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Effects of Land Use Change from Natural Forest to Livestock on Soil C, N and P Dynamics along a Rainfall Gradient in Mexico

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Abstract: The effects of converting native forests to livestock systems on soil C, N and P contents across various climatic zones are not well understood for the tropical region. The goal of this study was to test how soil C, N and P dynamics are affected by the land-use change from natural forests to livestock production systems (extensive pasture and intensive silvopastoral systems) across a rainfall gradient of 1611–711 mm per year in the Mexican tropics. A total of 15 soil-based biogeochemical metrics were measured in samples collected during the dry and rainy seasons in livestock systems and mature forests for land-use and intersite comparisons of the nutrient status. Our results show that land-use change from natural forests to livestock production systems had a negative effect on soil C, N and P contents. In general, soil basal respiration and C-acquiring enzyme activities increased under livestock production systems. Additionally, reduction in mean annual rainfall affected moisture-sensitive biogeochemical processes affecting the C, N and P dynamics. Our findings imply that land-use changes alter soil C, N and P dynamics and contents, with potential negative consequences for the sustainability of livestock production systems in the tropical regions of Mexico investigated.

Keywords: climate change; drought; rainfall regime; soil biogeochemistry

1. Introduction

Globally, soils store at least three times as much carbon (C) as is found in either the atmosphere or living plants [1–3], with the largest portion of it found in tropical forests [4,5]. A global examination of the terrestrial C stocks highlighted that the largest soil organic C stocks in tropical lands are subject to the greatest risks [2], and land-use change continues to pose a threat to tropical forests [6–8]. Moreover, earth-system models have shown that these C stocks in soils will become increasingly vulnerable during the twenty-first century, since reduced rainfall and large-scale agricultural transformation of forests, primarily to pastureland [9,10], are predicted for large areas of the tropics [11]. Tropical



ecosystems dominate the exchange of CO₂ between the atmosphere and terrestrial biosphere, yet our understanding of how nutrients control the tropical C dynamics remains far from complete. A better understanding of nitrogen (N) and phosphorus (P) balances in soils can help guide the implementation of mitigation policies and land-use management, since the supplies of one or both nutrients constrain C uptake in the tropics [12]. In contrast to the clear inventory-based assessments of aboveground C on global scales [4], C cycling in soils remains less well understood, due to high biogeochemical variation in the tropics [13].

Environmental factors such as rainfall decline, together with agricultural expansion, generate abrupt, large-scale changes in forestlands and alter soil C, N and P dynamics [14–16]. The impacts of converting natural forests to systems for livestock production on soil C, N and P dynamics have been well examined at the stand scales, with studies relating variations in above- and below-ground C input through litterfall and root exudation to these inherently different management practices [17]. However, the influence of wider regional or global-scale conversion of natural forests to livestock on soil C, N and P dynamics is not yet well understood. This is perceived as a key bottleneck in improving the prediction and evaluation of the results of soil C mitigation efforts related to land-use change; it is also an impediment to better understanding the degradation of soil quality. Previous studies have suggested that converting native forests to livestock systems significantly impacts the quantity and quality of C and nutrient inputs [18,19], and that these changes could be sensitive to rainfall regime. Converting annual cropland to perennial pastureland enhanced microbial biomass and enzyme activities involved in C, N and P cycling due to lower fluctuations in soil water content in pastureland [20]. Campo et al. [21] reported that changes in the land cover can increase surface soil C pools in the dry tropics, while converting native forests to pasturelands in the humid tropics significantly decreases C contents in soils. The changes in land use and management may decrease soil organic matter content and significantly alter soil water dynamics, which would have effects on soil organic carbon [22].

