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RESEARCH ARTICLE

Simulated elephant foraging alters tree root exudation rates: Species-specific responses and implications for belowground carbon dynamics in tropical forests

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Societal Impact Statement

Asian elephants play crucial roles in ecosystem functioning, and their interactions with plants influence above- and belowground carbon cycling. We tested whether their mechanically destructive foraging triggers short-term, stress-induced shifts in tree root exudation, an underappreciated pathway linking herbivory to belowground carbon processes. We found that elephant herbivory can increase root exudation (i.e., carbon release to soils), which shapes soil microbial activity and nutrient cycling. Recognizing this pathway clarifies elephants' indirect role in belowground carbon dynamics and strengthens the case for conserving ecologically functional populations to support resilient soils and ecosystems, with practical relevance for restoration and nature-based climate solutions.

Summary

- Asian elephants (*Elephas maximus*) have uniquely destructive foraging habits, damaging large numbers of saplings of fast-growing, early-successional trees. We hypothesized that elephant foraging might increase root carbon exudation rates as a stress response, potentially altering belowground carbon dynamics in tropical forests. We aimed to evaluate (1) how varying herbivory intensities affect root exudation rates; (2) how these effects vary among tree species and over time; and (3) how root exudation rates correlate with root traits and soil properties.
- We simulated elephant herbivory on saplings of three early-successional tree species commonly consumed by elephants, applying three levels of damage: control (no damage), mild (10% aboveground biomass removal), and severe (50% removal). We then quantified root exudation rates in situ at 24, 48, 72, and 96 h post-damage.
- The three tree species differed in their basal root exudation rates and displayed species-specific responses to herbivory. *Macaranga indica* doubled its exudation rate after mild damage but showed no response to severe herbivory; *Ficus hispida*

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exhibited elevated exudation rates following severe herbivory but not after mild herbivory; and *Bauhinia variegata* did not respond to either level. Exudation rates also correlated with root traits and soil properties, supporting a traits–environment–disturbance framework.

- We identified a previously underappreciated pathway by which large browsing herbivores—particularly elephants—influence belowground biogeochemical processes and soil organic carbon pools in tropical forests through short-term, species-specific shifts in root carbon exudation. These findings have implications for conservation, restoration, and nature-based solutions—via elephant-compatible forest mosaics, targeted species screening, and soil-function monitoring.

KEYWORDS
belowground, ecological impacts, elephants, herbivory, nature-based solutions, root exudates, soil carbon, tropical Asia

1 | INTRODUCTION

Large animals play critical roles in ecosystems, supporting biodiversity and ecosystem services essential for human well-being, yet defaunation threatens these functions worldwide (Dirzo et al., 2014; Galetti & Dirzo, 2013). Elephants, in particular, influence ecosystems through their foraging and movements, consuming large amounts of plant biomass and dispersing seeds and nutrients over long distances (Asner et al., 2016; Campos-Arceiz & Blake, 2011; Owen-Smith, 2013). These activities can enhance aboveground carbon storage by promoting slow-growing, high wood density species and altering forest structure (Berzaghi et al., 2023). Additionally, elephants influence belowground carbon and nutrient cycling through defecation, carcass decomposition, and woody biomass input (Bartel et al., 2024; Sandhage-Hofmann et al., 2021; Stephenson et al., 2024). Despite these effects, an indirect pathway—root exudation—remains unexplored. This process links plant metabolism to microbial processes and carbon storage, with important implications for soil carbon cycling, ecosystem resilience, and climate regulation (Bardgett & Wardle, 2010).

Root exudates are primary and secondary metabolites released by plants constitutively or in response to stressors, including herbivory (Badri & Vivanco, 2009; Karst et al., 2017; Vives-Peris et al., 2020). Through exudates, plants transfer 11%–40% of the net carbon fixed by photosynthesis into the soil (Lynch & Whipps, 1990; Zhalnina et al., 2018). This transfer can occur relatively quickly, ranging from a few hours in grasses to 4–5 days in trees (Kaiser et al., 2015; Kuzyakov & Gavrichkova, 2010). Exudates contribute more to soil organic carbon (SOC) formation than aboveground inputs (Broadbent & Nakashima, 1974; Rasse et al., 2005), providing labile substrates that microbial communities rapidly assimilate. This enhances nutrient uptake and benefits plant health and growth (Finzi et al., 2015; Hamilton & Frank, 2001; Oburger & Jones, 2018; Meier et al., 2020). However, the fate of exudates does not always lead to increased soil carbon stocks. While exudates can promote SOC formation by facilitating microbial assimilation, turnover, and binding with minerals to form persistent organo-mineral associations (Chari & Taylor, 2022; Shabtai et al., 2024), they can also stimulate SOC loss by accelerating the decomposition of existing organic carbon (Cotrufo & Lavallee, 2022).

Even small changes in root exudation rates can significantly influence microbial composition, abundance, and activity, thereby impacting nutrient cycling (Finzi et al., 2015; Li et al., 2025; Ma et al., 2022). Herbivory, as a disturbance factor, may serve as a potential driver of these changes. However, the relationship between herbivory and root exudation is complex and not yet well understood, with studies reporting varying responses (Hamilton et al., 2008; Kristensen et al., 2022). Current knowledge is largely based on grasslands, grazing herbivores, or laboratory assays, which have limited applicability to other ecosystems (Guitian & Bardgett, 2000; Hamilton et al., 2008; Wilson et al., 2018). Furthermore, root exudation responses to stressors, including herbivory, are influenced by root traits and local conditions. For example, root exudation rates may increase with root diameter and in nitrogen-poor soils but decrease with root tissue density (Meier et al., 2020; Sun et al., 2021; Williams et al., 2022). Exudation response to herbivory can be immediate or emerge over the next 1–4 days (Bazot et al., 2005; Hamilton et al., 2008; Paterson et al., 2005). Root exudates are primarily involved in nutrient acquisition and microbial signaling, but in response to herbivory, they may also function as a stress-related response. This stress-induced shift in exudation patterns can trigger changes in microbial communities, promoting nutrient mobilization to support plant recovery from herbivory.

