Ecosystem function associated with soil organic carbon declines with tropical dry forest degradation

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Abstract

Forest degradation is increasingly recognized as a major threat to global biodiversity and ecosystems' capacity to provide ecosystem services. This study examined the impacts of forest degradation on soil quality and function in a seasonally dry tropical forest (SDTF) of Ecuador. We compared soil physical-chemical properties, enzymatic activity, particulate organic carbon (POC) and mineral-associated organic carbon (MAOC) along a gradient of SDTF degradation in the dry and rainy season. Our findings showed a consistent and steady reduction in soil quality (total C and N) and function (dehydrogenase and β-glucosidase activity) that paralleled the loss of vegetative structure and diversity along the degradation gradient. Soil physical-chemical properties were less variable and enzymatic activity was generally higher in the dry season compared to the rainy season. We also showed for the first time a significant and uniform decrease in POC and MAOC with ecosystem degradation in a SDTF. The relative proportion of these two components was constant along the gradient except for the most degraded state (arid land), where POC was higher in proportion to MAOC, suggesting that a functional tipping point may be crossed with extreme forest degradation. These findings address an important knowledge gap for SDTFs by showing a consistent loss of soil quality and functionality with degradation and suggest that extreme degradation can result in an alternate state with compromised resilience.

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Abstract. Forest degradation is increasingly recognized as a major threat to global biodiversity and ecosystems' capacity to provide ecosystem services. This study examined the impacts of forest degradation on soil quality and function in a seasonally dry tropical forest (SDTF) of Ecuador. We compared soil physical-chemical properties, enzymatic activity, particulate organic carbon (POC) and mineral-associated organic carbon (MAOC) along a gradient of SDTF degradation in the dry and rainy season. Our findings showed a

consistent and steady reduction in soil quality (total C and N) and function (dehydrogenase and β-glucosidase activity) that paralleled the loss of vegetative structure and diversity along the degradation gradient. Soil physical-chemical properties were less variable and enzymatic activity was generally higher in the dry season compared to the rainy season. We also showed for the first time a significant and uniform decrease in POC and MAOC with ecosystem degradation in a SDTF. The relative proportion of these two components was constant along the gradient except for the most degraded state (arid land), where POC was higher in proportion to MAOC, suggesting that a functional tipping point may be crossed with extreme forest degradation. These findings address an important knowledge gap for SDTFs by showing a consistent loss of soil quality and functionality with degradation and suggest that extreme degradation can result in an alternate state with compromised resilience.

Keywords (max 6): forest degradation; seasonally dry tropical forest; soil function; enzyme activity; POC; MAOC

Introduction

Forest degradation resulting from chronic anthropogenic modification of ecosystem structure, composition or function is gaining increasing attention as a major issue affecting human societies and biodiversity (Ghazoul and Chazdon, 2017; Grantham et al., 2020). Degradation compromises many of the benefits that forests provide (IPBES, 2018), and evidence suggests that the environmental consequences of degradation are potentially as significant as those from deforestation (Walker et al., 2020). The effect of forest degradation on soil dynamics and function is of particular concern given the fundamental role soils play in the provision of multiple ecosystem services (Smith et al., 2015). Given the scale and impacts of forest degradation resulting from chronic disturbance, it is urgent to understand its effects on soil functionality and the implications for ecosystem resilience.

A critical global ecosystem that has experienced widespread degradation is seasonally dry tropical forest (SDTF) (Miles et al., 2006). Representing 42% of tropical ecosystems worldwide and recognized for their high levels of endemicity, species richness, and functional diversity (Dirzo, 2011; Banda-Rodríguez et al., 2016), SDTFs are considered to be one of the most threatened ecosystems globally due to centuries of land use conversion and chronic disturbance (Dimson and Gillespie, 2020; Portillo-Quintero and Sánchez-Azofeifa, 2010). As in tropical rain forests, the study of degradation has experienced a recent upsurge in SDTFs due to a growing recognition of its widespread impacts on biodiversity and ecosystem function (Ribeiro-Neto et al., 2016; Sfair et al., 2018; Souza et al., 2019). The focus of most studies of degradation in SDTFs has been on its effects on taxonomic and functional plant diversity (Arnan et al., 2022; Jara-Guerrero et al., 2021; Ribeiro et al., 2019; Sagar et al., 2003). However, how degradation of SDTFs affects the conditions and ecosystem functions underpinning this diversity, particularly those related to the soil, remains poorly understood (Mora et al., 2018; Schulz et al. 2016).

