sniegocki et al. 2022). However, these improvements may be limited by the influence of past land-uses (Chazdon et al. 2006). Forests with a legacy of agricultural activities may still retain high soil compaction, nutrient depletion, and shifts in plant species composition (van der Sande et al. 2022), all of which may limit the benefits of forest recovery on decomposition rates.

The changes in vegetation along a process of forest succession may also significantly modify the microclimatic conditions at the soil surface. Although temperature and water availability are typically the two main controlling factors of decomposition processes both above- (Salinas et al. 2011) and belowground (Aerts 1997), in tropical forests, where temperature is less restrictive, soil moisture plays a crucial role by regulating microbial activity (Meir et al. 2008; Schaap et al. 2024). For instance, in forests with closed canopies, higher moisture levels increase the solubility of organic carbon and diffusion, facilitating microbial carbon uptake and reducing physiological stress (Manzoni et al. 2014; Moyano et al. 2013). However, excessive moisture may reduce oxygen availability, which slows aerobic decomposition (Skopp et al. 1990; Keiluweit et al. 2016).

These changes in microclimate interact with environmental conditions to shape decomposition processes during forest regrowth (Schilling et al. 2016). For example, soil carbon-to-nitrogen (C:N) ratios can have contrasting effects on decomposition during the transition from open pasture to forest, with mass loss increasing with C:N ratio in forests but decreasing in grasslands (Blanco et al. 2023). Decomposition rates also vary across pH gradients, as soil pH influences microbial community composition and enzymatic activity (Sellan et al. 2020). Finally, topography can also influence decomposition via its effects on soil properties and microclimate. For instance, some studies report increased decomposition on steeper slopes due to enhanced solar exposure, temperature, and soil aeration (Hu et al. 2020), while others found no significant effects (Ma et al. 2024). Elevation is often closely associated with temperature and forest composition, thus affecting leaf litter decomposition, especially aboveground (Bohara et al. 2020).

Extensive areas of neotropical forests are commonly subject to low-impact forest degradation (Matricardi et al. 2020), resulting in plant and animal biomass removal. Such forest clearance activities modify microclimate, soil properties, disrupt decomposer communities, and hinder litter breakdown (Frouz 2018; Latterini et al. 2023). A long-term litter manipulation experiment in mature forest in Panama revealed that litter removal altered soil conditions, reduced nutrient cycling, and impacted soil fauna and microbial communities (Ashford et al. 2013; Sayer et al. 2006). In addition to plant biomass, the reduction in animal biomass can also modify decomposition dynamics. Vertebrates influence litter breakdown both directly and indirectly, as they alter litter quality through foraging, disturb the environment via movement and trampling, modify trophic interactions within decomposer communities, contribute nutrients through fecal deposition, and physically fragment litter (Tuo et al. 2024). However, experimental manipulations of forest clearance in tropical forests remain rare, and the immediate effects of such perturbations on decomposition dynamics remain uncharacterised.

Here, we address this research gap by investigating how different scales and types of disturbance influence above- and belowground decomposition in a tropical lowland forest of the Ecuadorian Chocó. With a chronosequence established through a space-for-time approach (described in Escobar et al. 2025), we studied how land-use legacy and environmental factors interact in forest areas at different stages of recovery from larger-scale disturbances (> 1 ha). In addition, we simulated low-impact forest degradation such as localized forest clearance (Sagarin and Pauchard 2010) or selective large animal exclusion (Dirzo et al. 2014; Granados et al. 2017) with two types of small-scale disruptions (100 m).

Our study addressed two key objectives: (a) to elucidate variations in leaf litter decomposition across stages of forest regeneration from different land-uses, and abiotic factors that differ among microhabitats; (b) to experimentally assess the recovery of decomposition following a pulse perturbation and evaluate the relative importance of large animal activity on decomposition dynamics. We hypothesized that: (a) decomposition rates will increase with forest succession, but the trajectory will differ between land-use legacies; these differences in decomposition with forest age and land-use legacy will be explained by distinct environmental conditions and soil properties; (b) small-scale disturbances simulating forest clearance and large mammal loss will strongly inhibit decomposition. Overall, we expect disturbances to have stronger effects on aboveground decomposition, as belowground processes are likely more buffered.

2 | Methods

2.1 | Study Design

This study is part of the *Reassembly* Research Unit (www.reassembly.de), which investigates tropical forest recovery in northwest Ecuador's lowland Chocó. The study area includes the Canandé and Tesoro Escondido reserves and nearby villages (La Yuca and Hoja Blanca, Esmeraldas). Climatic conditions at the site, based on pilot measurements (Escobar et al. 2025), are characteristic of equatorial lowland forests, with annual precipitation of approximately 4000–5000 mm, relative humidity consistently approaching saturation, and mean temperatures of 21°C–25°C (Table S1). The *Reassembly* chronosequence spans active cacao plantations and pastures to 38-year-old regenerating forests (described in Escobar et al. 2025). For the present study, we selected 32 plots (50 × 50 m) along the chronosequence: three active cacao plantations (monocultures of *Theobroma cacao*), three pastures (mainly consisting of grasses *Brachiaria* or *Axonopus scoparius*), 18 regenerating forests (nine each with cacao plantation and pasture legacies), and eight old-growth forests served as undisturbed benchmarks (Table S1). Forest age, defined by years since last human use, was evenly distributed across land-use histories (Figure S1). Old-growth plots were selected based on historical data provided by the Jocotoco Foundation (www.jocotoco.org).

2.2 | Perturbation-Recovery Experiment (PREX)

To study the short-term response of decomposition processes to disturbance, we conducted a perturbation-recovery experiment (PREX). We established four 10 × 10 m subplots within each forest plot along the chronosequence, distributed across the plot area. In the agricultural sites (active cacao and pasture plots), which were on private property, subplots were reduced to 8 × 8 m and positioned adjacent to each other. In March 2022, we applied one of four treatments to each subplot: (1) complete removal of litter, dead wood, seeds, shrubs, and understory plants and lianas with < 8 cm stem diameter at breast height, DBH (P_0), (2) large animal exclusion by surrounding the area with a *c.* 1 m high shade-cloth fence (CF); (3) combined understory clearance and fencing (PF_0); and (4) undisturbed open controls (C). A previous study on vertebrate activity and populations along the same chronosequence showed that the collared peccary *Dicotyles tajacu* and the white-lipped peccary *Tayassu pecari* were the main target of our exclusion fences and that they occur uniformly across all stages of forest succession (Grella et al. 2025). We therefore assumed that peccaries regularly visited the unfenced subplots throughout the chronosequence. In March 2023, we repeated the vegetation removal treatments within smaller areas of the previously perturbed subplots. The re-perturbation was applied at the southern end of each plot, while the northern end was left undisturbed as a one-year recovery reference for other studies. All new vegetation with stem DBH of < 8 cm, and all dead wood and leaf litter were removed from a 4 × 10 m area in the old-growth and regeneration subplots, and a 2.5 × 8 m area in the active cacao plantations and pastures. Because of the sloped terrain of some plots, a barrier was placed between the newly perturbed area and the one perturbed the year before to protect from eventual debris- and mudslides. The re-perturbation added two more treatments to the PREX experiment: open perturbed treatment (P) and perturbed-fenced (PF). Throughout this study, we utilized only the C, CF, P, and PF treatments; thus, when referring to perturbation treatments in the text, this corresponds only to P and PF.

