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Century-old land-use legacies outweigh hurricane disturbance in shaping soil microbial functioning in a tropical forest

Manar Bassam Talab

talabm@umich.edu

University of Michigan https://orcid.org/0009-0004-5774-4307

Aimée T. Classen

Brendan O'Neill

María Natalia Umaña

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Century-old land-use legacies outweigh hurricane disturbance in shaping soil microbial functioning in a tropical forest

Manar B. Talab[1]*, Aimée T. Classen[2], Brendan O'Neill[3], María Natalia Umaña[4]

[1,2,3,4] University of Michigan, Ecology and Evolutionary Biology, Ann Arbor, MI, USA

ORCID ID: 0009-0004-5774-4307

Keywords: Land-use legacy; hurricane disturbance; soil microbial functioning; soil enzyme activity; nutrient cycling; tropical forest soils

Abstract:

Aims:

Soil microbial communities are responsible for critical ecosystem functions like decomposition and nutrient cycling, yet their responses to long-term (press) versus episodic (pulse) disturbances remain poorly understood in tropical forests. Long-term land use can impose lasting changes to soil physical and chemical properties, constraining microbial functioning for decades. In contrast, short-term disturbances may temporarily disrupt soil structure but allow rapid recovery. This study aims to investigate the relative impacts of past land use change and recent hurricane disturbance on soil microbial functioning.

Methods:

We quantified soil abiotic properties, enzyme activity, and nutrient availability across adjacent cultivated and never cultivated forests in Puerto Rico. Within each forest, we compared the areas of uprooted trees and adjacent intact soils eight years after hurricanes Irma and Maria.

Results:

We found that land-use legacies structured soil conditions and microbial functioning nearly a century after abandonment. Never cultivated forests maintained higher soil moisture, lower bulk density and acidity, 2.3 fold greater potential complex carbon-degrading oxidative enzyme activity, and 22% higher ammonium availability. In contrast, cultivated forests had higher potential labile carbon-, nitrogen-, and phosphorus-degrading enzyme activity and 48% greater nitrate availability indicating divergent decomposition and soil nutrient cycling. By contrast, hydrolytic enzyme activity and nutrient availability did not differ between tree-fall and intact soil areas eight years after hurricane disturbance, despite differences in microtopography and soil temperature.

Conclusion:

Historic land-use legacies exert stronger and longer-lasting controls on soil microbial functioning than acute hurricane disturbance, with implications for ecosystem recovery under intensifying disturbance regimes.

Abbreviations: Cultivated (C) and Never Cultivated (NC)

* Corresponding author: Manar Talab, email: talabm@umich.edu

Introduction

Soil microbial communities play an essential role in terrestrial ecosystems through the decomposition of organic matter and cycling nutrients to support aboveground biomass (Bradford et al 2016; Wood, McGuire, and Hickman 2014). Disturbance reshapes the soil environment and the soil microbial communities that regulate decomposition and nutrient cycling rates, but disturbances can occur across broad magnitudes and timescales. Press disturbances, such as land-use change, impose long-term, directional shifts in soil conditions, whereas pulse disturbances such as hurricanes deliver acute, transient perturbations from which ecosystems may recover quickly (Bradford et al 2016; Wood, McGuire, and Hickman 2014; Eaton et al 2020). Many studies track how press and pulse disturbance shifts microbial community identity (Bachelot et al 2016; Waring et al 2024; Wood, McGuire, and Hickman 2014), yet whether different types of disturbances leave enduring legacies on microbial functional capacity, and therefore on the critical processes microbes regulate, remains unclear.

Land use change, a press disturbance, is a major driver of shifts in soil microbial communities and related decomposition rates. One prominent driver of land-use change, cultivation, reduces organic matter inputs, compacts soil, alters soil acidity, and reduces soil moisture (Weil and Brady 2016), favoring soil taxa adapted to these conditions, and reshaping community composition (Waring et al 2024; Wood, McGuire, and Hickman 2014). In Puerto Rico, forests that were historically clearcut, farmed, and abandoned 80 years past still showed reduced fungal beta diversity and greater evenness (Bachelot et al 2016). Similarly, comparable land-use shifts have altered microbial diversity, functional capacity, and microbial biomass in other systems (Azene et al 2023; Carney and Matson 2005; Moghimian et al 2017; Wood, McGuire, and Hickman 2014). The effects are both large and persistent. Potential soil enzyme activity in natural forest can fall 30 to 75% when converted to farmland (Azene et al 2023; Moghimian et al 2017), and deforestation still shapes decomposition and nutrient cycling 80 years after regrowth of tropical forest, with slightly higher decomposition in historically deforested lands and nitrogen immobilization in intact forest (Zou et al 1995).

Hurricanes, a pulse disturbance, restructure microbial communities through abrupt inputs of litter and rapid changes in soil biogeochemistry (Eaton et al 2020). A single storm deposits years worths of leaves and woody debris in days, altering microclimate and flooding the soil with organic matter in ways that reshape microbial composition, abundance, and function (Bradford et al 2016; Eaton and McGee 2025; Lauber et al 2008; Sandford et al 1991). Recovery follows a characteristic sequence. In the initial phase (0-2 years), canopy inputs stimulate decomposition of labile organic C, increase in microbial biomass, favor bacterial dominance, and accelerate nitrogen mineralization and uptake (Eaton and McGee 2025); in an intermediate phase (2-20 years) soil communities shift towards fungal dominance and the breakdown of more stable organic compounds while respiration stabilizes, and bacterial abundance declines until an eventual return to pre-hurricane levels (Eaton and McGee 2025). Consistent with this trajectory, decomposer communities move from bacterial to fungal dominance within five years post storm, and the elevated carbon, nitrogen, and phosphorus cycling found after the first year returns to pre-hurricane levels (Eaton et al 2020; Reed et al 2020).

In addition to the rapid influx of litter, hurricanes cause major physical disruptions to the soil by uprooting trees. Uprooting exposes and severs entire root systems, and excavates pits that can persist for decades, locally altering soil structure, moisture, aeration, and temperature (Waring et al 2024). Unlike canopy damage alone, uprooting directly disrupts belowground habitat by redistributing organic matter and exposing previously protected soil layers, with consequences for microbial communities and their function. In a temperate forest in the UK, stands with severe wind disturbance and uprooted trees led to reduced soil carbon, acidity, and root biomass, as well as an increase in microbial community turnover after one year (Waring et al 2024). In addition to the system-wide changes imposed by hurricane disturbance, the localized biogeochemical changes of tree uprooting have the potential to leave lasting effects on microbial community composition and function.