Two important indicators of soil quality and function are soil organic matter (SOM) content and enzyme activity. As with deforestation and land use conversion, forest degradation drives SOM loss (Jiang et al., 2023, Jiménez et al., 2011), which has major repercussions for the capacity of forests to store C, cycle nutrients, and self-regenerate (Zhou et al., 2018). However, persistent knowledge gaps exist pertaining to the accrual, decomposition and transformation pathways of SOM (Angst et al., 2021; Sokol et al., 2022). These knowledge gaps can be partially addressed by comparing the different components of SOM. Recent approaches distinguish particulate organic matter (POM) from mineral-associated organic matter (MAOM) as two operational physical fractions of SOM with different origins and rates of turnover (Lavallee et al., 2020; Wiesmeier et al., 2019; Yu et al., 2022). Considered to be primarily plant derived, POM contains many structural C compounds with low N content and is preserved in soil via biochemical recalcitrance, physical protection in micro aggregates, and microbial inhibition. MAOM originates largely from soil microbes, contains higher N, and has a longer residence time due to chemical bonding with minerals and physical protection in small aggregates (Cotrufo et al., 2019). It is generally assumed that POM is more accessible but its quality for decomposers varies, whereas MAOM provides labile C and nutrients to microbiota and plants only following destabilization. Thus, POM is considered to be less persistent and more sensitive to disturbance than MAOM (Cambardella and Elliott, 1992; Cotrufo et al., 2019; Poeplau et al., 2018). These functional differences underscore the utility of quantifying POM and MAOM separately in order to better understand the effect of forest degradation on SOM (Lavallee et al., 2020).

Soil enzyme activity is related to SOM fluxes and can provide a useful indicator of soil function in response to disturbance (Barbosa et al., 2023). Among the myriad biotic (e.g., microbial community structure and abundance, plant inputs) and abiotic (e.g., organo-mineral interactions, soil and climatic conditions, chemical quality of C inputs) factors influencing SOM dynamics, soil enzyme activity plays a prominent role (Panettieri et al., 2022). For example, Bernard et al. (2022) demonstrated that turnover rates of SOM integrated by different pools depend on its biochemical composition and accessibility to enzymes. Kandeler et al. (1999, 2019) identified higher rates of enzyme activity in the MAOM fraction due to a greater contribution of microbial compounds. Decomposition of compounds in POM depends on processes of microbial and enzymatic inhibition, while MAOM is more subject to spatial constraints such as mineral association (Lavallee et al., 2020). While studies have demonstrated that enzyme activity decreases with the conversion of STDF to agriculture (e.g., Medeiros et al., 2015; Oliveira Silva et al., 2019), few have addressed how this crucial aspect of soil function is affected by SDTF degradation.

In this study, we examined soil quality and function along a gradient of ecosystem degradation in the STDF of Ecuador in the dry and rainy season. Our objectives were to: (1) compare soil physical-chemical properties under different levels of forest degradation between seasons; (2) evaluate the response of dehydrogenase, β-glucosidase and urease to degradation to understand how enzyme activity affects soil carbon (C) and nitrogen (N) across the degradation gradient in each season; and (3) compare particulate organic carbon (POC) and mineral-associated organic carbon (MAOC) along the degradation gradient to gain insights into the underlying mechanisms of accrual, transformation and persistence of these components of SOM. We discuss the results in the context of the impact of forest degradation on soil functionality in SDTFs, the relationship between this functionality and vegetative structure and diversity, and how extreme degradation could lead to loss of ecosystem resilience.