2.3 | Decomposition Experiment

To assess the effects of forest age, land-use legacy, and disturbance on decomposition, we measured litter mass loss over three consecutive 45-day post-disturbance stages using litterbags. Aboveground (AG) litterbags (20 × 20 cm, 0.5-cm plastic mesh) and belowground (BG) litterbags (5 × 5 cm, 0.5-mm nylon mesh) contained a standardized litter mix from five common tree species (with equal proportions of species) that encompass a range of leaf traits across the chronosequence (Table S2, Figure S2). Litter consisted of mature, freshly fallen leaves to ensure reproducibility. Leaves were processed according to decomposition environment and litterbag size. For AG litterbags, leaves were cut into 5 × 5 cm pieces, frozen at −18°C for 30 days, and mixed in equal mass per species (30 g total). For BG litterbags, leaves were cut into 5 × 5 mm pieces, oven-dried at 70°C to constant weight, and combined at 0.2 g per species (1 g total). Leaf fragmentation and pre-treatment aimed to maximize standardization across treatments, along forest succession, and within decomposition environments, thereby enabling robust comparisons rather than reproducing natural decomposition rates. Freezing and oven-drying were used to reduce initial arthropod and microbial activity and, in the case of BG litterbags, to enable precise weight standardization given the small litter mass. In March 2023, we deployed the first set of litterbags on the same day the perturbation treatment was applied. We placed one AG litterbag and two BG litterbags (*c.* 10 cm depth) in all four PREX subplots per plot. This burial depth corresponds to the biologically active surface mineral soil layer that contains substantial root activity and diverse decomposer communities, while remaining shallow enough for retrieval (Trevathan-Tackett et al. 2024; Powers et al. 2009). In the fenced treatments, litterbags were placed away from the fence to prevent potential interference from the shadow cast by the shade cloth, which could affect soil moisture and, possibly, decomposition rates. AG litterbags were attached to tree stems or roots to prevent them from being displaced with rainfall. We used two BG litterbags per subplot as buried bags were more likely to be damaged or lost. To account for seasonal variation, all litterbags were deployed immediately following the start of the rainy season, so the 135-day experiment spanned a period of relatively consistent rainfall. After an incubation period of 45 days, we collected all litterbags, replaced them in each subplot and repeated this process two times. Thus, we measured decomposition at 45, 90 and 135 days post-perturbation, in four subplots within 32 study plots, giving a total of 386 AG litterbags and 772 BG litterbags. In the unfenced treatments, we consistently observed signs of vertebrate activity. Upon retrieval, litterbags were cleaned, dried (70°C) to constant weight, and decomposition was calculated as percentage litter dry mass loss (%) per 45-day incubation. BG decomposition was averaged across paired bags, provided both were recovered. Due to loss or damage, 62 AG and 67 BG litterbags were discarded, leaving 324 AG and 705 BG litterbags for analysis.

2.4 | Environmental Data

To establish whether differences in microclimate and environmental conditions might explain differences in decomposition with land-use legacy or forest age, we measured slope, elevation, aboveground tree biomass, litter standing crop, soil temperature at the surface and 0–6 cm depth, and soil properties (pH, moisture, and C:N ratio at 0–10 cm depth) in each plot. Soil temperature and moisture were recorded with a TMS-4 data logger (TOMST s.r.o., Czech Republic; method by Wild et al. (2019)) and summarized as the 95th percentile over the decomposition study period (see Supporting Information Methods). For soil pH and C:N ratio, eight soil samples (0–10 cm depth) were collected per plot, combined into one composite sample, and oven-dried at 40°C. Soil pH was measured in a 1:1 soil-water solution, and total C and N were analyzed using an Elemental Analyzer FlashSmart (Thermo Fisher Scientific, Italy). Litter standing crop was determined prior the first perturbation event from four 1 × 1 m samples per plot, which were dried to constant weight at 70°C. Topographical and botanical data were collected as part of the *Reassembly* project; methods are described in Escobar et al. (2025) and data is from Escobar et al. (2024). In brief, tree aboveground biomass was estimated according to Chave et al. (2014) using plot-level surveys of diameter at breast height (DBH) and tree height. Elevation and slope were extracted from a digital elevation model using bilinear interpolation at plot centroids.

2.5 | Statistical Analysis

Data analysis was conducted in R version 4.3.1 (R Core Team 2023, www.r-project.org) and all analyses were conducted for AG and BG litterbags separately. To assess the effects of forest age and land-use legacy on litter decomposition, we based the analyses on mass loss from litterbags in the PREX control subplots excluding the old-growth forests. We used generalized linear mixed models (GLMM) with Gaussian family (*lmer* function in the lme4 package; Bates et al. 2015). As preliminary analyses on both AG and BG litterbags showed that mass loss in the control subplots did not vary between times since the start of the PREX experiment (45, 90, or 135 days), we treated the three measurements as replicates, assuming no seasonal variation in decomposition (Table S3). Therefore, the initial models included study plot as a random intercept, forest age and land-use legacy (pasture or cacao) as fixed effects, and they were simplified by sequentially removing non-significant terms to derive a minimal adequate model (Crawley 2007; Laird-Hopkins et al. 2017). For AG decomposition, a quadratic forest age term provided the best model fit, based on likelihood ratio tests (*anova* function in base-R), and Akaike Information Criteria (AIC). To assess if the quadratic term was affected by legacy, we conducted further analyses on the cacao and pasture legacies separately (Table S4). We estimated fixed and random effects using the lmerTest package (Kuznetsova et al. 2017) and we assessed the significance of fixed effects using Type II ANOVA and an F-test (car package, Fox and Weisberg 2018). We performed model diagnostics and tested for overdispersion or zero inflation using the DHARMa package (Hartig 2016).

To examine microhabitat variation with forest succession, we modeled each environmental factor as a function of forest age (excluding old-growth forests) using generalized linear models (GLMs, Table S5). Since a preliminary assessment of correlations among all measured environmental factors showed a high correlation of leaf area index (LAI) with tree aboveground biomass (Table S6), we excluded the former from further analysis. To determine whether environmental factors explained differences in decomposition with forest age, we utilized GLMMs based on mass loss from the control subplots, including old-growth forests. We constructed separate models for each incubation site-specific environmental variable: tree aboveground biomass, elevation, leaf litter standing crop, soil surface temperature, terrain slope, soil pH, soil C:N, soil moisture, soil temperature belowground. Each model included its respective environmental variable as a fixed effect and study plot as a random intercept. The two temperature models additionally included land-use legacy as a fixed factor. For each level (cacao, pasture and old-growth) we calculated the estimated marginal means adjusted for model structure and conducted Tukey's post hoc pairwise comparisons (*emmeans* function and package). Predictors were log- or square-root transformed as necessary to meet model assumptions, and AG mass loss was square-root transformed (Table S7). However, to facilitate comparison among predictors within each specific incubation environment, we also refitted all models with standardized (scaled) environmental variables and extracted standardized coefficients ($\beta \pm$ SE). Models were inspected and evaluated as described above.

We assessed the impact of perturbation (P, PF treatments) and fencing (CF, PF treatments) using Kruskal-Wallis tests, comparing mass loss from each treatment to the control at each sampling time. We considered the sampling periods post-perturbation (45, 90, or 135 days) as recovery stages. To measure the treatments' effect sizes, we calculated epsilon squared (ε^2) for every recovery stage:

$$\varepsilon^2 = \frac{H - k + 1}{n - k} \tag{1}$$

where $n = 64$ (total sample size), $k = 2$ (control and one treatment), and H is the Kruskal-Wallis statistic (Vogt and Johnson 2016).

To easily visualize the effects of the experimental disturbances (PREX), we calculated treatment effects (TE) as response ratios for every subplot:

$$\left(\mathrm{TE}_i\right)_{\mathrm{days}} = \frac{(\text{Mass Loss\%CF, P or PF})_i}{(\text{Mass Loss\%C})_i} \quad (2)$$

where CF, P and PF are the treatments and C is the control, i represents study plot, and days is the time since perturbation (recovery stage). To further assess the effect of time since the perturbation event on each treatment, we compared TEs between the three recovery stages with Wilcoxon rank-sum tests, applying Benjamini-Hochberg correction for multiple comparisons. For all analyses, we report significant results at $p<0.05$ and non-significant trends at $p<0.1$.