Asian elephants (*Elephas maximus*) have a strong feeding preference for saplings of fast-growing, early-successional tree species (English et al., 2014), causing severe damage to large numbers of saplings (Ong et al., 2023). Despite this, many saplings resprout and recover (Terborgh et al., 2024). Based on these observations, we hypothesized that elephant foraging damage might increase root carbon exudation rates as a mechanism to enhance nutrient acquisition in saplings of tropical forest trees, potentially impacting belowground

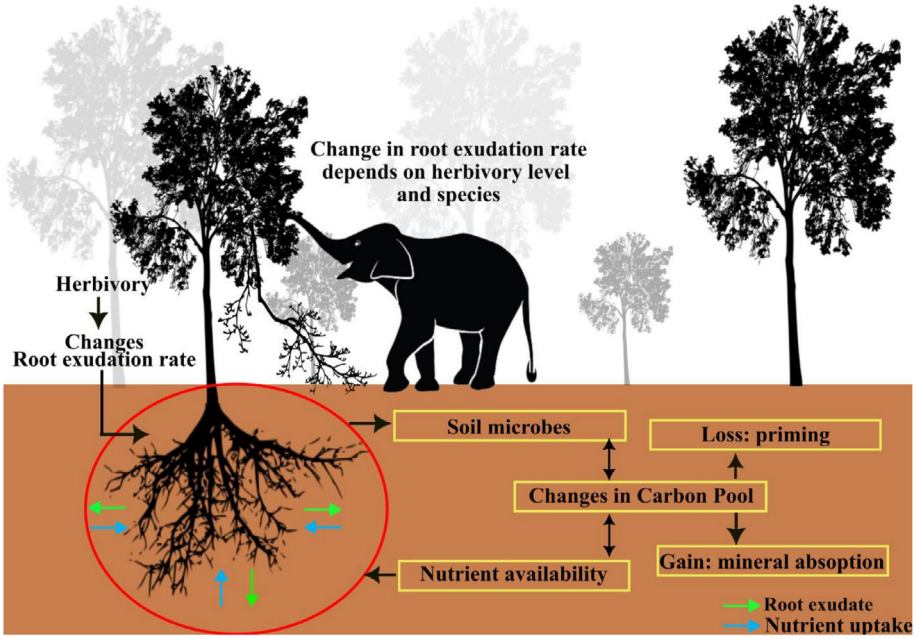


FIGURE 1 Conceptual model of the effects of elephant herbivory on root exudation and soil-carbon dynamics in tropical forests. Elephant-induced herbivory (e.g., branch breaking) alters plant resource allocation, leading to changes in root exudation rates. The magnitude and direction of this change depend on the intensity of herbivory and plant species. Altered root carbon exudation rate influences microbial activity and subsequently affects the soil carbon pool (herbivory → exudation → microbe → SOC pathway).

carbon dynamics. To test this, we evaluated whether (1) varying intensities of elephant-induced damage affect root exudation rates in saplings; (2) the effects of herbivory vary among tree species and over time, with species-specific responses shaped by root traits and growth strategies; and (3) root exudation rates correlate with root traits and soil properties.

We predicted that more severe foraging damage would lead to higher exudation rates as a mechanism to recruit beneficial microbes and enhance nutrient acquisition for regrowth (see Figure 1 for a conceptual model). Moreover, we expected variations in root exudation to be linked to species-specific root traits (e.g., root length (RL), surface area, root diameter, and branching intensity (BI)), with acquisitive traits (such as greater surface area and finer roots) promoting higher exudation rates. Conversely, species with more structural root investments (e.g., high tissue density) were expected to show weaker or negative correlations with exudation. Regarding soil properties, we hypothesized that lower nutrient availability (e.g., reduced SOC, dissolved organic carbon (DOC), or nitrogen) would promote higher exudation rates, as plants would increase belowground carbon allocation to enhance nutrient mobilization. In nutrient-rich soils, we expected exudation rates to be lower due to the reduced need for high carbon allocation (Jiang et al., 2023; Meier et al., 2020; Sun et al., 2021; Zhang et al., 2024).

To test these predictions, we conducted a manipulative experiment in a botanical garden in tropical China. Saplings of three early-successional tree species commonly consumed by elephants—*Bauhinia variegata*, *Ficus hispida*, and *Macaranga indica*—were subjected to three levels of simulated elephant herbivory intensity: control (no damage), mild (10% aboveground biomass removal), and severe (50% biomass removal). We recorded root exudation rates at 24-h intervals over a 4-day period and collected data on root morphological traits and soil properties. Our experimental design included five replicates per combination of herbivory treatment and species, totaling 45 saplings.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted at the Xishuangbanna Tropical Botanical Garden (XTBG; 21°55′N, 101°16′E; 568 m elevation) in Xishuangbanna, Yunnan, Southwest China. Xishuangbanna lies at the transition between tropical Southeast Asia and subtropical East Asia, characterized by a rich tropical flora and tropical seasonal rainforest as the predominant natural vegetation in the lowlands (Zhu, 2006). The region experiences a typical monsoon climate, with approximately 80% of the rainfall occurring during the rainy season (May–October). The dry season is divided into a cool dry period (November–February) and a hot dry period (March–April). XTBG has a mean annual temperature of 21.7°C and a mean annual precipitation of 1560 mm. Soils are typically clay loam, with a depth of about 2 m, containing 42% sand, 34% silt, and 24% clay (Yang et al., 2020).

2.2 | Focal tree species

The saplings of early successional trees are Asian elephants' preferred food in disturbed and secondary forests (Ong et al., 2023). Hence, for this experiment we selected 15 saplings for each of three early successional tree species known to be consumed by elephants in the region (Liu et al., 2016): *M. indica* (2.1–5.3 dbh), *F. hispida* (2.6–5.6 dbh), and *B. variegata* (2.0–4.6 dbh). Based on the garden layout, we haphazardly selected three replicate plots per tree species, with each individual at least 2 m apart. Although individuals of each species were grouped within separate plots rather than interspersed, which may have introduced plot-level effects, treatments were applied consistently across species.