2. Materials and methods

2.1. Study area

The study was carried out in the SDTF of southwestern Ecuador located in Zapotillo canton within the province of Loja (Fig. 1). This ecosystem lies within the Tumbesian biogeographic region, which extends from the central coast of Ecuador to north-western Peru and forms part of the Tumbes-Choco-Magdalena biodiversity hotspot (Mittermeier et al., 2011). As a consequence of chronic anthropogenic disturbance over decades (if not centuries), most of the original SDTF of the Tumbesian region has been degraded or lost (Mittermeier et al., 2005; Tapia-Armijos et al., 2015). This process of degradation has been more a consequence of low-intensity, chronic use and disturbance of SDTF over time than outright forest conversion to anthropogenic land uses (Jara-Guerrero et al. 2019). The resulting landscape is a mosaic of relatively undisturbed forest fragments, forest fragments with different levels of degradation caused by livestock grazing, selective logging, and firewood extraction, and highly degraded areas nearly devoid of woody vegetation (Tapia-Armijos et al., 2015).

Annual precipitation in the study area ranges from 300-700 mm and mean annual temperature varies between 20-26 °C, with daily temperatures reaching as high as 35 °C during the rainy season (Leal-Pinedo and Linares-Palomino, 2005). The climate is highly seasonal, with a rainy season occurring from January to April and a dry season lasting from May to December (Espinosa et al., 2018). The period from September to November is particularly dry with precipitation generally dropping to below 10 mm per month (Maass and Burgos, 2011). The region is affected by El Nino/Southern Oscillation (ENSO) every 3-7 years, which brings a dramatic rise in ocean surface temperatures and high levels of precipitation (Trenberth, 2019).

According to the geopedological map of Ecuador, soils of the area are primarily Inceptisols, Alfisols and Entisols and are considered eroded and poorly evolved with low to moderate depth, low stoniness, and textures ranging from sandy clay loam to loamy sand with some classfied as loam or sand (Espinosa et al.

2016; MAG, 2019). Elevation of the study sites ranges from 200 to 500 m above sea level.

2.2 Forest states

To define the gradient of ecosystem degradation in the region, we used the state-transition model developed by Jara-Guerrero et al. (2019). Based on expert scientific and local knowledge, this model identifies five states of the SDTF of Ecuador, which can be differentiated according to vegetation structure, species diversity, and the drivers leading to each state. These states are:

- **Natural forest** : High richness of woody plants and high canopy cover with three clear strata (arboreal, shrub and herbaceous) and abundant natural regeneration. Resource extraction is low and limited to small areas.
- **Semi-natural forest** : Lower woody species richness, tree density and natural regeneration compared to natural forest, as well as higher density of herbaceous and shrub species. Persistent livestock grazing (primarily by goats) and/or selective logging drive the transition from natural to semi-natural forest over time.
- **Shrub-dominated forest** : Significantly reduced woody species richness, tree density and regeneration. Trees are isolated or absent and the shrub and herbaceous strata dominate. Common species tend to have high wood density that likely enables them to resist browsing by livestock. Intensification of grazing pressure and logging trigger the transition from semi-natural forest to this state over time.
- **Simplified forest:** Dominance of the tree layer by one or a few species (e.g., *Handroanthus chrysanthus* or *Bursera graveolens*), moderate canopy cover, and regeneration of few species compared to natural forest. This state results from a history of land use favouring few species followed by a transition from shrub-dominated forest when livestock have been removed.
- **Arid land**: Nearly complete absence of woody species except for isolated trees and shrubs. Herbaceous species comprise the only stratum and are highly seasonal, proliferating in the rainy season. Regeneration is low to absent and the soil is highly exposed and eroded. This state results from a transition from shrub-dominated forest when extensive livestock grazing and logging are practiced continually over time.

2.3. Soil sampling and chemical and enzyme analysis

Soil samples were collected from 25 sites representing the five forest states (Fig. 1). Sampling sites were located at least 500 m from one another and are considered independent. Soils were sampled from each site once in the middle of the dry season in October 2021 and once towards the end of the rainy season in May 2022. Four samples were extracted from the topsoil (0-10 cm) at each site and combined to produce a composite sample. After sieving at 2 mm, samples were split into two subsamples: the first was stored at 4 °C prior to biochemical analysis and the second was air dried, crushed and sieved (<60 µm) for chemical analysis.