3 | Results

3.1 | Decomposition Dynamics Across the Chronosequence

Mass loss (%) was the highest in the old-growth forest, followed by cacao plantations, and was lowest in pastures (Table S8). AG mass loss revealed a quadratic pattern of mass loss with lower decomposition rates in intermediate-aged forest plots (forest age^2: estimate = 19.70; SE = 6.45; $p=0.007$). Although there was no overall difference in mass loss among land-use types, the quadratic trend was apparent only in the sites with cacao legacy (forest age^2: estimate = 19.97; SE = 6.34; $p=0.035$). There was a trend of declining BG mass loss with forest successional stage (estimate = −0.04, SE = 0.07), but the effect was not significant and land-use legacy had no detectable influence (Figure 1).

3.2 | The Influence of Environmental Factors

A detailed description of the results of the individual measured variables and their respective trends with forest age is reported in the Supporting Information (Tables S9–S13). Environmental variables differed markedly among sites along the regeneration gradient (Table S14, Figure 2). Tree aboveground biomass and leaf area index (LAI) increased with forest age, a trend that persisted in old-growth forests. Soil C:N also increased with successional stage but old-growth forests had lower soil C:N values. Temperature and pH decreased with forest age, reaching lower levels in old-growth stands. Leaf litter standing crop followed a bell-shaped trajectory, with the highest values in 10–20 year-old forests and lower litter standing crop in old-growth forests. Litter standing crop was much lower at former pasture sites than at former cacao plantations at the start of the chronosequence, as pastures lacked leaf litter due to minimal tree cover.

AG mass loss was related to differences in tree aboveground biomass, surface temperature and elevation across plots, whereas BG mass loss was related to soil C:N and soil moisture (Table S15). AG mass loss increased linearly with tree aboveground biomass ($\beta=0.27$, SE = 0.08, $p=0.003$) and elevation ($\beta=0.20$, SE = 0.09, $p=0.027$) but exhibited a bell-shaped relationship with leaf litter biomass ($\beta=-0.21$, SE = 0.08, $p=0.023$; ANOVA: $p=0.061$), with peak values at a leaf litter biomass of approx. 1 t/ha. AG mass loss declined with increasing surface temperature ($\beta=-0.17$, SE = 0.08, $p=0.026$) but the relationship differed among land-use legacies (ANOVA: $p=0.012$), whereby mass loss increased with

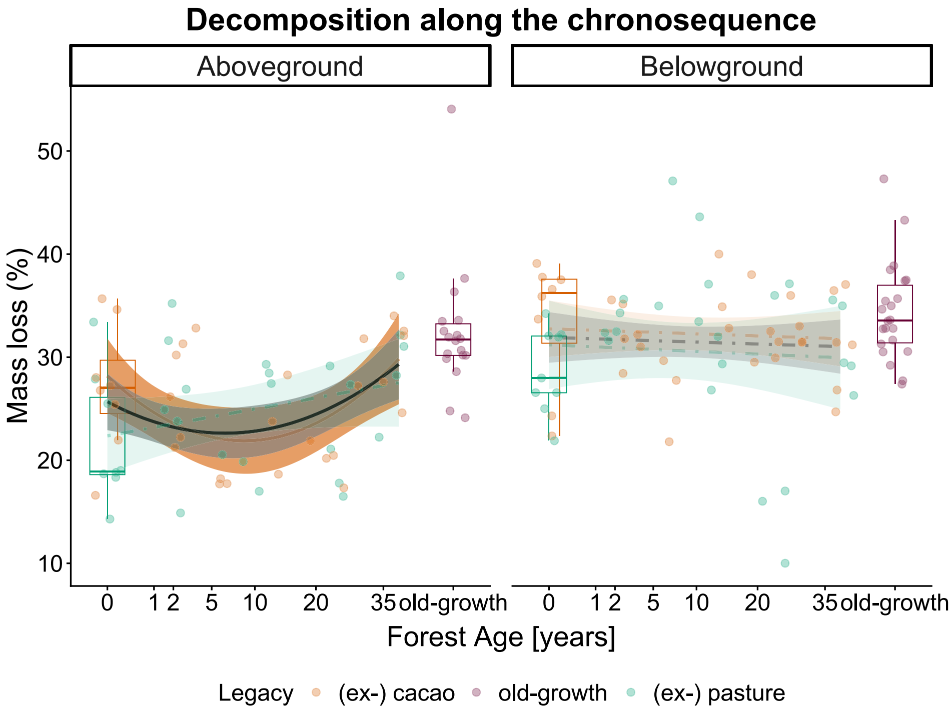

FIGURE 1 | Leaf litter decomposition dynamics measured above- and belowground at three time points along a chronosequence of tropical forest regeneration from two different land-uses, where dots represent mean mass loss per subplot and timepoint; lines with shading represent modeled relationships with confidence intervals; solid lines with opaque CIs stand for statistical significance as opposed to dashed lines with transparent CIs; green is pasture, orange is cacao plantation, purple is old-growth forest; black/gray is the overall chronosequence model in which old-growth forests were not included; the data distribution of old-growth plots is instead represented by boxplots, showing medians, interquartile range and whiskers.