Mexico, with a land area of 1.96 million km², covers climatic gradients, from humid to dry climate zones, and has experienced diverse and intensive land-use change for animal production, mainly in the tropical regions of the country [23], which are responsible for 50% of national livestock production [24]. Today, beef production in the tropics of Mexico is undergoing major changes with the introduction of management practices for long-term sustainable intensification (intensive silvopastoral systems) through more efficient use of water, materials, and energy [25,26]. Intensive silvopastoral systems are an emerging response to the increasing consumption of animal protein in the country [27] and an alternative to extensive pasture systems, which clear the natural cover to open space for cattle grazing [28,29], reducing the biodiversity and ecological services [30–34], and this intensification of livestock production systems could become a key climate change mitigation technology [35]. For example, intensive silvopastoral systems can produce 12 times more meat than extensive pasture systems [36], and their annual methane emissions per tonne of meat produced are 1.8 times lower than those of extensive pastures systems [37]. With its variety of tropical climates and livestock production systems, Mexico can be viewed as a unique laboratory containing complex interactions between climatic zones and human activities, and thus providing an excellent opportunity to examine simultaneous climate and livestock production impacts on soil fertility, particularly on soil C sequestration and background nutrient status.

To better understand the complex interactions among rainfall, livestock strategies, soil, and C, N and P dynamics, we analyzed C and nutrient dynamics across a gradient of sites varying in rainfall amount (from 1661 to 711 mm year⁻¹), using a robust experimental design. The gradient contains 12 sites, including mature tropical forests (as natural forests), extensive pasture and intensive silvopastoral systems located in humid, subhumid and semiarid climates in the southeast of Mexico. In particular, we studied how C, N and P dynamics in the topsoil layer (upper 10 cm of soil) differed between adjacent native forests and livestock systems, and if those differences were related to rainfall amount or livestock production system (i.e., pastures and silvopastoral). We examined soil bulk organic

2. Material and Methods

as indicators of soil C and nutrient biogeochemistry.

2.1. Study Areas

The study was carried out at four sites with different mean annual rainfall (MAR) in Mexico; two located in a dry tropical region, where MAR decreases from 917 to 711 mm, and two in a humid tropical region, where MAR decreases from 1661 to 1232 mm (Table 1). At each location, we evaluated two types of livestock system: extensive pastures systems and intensive silvopastoral systems. In addition, at each location, a natural forest site (tropical forest in all cases) was used as a reference for original soil fertility conditions. The criteria used for the selection of sites were: (i) sites that shared the same mean annual temperature, but located across a gradient of MAR; (ii) the presence of natural forests, pastures and silvopastures within the same edaphic conditions within each site; (iii) extensive pastures with around 25 years of land use; (iv) silvopastures with around 5 years of land use after around 20 years of extensive pasture systems; (v) both livestock production systems located at a distance of no more than 5 km from the reference (i.e., natural forests). To ensure that none of the sites had been subjected to other human activity, sites were selected following consultations with local owners and a review of the regional government's land-use database.

Long-term climate data from weather stations show that all sites are characterized by a distinct period of low precipitation (four to seven months with rainfall below 100 mm; Table 1). The four sites differ strongly in aridity index (i.e., mean annual rainfall divided by mean annual evapotranspiration). Across the sites, variation in mean annual temperature is less than 1.5 °C, and the climate, semiarid to subhumid, would support from tropical dry to humid forests in the Holdridge Life Zone System [38]. Soils (Inceptisols at the wettest end of the rainfall gradient, and Entisols at all three drier sites) have bulk density and clay content that decrease across sites with decreased rainfall amount, and pH that increases from the wettest site to the driest site of the gradient.

Location	20°51′ N, 89°37′ W	21°08′ N, 88°09′ W	19°24' N, 96°22' W	20°01′ N, 97°06′ W
Altitude (m)	10	20	14	121
Mean annual temperature (°C) ²	25.7	25.3	25.4	24.4
Mean annual rainfall (mm year ⁻¹) ²	711	917	1232	1661
Potential evapotranspiration (mm year ^{-1}) ¹	1719	1677	1561	1215
Aridity index ²	0.41 (semiarid)	0.55 (dry subhumid)	0.79 (humid)	1.37 (humid)
Water stress months	October-May	November-May	October-May	January–April
Mean month rainfall in water stress months				
$(\text{mm month}^{-1})^3$	27	53	29	80
Soil bulk density (g cm ⁻³)	0.8	0.8	0.9	1.1
Soil clay content (%)	12.1	12.5	15.4	15.5
Soil pH (H ₂ O)	8.0	7.6	7.4	5.1

Table 1. Location and characteristics of four study sites across the southeast of Mexico.