Here, we compare the long-lasting effects of land-use history (90 years) and hurricane disturbance (7 years) on soil properties, microbial functional capacity, and nutrient cycling in a forest in Puerto Rico. From the 1800s, areas of the forest were clearcut and cultivated for coffee, rice, yams, sweet potatoes, sugarcane, and gandules (pigeon peas). After Hurricane Felipe II in 1928, and the Forest Service purchase of the land in 1934, all farms were abandoned, leaving a mosaic of previously cultivated (C) and never cultivated (NC) forest. Major hurricanes struck in 1989 (Hugo, category 3), 1998 (Georges, category 3), and in 2017, when hurricane Irma (category 5) passed just north of the Island and hurricane Maria (category 4) made landfall two weeks later (NOAA 2017). We focus on the 2017 hurricanes, which doubled tree mortality relative to earlier storms (Uriarte, Thompson, and Zimmerman 2019). Storms of this intensity will increasingly affect our most productive forests (Emanuel 2020). Recurring canopy loss, stem breakage, and uprooting may now shape decomposition in concert with the signature of past land use.

To this end, we investigated the impacts of hurricane disturbance and cultivation on soil functioning in a subtropical forest through three primary questions: 1) What are the long-lasting impacts of disturbance on **soil abiotic properties** seven years after a hurricane (uprooted vs intact) and 90 years after divergent land use (cultivated vs never cultivated)? 2) How do these disturbances alter **soil microbial activity**? And finally, 3) How does disturbance affect **soil ecosystem function,** such as decomposition and nutrient cycling, on both short- and long- term time scales?

We predicted that past cultivation will have lasting impacts on the soil environment and soil microbial functioning due to the long-term impacts of farming on soil structure, chemistry, and subsequent changes in microbial biomass and community composition. Compared to never cultivated forest soil, previously cultivated soils will retain a legacy of disturbance to the soil environment and microbial function decades after abandonment from agriculture, observed as reduced microbial activity, enzyme potential, and available soil nutrients. Furthermore, recent tree uprooting from Hurricane Maria and Irma will produce lasting impacts on the soil environment and soil microbial function– to a lesser extent than historic cultivation, through the physical and chemical impacts of soil turbation that will cascade to impact soil microbial

activity. The altered soil structure and severed rhizosphere will reduce soil microbial activity, enzyme potential, and available nutrients compared to intact soil.

Materials and Methods

Study Site and Land Use History

We conducted this project in the 16-ha Luquillo Forest Dynamics Plot (LFDP) in the Luquillo Experimental Forest in the northeast of Puerto Rico (18.321482, -65.819958790). The LFDP is a subtropical rainforest with average yearly rainfall of 3500mm and mean annual temperatures between 19 and 25℃, with a history of severe hurricanes every 50-60 years (Thompson 2002). This long-term research site has a detailed census of each tree over a 10 cm diameter at breast height (Thompson 2002). The soils of this forest are formed from volcaniclastic sandstone with Zarzal (67%), Cristal (22%), and Prieto (6%) clays of low to moderate fertility (Thompson 2002). The LFDP is a mosaic of different forest types that represent four areas of different land-use histories, with cover class 1 having the lowest basal area and species richness, and cover class 4 having the highest basal area, species richness, and number of rare or endemic species (Thompson 2002). Cover class 4 was only selectively cleared due to undesirable topography for farming with large boulders and rocky elevation. Under current knowledge, decisions to cultivate across this forest were driven by topography and not stark differences in soil fertility, which is supported by the broad distribution of low fertility soil types across the plot (Thompson 2002). Cleared areas in cover classes 1, 2, and 3, were previously used for farming coffee, rice, yams, sweet potatoes, and sugar cane, with class 1 being the most recently cleared before 1936 when all activity ceased (Thompson 2002). In the literature, the cover classes 1, 2, and 3 are classified as mid successional forest, and cover class 4 as mature tabonuco forest (Zou et al 1995). Other studies have classified cover class 1, 2, and 3, as “high use” areas, and cover class 4 as “low use” areas (Bachelot et al 2016). In this study, cover classes 1–3 were classified as *cultivated* and cover class 4 as *never cultivated* (C and NC) to reflect differences in historical soil disturbance; these groupings were supported in Hogan et al 2016 using statistical analyses of indicator species. Separating analysis on the basis of cover class did not produce any deeper insight than the separation of cultivated and never cultivated. Therefore, cover classes were not reported in results.

Field Sampling Method

During May 2025, we used a paired design to establish 80 plots across the 500 × 300-meter research plot in the LFDP. We conducted a search for tagged uprooted trees along the main trail across the cultivated, non-cultivated forest binary. We then referenced the 2016 Luquillo census to confirm that the tree was alive before the 2017 landfall of Hurricane Maria. For each uprooted tree plot, we established a paired “intact” control plot one pit diameter away from the uprooting. To address our goal of comparing soil characteristics, microbial activity, and nutrient cycling across areas of different land use history and hurricane disturbance, we defined two treatment types based on visible hurricane damage: (1) uprooted areas, corresponding to tree uprooting pits where a visible soil depression was formed, and (2) intact plots, located adjacent,

in a random direction to uprooted plots where the soil surface appeared undisturbed. We identified these treatment areas along the entire LFDP, with equal number sites of cultivated (C) and never cultivated (NC) land use history (supp. Figure 1).

At each plot, we collected a 5 ×15 cm (diameter × depth) surface soil sample using a hammer core from the center of the plot. Light availability, soil moisture, and soil temperature were measured weekly between 0800–1000 A.M. for three weeks. Light availability was measured in Lux six inches above the soil surface using the LightMeter app. Percent soil moisture was collected with an electric probe measuring at 10cm depth. We also measured tree pit area, litter cover, and litter depth of each plot.

The 5 × 15cm soil cores were shipped on ice and stored in 4℃ until analysis. We subset soil cores into topsoil and subsoil (0-7cm and 8-15cm), sieved soils to 2mm, and extracted root fragments.

Laboratory Analysis

We analyzed variables (Table 1) that correspond to the three processes evaluated in this study (1) The soil abiotic environment through gravimetric water content, soil acidity, bulk density, and light; (2) Microbial activity through enzyme analysis, relative carbon mineralization, and root biomass; (3) Nutrient availability through concentrations of ammonium and nitrate. Below we describe the methods for analyzing these variables.

Abiotic Environment

To evaluate soil abiotic properties, we measured **gravimetric water content (GWC) (**Rome 2023)**. Bulk density** was calculated using the intact weight of the soil core (Rome 2023). Rock and root fragments were negligible and therefore not taken into consideration for calculations, except for sample 36 which contained substantial non-soil, coarse material, with only 94g of soil out of the total core mass of 254g. To evaluate soil chemical properties, we measured active **soil acidity (pH)** using deionized water and a calibrated pH meter.