Soil pH was measured in a 1 M KCl extract (1:2.5, m/v) after shaking for one hour (Hesse, 1971) using a pH meter (CRISON micro pH 2002). Electrical conductivity (EC) was determined in water extract (1:5, m/v) after shaking for one hour using a Conductivity Meter (CRISON micro CM 2201). Sample dry weights were used to calculate soil water content (SWC) by the gravimetric method. Water-soluble carbon (WSC) content was determined using a TOC-VE Shimadzu analyser after extraction with water using a sample-to-extractant ratio of 1:10. Dehydrogenase activity (DHA) was determined according to Trevors (1984) after soil incubation with p-Iodonitrotetrazolium chloride (2-(4-Iodophenyl)-3-(4-nitrophenyl)-5-phenyl-2H-tetrazolium chloride, INT) and measurement of the Iodonitrotetrazolium formazan (1-(4-Iodophenyl)-5-(4-nitrophenyl)-3-phenylformazan, INTF) absorbance at 490 nm. Glucosidase activity (β-Glu) was measured according to Eivazi and Tabatabai (1988) following soil incubation with p-Nitrophenyl-β-D-glucopyranoside and measurement of the p-Nitrophenol absorbance at 400 nm. Urease activity was determined according the method proposed by Kandeler and Gerber (1988) and modified by Kandeler et al. (1999).

2.4 Physical fractionation of soil organic matter

Total organic carbon (TOC) and total nitrogen (TN) were determined using a ThermoFlash 2000 NC Soil Analyzer. For organic C analysis, carbonates were removed from soil samples by acid fumigation with HCl prior to analysis (Harris et al., 2001).

Soils were fractionated by size after aggregate dispersion following the method described by Cambardella and Elliott (1992) and Sokol and Bradford (2019). A 10.5-g portion of each sample, sieved at 2 mm, was shaken for 18 hr in 5 g L^{-1} sodium hexametaphosphate, $Na_6[(PO_3)_6]$. After dispersion, samples were sieved again at 53 µm using a vibratory sieve shaker (AS 200, Retsch). Soil POM and MAOM represented the fraction remaining on the sieve (>53 µm) and that which passed through the sieve (<53 µm), respectively. All fractions were oven-dried at 60°C, weighed, and ground with a zirconium ball mill (MM 400, Retsch) for analyses. Carbon and nitrogen contents of POM and MAOM fractions were analysed as described for TOC and TN. Hereafter, particulate organic and mineral-associated organic C contents are referred to as POC and MAOC, respectively.

2.5 Statistical analysis

To characterize the physical-chemical differences among the five forest states and reduce these parameters to a limited number of factors, we applied principal components analysis (PCA). Differences between states were examined using biplots displaying the first two PCA factor scores. To analyse the effects of ecosystem degradation and seasonality on soil physical-chemical properties and enzymatic activity, generalized linear models (GLMs) followed by Tukey's post hoc test were applied. The five forest states and dry/rainy season were established as the independent variables and soil physical-chemical variables, enzymatic activity, and POC and MAOC fractions were the dependent variables. Given that the interaction between forest state and season was not significant for any of the variables, only their principal effects were interpreted. Levene's test was applied in the GLMs to ensure that the assumption of homogeneity of variance was met. All data are represented as means ± standard error of the mean (SEM).

Pearson correlations were used to assess relationships between variables. For all statistical tests, $p < 0.05$ was selected as the level of significance. Statistical analyses were performed with R version 4.2.3 (R Core Team 2023) and SPSS v25 for Windows (IBM Corp., Armonk, NY, USA).