We simulated elephant herbivory by manually breaking branches with a pole pruner and our hands. For each sapling, we first counted the number of branches and leaves (counting leaves was not feasible for *B. variegata* due to its numerous small leaves). Based on these counts, we removed approximately 10% and 50% of aboveground biomass to represent mild and severe herbivory, respectively. To more closely replicate elephant feeding behavior, we also pulled the plants to mimic the mechanical damage typical of elephant foraging. Each sapling was subjected to one of three herbivory treatments: i.e., control (no intervention), mild herbivory (10% biomass removal), and severe herbivory (50% biomass removal), with five replicates per treatment per species (see Method S1 for more details).

2.3 | Root exudate collection and calculation

We collected root exudates using a culture-based cuvette system modified from Phillips et al. (2008; following Sun et al., 2021). First, we carefully excavated two to three fine roots (length 15–20 cm, ≤2 mm in diameter) from the upper 5–10 cm of undisturbed soil around the target trees. The roots were traced back to the parent trees to assure the roots belonged to the target individuals (Guo et al., 2008). For each individual tree, two intact fine root systems were selected for sampling. Roots were washed gently with C-free nutrient solution (0.1 mM KH_2PO_4, 0.2 mM K_2SO_4, 0.2 mM $MgSO_4$, and 0.3 mM $CaCl_2$) and were inserted into a 60-mL transparent syringe, which was filled with 1-mm diameter sterile glass beads. The syringe was then injected with 20-mL nutrient solution. The cuvette containing the intact root system was then sealed with parafilm and covered with moist Kimwipes (Kimberly-Clark Corp., Roswell, New Mexico, USA) and aluminum foil to prevent the exposed portion of the root from drying out and to protect from sunlight. The cuvette system was then returned to the soil and covered with litter to allow the root system to equilibrate with the cuvette environment for 24 h.

After the 24 h equilibration period, the solution in the cuvettes was discarded, and the cuvettes containing roots were rinsed five times with 10 mL of fresh nutrient solution to remove any residual carbon. We then added 20 mL of fresh nutrient solution, reburied the cuvette, and immediately applied the herbivory treatment. Root exudates were subsequently collected at 24-h intervals for 4 days (24, 48, 72, and 96 h; Phillips et al., 2008, Jiang et al., 2023). At each sampling, the solution in the cuvette was recovered, and the cuvette was flushed twice with 10 mL of fresh nutrient solution to ensure complete recovery of the exudates. The recovered solutions were filtered immediately using 0.22-μm Minisart syringe filters, transferred to carbon-free glass vials, and transported to the laboratory in a cool box. The samples were stored at 4°C until analysis. Three cuvettes with no root system were prepared as a control in each plot.

The collected exudate samples were analyzed for total carbon using a TOC analyzer (Vario TOC cube, detection limit of 0–60,000 mg L^{-1} and measurement deviations of ≤1% for C concentrations >5 mg L^{-1}; Elementar Analysensysteme, Germany). Root exudate flux rates were calculated as the amount of carbon released over the 24-h incubation period (after subtracting the carbon detected in root-free control cuvettes) and normalized by root biomass (mg C g^{-1} root biomass day^{-1}).

2.4 | Root sampling, processing, and assessment of morphological and architectural traits

After exudate sampling, the fine roots in the cuvette system were harvested to measure root morphological traits. Roots were transported to the laboratory on ice packs and stored at 4°C. The roots were scanned using an EPSON Perfection V800 scanner at a resolution of 1200 dpi and analyzed using WINRHIZO PRO 2015 software (Regents Instruments Canada Inc.) to measure average diameter (D), total RL, total root area (RA), root volume (RV), and tip number (TN). Roots were then oven-dried to constant weights at 65°C and weighed. Specific root length or area (SRL/SRA) was calculated by dividing total RL or area by root dry weight. Root tissue density (RTD) was calculated by dividing root dry weight by volume. BI was calculated by dividing root tip number by RL.

2.5 | Soil sampling

Rhizosphere soil was collected from each target tree within a 1-m radius of the trunk by gently excavating fine roots and collecting the soil that remained attached after lightly shaking. The collected soil was divided into two parts: (1) air-dried samples to measure soil physical and chemical properties and (2) fresh soil stored at 4°C for microbial biomass carbon (MBC) and DOC analysis.

Soil moisture (SM) content was determined by overnight drying at 105°C (Gardner, 1986). Soil pH was measured in a 1:2.5 soil-to-water suspension with a digital pH meter (Mettler-Toledo GmbH, Switzerland). SOC was determined by acid dichromate wet oxidation (Nelson & Sommers, 1982). MBC was measured by a fumigation-extraction method (Vance et al., 1987). Mineral-associated organic carbon (MAOC) and particulate organic carbon (POC) were measured using a modified version of the approach outlined by Cambardella and Elliott (1992). Specifically, 30 mL of sodium hexametaphosphate $(NaPO_3)_6$ solution (5 g L^{-1}) was added to 10 g of soil sample and mixed for 18 h at 100 rpm. The soil suspension was sieved using a 53-μm sieve. Fractions recovered on the sieve (>53 μm) were classified as POC, while those collected through rinsing with deionized water (<53 μm) were classified as MAOC. Both fractions were oven-dried at 60°C for 48 h. DO and dissolved organic nitrogen (DON) were extracted by adding 0.5 M K_2SO_4 (1:5 m/v) to the soil sample and quantified using a TOC-2000 analyzer (Shimadzu, Japan; McGill et al., 1986). Permanganate oxidizable carbon (POXC) was quantified by oxidation with 330-mM $KMnO_4$ solution (Blair et al., 1995).

2.6 | Statistical analyses

All statistical analyses were conducted in R (4.4.2). We calculated the mean, standard deviation (SD), minimum, maximum, median, standard error, and coefficient of variation (CV) for root exudation rate by species and treatment (Table S1). To address non-normality in the data, we applied appropriate transformations (log, square root, or Box-Cox) where necessary before statistical analyses.