¹ Long-term climatic data (1975–2019 period; *Comisión Nacional de Aguas* personal communication). ² Aridity Index [39,40]. ³ Water stress months are the number of months per year with rainfall < 100 mm.

Three mature forest stands at each site were selected. The predominant vegetation at the three drier sites is the seasonally dry tropical forest (i.e., forests subjected to prolonged dry season; [41]), while humid tropical forests dominate at the wettest end of the rainfall gradient. Floristically, *Leguminosae* is the most important family across studied sites [42–44], and the abundance of *Leguminosae* trees increases with the decrease in MAR.

The average size of extensive pasture system generally increases with the rainfall amount (87.3 ha in the 1232 mm site, 100 ha in the 711 mm site, 123 ha in the 917 mm and 170 ha in the 1661 mm of MAR site). The extensive pasture system at all sites is dual-purpose, for dairy and meat productions. The average age of pastures of this type was 25 years at the four study sites. At the drier sites (711 and 917 mm of MAR), in pasture systems, one head of cattle per hectare graze for ~2 days and rotate every ~35 days, while an average of 1.3 animals per hectare graze for ~7 days and rotate every ~45 days at the wetter locations (1232 and 1661 mm of MAR). Livestock are usually supplemented with poultry litter and mineral salts at both drier sites, and the pastures do not receive applications of inorganic fertilizers. The most common species used as forage are *Penniseptum purpureum*—Heinrich C.F. Schumacher, *Pannicum maximum*—Jacq., *Cynodon nlemfuensis*—McVaugh, and *Brachiaria brizantha*—Hochst. ex A. Rich. Stapf [45]. Pastures do not receive fertilization at the wetter sites of the rainfall gradient, and the species used as forage are *Brachiaria brizantha*—Hochst. ex A. Rich. Stapf, *Paspalum vaginatum* Swartz, *Cynodon plectostachyus* (K. Schum.) Pilg., *Digitaria decumbens* Stent., *Pennisetum clandestinum* Hochst. ex Chiov, and *Panicum maximum* Jacq. [45]. The establishment of pastures at all study sites was carried out via traditional slash-and-burning of natural forests, followed by ploughing.

The implementation of silvopastoral systems along the rainfall gradient is relatively recent, since the age of the plots range from 4 to 6 years. The establishment of the silvopastoral systems was carried out at sites previously dedicated to extensive pastures for around 20 years, followed by ploughing and the planting of a monoculture of native trees (*Leucaena leucocephala* (Lam.) de Wit.) in high density (~10,000 per hectare). The average animal load in silvopastoral systems is 3 animals per hectare at both drier sites, which graze for ~1 day, while a larger number of livestock (4 to 6 animals per hectare) graze for ~4 days in the wetter sites; cattle are rotated every ~30 days at all four study sites.

2.2. Soil Sampling and Analysis

Sampling of soils was carried out in the dry (April) and rainy (October) seasons of 2017. One plot $(10 \times 50 \text{ m})$ was established at each forest stand, pasture and silvopastoral system, and five equidistant (10 m) samples were taken for each type of land use. The topography of all selected plots was even to minimize the effects of local terrain on soil fertility [46]. Samples were taken from the topsoil (0–10 cm in depth), combined into one composite sample per plot and stored at 4 °C prior to analysis. A total of three composite samples (from three independent landowners) per site for each type of land use were taken. The upper 10 cm of the soil profile concentrates organic C in tropical dry and tropical humid forests of Mexico [21]. Soil samples were air-dried and sieved (2 mm mesh), and gravimetric water content in fresh soil samples was determined prior to analysis to correct the soil weight used in each determination. Although water content in fresh soils did not vary among land uses or across sites, samples taken in the dry season had less moisture than those taken in the rainy season (23.7 ± 2.1 and 43.9 ± 4.1%, respectively; mean ± 1 standard error).

Soil texture [47] and pH (in water) were determined prior to C, N and P analyses. Total and inorganic C (carbonates) concentrations were analyzed in an automated C analyzer (SCHIMADZU 5005A), by grinding a 5-g air-dried subsample (100-mesh screen). Organic C was estimated from the difference between total and inorganic C concentrations. The concentration of total N and total P was determined by acid digestion [48] using an NP analyzer (Technicon Autoanalyzer III). Soil available P was extracted using the Bray and Kurtz [49] method for acidic soil (pH \leq 7), and the Olsen method was used for alkaline soils (pH > 7). After extraction, available soil P concentrations were determined with the colorimetrical method [48].