3. Results

3.1 Soil physical-chemical properties

PCA of the soil physical-chemical variables among the five forest states ($n = 25$) identified two principal components (PC) which together explained 87.8% and 69.2% of the total variance in the dry and rainy season, respectively (Fig. 2). Represented by cluster centroids (i.e., the average score on both PC1 and PC2 with standard errors), the forest states were aligned in the two-dimensional PC space along a gradient of ecosystem degradation from natural, semi-natural, simplified and shrub-dominated forests to arid land. In both seasons, natural and semi-natural forest were associated with high levels of C/N, TOC, TN and WSC as opposed to simplified forest, shrub-dominated forest and arid land, which were associated with low levels of these parameters. In general, these variables declined with ecosystem degradation. For example, TOC on average showed a significant reduction of 15, 37, 54, and 68% and TN decreased significantly by 11, 32, 47 and 55% from natural forest to semi-natural, simplified, shrub-dominated forests, and arid land, respectively (Table 1). Likewise, WSC decreased significantly by 3, 19, 29 and 42% along the same gradient. In contrast, SWC, pH, EC and C/N did not decrease significantly along the gradient although arid land was consistently and, in some cases, significantly lower than natural and/or semi-natural forest for these variables.

In terms of seasonal differences, in the rainy season, natural, semi-natural and simplified forest were clustered with overlapping standard errors while shrub-dominated forest and arid land were separated from this cluster (Fig 2). Variation in the PC1 and PC2 scores of each forest state, as measured by the size of the centroids, was generally greater in natural, semi-natural and simplified forest than shrub-dominated forest and arid land and during the rainy season compared to the dry season. The only soil properties that differed significantly between seasons were SWC and WSC, which, on average, increased by 42.2% +- 5.1 and decreased by 58.7%

+- 1.4 across all forest states from the dry to the rainy season, respectively.

3.2 Enzymatic activity

Enzymatic activity generally declined with ecosystem degradation although differences among forest states were more exacerbated during the dry season (Fig. 3). Dehydrogenase and β-glucosidase in both seasons declined significantly and at a near constant rate with increasing degradation from natural forest to arid land. Relative to natural forest, dehydrogenase activity decreased by 33, 64 and 70% on average in simplified forest, shrub-dominated forest and arid land, respectively for the dry season whereas for the rainy season this enzyme activity was reduced by 11, 22, 28 and 62% from the natural forest compared to semi-natural, simplified, shrub-dominated forests and arid land respectively (Fig. 3a). β-glucosidase activity declined by 12, 41, 62 and 72% on average for both seasons among the natural forest and the gradient of forest degradation (Fig. 3b). In each case, the difference between natural and semi-natural forest was not significant. Urease activity followed the same trend, although the only significant difference was in arid land, where the activity was approximately 63 and 72% less on average compared to the other states for the dry and the rainy seasons respectively (Fig. 3c).

Overall, the rainy season entailed both a reduction in soil enzymatic activity and a weakening of the association between enzymatic activity and most soil properties compared to the dry season. Dehydrogenase and urease activity declined significantly by 63% and 33% in the rainy season relative to the dry season across all forest states, respectively (Fig. 3). β-glucosidase activity also decreased in the rainy season but this difference (12%) was not significant. During the dry season, the activity of the three enzymes was significantly and positively correlated with all soil properties except the POC/MAOC ratio, which showed a significant negative correlation, and pH, which was not significantly correlated with urease activity (Fig. S1a). During the rainy season, the correlation between both dehydrogenase and β-glucosidase activity and SWC, pH, EC and POC/MAOC was no longer significant, while the correlation between urease activity and most properties remained significant but less so (Fig. S1b).

3.3 Organic carbon allocation in soil organic matter fractions

Both POC and MAOC declined along the gradient of ecosystem degradation, whereas the POC/MAOC ratio was nearly constant across all forest states and seasons except in arid land, where it was significantly higher (Fig. 4). POC content was significantly higher in natural and semi-natural forest compared to other forest states by ca. 45% on average (Fig. 4a). MAOC content followed the same pattern, with a reduction during the dry season of 8, 33, 56 and 54% from natural forest to semi-natural forest, simplified forest, shrub-dominated forest and arid land, respectively, and a similar reduction of 21-55% during the rainy season.

Regarding changes in SOM fractions between seasons within the same forest state, the greatest POC losses were detected in semi-natural forest and simplified forest (~30%) followed by natural forest (17%), shrub-dominated forest (14%) and arid land (12%). Losses of MAOC between seasons were less intense and no significant, showing a decrease of 7% for natural forest and 4% for shrub-dominated forest and arid land, while reaching 26% for semi-natural and simplified forest. POC/MAOC ratios remained constant across forest states and seasons, with the exception of a slight but non-significant decline of ca. 17% from the dry to rainy season in shrub-dominated forest and a significant increase in arid land in both seasons.