To assess the effects of herbivory, time, and species on root exudation rates, we used linear mixed-effects models fitted with *lmer* (*lme4* package), with individual plant and root nested as random effects. First, we analyzed the effect of species and time on root exudation rates under control conditions ($rer_c \sim species*time+[1|plant.id_c/root_c]$, only control data). Next, we evaluated the effects of herbivory, species, and time on root exudation rates (rer ~ species + treatment + time + species: treatment + species: time + treatment: time + [1|plant.id/root], full data). Then, we investigated the effects of herbivory and time on root exudation rates for each species separately ($rer_{sps} \sim treatment \times time + [1|plant.id_{sps}/root_{sps}]$) for analyzing species-specific responses. To assess the significance of the fixed effects (species, time, and their interaction), we performed ANOVA (Type II Wald chi-square tests) using the *Anova*() function from the *car* package. And further Tukey's HSD post hoc analyses were done for pairwise comparisons of the models using *emmeans* package.

We conducted nested ANOVA to examine differences in root morphological traits among species, while differences in soil properties between species were assessed using a two-way ANOVA. To explore pairwise differences among species, we performed Tukey's HSD post hoc analysis. Spearman correlations were used to determine the correlation between root traits and root exudation rates. We also used a linear mixed-effects model to investigate the effects of soil properties on root exudation rates with sampling dates as random effects and used Pearson correlations to examine their relationships.

To assess statistical power, we conducted a simulation-based power analysis using the *simr* package (Green et al., 2016). The analysis was based on the fitted linear mixed models and the observed variance structure of our data. Specifically, we simulated 1000 iterations at $\alpha = 0.05$ to estimate the power for key fixed effects, including the herbivory × time interaction, species × herbivory, and species × time interactions. For each effect, we report the power with 95% confidence intervals, helping to identify the effects that could be reliably detected given the sample size.

3 | RESULTS

3.1 | Herbivory impacts

In undamaged saplings, root exudation rates varied among species over time (species × incubation time interaction: $\chi^2 = 22.47$, df = 6, $p < 0.001$; Figures S1, S2, and Table S2). Pairwise comparisons revealed interspecific differences, with root exudation rates in *B. variegata* being approximately twice as high as in *F. hispida* and three times higher than in *M. indica* (1.98 ± 0.84, 1.26 ± 0.47, and 0.66 ± 0.39 mgC g^{-1} root biomass day^{-1}, respectively; Figures S1, S2, and Table S3).

For the herbivory treatments across all species, we detected a time-dependent effect of herbivory (herbivory × time: $\chi^2 = 19.22$, df = 6, $p = 0.003$), with high power (92%) for this interaction (simulation-based power analysis, 1000 simulations; $\alpha = 0.05$). In contrast, the species × herbivory ($\chi^2 = 8.14$, df = 4, $p = 0.08$) and species × time ($\chi^2 = 108.35$, df = 6, $p < 0.001$; Table S2) had moderate power (52% and 54%, respectively). The global herbivory main effect was underpowered (7%) as expected when effects are conditional on time and species (Table S2 for details). Given these power analyses, we interpret the herbivory effects cautiously, as some may not be robust enough for definitive conclusions.

3.2 | Species-specific responses

3.2.1 | Macaranga indica

In *M. indica*, the overall (omnibus) herbivory effects were not statistically distinguishable ($\chi^2 = 5.68$, df = 2, $p = 0.06$, Table S2), though the analysis had moderate power (54%; Table S2). At 24 h, moderate herbivory (10% biomass removal) resulted in a twofold increase in exudation rates, compared to control conditions (estimate = 0.36, df = 36, $p = 0.03$, Tables S3, S4). However, severe herbivory (50% removal) did not differ significantly from the control (estimate = −0.02, df = 36, $p = 0.9$). At later time periods (48–96 h), differences between moderate herbivory and control conditions disappeared (Figure 2). The herbivory × time interaction had moderate power (61%), indicating some temporal effects of herbivory.

3.2.2 | Ficus hispida

In *F. hispida*, there was a significant interaction between herbivory and time ($\chi^2 = 12.72$, df = 6, $p = 0.04$, Table S2), with moderate-to-good power (73%, Table S2). At 72 and 96 h, severe herbivory resulted in higher exudation rates compared to moderate herbivory (estimate = 0.35, df = 31, $p = 0.07$ and estimate = 0.37, df = 31, $p = 0.05$; Figure 2, Tables S3, S4). However, contrasts between severe and moderate herbivory were not consistently significant, and the overall herbivory effect was underpowered (43%), which limits our interpretation of the main effects.

3.2.3 | *Bauhinia variegata*

For *B. variegata*, root exudation rates varied with time ($\chi^2 = 26.83$, df = 3, $p < 0.001$; Figure 2), but there was no detectable effect of herbivory under our design (treatment $p = 0.70$; power 7.5%; treatment × time = 43%; Table S2). The low power and lack of significant effects suggest that herbivory did not affect root exudation in *B. variegata* under the current experimental conditions.