Carbon and N concentrations in soil microbial biomass were determined by chloroform fumigation– extraction methods [50] using replicated samples of fresh soil. Fumigated and non-fumigated samples were incubated at 24 °C for 24 h. Microbial biomass C was extracted with 0.5 MK₂SO₄, filtered (Wathman No. 42 paper), and the concentration of C was measured using an automated C analyzer. Microbial C was estimated from the difference between C concentrations in the fumigated and the non-fumigated extracts, and a conversion factor k_C equal to 0.45 [50] was used. Microbial biomass N was extracted in a similar way, after filtering through Wathman No. 1 paper, the filtrate was digested in acid and the total concentration of N was determined using an automated NP analyzer. Microbial N concentration was calculated in a similar way to microbial C, using a conversion factor k_N of 0.57 [51].

Soil basal respiration was determined from duplicated fresh subsamples (20 g) incubated at 25 °C. Soil subsamples were moistened to 50% water-filled pore space following light tamping in a jar (700 mL) containing vials of water to maintain humidity and 10 mL of 1.0 M NaOH to absorb CO_2 . Alkali traps were replaced at 1, 2, 3, 5, 7, 14, 21 and 28 days and were removed at 35 days. Evolved CO_2 was determined by titration of alkali with 0.5 M HCl [52]. Soil basal respiration was calculated using measurements from days 3 to 35 to avoid the majority of flush due to drying and rewetting. The CO_2 flux produced was standardized per gram of soil organic C.

We measured mineral N concentrations (NO₃ plus NH₄) and net N mineralization and nitrification rates using 2 M KCl extraction and aerobic incubation methods. Mineral N concentrations were measured by extracting a 15-g sub-sample in 100 mL 2 M KCl [53]. The soil KCl solution was shaken for 1 h and allowed to settle overnight. A 20 mL aliquot supernatant was transferred to vials and frozen for analysis (initial mineral N concentration). Nitrogen mineralization and nitrification rates were measured during 15-day aerobic incubations [53]. A second sub-sample was wetted to field water holding capacity with distilled water, maintained at field capacity moisture and incubated at 25 °C for 15 days before extraction, using KCl (final mineral N concentration). Analysis of both initial and final mineral N concentrations was done on an Autoanalyzer system using procedures to determine NO₃–N plus NO₂–N, which were reported as NO₃–N, and using the salycilate–hypochlorite procedure for NH₄–N. Nitrogen mineralization rate was determined from the difference between mineral N concentrations at the start and end of the incubation, and results were expressed on a basis of mean daily mineral N production. Likewise, nitrification rate was determined from the difference in NO₃–N

We measured the indicator enzymes most commonly used to infer growth-limiting C sources and nutrients: β -1, 4-glucosidase (BG; enzyme commission number: EC 3.2.1.21) and polyphenol oxidase (POX; EC 1.10.3.1) to infer C-acquiring enzymes, β -1, 4-N-acetylglucosaminidase (NAG; EC 3.2.1.14) to infer N acquiring enzymes, and acid phosphatase (AP; EC 3.1.3.1) to infer P acquiring enzymes [54], following the method proposed by Jackson et al. [55]. The enzyme assays were incubated at 25 °C for 2 h and their absorbance was recorded using a microplate reader at 410 nm for β -1, 4-glucosidase, β -1, 4-N-acetylglucosaminidase and acid phosphatase activities, and at 460 nm for polyphenol oxidase activity. The concentration of pNP (or tyrosine, for polyphenol oxidase) detected in the soil sample was corrected by subtracting the sum of absorption from the sample and substrate control wells, and enzyme activities were calculated as follows:

$EA = (\text{final absorbance})/(C \times \text{incubation time} \times \text{soil dry mass})$

where *EA* is the enzyme activity expressed in μ mol of pNP (or tyrosine, for polyphenol oxidase) released per gram of soil per hour (μ mol g⁻¹ h⁻¹), and *C* is the conversion factor that relates absorbance to μ mol of pNP (or tyrosine, for polyphenol oxidase) for each enzyme activity.