4. Discussion

Our results showed a consistent and steady reduction in soil quality and function along the gradient of ecosystem degradation in SDTF. While previous studies have shown loss of soil organic carbon (SOC) (Andrade et al., 2020; Maestre et al., 2022; Menezes et al., 2021) and total nitrogen (Andrade et al., 2020) resulting from the conversion of SDTF to different land uses, few studies have focused explicitly on the soil effects of SDTF degradation (Schulz et al., 2016). We show for the first time a significant and uniform decrease in POC and MAOC along a broad gradient of ecosystem degradation in SDTF. The relative proportion of these two components of SOC was constant along the gradient except for the most degraded state (arid land), where POC was higher in proportion to MAOC, suggesting that a functional tipping point may be crossed in the transition from shrub-dominated forest to arid land (Ghazoul and Chazdon, 2017). The patterns of soil C were corroborated by a reduction in the activity of dehydrogenase and β-glucosidase, while those of N led to a decrease in urease activity. These findings address an important knowledge gap for SDTFs by showing a consistent loss of SOM and soil functionality with degradation and suggest that extreme degradation can result in an alternate state with compromised resilience (Oliver et al., 2015).

4.1 Soil quality declines with ecosystem degradation

The alignment of forest states in the PCA biplots indicates a clear gradient of declining soil quality that parallels the decline in vegetation biomass, complexity, and diversity from natural forest to arid land (Jara-Guerrero et al., 2021; Ribeiro et al., 2019). Similar to other studies that have found differences in total C and N between undisturbed and disturbed SDTF (Andrade et al. 2020; Menezes et al. 2021; Schulz et al., 2016), these two important constituents of SOM decreased steadily with degradation. SDTFs tend to have a larger proportion of biomass belowground compared to wet tropical forests (Murphy and Lugo, 1986), with high biomass of roots in the upper soil layers, especially that of fine roots (Castellanos et al. 1991). Thus, belowground biomass associated with the abundant woody vegetation found in natural, semi-natural and, to a lesser degree, simplified forest, can partly explain why these states have high C, N and WSC content as well as a high C/N ratio relative to shrub-dominated forest and arid land. Higher C and N stocks may also be attributed to the different quality and quantity of the litter input in less degraded forests (Machado et al., 2019). Furthermore, variation in the PC scores was higher in these three states than shrub-dominated forest and arid land, likely due to greater heterogeneity in species composition and functional diversity between sampling sites (Ribeiro et al., 2019; Sagar et al., 2003). The scarcity of woody vegetation in shrub-dominated forest and arid land likely increased water stress and had a homogenizing effect on environmental conditions (Andrade et al. 2020; Jara-Guerrero et al., 2019; Menezes et al. 2021), which was reflected as reduced variation in physical-chemical properties.

Plant growth flourishes in all SDTF states during the rainy season, which probably explains the apparent mitigation of the effects provoked by of the degradation gradient relative to the dry season. Most plants in SDTFs shed their leaves during the dry season, contributing a high flux of nutrients (Anaya et al. 2007) that likely exacerbated physical-chemical differences between natural and semi-natural forest and the other states in this season. WSC was especially high in these two states in the dry season, accumulating in substantial quantities due to limited leaching and decomposition in the absence of significant rainfall. In the rainy season, such differences abated because growth in all vegetative strata and functional types attenuated differences in biomass and fresh organic matter among states. This was especially evident for simplified forest, which overlapped with semi-natural forest in the rainy season. Increased variation in PC scores in the rainy season was also probably due to plant growth in all states, revealing heterogeneity among sites within each state (Waring et al., 2021). Despite these seasonal differences, the consistency in the order of forest states in both seasons reinforces the notion that soil quality declined along the gradient of SDTF degradation.