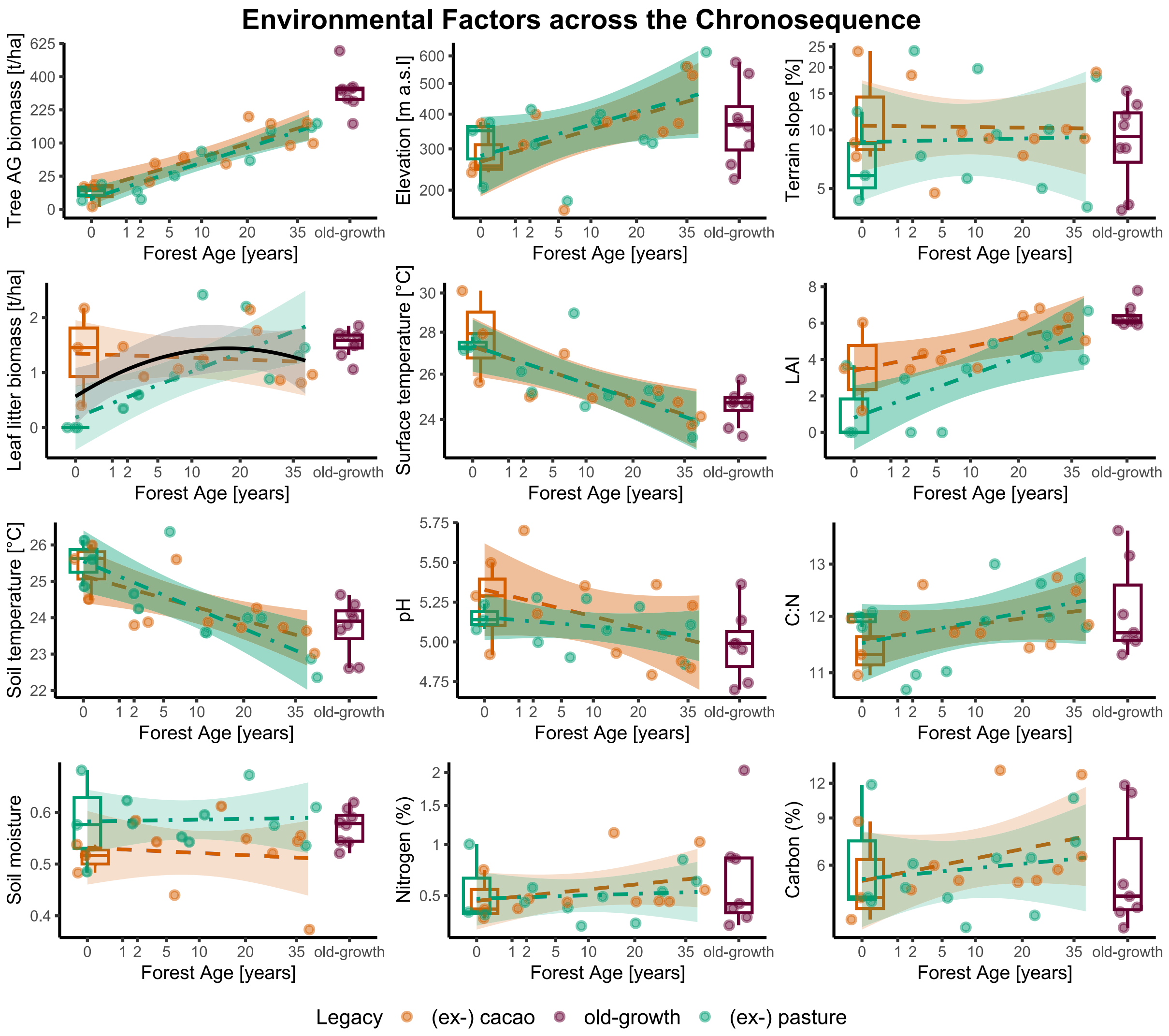

FIGURE 2 | Environmental and soil variables measured along the studied chronosequence; lines with shading represent modeled relationships with confidence intervals and their opacity stands for statistical significance; leaf litter biomass showed a bell-shaped relationship with forest age; in all models we differentiated the trends of each variable with forest age by land-use legacy; green is pasture, orange is cacao plantation and purple is old-growth forest; old-growth forests were not included in the models and the data distribution is instead represented by boxplots, showing medians, interquartile range and whiskers.

soil surface temperature in old-growth forests but declined in plots with cacao and pasture legacy (Figure S3). BG mass loss declined with increasing soil C:N ($\beta = -1.84$, SE $= 0.83$, $p = 0.034$) but showed a bell-shaped relationship with soil moisture ($\beta = -2.74$, SE $= 0.68$, $p < 0.001$), with peak mass loss at a soil moisture of c. 0.57 (unitless, scale 0–1).

3.3 | Effects of Small-Scale Perturbation and Animal Exclusion

In the control treatment, neither AG nor BG mass loss differed over time (Table S3). The effects of each experimental disturbance (PREX treatments) on AG and BG mass loss were overall comparable (Figure 3, Tables S16–S18). Perturbation inhibited mass loss from both AG ($p < 0.001$, $\varepsilon^2 = 0.20$) and BG litterbags ($p = 0.022$, $\varepsilon^2 = 0.07$) after 45 days, but only from AG bags after 90 days ($p < 0.001$, $\varepsilon^2 = 0.22$). In the perturbed-fenced treatments, BG mass loss was marginally lower than the control after 45 days ($p = 0.095$, $\varepsilon^2 = 0.03$) but there was no effect at later timepoints. However, AG mass loss in the perturbed-fenced treatment was strongly reduced compared to the controls at all three time points (45 days: $p = 0.004$, $\varepsilon^2 = 0.12$; 90 days: $p < 0.001$, $\varepsilon^2 = 0.23$; 135 days: $p = 0.002$, $\varepsilon^2 = 0.14$). Fencing alone had no influence on mass loss at any time.

4 | Discussion

This study examined how small- and large-scale disturbances influence leaf litter decomposition along a forest regeneration chronosequence, exploring variation across succession stages in sites with different land-use legacies and microhabitat conditions, and evaluating decomposition recovery after a strong pulse perturbation, including the contribution of large animal activity.

We found that both large and small-scale disturbances impact the recovery of decomposition processes during forest

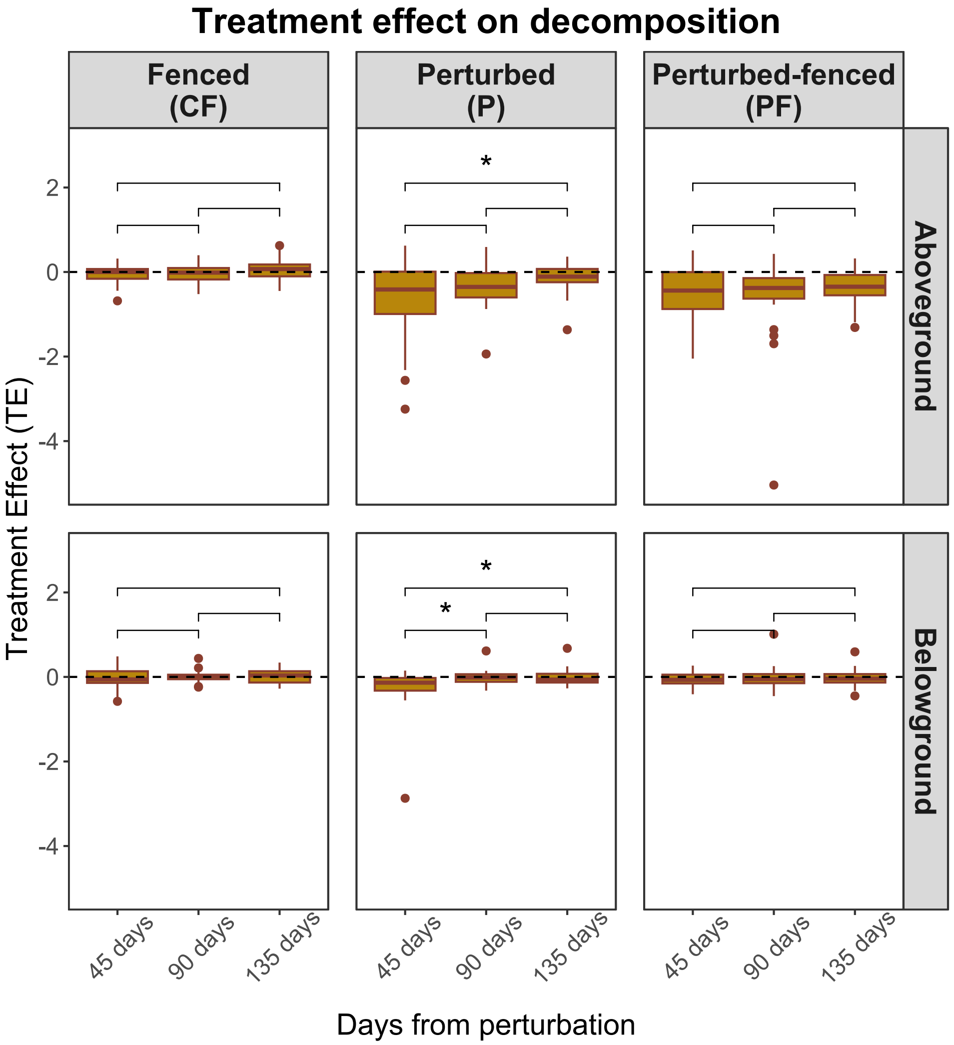

FIGURE 3 | Treatment effect (TE) on above- and belowground decomposition in the experimental treatments (CF, P and PF) at the three time points from the installation of the experimental disturbances (PREX event); the dashed black line at TE = 0 indicates no effect of CF, P nor PF hence when mass loss in the treatment was the same as the control, TE < 0 when mass loss in the treatment was less than the control, TE > 0 when mass loss in the treatment was higher than the control; the significancy levels refer to the *p*-values of the Wilcoxon rank-sum test to compare the TE in the three time points (days from perturbation) within each treatment and sample position.

regeneration. Mass loss during secondary forest succession followed different trajectories at sites with pasture legacy compared to former cacao plantations, which are largely explained by microclimate differences in the earlier stages of the forest chronosequence. Our perturbation treatment simulating initial land clearance inhibited litter decomposition, and although animal exclusion had no immediate effect, the impact of perturbation lasted much longer in fenced treatments, suggesting that animal activity accelerates the recovery of decomposition processes after disturbance.