Microbial Activity

We measured **root biomass** using root fragments collected from each soil sample that were dried at 60C for at least 48 hours. To evaluate microbial activity, air-dried soil was rewet and incubated over 24 hours to evaluate **carbon mineralization** ($\mu g\ CO_2\text{-}C\ g\ soil^{-1}\ day^{-1}$) (Franzleubbers et al 2000). To assess decomposition activity, we measured potential soil **extracellular enzyme activity** ($\mu mol\ substrate\ g\ soil^{-1} day^{-1}$) using microplate assays incubated in the dark at room temperature using methods adapted from Bell et al. (2013). Using soil slurries, we measured hydrolytic enzyme activities associated with carbon, nitrogen, and phosphorus cycling– β-glucosidase (BG), N-acetylglucosaminidase (NAG), and phosphatase (PHOS), fluorometrically using 4-methylumbelliferyl (MUB)–linked substrates. We incubated hydrolytic enzyme assays for 24 h and read them without the addition of a stop buffer. We assessed oxidative enzyme activity associated with lignin degradation using L-3,4-dihydroxyphenylalanine (L-DOPA). We quantified oxidative enzyme activity (LDOPA) colorimetrically by measuring absorbance at 480 nm 60 minutes after L-DOPA addition. We

diluted soil slurries (soil was allowed to settle for 1 minute and supernatant was collected from the surface) of oxidative enzymes.

Nutrient Availability

To assess differences in nutrient availability, we estimated **nitrate and ammonium** concentrations (mg NH_4/NO_3 kg $soil^{-1}$) according to Sinsabaugh, Reynolds, and Long 2000; Doane and Horwath 2003, with two replicates of 8g $\pm$ 0.05g of each sample. To assess differences in subsoil fertility**,** we sent a subset of 30 soil samples (8-15cm depth) for analysis of organic matter, available phosphorus, exchangeable potassium, magnesium, and calcium at A&L Great Lakes Laboratories, Inc. (Fort Wayne, IN).

Data Analysis

To examine how land use history (cultivated vs. never cultivated) and hurricane disturbance (intact/uprooted) influenced microbial and decomposition activities, we fit multiple generalized linear models (GLM) with predictors land use history (C/NC) and hurricane disturbance (intact/uprooted). In addition, we included pit size as a fixed effect to account for variation in topography. All variables were checked for normality to confirm the assumptions of the linear models. We then compared models using the Akaike Information criterion (AIC) information testing (AICctab) to determine the best model. Unless log transformed to meet model assumptions, all abiotic measurements were analyzed using linear models in their original distributions. Analyses utilizing the paired uprooting design were tested but revealed no difference to unpaired analyses. Nitrate presence was tested using a generalized linear model with binomial distribution, and nitrate concentration was modeled with a generalized linear model with a gamma (log link) distribution. All enzymes were analyzed with a gamma (log link) distribution in a generalized linear model. All analyses were performed in R version 2025.09.2 Build 418 (Posit team 2025).

Table 1. Summary of methods. Variables and metrics used in this study. Group refers to four different types of variables that we considered in our study, variable refers to the properties measured, role refers to the expected biological interpretation for each variable, and Predicted Response refers to the author's predictions and applies to the group of variables.

Group	Variable	Role	Expected response
Disturbance and litter characteristics	Litter depth (cm)	Assess whether litter quantity is associated with response variables	No difference between past land use (C/NC) or disturbance (Intact/Uprooted)

	Litter cover (%)	Assess whether litter quantity is associated with response variables	
	Pit area (m^2)	Assess whether disturbance magnitude is associated with response variables	—
Abiotic soil properties	Gravimetric water content (g H_2O g^{-1} soil)	Characterize the soil environment, an important determinant of microbial community and function	Differs between past land use (C/NC) and disturbance (Intact/Uprooted)
	Bulk density (g soil cm^{-3})	Characterize the soil environment, an important determinant of microbial community and function	
	Soil acidity (pH)	Characterize the soil environment, an important determinant of microbial community and function	
	Light availability (lux)	Characterize the aboveground environment	
Microbial activity	Root biomass (g)	Characterize belowground biomass	Differs between past land use (C/NC) and disturbance (Intact/Uprooted)

	Carbon mineralization (μg CO_2-C g^{-1} soil day^{-1})	Assess microbial activity and decomposition potential	
	Enzyme activities BG, NAG, PHOS, PHENOX (μmol substrate g^{-1} soil day^{-1})	Assess microbial activity and decomposition potential	
Nutrient availability	Extractable NH_4^+ (mg NH_4^+ kg^{-1} soil)	Assess potential functional capacity and soil fertility	Differs between past land use (C/NC) and disturbance (Intact/Uprooted)
	Extractable NO_3^- (mg NO_3^- kg^{-1} soil)	Assess potential functional capacity and soil fertility	
	Subsoil measurements	Assess whether treatment effects extend below the surface soil layer	

Results

Abiotic Properties

What are the long-lasting impacts on abiotic soil properties eight years after hurricane disturbance (tree uprooting) and 90 years after historic land use (cultivation)?