4.2 Enzymatic activity declines with ecosystem degradation

The likely driver of differences in soil quality among forest states was enzymatic activity, which decreased at a steady rate along the gradient of SDTF degradation. In a global meta-analysis, enzyme activity was also found to decrease due to less substrate availability in intensive management practices (Sinsabaugh et al., 2008). The decline in enzymatic activity found in this study paralleled that of soil C and N, which again can be attributed to differences in vegetation biomass and diversity among forest states. The largest declines were in dehydrogenase and β-glucosidase activity, indicating their usefulness as indicators of soil quality, whereas urease activity also decreased but not significantly, except in arid land. Likewise, Oliveria Silva et al. (2019) found that β-glucosidase activity was the best indicator of dry forest conversion to agriculture in the Brazilian Caatinga. However, Sandoval-Pérez et al. (2009) found that urease and dehydrogenase were not good indicators of land-use effects on soil fertility in a Mexican dry forest. Thus, while enzymatic activity can provide a useful indicator of soil function in response to anthropic disturbance, these studies underscore the need for further research to generalize results for SDTFs.

The activity of all three enzymes was similar between natural and semi-natural forest, indicating minimal loss of soil function with moderate degradation of SDTF. In contrast, activity of dehydrogenase and β-glucosidase was significantly reduced in shrub-dominated forest and arid land, and urease activity was significantly lower in arid land. Loss of canopy cover and woody species richness in shrub-dominated forest and arid land likely caused this severe reduction in soil function (Singh et al., 2018). This may result from the direct effects of plant species loss or indirect effects like increased soil erosion and water stress due to removal of the canopy (Jara-Guerrero et al., 2021; Singh et al., 2018). However, the results also showed that the transition to simplified forest that occurs when livestock are excluded from shrub-dominated forest and natural regeneration is allowed to proceed (Jara-Guerrero et al., 2019) facilitated the recovery of moderate levels of dehydrogenase and β-glucosidase activity. Given that simplified forest is species poor relative to natural and semi-natural forest, these results suggest that a threshold of canopy cover and tree density is more important than species diversity to recover the functionality associated with these enzymes (Singh et al., 2018).

Higher enzymatic activity in the dry season than the rainy season was counterintuitive, but could be explained by the exact moment soils were sampled in each season. For the rainy season, samples were collected near the end of the season in May when the leaf litter and SOM had largely been decomposed and leaf fall had not yet occurred (Anaya et al., 2007). The low quantity of substrate may explain why enzymatic activity was significantly reduced in the rainy season. For the dry season, soils were sampled in October following the peak of leaf fall and after several months of accumulation of plant litter and exudates (Anaya et al., 2007), which increase the OM content of the soil and in the process mitigate the conditions to which soil microbes are exposed, particularly soil moisture. Both urease and β-glucosidase are extracellular enzymes, meaning they can continue to function as long as some moisture remains, even after the cells that synthesized them are gone (Barbosa et al. 2023). Strong correlations between most soil properties and the three enzymes indicated the importance of these parameters for enzyme function in the dry season, whereas total N and WSC were highly correlated with enzyme function in the rainy season, which were likely related to OM flush events caused by rainfall (Murphy and Lugo, 1986; Oliveria Silva et al., 2019).