4.1 | Land-Use Legacy and Microhabitat Influence Decomposition Dynamics During Forest Regeneration

Land-use legacy influenced aboveground litter decomposition, whereby the U-shaped relationship between decomposition and regeneration time at former cacao plantation sites is likely due to changes in decomposer communities and microclimatic conditions (Guariguata and Ostertag 2001; Paudel et al. 2015). Although we did not assess decomposer communities in this study, work on temperate forest succession showed that arthropod richness and density (individuals/m^2) declined in mid-successional stages before increasing in mature forests (Cole et al. 2020; Deng et al. 2022). The initial decline in mass loss in former cacao plantations could also reflect transient changes in vegetation structure, soil chemistry, and nutrient availability as the forest regrows (Gessner et al. 2010; Thom and Keeton 2020; Toro et al. 2025). For instance, recently abandoned croplands and high-activity clay soils are often strongly compacted and depleted in carbon and nitrogen. As succession progresses, bulk density decreases while soil C and N increase, promoting greater fine root growth and litter input (van der Sande et al. 2022). At the same time, leaf traits such as specific leaf area (SLA) and nitrogen concentration decline, reflecting a shift toward more conservative resource-use strategies (Sánchez-Silva et al. 2018). In contrast, mass loss increased linearly with forest age at sites with pasture legacies, where harsh conditions in pastures—high temperatures, intense solar radiation, and the absence of canopy cover—create unfavorable environments for decomposer communities (Lorenzo et al. 2014; Wallace et al. 2018). Accordingly, litter decay rates are often lower in pastures compared to forest sites (Röder et al. 2024; Stone et al. 2020) but increase as ecosystems regenerate. In our study, the soil surface temperatures in open pastures were up to 11°C higher than in forest sites (Table S9), frequently exceeding 30°C, with no canopy cover to provide shade or protection (Table S12). These findings support our first hypothesis, emphasizing the role of microclimate in the recovery of decomposition processes during forest regrowth. Site-specific microclimates likely also explain the positive relationship between decomposition and elevation. Our study spanned a narrow elevation range (159–615 m a.s.l.), and mid- to high-elevation plots provided more favorable conditions, with increased humidity and moderate temperatures (Röder et al. 2024).

While land-use legacy can induce lasting structural changes in forests, its influence may weaken as forests mature (Foster et al. 2003). Greater AG mass loss in old-growth forests and increasing AG decomposition with forest age and the concurrent accumulation of tree aboveground biomass ($p = 0.005$) reinforce the "vegetation quantity effect" (Lohbeck et al. 2015), whereby greater live biomass promotes decomposer microhabitats by increasing organic inputs, moisture retention, and temperature stability (Schilling et al. 2016). In our study, greater decomposition rates in old-growth forests were likely due to stable surface temperatures (23°C–26°C; Table S9) maintained by the dense canopy, indicated by the high LAI (Table S12). By contrast, BG decomposition showed no relationship with successional age or land-use legacy, suggesting a distinct recovery trajectory from decomposition of litter on the soil surface and weaker dependence on forest structure (Toro et al. 2025). Instead, mass loss declined with increasing soil C:N, likely reflecting greater microbial N limitation belowground (Schaap et al. 2024) compared to at the soil surface. High soil C:N also indicates that organic matter is still relatively undecomposed, which further limits decomposition and contributes to slower litter mass loss. Soil microbial activity can be strongly constrained by factors such as soil pH (Rousk et al. 2010; Shi et al. 2019) or nutrient content (Cornwell et al. 2008), soil moisture and C:N ratios (Pausas and Bond 2020; Wieder et al. 2009). The importance of soil conditions for BG mass loss was further evident in the bell-shaped response of decomposition to soil moisture (Figure S3). Mass loss peaked at intermediate moisture levels but declined at a soil water content of *c.* 53%, at which point it is possible that anoxic conditions inhibited microbial activity. In tropical wet forests, this threshold is easily reached, as seen in our study: active pastures, lacking canopy cover and root biomass, had the highest soil moisture levels (Table S10) and also exhibited the lowest decomposition rates. Conversely, active cacao plots exhibited very low soil moisture levels, likely due to increased evaporation due to the elevated surface temperatures and water uptake by cacao plants (Foster et al. 2003). In addition, active pastures are associated with soil compaction and nutrient depletion (Souza et al. 2013), whereas cacao plantations, with higher pH (Table S13), may have enhanced microbial activity (Corre et al. 2003; Luizão et al. 2007), despite the similar nitrogen levels across sites (Gill et al. 2021). Cacao plantations also maintained a substantial litter layer (up to 2 t/ha; Table S11), owing to the leaf shedding of cacao trees (Rodríguez et al. 2023; Sari et al. 2022), which reduces temperature extremes (Sayer et al. 2006) and creates a favorable microclimate for decomposition (Liu et al. 2005). As a result, BG decomposition was lowest in active pastures, while cacao plantations showed greater mass loss, likely due to differences in soil conditions (Figure 2).

AG decomposition followed a bell-shaped relationship with litter standing crop biomass (Figure S3), suggesting that decomposition is promoted at intermediate levels of litter on the soil surface. While low litter biomass may limit decomposition due to microclimatic effects such as lack of water retention (Sayer et al. 2006), excessive accumulation could constrain decomposer activity through nutrient immobilization.

4.2 | Forest Clearance Inhibits Decomposition and Exclusion of Large Animal Slows Down Recovery

Our results indicate that the presence of the fence alone had no substantial effect on decomposition. At first glance, this appears to contradict our initial hypothesis that mechanical disturbance by large animals would accelerate decomposition by promoting litter fragmentation and soil mixing. However, the perturbation treatment strongly reduced AG decomposition, supporting our hypothesis and aligning with previous research showing that disturbances such as logging or clearing can slow decomposition by disrupting decomposer communities and altering soil conditions (Laigle et al. 2021; Latterini et al. 2023). However, with perturbation alone, mass loss both above and belowground only initially decreased (45 days) and then recovered to control levels within 135 days. No such recovery was observed for AG mass loss when in the fenced perturbed plots, indicating that excluding large animals inhibited the recovery of decomposition processes after disturbance, at least within the timeframe of this study. This finding reinforces the crucial role of large animals in forest nutrient cycling by promoting litter breakdown, soil mixing, and bioturbation. The influence of animal exclusion on the recovery of decomposition processes was not observed for BG mass loss, suggesting that decomposition beneath the soil surface is less sensitive to pulse disturbances and exhibits greater resilience overall. Thus, large animals appear to play a key role in facilitating the recovery of aboveground litter decomposition post-disturbance, offering novel insights into their ecological function in tropical forests.

5 | Conclusion

Our study highlights the intricate and dynamic nature of leaf litter decomposition in regenerating tropical forests, emphasizing the impact of land-use legacy. We show that historical land use shapes early recovery, with its influence on ecosystem processes slowly fading as time passes from abandonment, underscoring the importance of the complex interactions among decomposer communities, microclimate, and vegetation structure. Key environmental drivers played distinct yet interconnected roles in shaping decomposition across forest age and land-use legacy. We also provide novel insights into the role of large animals and disturbance in decomposition recovery. Small-scale perturbation initially slowed mass loss but recovery of decomposition rates over time occurred only when animals remained present. By illustrating how vegetation structure, land-use legacy, and decomposition processes interact, our study provides key insights into tropical forest recovery. These findings have direct implications for conservation and restoration, emphasizing the need to account for historical land-use impacts, prioritize vegetation recovery, and favor the presence of large animals to restore decomposition cycles. As tropical forests regenerate under diverse anthropogenic pressures, understanding these ecological processes is crucial for effective management and ecosystem resilience. Nutrient cycling through litter decomposition supports plant growth and soil communities, forming the basis for long-term forest recovery. Without functioning soil processes, restoration efforts risk failure as ecosystems may lack foundational resources needed to sustain biodiversity and productivity.