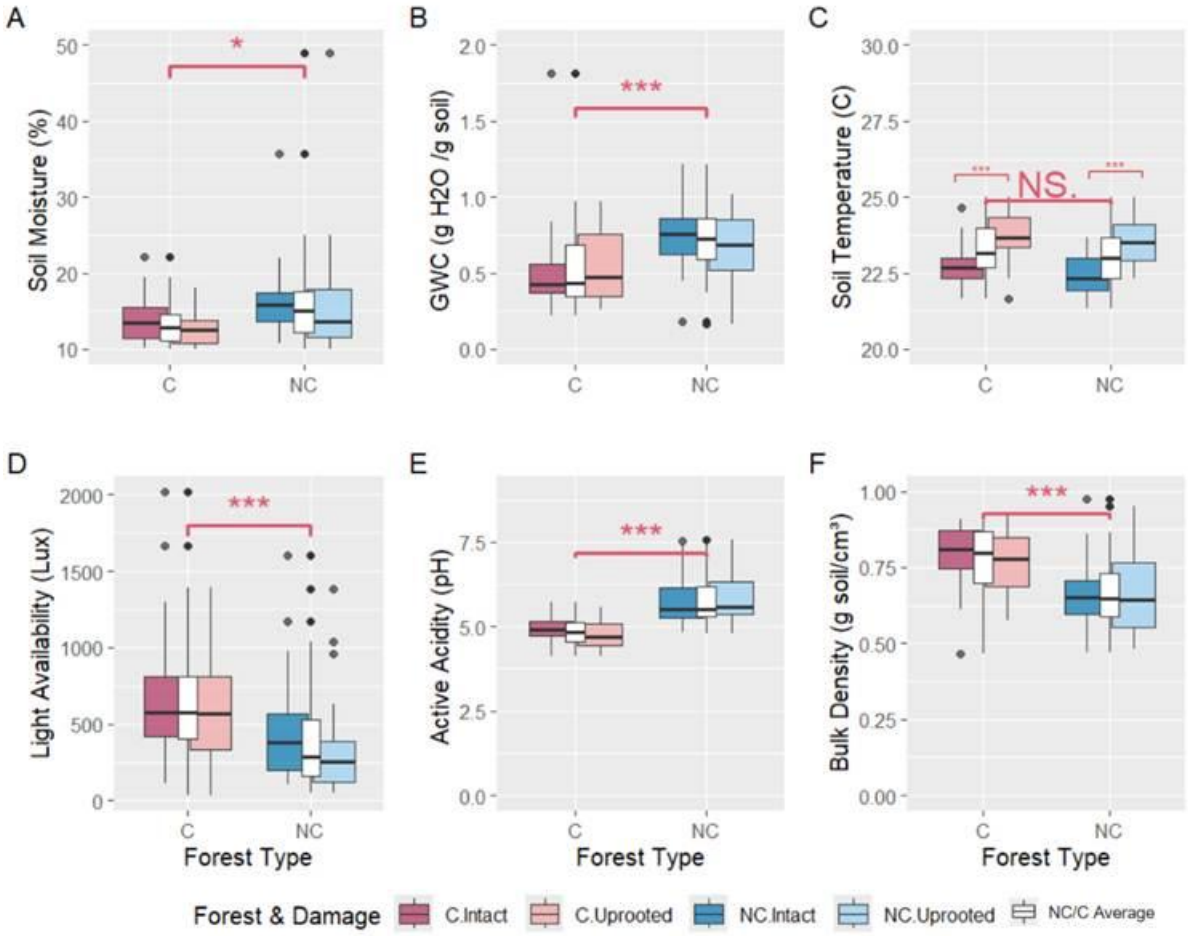


Figure 1. Boxplots showing the difference in microclimate between cultivated (C) and never cultivated (NC) forests. Log transformed and original distribution linear models used where appropriate and detected significant differences in A. Soil moisture, B. Gravimetric water content, C. Soil temperature, D. Light availability, E. Active acidity (Water extracted pH) and F. Bulk density, (alpha= 0.05). Error bars indicate one standard deviation. Box plot center line indicated median and box plot contains interquartile range. Red bars indicate significance of models: * indicates $p < 0.05$, ** indicates $p < 0.01$, and *** indicates $p < 0.001$.

A comparison of land use history and uprooting disturbance revealed significant differences in soil environment. Soils from the NC (Never Cultivated) plot had 38% greater moisture in field measurements than C (Cultivated) soils ($p < 0.001$, Figure 1A). Soil temperature did not differ between C and NC soils, but across both forests, uprooted soil was on average 1°C warmer than intact soils ($p < 0.001$, Figure 1C). Soils in C forest received 46% more light than NC forest ($p < 0.001$, Figure 1D). Soils in NC forest had 0.1 g/cm^3 less dense soil than cultivated soils. Soils in NC forest featured 36% higher gravimetric water content than C soils ($p=0.002$, Figure 1B). Our analysis of active acidity revealed significant differences across land use history but not uprooting disturbance, with C soils being strongly acidic and NC soils being moderately acidic ($p < 0.001$, Figure 1E).

Decomposition Potential

How does soil microbial activity change over areas of different historic land use and hurricane disturbance?

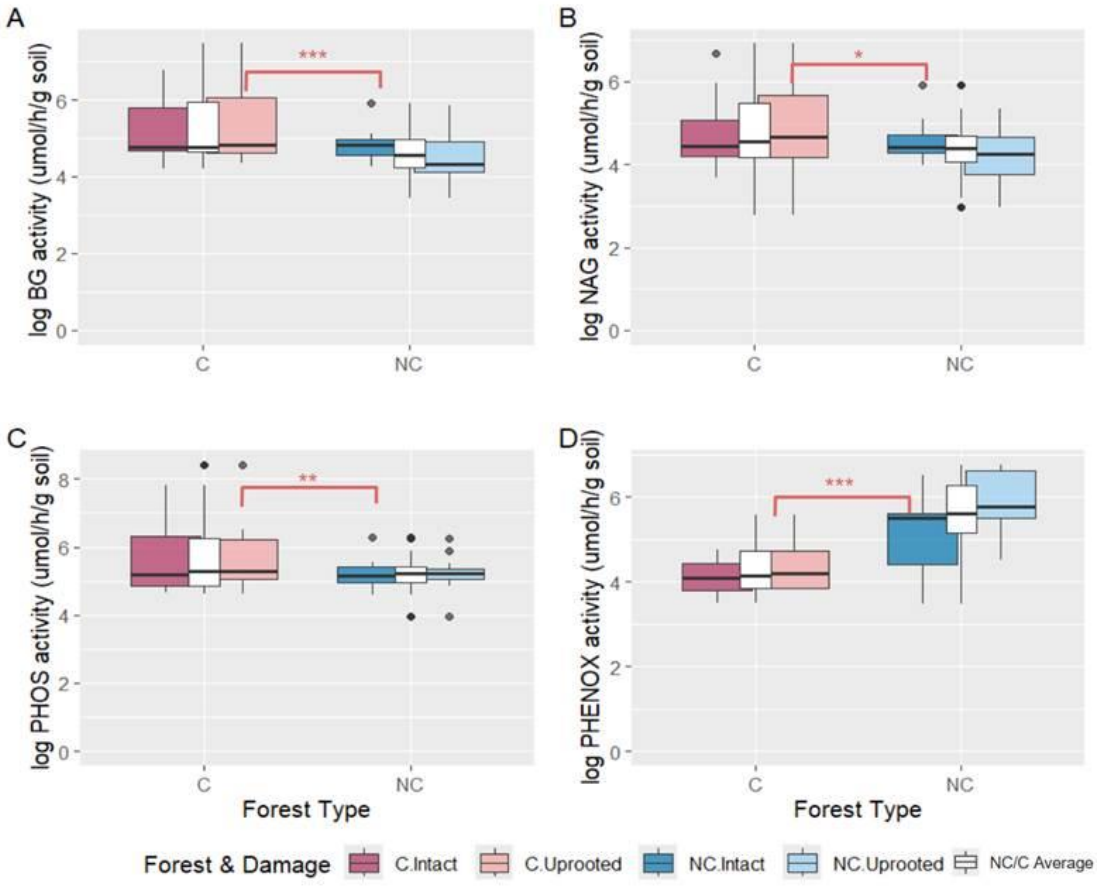


Figure 2. Boxplots showing significant differences in potential enzyme activity between C and NC forests. Gamma (log link) generalized linear models found significant differences in **A)** BG (Beta Glucosidase), sample size= 80, **B)** NAG (N-acetyl glucosaminidase), sample size= 80, **C)** PHOS (phosphatase), sample size= 80, and **D)** PHENOX (phenol oxidase), sample size= 20, (µmol substrate h^{-1} g^{-1} soil) activity across forest types. Error bars represent one standard deviation (alpha=0.05). Red bars indicate significance of models: * indicates $p < 0.05$, ** indicates $p < 0.01$, and *** indicates $p < 0.001$.