4.3 Drivers of soil organic matter fractions

The uniform decline in POC and MAOC in the same relative proportion among forest states except arid land indicated similar effects of degradation on both fractions. POM and MAOM are assumed to have different C turnover rates and degrees of physical-chemical protection owing to distinct origins (Lavallee et al., 2020; Nicolás et al., 2012). Comparing these fractions between different ecosystems, Yu et al. (2022) found that 90% of grassland/shrubland soils stored more SOC as MAOM than POM, whereas 40% of forest soils exhibited a higher POM fraction, which was attributed to the contribution of woody vegetation. Similarly, POC was shown to be highly sensitive to soil changes resulting from the conversion of dry forest to crops in the semiarid Chaco (Villarino et al., 2017). Focusing on the C component in POM and MAOM, we thus expected a proportionally larger fraction of POC in less degraded SDTF states given its origin primarily from plants (Baldock and Skjemstad, 2000). Contrary to our expectations, however, the POC/MAOC ratio was constant across natural, semi-natural, simplified and shrub-dominated forests in both seasons, despite large differences in vegetative biomass and structure among these states. This suggests that POC and MAOC were equally susceptible to forest degradation and, in general, degradation resulted in SOC loss despite mineral protection in soil aggregates. In contrast, studies from other ecosystems show a decoupling of POC and MAOC. For example, soils with high SOC tend to store more C as POC given that MAOC reaches saturation (Cotrufo et al., 2019). In disturbed soils, MAOC is more stable and less sensitive to disturbance (Sokol and Bradford, 2019). However, our results support the hypothesis that the two fractions are coupled, suggesting that microbial and plant residues contribute to both components to a similar extent and with the same dynamics (Angst et al., 2021; Córdova et al., 2018; Yu et al., 2022). It is also possible that soil texture, SOC content, and precipitation play important roles in the distribution of organic C within physically and chemically defined pools (Haddix et al., 2020; Yu et al., 2022). Despite significant progress toward understanding the intrinsic mechanisms of POC and MAOC distribution and functions in soils, further research is needed to identify the primacy of biotic versus abiotic controls on their dynamics in SDTFs subjected to different degrees of disturbance.

The higher POC/MAOC ratio in arid land compared to the other forest states implies a functional tipping point with extreme degradation (Ghazoul and Chazdon, 2017). This anomaly in arid land is likely the outcome of several related factors. First, the microbial C pump conceptualized by Liang (2020) that transforms plant residues to POC and finally to MAOC through microbial anabolism was probably disrupted by the harsh biotic and abiotic conditions of this state. Functioning of this mechanism occurs via microbial transformation of POC through microbial biomass and ultimately conversion into MAOC. Low inputs of leaf litter and root exudates as well as water stress inhibit microbial activity and biomass and constrain the C pump (Liang 2020), which could lead to changes in the proportions of POC and MAOC. Likewise, low vegetative cover means that arid land is prone to erosion, which leads to nutrient leaching and depletion of SOC stocks (Villarino et al., 2017). Second, lower quality litter tends to favour the formation of POC over MAOC (Cotrufo et al., 2013). Therefore, low litter quantity and quality combined with water stress in arid land likely contributed low decomposition rates (Machado et al., 2019) which, in turn, inhibited the conversion of POC into MAOC. Third, sandier soils in arid land could inhibit the formation of MAOC given that it tends to associate with fine silt and clay particles (Lavallee et al., 2020; Machado et al. 2019; Schulz et al. 2016). Any or all of these factors could result in a lower proportion of MAOC compared to less degraded states, altering the delicate balance between these two fractions and disrupting an important function of SOC storage and turnover. Given the implications of this tipping point for the resilience of the STDF ecosystem, we urgently need to better understand the mechanism underlying this result.

5. Conclusions

Forest degradation is increasingly recognized as a major threat to global biodiversity and ecosystems' capacity to provide ecosystem services. This study contributes to our understanding of the impacts of forest degradation on soil quality and function in SDTFs. Whereas previous studies of this ecosystem have focused on the effects of land-use conversion on soils, particularly agriculture, our study is among the first to examine soil impacts of forest degradation resulting from chronic disturbance. The effects of forest degradation might not be as obvious as those from deforestation, but understanding them is as important for ensuring ecosystem integrity and resilience as fathoming the impacts of land-use change.

Our findings showed a consistent and steady reduction in soil quality and function that paralleled the loss of vegetative structure and diversity along a gradient of SDTF degradation. Above and belowground conditions were clearly linked in the different forest states and between seasons. This implies that while degradation can drive the loss of soil C, N and enzymatic activity through the depletion of vegetation biomass and richness, well-designed restoration strategies can help reverse those losses.

The case of arid land, however, suggests that extreme forest degradation could lead to an alternate state in which critical biochemical pathways cease to function. Diminished soil quality, low enzymatic activity, and a high POC/MAOC ratio suggested that this state lies beyond a critical threshold of ecosystem resilience and requires serious intervention to recover soil functionality. The question as to whether continued disturbance to this state would lead to desertification requires urgent attention.

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Declarations

Conflict of interest The authors declare that there is no conflict of interest

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