Acknowledgments

We are grateful to Fundación Jocotoco and Fundación Reserva Tesoro Escondido (Martin Schaefer and Citlalli Morelos) for their permission to conduct research on their reserves. We thank Chocó lab staff Katrin Krauth, Julio Carvajal, Chiara Correa, and Yadira Giler for their logistical support, parabiologists Miguel Ángel Tacuri, Bryan Tamayo, Leonardo Alexis de la Cruz, Franklin Quintero, Lady Condoy, Jefferson Tacuri, and Jordy Ninabanda for their invaluable assistance, and Karen Pedersen and Constance J. Tremlett for their coordination in the field. We warmly thank Michael Staab for his statistical mentoring. We acknowledge the Ministerio del Ambiente, Agua y Transición Ecológica of Ecuador for granting research and collection permits under the Genetic Resources Access Agreement (MAATE-DBI-CM-2021-0187). This study was funded by the Deutsche Forschungsgemeinschaft (DFG) through the Research Unit REASSEMBLY (FOR 5207; sub-project SP2: HE4593/12-1).

Funding

This work was supported by Deutsche Forschungsgemeinschaft, FOR 5207, HE4593/12-1.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.30693650.v1.

References

Aerts, R. 1997. "Climate, Leaf Litter Chemistry and Leaf Litter Decomposition in Terrestrial Ecosystems: A Triangular Relationship." *Oikos* 79, no. 3: 439–449. https://doi.org/10.2307/3546886.

Ashford, O. S., W. A. Foster, B. L. Turner, E. J. Sayer, L. Sutcliffe, and E. V. J. Tanner. 2013. "Litter Manipulation and the Soil Arthropod Community in a Lowland Tropical Rainforest." *Soil Biology and Biochemistry* 62: 5–12. https://doi.org/10.1016/j.soilbio.2013.03.001.

Attignon, S. E., D. Weibel, T. Lachat, B. Sinsin, P. Nagel, and R. Peveling. 2004. "Leaf Litter Breakdown in Natural and Plantation Forests of the Lama Forest Reserve in Benin." *Applied Soil Ecology* 27, no. 2: 109–124. https://doi.org/10.1016/j.apsoil.2004.05.003.

Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67, no. 1: 1. https://doi.org/10.18637/jss.v067.i01.

Blanco, J. A., M. Durán, J. Luquin, L. San Emeterio, A. Yeste, and R. M. Canals. 2023. "Soil C/N Ratios Cause Opposing Effects in Forests Compared to Grasslands on Decomposition Rates and Stabilization Factors in Southern European Ecosystems." *Science of the Total Environment* 888: 164118. https://doi.org/10.1016/j.scitotenv.2023.164118.

Bohara, M., K. Acharya, S. Perveen, et al. 2020. "In Situ Litter Decomposition and Nutrient Release From Forest Trees Along an Elevation Gradient in Central Himalaya." *Catena* 194: 104698. https://doi.org/10.1016/j.catena.2020.104698.

Chave, J., M. Réjou-Méchain, A. Búrquez, et al. 2014. "Improved Allometric Models to Estimate the Aboveground Biomass of Tropical Trees." *Global Change Biology* 20, no. 10: 3177–3190. https://doi.org/10.1111/gcb.12629.

Chazdon, R. L., S. G. Letcher, M. van Breugel, M. Martínez-Ramos, F. Bongers, and B. Finegan. 2006. "Rates of Change in Tree Communities of Secondary Neotropical Forests Following Major Disturbances." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 362, no. 1478: 273–289. https://doi.org/10.1098/rstb.2006.1990.

Cole, R. J., P. Selmants, S. Khan, and R. Chazdon. 2020. "Litter Dynamics Recover Faster Than Arthropod Biodiversity During Tropical Forest Succession." *Biotropica* 52, no. 1: 22–33. https://doi.org/10.1111/btp.12740.

Cornwell, W. K., J. H. C. Cornelissen, K. Amatangelo, et al. 2008. "Plant Species Traits Are the Predominant Control on Litter Decomposition Rates Within Biomes Worldwide." *Ecology Letters* 11, no. 10: 1065–1071. https://doi.org/10.1111/j.1461-0248.2008.01219.x.

Corre, M. D., F. O. Beese, and R. Brumme. 2003. "Soil Nitrogen Cycle in High Nitrogen Deposition Forest: Changes Under Nitrogen Saturation and Liming." *Ecological Applications* 13, no. 2: 287–298. https://doi.org/10.1890/1051-0761(2003)013%255B0287:SNCIHN%255D2.0.CO;2.

Crawley, M. J. 2007. *The R Book*. Wiley.

Deng, Y., Y. Bai, R. Cao, et al. 2022. "Key Drivers of Soil Arthropod Community Shift Across a Subalpine Forest Series Vary Greatly With Litter and Topsoil Layers." *European Journal of Soil Biology* 111: 103421. https://doi.org/10.1016/j.ejsobi.2022.103421.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. "Defaunation in the Anthropocene." *Science* 345, no. 6195: 401–406. https://doi.org/10.1126/science.1251817.

Escobar, S., F. L. Newell, M. Endara, et al. 2024. "Data From: Reassembly of a Tropical Rainforest: A New Chronosequence in the Chocó Tested With the Recovery of Tree Attributes (Version 7, p. 816839 Bytes) [Data Set]." Dryad. https://doi.org/10.5061/DRYAD.C59ZW3RGB.

Escobar, S., F. L. Newell, M. Endara, et al. 2025. "Reassembly of a Tropical Rainforest: A New Chronosequence in the Chocó Tested With the Recovery of Tree Attributes." *Ecosphere* 16, no. 2: 70157. https://doi.org/10.1002/ecs2.70157.

Foster, D., F. Swanson, J. Aber, et al. 2003. "The Importance of Land-Use Legacies to Ecology and Conservation." *Bioscience* 53, no. 1: 77–88. https://doi.org/10.1641/0006-3568(2003)053%255B0077:TIOLUL%255D2.0.CO;2.

Fox, J., and S. Weisberg. 2018. *An R Companion to Applied Regression*. SAGE Publications.

Frouz, J. 2018. "Effects of Soil Macro- and Mesofauna on Litter Decomposition and Soil Organic Matter Stabilization." *Geoderma* 332: 161–172. https://doi.org/10.1016/j.geoderma.2017.08.039.

García-Palacios, P., F. T. Maestre, J. Kattge, and D. H. Wall. 2013. "Climate and Litter Quality Differently Modulate the Effects of Soil Fauna on Litter Decomposition Across Biomes." *Ecology Letters* 16, no. 8: 1045–1053. https://doi.org/10.1111/ele.12137.

Gessner, M. O., C. M. Swan, C. K. Dang, et al. 2010. “Diversity Meets Decomposition.” *Trends in Ecology & Evolution* 25, no. 6: 372–380. https://doi.org/10.1016/j.tree.2010.01.010.

Gill, A. L., J. Schilling, and S. E. Hobbie. 2021. “Experimental Nitrogen Fertilisation Globally Accelerates, Then Slows Decomposition of Leaf Litter.” *Ecology Letters* 24, no. 4: 802–811. https://doi.org/10.1111/ele.13700.

Granados, A., J. F. Brodie, H. Bernard, and M. J. O'Brien. 2017. “Defaunation and Habitat Disturbance Interact Synergistically to Alter Seedling Recruitment.” *Ecological Applications* 27, no. 7: 2092–2101. https://doi.org/10.1002/eap.1592.

Grella, N., K. Pedersen, N. Blüthgen, et al. 2025. “Vertebrate Diversity and Biomass Along a Recovery Gradient in a Lowland Tropical Forest.” *Biotropica* 57, no. 1: e13417. https://doi.org/10.1111/btp.13417.

Guariguata, M. R., and R. Ostertag. 2001. “Neotropical Secondary Forest Succession: Changes in Structural and Functional Characteristics.” *Forest Ecology and Management* 148, no. 1: 185–206. https://doi.org/10.1016/S0378-1127(00)00535-1.

Hartig, F. 2016. “DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models.” CRAN: Contributed Packages. https://doi.org/10.32614/cran.package.dharma.

Heinrich, V. H. A., R. Dalagnol, H. L. G. Cassol, et al. 2021. “Large Carbon Sink Potential of Secondary Forests in the Brazilian Amazon to Mitigate Climate Change.” *Nature Communications* 12, no. 1: 1785. https://doi.org/10.1038/s41467-021-22050-1.