Cultivation history explained significant differences in labile carbon (BC), nitrogen (NAG), phosphorus (PHOS), and complex carbon (PHENOX) degrading enzymes, unlike hurricane disturbance. Plots in C forest had 46% more labile carbon degrading activity than NC soils ($p < 0.001$, Figure 2A). Similarly, the C soil plots had 36% more N degrading activity than NC forest soil ($p = 0.020$, Figure 2B). Soils from C forest plots featured 44% greater potential phosphorus degrading activity than NC forest ($p= 0.020$, Figure 2C). Plots in NC forest soils had 2.3x greater complex carbon degrading activity than C soils ($p=0.020$, Figure 2D). As for microbial activity, carbon mineralization did not differ between land use or uprooting damage (Figure 2). Plots in the C forest had an average of 3.08 µg CO_2-C g $soil^{-1}$ day^{-1} and never cultivated soil had an average of 2.80 µg CO_2-C g $soil^{-1}$ day^{-1} (supp. Table 1). Similarly, root

biomass showed no meaningful difference over cultivation or uprooting damage with an average biomass of 1.19g in C soils and 1.64g in NC soils (supp. Table 1).

Nutrient Availability

How does this affect larger ecosystem functioning following disturbance in the system?

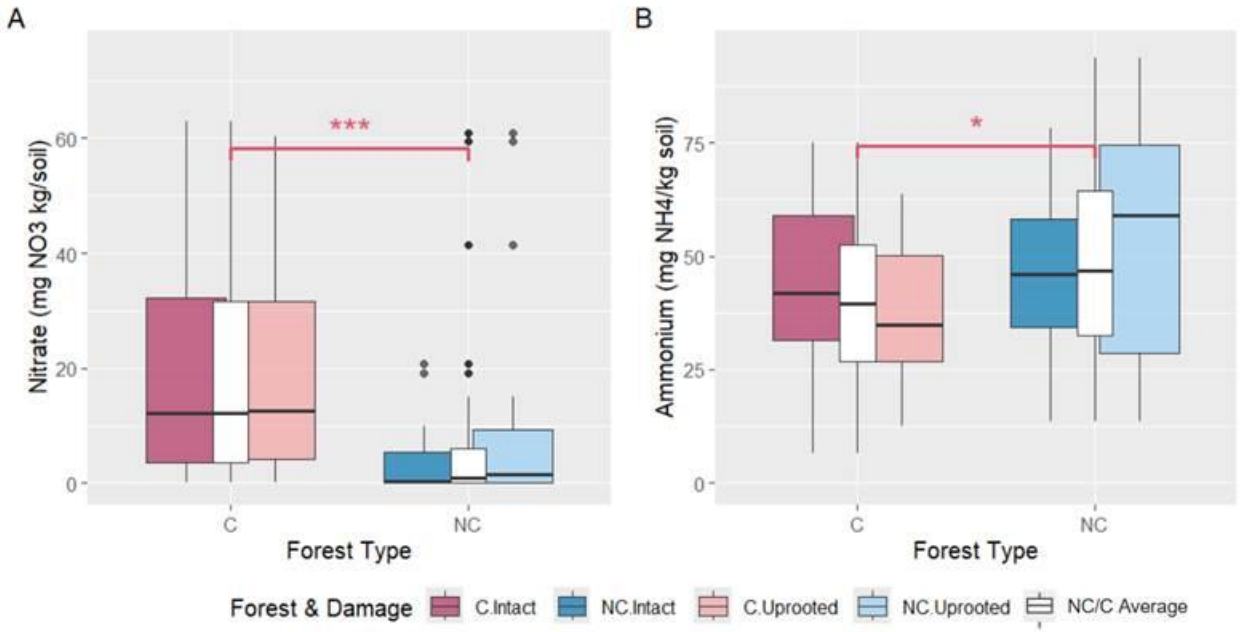


Figure 3. Boxplots showing significant differences in nitrate and ammonium availability between C and NC forests. **A)** NO_3, sample size= 80 and **B)** NH_4, sample size= 80. Concentrations were modeled with Gamma Log link distributed GLM (NO_3) and linear model (NH_4). Error bars represent standard deviation (alpha=0.05). Red bars indicate significance of models * indicates $p < 0.05$ and *** indicates $p < 0.001$.

We observed significant differences in occurrence and concentrations of nitrate and ammonium over past cultivation but not hurricane damage (Figure 3). Never-cultivated soils had approximately 86% lower odds of detectable nitrate than C soils, with 25 of 80 plots having no detectable nitrate ($p=0.002$, Figure 3A). Nitrate was 48% less available in NC forest ($p=0.030$, Figure 3B). In contrast, NC forest possessed more ammonium than the C forest by 10.87 mg NH_4 kg $soil^{-1}$ ($p=0.020$, Figure 3B). Overall, both forests had a much lower concentration of nitrate than ammonia, with the whole forest average around 13.7 mg NO_3 kg $soil^{-1}$ compared to 44.5 mg NH_4 kg $soil^{-1}$ ($p < 0.001$, Figure 3).

Discussion

Overall, we found that forests with different land use histories differ in patterns of soil ecosystem function through soil abiotic properties, decomposition patterns, and nutrient availability more than 90 years after abandonment, suggesting that agriculture leaves long lasting legacies in soil. Interestingly, seven to eight years post disturbance, there were no differences in soil microbial activity or nutrient availability between uprooted and intact soils, despite persistent differences in temperature and topography. Together these results suggest that land use legacies outweigh recent uprooting disturbance effects on soil microbial function, potentially

indicating microbial resilience to recent pulse disturbance while agricultural press disturbance has a cascading impact on soil function and nutrient availability and has a much longer recovery time. Together, these results highlight the complexity of legacy effects and emphasize the role of soil legacies in shaping the trajectory of forest recovery.