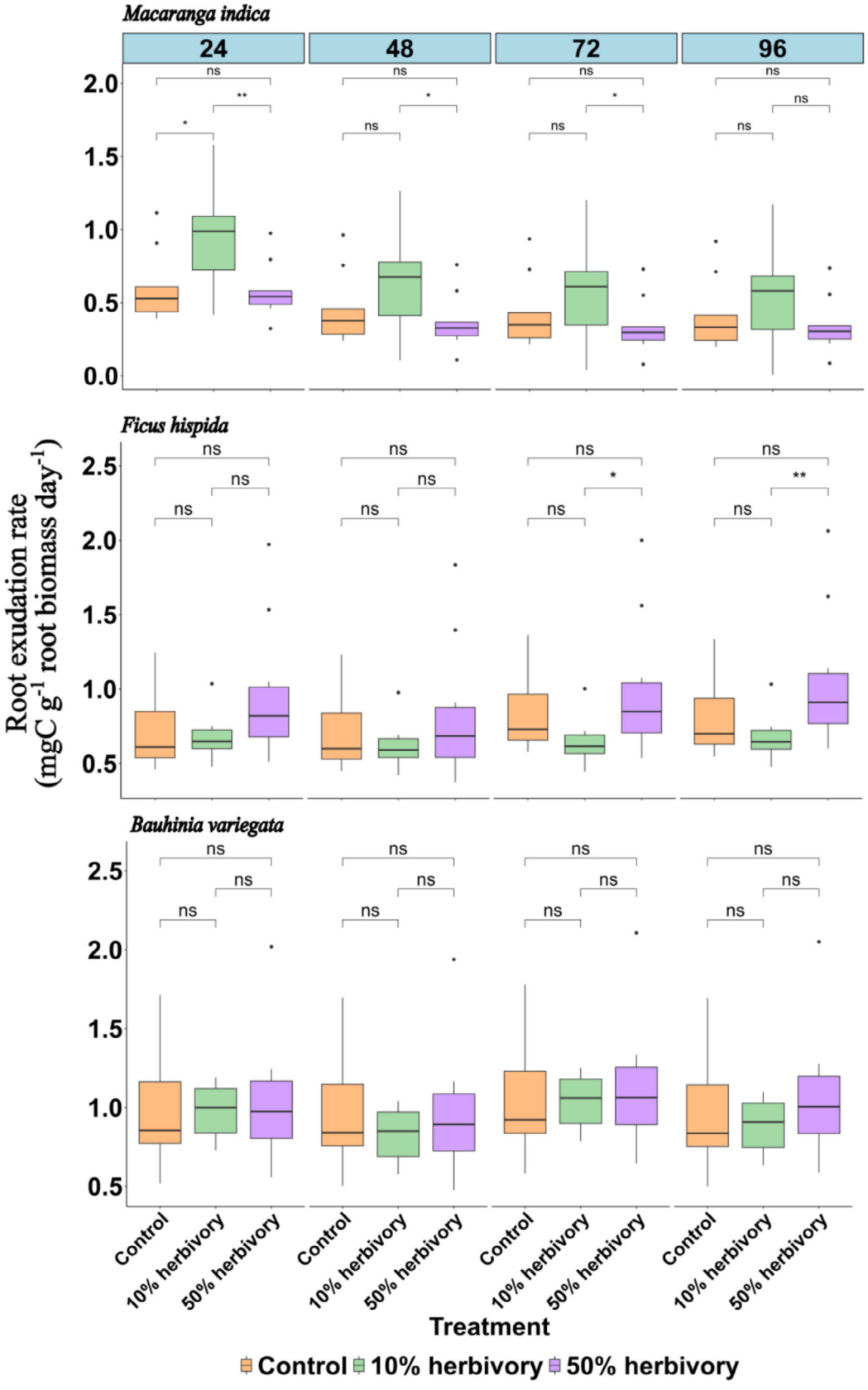


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FIGURE 2 Root exudation rates of saplings from three tree species (*Macaranga indica*, *Ficus hispida*, and *Bauhinia variegata*) were influenced by simulated elephant herbivory (three treatments: control, 10%, and 50% aboveground biomass removal) and incubation time (four treatments: 24, 48, 72, and 96 h post-disturbance); $n = 5$ saplings per species and herbivory treatment. Boxes represent the interquartile range (1st and 3rd quartiles), with horizontal black lines indicating median values. Dots represent extreme values. Statistical significance: ns = not significant; * = $p < 0.05$; ** = $p < 0.01$.