Hu, A., J. Angerer, Y. Duan, et al. 2020. “Effects of Terrain on Litter Decomposition and Nutrient Release in Typical Steppe of Eastern Gansu Loess Plateau.” *Rangeland Ecology & Management* 73, no. 5: 611–618. https://doi.org/10.1016/j.rama.2020.06.004.

Kallenbach, C. M., and A. Stuart Grandy. 2015. “Land-Use Legacies Regulate Decomposition Dynamics Following Bioenergy Crop Conversion.” *GCB Bioenergy* 7, no. 6: 1232–1244. https://doi.org/10.1111/gcbb.12218.

Keiluweit, M., P. S. Nico, M. Kleber, and S. Fendorf. 2016. “Are Oxygen Limitations under Recognized Regulators of Organic Carbon Turnover in Upland Soils?” *Biogeochemistry* 127, no. 2: 157–171. https://doi.org/10.1007/s10533-015-0180-6.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. “lmerTest Package: Tests in Linear Mixed Effects Models.” *Journal of Statistical Software* 82: 1–26. https://doi.org/10.18637/jss.v082.i13.

Laigle, I., M. Moretti, L. Rousseau, et al. 2021. “Direct and Indirect Effects of Forest Anthropogenic Disturbance on Above and Below Ground Communities and Litter Decomposition.” *Ecosystems* 24, no. 7: 1716–1737. https://doi.org/10.1007/s10021-021-00613-z.

Laird-Hopkins, B. C., L. M. Bréchet, B. C. Trujillo, and E. J. Sayer. 2017. “Tree Functional Diversity Affects Litter Decomposition and Arthropod Community Composition in a Tropical Forest.” *Biotropica* 49, no. 6: 903–911. https://doi.org/10.1111/btp.12477.

Latterini, F., M. K. Dyderski, P. Horodecki, et al. 2023. “The Effects of Forest Operations and Silvicultural Treatments on Litter Decomposition Rate: A Meta-Analysis.” *Current Forestry Reports* 9, no. 4: 276–290. https://doi.org/10.1007/s40725-023-00190-5.

Liu, Q., S. L. Peng, H. Bi, et al. 2005. “Decomposition of Leaf Litter in Tropical and Subtropical Forests of Southern China.” *Journal of Tropical Forest Science* 17, no. 4: 543–556.

Lohbeck, M., L. Poorter, M. Martinez-Ramos, and F. Bongers. 2015. “Biomass Is the Main Driver of Changes in Ecosystem Process Rates During Tropical Forest Succession.” *Ecology* 96, no. 5: 1242–1252. https://doi.org/10.1890/14-0472.1.

Long, J., M. Zhang, J. Li, H. Liao, and X. Wang. 2021. “Soil Macro- and Mesofauna-Mediated Litter Decomposition in a Subtropical Karst Forest.” *Biotropica* 53, no. 6: 1465–1474. https://doi.org/10.1111/btp.12980.

Lorenzo, L., N. Pérez-Harguindeguy, F. Casanoves, and A. A. de Oliveira. 2014. “Recovering From Forest-To-Pasture Conversion: Leaf Decomposition in Central Amazonia, Brazil.” *Journal of Tropical Ecology* 30, no. 1: 93–96. https://doi.org/10.1017/S0266467413000771.

Luizão, F. J., R. C. C. Luizão, and J. Proctor. 2007. “Soil Acidity and Nutrient Deficiency in Central Amazonian Heath Forest Soils.” *Plant Ecology* 192, no. 2: 209–224. https://doi.org/10.1007/s11258-007-9317-6.

Ma, S., S. Chen, Y. Ding, et al. 2024. “What Controls Forest Litter Decomposition? A Coordinated Distributed Teabag Experiment Across Ten Mountains.” *Ecography* n/a: e07339. https://doi.org/10.1111/ecog.07339.

Makkonen, M., M. P. Berg, I. T. Handa, et al. 2012. “Highly Consistent Effects of Plant Litter Identity and Functional Traits on Decomposition Across a Latitudinal Gradient.” *Ecology Letters* 15, no. 9: 1033–1041. https://doi.org/10.1111/j.1461-0248.2012.01826.x.

Manzoni, S., S. M. Schaeffer, G. Katul, A. Porporato, and J. P. Schimel. 2014. “A Theoretical Analysis of Microbial Eco-Physiological and Diffusion Limitations to Carbon Cycling in Drying Soils.” *Soil Biology and Biochemistry* 73: 69–83. https://doi.org/10.1016/j.soilbio.2014.02.008.

Matricardi, E. A. T., D. L. Skole, O. B. Costa, M. A. Pedlowski, J. H. Samek, and E. P. Miguel. 2020. “Long-Term Forest Degradation Surpasses Deforestation in the Brazilian Amazon.” *Science* 369, no. 6509: 1378–1382. https://doi.org/10.1126/SCIENCE.ABB3021.

Meir, P., D. B. Metcalfe, A. C. L. Costa, and R. A. Fisher. 2008. “The Fate of Assimilated Carbon During Drought: Impacts on Respiration in Amazon Rainforests.” *Philosophical Transactions of the Royal Society, B: Biological Sciences* 363, no. 1498: 1849–1855. https://doi.org/10.1098/rstb.2007.0021.

Morffi-Mestre, H., G. Ángeles-Pérez, J. S. Powers, et al. 2023. “Leaf Litter Decomposition Rates: Influence of Successional Age, Topography and Microenvironment on Six Dominant Tree Species in a Tropical Dry Forest.” *Frontiers in Forests and Global Change* 6: 1082233. https://doi.org/10.3389/ffgc.2023.1082233.

Moyano, F. E., S. Manzoni, and C. Chenu. 2013. “Responses of Soil Heterotrophic Respiration to Moisture Availability: An Exploration of Processes and Models.” *Soil Biology and Biochemistry* 59: 72–85. https://doi.org/10.1016/j.soilbio.2013.01.002.

Ngo Bieng, M. A., M. Souza Oliveira, J. Roda, et al. 2021. “Relevance of Secondary Tropical Forest for Landscape Restoration.” *Forest Ecology and Management* 493: 119265. https://doi.org/10.1016/j.foreco.2021.119265.

Ostertag, R., C. Restrepo, J. W. Dalling, et al. 2022. “Litter Decomposition Rates Across Tropical Montane and Lowland Forests Are Controlled Foremost by Climate.” *Biotropica* 54, no. 2: 309–326. https://doi.org/10.1111/btp.13044.

Paudel, E., G. G. O. Dossa, M. De BleCourt, P. Beckschafer, J. Xu, and R. D. Harrison. 2015. “Quantifying the Factors Affecting Leaf Litter Decomposition Across a Tropical Forest Disturbance Gradient.” *Ecosphere* 6, no. 12: 1–20. https://doi.org/10.1890/ES15-00112.1.

Pausas, J. G., and W. J. Bond. 2020. “On the Three Major Recycling Pathways in Terrestrial Ecosystems.” *Trends in Ecology & Evolution* 35, no. 9: 767–775. https://doi.org/10.1016/j.tree.2020.04.004.

Poorter, L., F. Bongers, T. M. Aide, et al. 2016. “Biomass Resilience of Neotropical Secondary Forests.” *Nature* 530, no. 7589: 211–214. https://doi.org/10.1038/nature16512.

Powers, J. S., R. A. Montgomery, E. C. Adair, et al. 2009. “Decomposition in Tropical Forests: A Pan-Tropical Study of the Effects of Litter Type, Litter Placement and Mesofaunal Exclusion Across a Precipitation Gradient.” *Journal of Ecology* 97, no. 4: 801–811. https://doi.org/10.1111/j.1365-2745.2009.01515.x.

R Core Team. 2023. "R: A Language and Environment for Statistical Computing." R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Röder, J., T. Appelhans, M. K. Peters, T. Nauss, and R. Brandl. 2024. "Disturbance Can Slow Down Litter Decomposition, Depending on Severity of Disturbance and Season: An Example From Mount Kilimanjaro." *Web Ecology* 24, no. 1: 11–33. https://doi.org/10.5194/we-24-11-2024.