Soil legacies of agriculture remain after ~100 years

In fact, we find that previously cultivated forests had lower soil moisture and higher bulk density relative to uncultivated forests. The NC forest featured higher soil water content and lower soil compaction in never cultivated forest, which supports our prediction that never cultivated soils have a more favorable environment for microbial activity, (Weil and Brady 2016; Wood, Detto, and Silver 2013). Interestingly, relative to previously cultivated forests, we found that never cultivated forests had a reduction in light availability. This may indicate that the mixed canopy structure of the previously cultivated forest, as described in Hogan et al 2016, allows more light to reach the forest floor, which may also explain the reduced soil moisture in cultivated plots. Overall, we find that physical properties of soil remained altered nearly 100 years after agricultural abandonment, with less-than-optimal soil abiotic conditions for microbial activity in cultivated forests. The long-lasting impact of past land use on current soil conditions is not uncommon. For example, the Australian bushland and other Neotropical forests recorded long lasting alterations in soil environment following cultivation (Jakovac et al 2021; Peddle et al 2024).

Soil acidity was markedly different across forest types, with the never cultivated soils being less acidic, and the cultivated soils more acidic with nearly 10 fold lower pH, supporting our predictions of altered abiotic properties with potential consequences for soil community identity and function. Strong acidity can shift microbial diversity and nutrient availability particularly for nitrogen, phosphorus, and potassium, while potentially increasing concentrations of iron, manganese, and aluminum to toxic levels (Khaled and Sayed 2023). Soil acidity is a dominant driver of microbial community assembly. Bacterial diversity has been shown to be more sensitive to pH changes and successional shifts than fungal diversity (Xiong et al 2024; Zheng et al 2019), often peaking at near- neutral pH soils, and dramatically dropping off at lower pH (Feng and Deng 2025). The possible differences in the bacterial/fungal ratio have further implications on microbial functional capacity, with bacteria specializing in labile nutrient cycling and fungi specializing in more complex compound degradation (Eaton and McGee 2025; Feng and Deng 2025). Furthermore, acidity controls enzymatic activity, so persistent differences in pH between cultivated and never cultivated sites may drive differences in both community identity and extracellular enzymatic activity that ultimately result in differences in function.

Our analysis of potential enzymatic activity further reveals clear functional differences between cultivated and never cultivated forests. Enzymes degrading labile substrates, carbon (BG), phosphorus (PHOS), and nitrogen (NAG) were more active in cultivated soils, while complex carbon degrading enzyme (PHENOX) was higher in never cultivated soils. This is surprising since we predicted an overall greater decomposition potential in never cultivated forest. On the contrary, these results suggest that cultivated soils harbor a more rapid cycling

microbial community, potentially dominated by bacteria, while never cultivated soils support a slower, potentially fungal dominated nutrient cycling regime, a pattern that is supported across a similar successional gradient in a montane riparian forest (Han et al 2025). The reduced capacity for labile carbon, nitrogen, and phosphorus cycling in never cultivated (late successional) forest is supported in an analysis of soil microbial functional potential in another Puerto Rican forest (Pressler et al 2020). Together, higher nitrogen-degrading enzyme activity and higher nitrate concentrations indicate efficient and specialized (nitrogen) nutrient cycling in cultivated forest. Moreover, the higher labile carbon degrading activity in cultivated soils points to microbial investment in accessible labile carbon, indicating a tighter nutrient economy. Meanwhile, the higher complex carbon degrading activity in never cultivated forests indicates a microbial investment in accessing more recalcitrant carbon, indicating a slower, more stable cycling regime by a potentially fungal-dominated soil microbial community.

Interestingly, despite enzymatic differences, carbon mineralization rates were similar between forest types, suggesting similar microbial biomass. This does not support our prediction that there would be overall lower microbial activity in previously cultivated forests but instead suggests that differences in function are not arising from differences in microbial abundance but in microbial community identity. This result is supported in a montane riparian forest study finding differences in function by an altered microbial community structured by its soil environment (Han et al 2025). They found that younger, previously deforested soils harbor a more rapid cycling microbial community, potentially dominated by bacteria, while older, less disturbed soils support slower, potentially fungal dominated nutrient cycling regime (Han et al 2025). Litter quality may also drive enzymatic differences. Previous studies of litter and decomposition in these forests reveal key information to contextualize these results. Though never cultivated and cultivated forests differ in tree community composition, they do not differ in litterfall rate, litter quantity, or lignan content, which is supported by our observations of similar litter cover and litter depth across the system (Gonzalez, Murphy, and Belen 2012; Oliveira and Carvalho 2009; Zou et al 1995). With this information, we infer that differences in function arise from differing microbial communities determined by soil abiotic properties and nutrient economies, not altered litter inputs. With the slightly higher decomposition (measured by mass loss) in the cultivated forest, which is supported by our potential enzymatic assays (Zou et al 1995), this indicates that differences in decomposition and turnover between cultivated and never cultivated forests are driven by differences in soil microbial community structure. However, land use change strongly impacted subsequent tree species composition, even stronger than hurricane impacts (Hogan et al 2016; Thompson et al 2002). Alterations to the aboveground community from land use change may have caused connected and parallel changes in belowground functioning (Uriarte et al 2015). Future research may explore differences in microbial community composition and above-ground community composition to better link observed enzymatic activity to community identity. Analysis of other important members of the soil community like earthworms and arthropods could further illuminate these differences. Additionally, direct measurements of decomposition, such as litter bag experiments, could

provide further insight into how historical land use and acute disturbances shape nutrient cycling and decomposition capacity.

The observed differences in the magnitude of important soil ecosystem functions should ultimately drive differences in the availability of nutrients nitrate and ammonium. In this sense, our results demonstrate the long-term effects of land use on soil microbial functioning. Contrary to our predictions, there was no overall difference in nutrient availability, but there were meaningful differences in the relative availability of each nutrient in each forest. In particular, never cultivated soils contained 22% more extractable ammonium than cultivated soils, suggesting a more closed and stable nitrogen nutrient cycle, as its positive charge allows it to cling to soil more strongly than nitrate. Additionally, a study in a tropical coffee farm found that intensely managed soils have less nitrogen fixing bacteria (Carrasco-Espinosa et al 2022). In line with this, a recent study of forest succession found that more mature forests have greater capacity for nitrogen fixation and retain very little nitrate (Han et al 2025), which aligns with our results from the never cultivated forest, and the long-lasting legacy of agriculture. Contributing to this pattern, we found that never cultivated soils had higher complex carbon degrading enzyme activity, which suggests a higher degradation of lignin, which slowly releases carbon. This slow release, along with the phosphorus limitation of never cultivated/mature forests, prompts the buildup of stable organic nitrogen in forests (ammonium) (Weil and Brady 2016; Wong et al 2024).