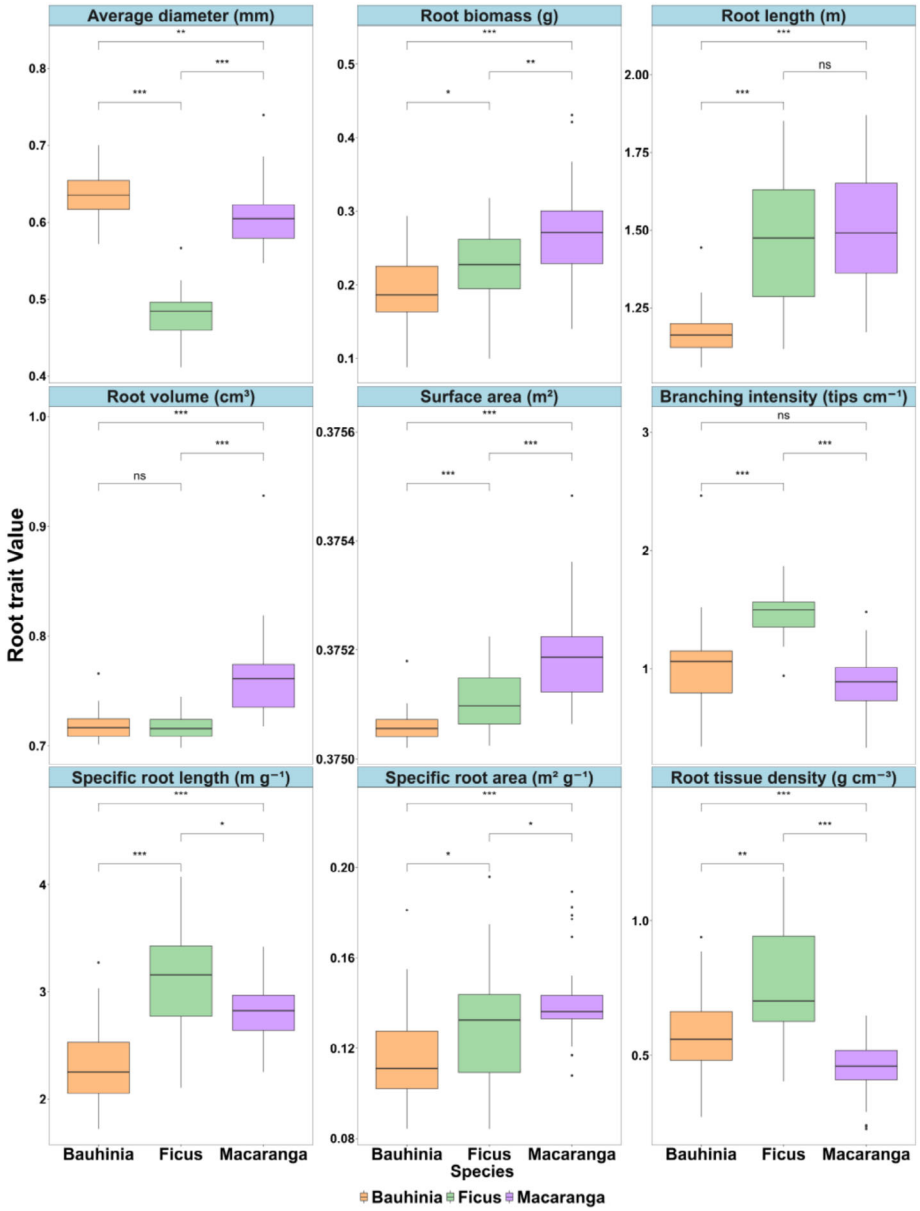


FIGURE 3 Interspecific variation in root traits of *M. indica*, *F.hispida*, and *B. variegata* ($n = 15$ saplings per species). Boxes represent the interquartile range (1st and 3rd quartiles), with horizontal black lines indicating median values. Dots represent extreme values. Note that the scale differs among panels. Statistical significance: ns = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

3.3 | Simulation-Based Power Analysis and Minimum Detectable Effect (MDE)

We conducted a simulation-based power analysis (Table S2, $\alpha = 0.05$, 1000 simulations, likelihood-ratio tests on fixed terms) to assess statistical power (Figures S3, S4). For species-specific herbivory effects, *Macaranga indica* had moderate power to detect effects, while *Ficus hispida* showed higher power for detecting interaction effects over time. For *B. variegata*, the sample size was insufficient to detect any herbivory-related changes in root exudation. Effect sizes with 95% confidence intervals for focal contrasts are reported in Table S2, providing clarity on the magnitude and uncertainty of our estimates.

3.4 | Root traits

Root morphological and architectural traits differed significantly among the three species (nested ANOVA, all $p < 0.001$; Figure 3, Table S5). For these analyses, we used all plant individuals, regardless

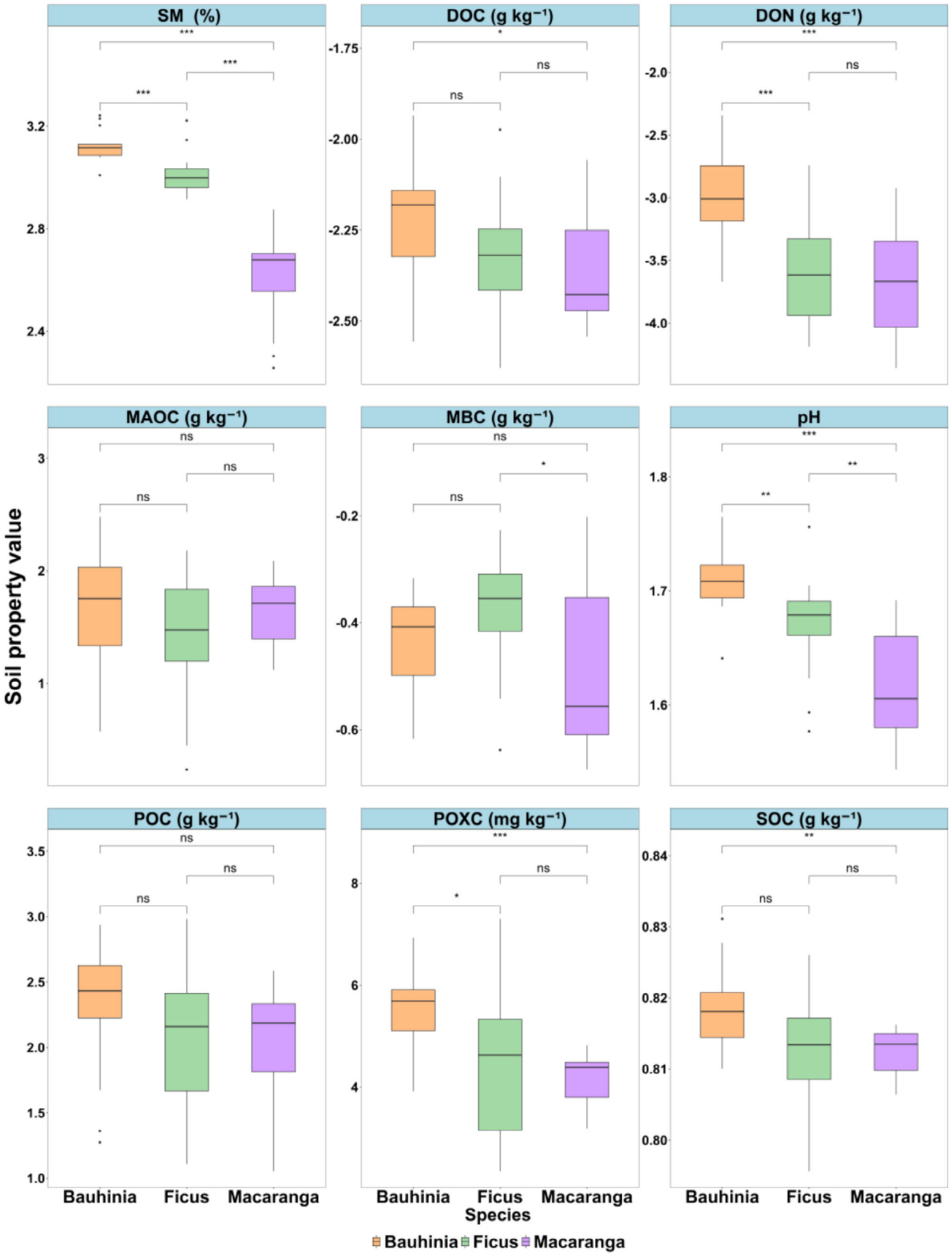


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FIGURE 4 Interspecific variation in soil properties of *M. indica*, *F. hispida*, and *B. variegata* ($n = 15$ soil samples per species). DOC = dissolved organic carbon, DON = dissolved organic nitrogen, MAOC = mineral-associated organic carbon, MBC = microbial biomass carbon, POC = particulate organic carbon, POXC = permanganate oxidizable carbon, SM = soil moisture, and SOC = soil organic carbon. Boxes represent the interquartile range (1st and 3rd quartiles), with horizontal black lines indicating median values. Dots represent extreme values. Note that the scale differs among panels. Statistical significance: ns = not significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