Rodríguez, W., J. C. Suárez, and F. Casanoves. 2023. "Total Litterfall and Leaf-Litter Decomposition of *Theobroma grandiflorum* Under Different Agroforestry Systems in the Western Colombian Amazon." *Agroforestry Systems* 97, no. 8: 1541–1556. https://doi.org/10.1007/s10457-023-00876-6.

Rousk, J., E. Bååth, P. C. Brookes, et al. 2010. "Soil Bacterial and Fungal Communities Across a pH Gradient in an Arable Soil." *ISME Journal* 4, no. 10: 1340–1351. https://doi.org/10.1038/ismej.2010.58.

Sagarin, R., and A. Pauchard. 2010. "Observational Approaches in Ecology Open New Ground in a Changing World." *Frontiers in Ecology and the Environment* 8, no. 7: 379–386. https://doi.org/10.1890/090001.

Salinas, N., Y. Malhi, P. Meir, et al. 2011. "The Sensitivity of Tropical Leaf Litter Decomposition to Temperature: Results From a Large-Scale Leaf Translocation Experiment Along an Elevation Gradient in Peruvian Forests." *New Phytologist* 189, no. 4: 967–977. https://doi.org/10.1111/j.1469-8137.2010.03521.x.

Sánchez-Silva, S., B. H. J. De Jong, D. R. Aryal, E. Huerta-Lwanga, and J. Mendoza-Vega. 2018. "Trends in Leaf Traits, Litter Dynamics and Associated Nutrient Cycling Along a Secondary Successional Chronosequence of Semi-Evergreen Tropical Forest in South-Eastern Mexico." *Journal of Tropical Ecology* 34, no. 6: 364–377. https://doi.org/10.1017/S0266467418000366.

Sari, R. R., D. M. A. Rozendaal, D. D. Saputra, K. Hairiah, J. M. Roshetko, and M. van Noordwijk. 2022. "Balancing Litterfall and Decomposition in Cacao Agroforestry Systems." *Plant and Soil* 473, no. 1: 251–271. https://doi.org/10.1007/s11104-021-05279-z.

Sayer, E. J., E. V. J. Tanner, and A. L. Lacey. 2006. "Effects of Litter Manipulation on Early-Stage Decomposition and Meso-Arthropod Abundance in a Tropical Moist Forest." *Forest Ecology and Management* 229, no. 1: 285–293. https://doi.org/10.1016/j.foreco.2006.04.007.

Schaap, K. J., L. Fuchslueger, F. Hofhansl, O. Valverde-Barrantes, C. A. Quesada, and M. R. Hoosbeek. 2024. "Intra-Annual Dynamics of Soil and Microbial C, N, and P Pools in a Central Amazon Terra Firme Forest." *Journal of Plant Nutrition and Soil Science* 187, no. 6: 725–736. https://doi.org/10.1002/jpln.202300107.

Schilling, E. M., B. G. Waring, J. S. Schilling, and J. S. Powers. 2016. "Forest Composition Modifies Litter Dynamics and Decomposition in Regenerating Tropical Dry Forest." *Oecologia* 182, no. 1: 287–297. https://doi.org/10.1007/s00442-016-3662-x.

Sellan, G., J. Thompson, N. Majalap, R. Robert, and F. Q. Brearley. 2020. "Impact of Soil Nitrogen Availability and pH on Tropical Heath Forest Organic Matter Decomposition and Decomposer Activity." *Pedobiologia* 80: 150645. https://doi.org/10.1016/j.pedobi.2020.150645.

Shi, L., G. G. O. Dossa, E. Paudel, H. Zang, J. Xu, and R. D. Harrison. 2019. "Changes in Fungal Communities Across a Forest Disturbance Gradient." *Applied and Environmental Microbiology* 85, no. 12: e00080. https://doi.org/10.1128/AEM.00080-19.

Skopp, J., M. D. Jawson, and J. W. Doran. 1990. "Steady-State Aerobic Microbial Activity as a Function of Soil Water Content." *Soil Science Society of America Journal* 54, no. 6: 1619–1625. https://doi.org/10.2136/sssaj1990.03615995005400060018x.

Sniegocki, R., J. Moon, A. Rutrough, et al. 2022. "Recovery of Soil Microbial Diversity and Functions Along a Tropical Montane Forest Disturbance Gradient." *Frontiers in Environmental Science* 10: 853686. https://doi.org/10.3389/fenvs.2022.853686.

Souza, R. C., M. E. Cantão, A. T. R. Vasconcelos, M. A. Nogueira, and M. Hungria. 2013. "Soil Metagenomics Reveals Differences Under Conventional and No-Tillage With Crop Rotation or Succession." *Applied Soil Ecology* 72: 49–61. https://doi.org/10.1016/j.apsoil.2013.05.021.

Stone, M. J., L. Shoo, N. E. Stork, F. Sheldon, and C. P. Catterall. 2020. "Recovery of Decomposition Rates and Decomposer Invertebrates During Rain Forest Restoration on Disused Pasture." *Biotropica* 52, no. 2: 230–241. https://doi.org/10.1111/btp.12682.

Thom, D., and W. S. Keeton. 2020. "Disturbance-Based Silviculture for Habitat Diversification: Effects on Forest Structure, Dynamics, and Carbon Storage." *Forest Ecology and Management* 469: 118132. https://doi.org/10.1016/j.foreco.2020.118132.

Toro, L., L. K. Werden, S. D. Addo-Danso, et al. 2025. "Integrating Belowground Recovery Into Tropical Forest Restoration Design and Monitoring." *Bioscience* 75, no. 11: 937–952. https://doi.org/10.1093/biosci/biaf097.

Trevathan-Tackett, S. M., S. Kepfer-Rojas, M. Malerba, et al. 2024. "Climate Effects on Belowground Tea Litter Decomposition Depend on Ecosystem and Organic Matter Types in Global Wetlands." *Environmental Science & Technology* 58, no. 49: 21589–21603. https://doi.org/10.1021/acs.est.4c02116.

Tuo, B., P. García-Palacios, C. Guo, E.-R. Yan, M. P. Berg, and J. H. C. Cornelissen. 2024. "Meta-Analysis Reveals That Vertebrates Enhance Plant Litter Decomposition at the Global Scale." *Nature Ecology & Evolution* 8, no. 3: 411–422. https://doi.org/10.1038/s41559-023-02292-6.

van der Sande, M. T., J. S. Powers, T. W. Kuyper, et al. 2022. "Soil Resistance and Recovery During Neotropical Forest Succession." *Philosophical Transactions of the Royal Society, B: Biological Sciences* 378, no. 1867: 20210074. https://doi.org/10.1098/rstb.2021.0074.

Vogt, W. P., and R. B. Johnson. 2016. *The SAGE Dictionary of Statistics & Methodology: A Nontechnical Guide for the Social Sciences*. SAGE Publications, Inc. https://doi.org/10.4135/9781071909751.

Wallace, K. J., D. C. Laughlin, B. D. Clarkson, and L. A. Schipper. 2018. "Forest Canopy Restoration Has Indirect Effects on Litter Decomposition and no Effect on Denitrification." *Ecosphere* 9, no. 12: e02534. https://doi.org/10.1002/ecs2.2534.

Wieder, W. R., C. C. Cleveland, and A. R. Townsend. 2009. "Controls Over Leaf Litter Decomposition in Wet Tropical Forests." *Ecology* 90, no. 12: 3333–3341. https://doi.org/10.1890/08-2294.1.

Wild, J., M. Kopecký, M. Macek, M. Šanda, J. Jankovec, and T. Haase. 2019. "Climate at Ecologically Relevant Scales: A New Temperature and Soil Moisture Logger for Long-Term Microclimate Measurement." *Agricultural and Forest Meteorology* 268: 40–47. https://doi.org/10.1016/j.agrformet.2018.12.018.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** Supporting Information.