Conversely, we found that cultivated soils contained 48% more extractable nitrate than NC forest, suggesting that cultivated forest relies on a more transient form of nitrogen for plant growth. Nitrate is a less stable form of nitrogen because its negative charge makes it more prone to leaching and denitrification. While the production of ammonia is a common function among soil microbes, nitrification is much more specialized and environmentally sensitive (Weil and Brady 2016). One explanation is that taxa specialized in nitrification may be more abundant in cultivated soils, promoting a greater conversion of ammonia to nitrate. Another explanation could be that uptake of nitrate and ammonium by plants is driving these differences. Overall, nitrate represented a higher proportion of available nitrogen (33%) in the cultivated forest, whereas it made up a small fraction (12%) of available nitrogen in never cultivated forest. In a tropical intercropping system, reduced soil acidity was associated with greater expression of genes associated with nitrogen fixation (produces ammonia) and reduction of gene expression involving nitrification (produces ammonia) (Bossolani et al 2020). In our system, this could support our results that the reduced acidity, never cultivated system featured more ammonium and less nitrate than cultivated systems, and further demonstrate how long lasting the effects of cultivation are on soil microbial functioning. The alteration of acidity by long term cultivation in these soils is driving differences in microbial functioning and nutrient availability almost a century after agricultural abandonment. The difference in ammonium and nitrate in these forests may have larger ecological consequences (Reed et al 2020), such as influencing soil acidity, microbial community, soil organic carbon, and plant growth (Guo, Yang, and Dong 2022). Together, these results suggest that never cultivated forest has a more stable stock of extractable nitrogen than cultivated forest, which will impact plant growth and ultimately forest recovery.

The observed differences in acidity, enzymatic potential, and similarity in carbon mineralization between cultivated and never cultivated soils indicate differences in microbial community structure, which seems to ultimately drive differences in nutrient availability. Differences in soil properties and microbial functioning structuring altered microbial communities have also been found after habitat recovery of cultivated soils in a similarly nutrient-depleted system (Peddle et al 2024). We suggest that these observed differences between cultivated and never cultivated represent two alternative functional pathways, with the cultivated forest hosting less moist, more acidic soils, with microbial communities that are more adept at cycling easily accessible carbon and producing nitrate. The never cultivated forest features more moist, less dense, and less acidic soils, with cycling of more complex carbon substrates, and higher ammonium stocks. The land use change from forest to cultivation is associated with lower soil pH, higher C:N ratios, and an increase in R strategist type microbes that grow and reproduce quickly (Carrasco- Espinosa et al 2022). This is another parallel of the century past cultivated system reflecting current agricultural systems, demonstrating the magnitude of cultivation legacies. This evidence for the structuring of alternative decomposition pathways by past land use is supported in other forests and biodiversity hotspots (Jakovac et al 2021; Peddle et al 2024).

Disturbances have different impacts on ecosystem function

Despite the observed, persistent effects of land use legacies, microbial communities in this system appear resilient to acute physical disturbances, such as hurricane- induced tree uprooting, contrary to our predictions. More than eight years after Hurricane Maria, we found no differences in microbial activity, enzymatic potential, or nutrient availability between tree pit soils and adjacent intact soils despite measurable differences in topography and soil temperature. Even with tree pit soils being 1°C warmer than surrounding soils, a condition that typically enhances metabolic activity (Wood, Detto, and Silver 2013), microbial function and nutrient availability remained the same, at least on a decadal time scale. Since we lack information about the activity before the hurricane and in the immediate aftermath, we can only speculate based on what past studies like Waring et al 2024 discovered, namely that pit soil and intact soil differed in biogeochemistry with implications for function one year after uprooting. One explanation is that soil microbial communities in these frequently disturbed forests are buffered against short term physical disturbances and can maintain functional stability despite physical damage and severing of the rhizosphere. Other studies have had similar conclusions, a study from an arid ecosystem found that human made disturbances (past agricultural use featuring daily flood-drought cycles) had greater negative consequences on the structure and stability of soil microbial communities than natural disturbances (yearly flood-drought cycles) (Maurice et al 2024). Perhaps the high frequency of hurricanes (natural, pulse disturbances) in this system selects for resilient microbial communities. In fact, soil microbial resilience to disturbance is influenced by soil properties like organic matter, aggregation, and acidity (Griffiths and Philippot 2012), which in our study, did not differ between hurricane disturbance types (uprooted and intact) but did differ between cultivated and never cultivated soils. In this sense, past land use ultimately determines soil microbial resilience. However, we cannot ignore the possible

influence of trees expanding their root systems into uprooted tree pits, which may explain similarities in nutrient availability and microbial activity, with new roots taking up excess nutrients that may have accumulated in pits shortly after the hurricane and encouraging microbial activity. This also suggests that trees help to reestablish microbial function after disturbance through the expansion of roots into pit areas. To this point, we found no difference in root biomass between pits and intact soil, suggesting that their similar levels of function may be overcoming abiotic differences through the establishment of a rhizosphere.

Conclusion

This study demonstrates the complexity of soil legacies, with the system responding differently to historical press disturbance than recent pulse disturbance. We found that historical land use exerts a stronger and more persistent influence on abiotic properties, soil microbial function, and nutrient availability than more recent hurricane disturbance. Even 90 years after the cessation of cultivation, historical land use continues to drive differences in microclimate, soil moisture, and bulk density. These abiotic conditions, in turn, influence soil acidity, which exerts strong control over microbial communities and their functional capacity, ultimately shaping nutrient cycling dynamics. In contrast, eight years after a category five hurricane, no measurable differences in microbial activity, enzymatic potential, or nutrient availability were observed between uprooted and intact soils. This suggests a high level of functional resilience of soil microbial communities to periodic physical disturbance, with belowground processes recovering more rapidly from canopy disruption than from historical land use change. Overall, these findings indicated that historical land use represents an enduring ecological control that creates persistent abiotic conditions that drives alternate trajectories of forest ecosystem functioning. Belowground processes retain ecological signatures of past land use over nearly centennial timescales, with implications for current microbial function, nutrient cycling, and ultimately forest regeneration. Together, these results highlight the importance of incorporating historical land use context into assessments of ecosystem resilience and recovery.

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Statements and Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contribution Statement

Manar Talab and Natalia Umaña conceived of the study. Aimée Classen assisted in developing the theoretical framework and provided feedback on writing. Manar Talab conducted lab analyses with the assistance and guidance of Brendan O'Neill. Manar Talab conducted data analysis, writing, and formatting. Brendan O'Neill provided writing feedback and refinement of the discussion. All authors discussed the results and final conclusions and edited writing.