of treatment. Root dry weight ranged from 0.0078 to 0.1857 g (CV = 57.25%), and the average diameter of root segments ranged from 0.17 to 0.55 mm (CV = 24.89%). *B. variegata* had the thickest and shortest roots; *F. hispida* had the thinnest and longest roots, with the highest BI and root tissue density (RTD); and *M. indica* had the highest SRA and the lowest RTD and BI (Figure 3, Table S5).

During all incubation periods, root exudation rates showed strong negative correlations with RL, RA, and RV (Spearman correlation; Figure S5). BI was negatively correlated with RV, RA, and average diameter (D), and positively correlated with RTD. SRA was positively correlated with other morphological traits except RTD; SRL was positively correlated with other morphological traits except D (Figure S5).

3.5 | Soil properties

Soil properties differed significantly among species for SOC ($F_{2,40} = 4.33$, $p = 0.01$), POXC ($F_{2,40} = 7.441$, $p = 0.002$), SM ($F_{2,40} = 78.37$, $p < 0.001$), pH ($F_{2,40} = 19.38$, $p < 0.001$), DON ($F_{2,40} = 11.68$, $p = 0.0001$), MBC ($F_{2,40} = 11.68$, $p = 0.07$), and DOC ($F_{2,40} = 2.8$, $p = 0.06$; Figure 4, Table S6). Pairwise comparisons showed that *B. variegata* had significantly higher SOC, POXC, SM, pH, and DON than *F. hispida* and *M. indica* (Table S7).

Combining all species, SOC was negatively associated with root exudation rate ($\chi^2 = 6.8$, df = 1, $p = 0.01$), while POXC and SM showed positive associations ($\chi^2 = 4.1$, df = 1, $p = 0.04$ and $\chi^2 = 4.01$, df = 1, $p = 0.04$ respectively; Table S2).

For all herbivory treatments, root exudation rates were positively correlated with SM, pH, POXC, DOC, and POC, but negatively correlated with MAOC in the control treatment (Figure S6). Additionally, root exudation rates were negatively correlated with MBC under mild herbivory and with SOC and DON under severe herbivory (Figure S6).

4 | DISCUSSION

Elephant herbivory—simulated here as mechanical removal of aboveground biomass—altered sapling root carbon exudation in a species- and time-dependent manner. Within 4 days, *M. indica* showed a short-lived spike under mild damage at 24 h, *F. hispida* increased exudation under severe damage at 72–96 h, and *B. variegata* showed no detectable change. These patterns indicate rapid belowground responses to herbivory damage, with direction and timing contingent on species' resource-use strategies and local soil properties. Because root-derived inputs can be an important pathway by which plant carbon enters microbial and mineral pools, even short-term exudation pulses may influence rhizosphere processes and, over longer periods, soil-carbon dynamics. Our experiment captures acute responses rather than long-term allocation or recovery, framing our findings as evidence for a mechanistic pathway—rather than a direct estimate—of elephant impacts on belowground carbon cycling.

4.1 | Species-Specific Responses

Baseline exudation, root traits, and soil properties differed among the three tree species. Although all are fast-growing pioneers, they differed substantially in root economic strategies (conservative vs acquisitive) and soil properties (Figures 3 and 4), which likely influenced their distinct root exudation responses. *M. indica* (acquisitive strategy: low root tissue density, SRA, and growing in more acidic, nutrient-poor soils) showed a short-lived exudation increase under mild, but not severe, damage. This pattern is consistent with previous studies linking low root tissue density and resource-limited soils with increased exudation (Meier et al., 2020; Sun et al., 2021). *F. hispida* (more conservative: finer, denser, highly branched roots) exhibited a delayed increase only under severe herbivory, in line with reports of lower exudation with high root tissue density, fine, and highly branched roots (Groleau-Renaud et al., 1998; Sun et al., 2021; Zhang et al., 2024). The capacity of *Ficus* species to form adventitious roots during stress (Yuan et al., 2024) further supports a conservative strategy that may switch to a more acquisitive strategy under acute damage. Similar conservative-to-acquisitive transitions with sustained grazing have been reported in grasses (Zhou et al., 2024), as grazing time increases. *B. variegata* (intermediate-to-conservative, with thicker, shorter roots and the highest baseline exudation) did not change with damage, plausibly because it occurred in comparatively resource-rich soils (higher SOC, POXC, SM, pH, and DON). The positive association between its exudation and POXC is consistent with a resource-replete rhizosphere reducing the need to upregulate exudation after canopy loss. Overall, our results fit a traits–environment–disturbance framework: Exudation responses depend on root economic strategy and resource context and manifest only at certain damage intensities and timescales.

4.2 | Temporal dynamics

The timing of root exudation responses differed strongly by species: *M. indica* exhibited an immediate peak at 24 h, whereas *F. hispida* showed a relatively delayed response, with increased exudation occurring at 72 and 96 h. This variation highlights the complexity of

plant responses to herbivory and suggests that root exudation may be triggered immediately or after a delay (Hamilton & Frank, 2001; Hamilton et al., 2008), reflecting differences in carbon allocation strategies and stress physiology. Bazot et al. (2005) reported increased root exudation for up to four days after defoliation in *Lolium perenne*, and Hamilton et al. (2008) observed elevated rates within 24–72 h in *Poa pratensis*, supporting our findings of both immediate and delayed species-specific responses.