Data Availability

The datasets generated during and analysed in the current study are available from the corresponding author on reasonable request.

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Supplementary Materials

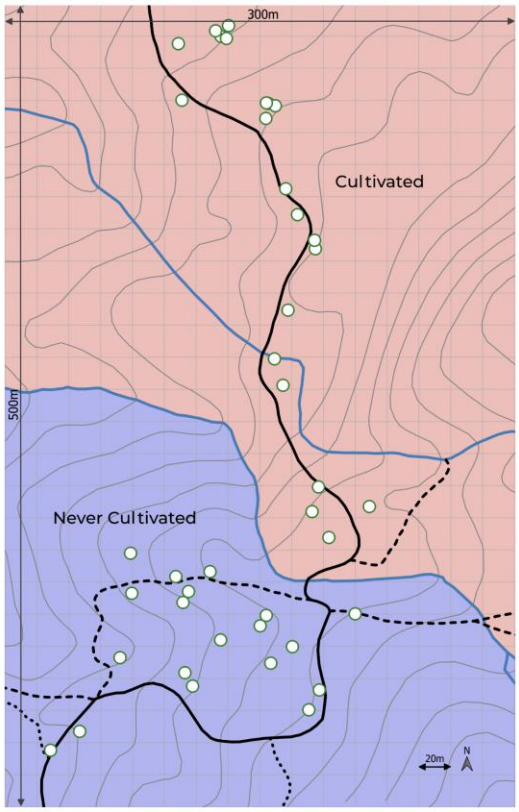


Figure 1. Map of Uprooted Plots on LFDP (large rectangle). Blue lines indicate rivers, black lines indicate the trail, and white circles indicate uprooted-intact soil plots.

Table 1. Average (standard deviation) of soil respiration over 24 hours and average root biomass within soil cores across land use history- cultivated (C) and never cultivated (NC), and hurricane damage-- intact and uprooted soil, with standard deviation over hurricane disturbance and historic land use. Variables were modeled with log transformed linear regression and showed no meaningful difference.

Land Use History	Hurricane Damage	C-Flux/day (µg CO_2 L^{-1} day^{-1}) (SD)	Root Biomass (g) (SD)
C	Intact	2.11 (1.58)	1.23 (1.24)
C	Uprooted	1.74 (1.01)	1.15 (1.24)
NC	Intact	1.97 (2.01)	1.88 (1.24)

NC	Uprooted	1.51 (1.54)	1.39 (1.24)

Table 2. Summary of models with significant fixed effects. Response variable column indicates the response variable in a given model with transformations reported in parenthesis predictor reflects significant fixed effects. The predictor column reflects significant fixed effects (alpha=0.05). NC refers to never cultivated soils. GWC indicating Gravimetric Water Content, BG indicating Beta glucosidase enzyme, NAG indicating N- Acetyl Glucosinamide enzyme, PHOS indicating phosphatase enzyme, and PHENOX indicating phenol oxidase enzyme. *Pseudo-R^2 was calculated as 1 - (residual deviance/null deviance). † Response variable was log-transformed prior to analysis. †† Generalized linear model with a log link.

Response Variable	Predictor	Estimate	SE	z value	P value	R^2
Active acidity	Forest: NC	1.00	0.15	6.84	<0.001	0.36
Soil temperature	Disturbance: Uprooted	1.03	0.17	5.91	<0.001	0.30
Moisture†	Forest: NC	0.32	0.08	4.32	<0.001	0.19
Light†	Forest: NC	−0.62	0.18	−1.58	<0.001	0.16
Bulk density	Forest: NC	−0.11	0.03	−4.04	<0.001	0.15
GWC†	Forest: NC	0.31	0.10	3.22	0.002	0.10
BG††	Forest: NC	−0.62	0.17	−3.75	<0.001	0.02*
NAG††	Forest: NC	−0.44	0.18	−2.43	0.018	0.09*
PHOS††	Forest: NC	−0.57	0.18	−3.19	0.002	0.17*
Phenol oxidase††	Forest: NC	0.82	0.32	2.60	0.020	0.26*
Ammonium	Forest: NC	10.87	4.42	−2.46	0.016	0.05

Nitrate††	Forest: NC	−0.65	0.30	−2.20	0.032	0.07*
Nitrate presence††	Forest: NC	−1.94	0.62	−3.14	0.002	0.13

Table 3. Nutrient analysis of soil cores (7-15 cm depth). C refers to cultivated soil and NC refers to never cultivated soil. SOM refers to soil organic matter. No significant differences found among any variable.

Land Use History	Hurricane Damage	SOM (%)	P (mg/kg)	K (mg/kg)	Mg (mg/kg)	Ca (mg/kg)
C	Intact	9.31 ± 1.58	1.10 ± 0.32	43.8 ± 9.2	261 ± 155	410 ± 235
C	Uprooted	9.78 ± 1.48	1.40 ± 0.84	52.6 ± 21.4	307 ± 241	505 ± 339
NC	Intact	10.68 ± 1.70	1.40 ± 0.55	73.4 ± 21.1	225 ± 110	380 ± 297
NC	Uprooted	8.10 ± 1.97	1.20 ± 0.45	51.2 ± 18.7	208 ± 79	320 ± 144

Table 4. Equations used to calculate soil physical properties and carbon mineralization.

Variable	Equation	Units / notes
Gravimetric water content (GWC)	GWC = (Mwet − Mdry) / Mdry	g H_2O g^{-1} dry soil
Bulk density (Db)	Db = Msoil / Vcore = Msoil / 308.8 cm^3	g soil cm^{-3}
Soil porosity (φ)	$\varphi = 1 - (Db / Dp)$	Unitless; Dp = particle density

Volumetric water content (VWC)	$VWC = Db \times GWC$	$cm^3\ H_2O\ cm^{-3}$ soil
Water-filled pore space (WFPS)	$WFPS = (VWC / \varphi) \times 100$	%
Water required for 50% WFPS	$W50 = (VWC \times 50) / WFPS$	Water added per g soil
CO_2-C concentration (Cm)	$Cm = (Cv \times 12.01) / (R \times T)$	µg CO_2-C L^{-1}
CO_2-C flux	$Flux_{min} = (Cm \times Vh) / (Mass_{soil} \times t)$	µg CO_2-C g^{-1} soil min^{-1}; Vh = 0.875 L
CO_2-C flux per day	$Flux_{day} = [(Cm \times Vh) / (Mass_{soil} \times t)] \times 1440$	µg CO_2-C g^{-1} soil day^{-1}

676