4.3 | Mechanistic pathways and context-dependence

Herbivory can alter exudation via acute stress responses that rapidly divert recently fixed or stored carbon belowground, and via subsequent adjustments as plants meet nutrient demand for regrowth. Over our 4-day window, observed changes most likely reflect the first mode. Once released, exudate chemistry (sugars, amino acids, organic acids, phenolics, and polysaccharides) governs microbial metabolism and soil-carbon fate. Labile compounds such as organic acids and amino acids can boost microbial growth and carbon-use efficiency, leading to the production of microbial residues that sorb to minerals and become mineral-associated organic matter (MAOM/MAOC). In contrast, oxalic acids and simple sugars can destabilize existing MAOM by promoting the desorption of bound organic compounds. Depending on environmental conditions, this process may either reduce SOC through accelerated microbial metabolism and CO_2 efflux or enhance SOC through efficient microbial assimilation and necromass formation (Chari & Taylor, 2022; Keiluweit et al., 2015; Shabtai et al., 2024). Thus, the herbivory-mediated effect of exudates on soil carbon depends on chemistry and microbial response. Context matters: plant traits (acquisitive vs. conservative roots), local soil properties (e.g., POXC, SOC, mineral-surface saturation, and pH), and moisture help determine whether exuded carbon is stabilized in mineral-associated pools (MAOM/MAOC) or lost via microbial respiration.

In sum, we document species- and time-specific exudation pulses after simulated elephant herbivory—necessary first steps in the herbivory → exudation → microbe → SOC pathway. Determining the net SOC effect requires pairing exudation rates and composition with microbial activity, mycorrhizal metrics, and direct measurements of MAOM/POC dynamics over longer timescales and across environmental contexts.

4.4 | Ecological and conservation implications

Given the scale of elephant damage in tropical forests—for example, a single adult female has been reported to damage over 39,000 tree saplings annually in a mature forest and ~73,000 in early successional habitats (Ong et al., 2023)—even transient, species-specific exudation pulses could cumulatively influence microbial activity, nutrient cycling, and the balance between mineral-associated carbon formation and losses in tropical soils. Effects are likely strongest (i) in stands dominated by acquisitive species with fine, high-surface-area roots, (ii) in nutrient-poor or acidic soils where exudation aids nutrient mobilization, and (iii) in landscapes with frequent elephant use and abundant regenerating forest.

These insights have important implications for people and policy. Elephants provide multiple ecosystem services aboveground (e.g., seed dispersal; altered vegetation structure, composition, and diversity; and carbon sequestration; Campos-Arceiz et al., 2008; Ong et al., 2023; Berzaghi et al., 2019) and belowground via defecation (Sandhage-Hofmann et al., 2021; Stephenson et al., 2024), carcass decomposition (Bartel et al., 2024; Burcham et al., 2024), and—as shown here—root exudation. Taken together, our results suggest that conserving elephants at ecologically functional densities can aid soil-function recovery in regenerating tropical forests by eliciting short-term, species-specific increases in root exudation that support microbial nutrient cycling. In practice, restoration in elephant landscapes should be elephant-compatible: Maintain early–mid-successional mosaics accessible to elephants; include species mixes that pair acquisitive pioneers with structural species on nutrient-poor or acidic sites; apply targeted screening of locally common, elephant-preferred pioneers to identify exudation-responsive species; and monitor simple soil-function indicators (POXC, DOC/DON, and MAOM/POC) to verify gains—aligning with emerging megafauna–tree–soil C frameworks (e.g., Sandhage-Hofmann et al., 2021), and without presuming net carbon gains a priori.

Optimizing these pathways by protecting elephant populations at ecologically functional densities, restoring habitats, and enhancing connectivity may sustain not only visible vegetation processes but also underappreciated belowground processes that underpin tropical forest resilience and carbon sequestration. For restoration and nature-based solutions, our results argue for explicitly and routinely monitoring soil function (e.g., POXC, DOC/DON, and MAOM/POC) and selecting species mixes with contrasting root traits, while treating belowground carbon outcomes as a potential cobenefit.

4.5 | Future directions

To move from mechanisms to net carbon outcomes, future work should extend measurements from days to months to capture recovery and regrowth, pairing exudation rates and composition (metabolite profiling) with microbial responses (enzyme activity, carbon-use efficiency) and SOC fractions. Designs should use randomized, interspersed, or blocked layouts to minimize plot effects and higher replication calibrated by our power curves. Because context mediates outcomes, experiments should span contrasting soils (pH, POXC, mineral-surface saturation, and moisture) and root economic strategies (acquisitive to conservative), and include field validation along gradients of elephant use and successional stage. Clarifying mycorrhizal roles is a priority: Quantify colonization and guilds to test their moderating effects on herbivory–exudation–SOC linkages. Finally, targeted species screens aligned with elephant browsing preferences

can inform restoration species mixes and nature-based solutions aimed at sustaining soil function under active herbivory.

5 | CONCLUSIONS

This study identifies a previously underappreciated pathway by which large browsing herbivores—particularly elephants, due to their destructive foraging habits—may influence belowground carbon cycling in tropical forests through short-term, species-specific shifts in root exudation. While preliminary, these findings generate testable predictions about when and where elephant conservation and restoration efforts may also enhance soil function and climate resilience, and they point to the measurements needed to move from mechanism to quantified net carbon outcomes.

AUTHOR CONTRIBUTIONS

Pratibha Khatri and Ahimsa Campos-Arceiz designed the research. Pratibha Khatri and BS conducted the experiments. Pratibha Khatri analyzed the data. Pratibha Khatri and Ahimsa Campos-Arceiz wrote the manuscript. Pratibha Khatri, Bimal Sharma, Lisa Ong, and Ahimsa Campos-Arceiz contributed to data interpretation and the revision of the final manuscript.

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DATA AVAILABILITY STATEMENT

All data analyzed in this study, including root exudation rates, root morphological traits, and rhizosphere soil properties, are provided in Dataset S1.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

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

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