2.3. Statistical Analyses

For each metric, a one-way ANOVA was performed, testing the effects of the rainfall regimen and the effect of the land-use change. The ANOVA residuals were explored for normality using the Shapiro–Wilk's test. Data were transformed logarithmically when the assumptions of normality did not occur; the following soil metrics violated the normality assumptions: microbial biomass C and N concentrations, net N transformation rates and the activity of the β -1, 4-glucosidase. The honest significant difference (HSD) test was used when statistical differences (p < 0.05) were observed across sites, or among land uses in each site. The interactions between soil metrics, land uses (natural forests, pastures and silvopastoral systems) and rainfall regime (MAR) were explored using a principal component analysis (PCA). In addition, correlation matrices were used as a way to depict the relationships between soil metrics within each site in both sampling seasons (i.e., dry and rainy seasons). All statistical analyses were performed using R statistical software [56].

3. Results

3.1. Carbon, Nitrogen and Phosphorus Concentrations

Soil organic C, total N, total P and, microbial biomass C and N concentrations were the highest at the driest end of the rainfall gradient and decrease with rainfall increase, meanwhile NH_4 concentration was higher in the wettest end of the rainfall gradient (Figures 1–3, Table 2). Rainfall regime did not have a significant effect on soil NO_3 and available P concentrations (Figure 2). Rainfall seasonality did not affect the organic C, total N, total P, and microbial biomass C and N concentrations in soils. However, NH_4 and NO_3 concentrations were higher in the rainy season than in the dry season. In contrast to the seasonal variation in soil inorganic N concentrations, available P concentration was consistently higher in soils taken in the dry season than those taken in the rainy season.

Land-use change from natural forests to both livestock production systems (i.e., extensive pasture and intensive silvopastoral systems) decreased soil organic C, total N and P available concentrations (Figures 1 and 2, Table 2). In contrast, no significant changes in NO₃, NH₄, total P and microbial biomass C and N concentrations were detected with land-use change (Figures 1–3). Finally, no significant changes in soil C, N and P concentrations were detected between livestock production systems.

Metric	Source of Variation		
	Site	Season	Land Use
		F	
Organic C (OC)	34.6 ***	0.595 NS	8.45 **
Total N (TN)	50.5 ***	1.33 NS	6.47 **
NH_4	23.0 ***	13.9 ***	0.626 NS
NO ₃	4.36 NS	59.8 ***	1.55 NS
Total P (TP)	43.0 ***	0.676 NS	2.61 NS
Available P (AP)	0.565 NS	29.9 ***	6.48 **
Microbial biomass C (MBC)	32.0 ***	1.14 NS	3.44 NS
Microbial biomass N (MBN)	16.4 ***	0.860 NS	0.042 NS
Soil basal respiration (SBR)	2.95 *	0.124 NS	6.76 **
Net N mineralization (MIN)	17.4 ***	4.20 *	1.13 NS
Net nitrification (NIT)	32.9 ***	4.15 *	1.05 NS
ß-1, 4-glucosidase (BG)	8.06 *	8.94 **	3.36 NS
Polyphenol oxidase (POX)	37.0 ***	2.85 NS	2.21 NS
ß-1, 4-N-acetylglucosaminidase (BNA)	10.1 **	0.851 NS	4.69 *
Acid phosphatase (PHO)	70.1 ***	0.305 NS	6.84 *

Table 2. Site, season and land-use effects on soil carbon, nitrogen and phosphorus metrics along a rainfall gradient in Southeast Mexico.

Significance main effect: NS, *p* > 0.05; *, *p* < 0.05; **, *p* < 0.01; ***, *p* < 0.001.

500

400

300

200

а





350

300

250

200 150

Figure 1. Soil organic carbon, total nitrogen and total phosphorus concentrations in dry (a-c) and rainy (d-f) seasons under natural forests, pastures and silvopastoral systems along a rainfall gradient. Data are means and confidence intervals.



Figure 2. Cont.



Figure 2. Soil ammonium, nitrate and available phosphorus concentrations in dry (**a**–**c**) and rainy (**d**–**f**) seasons under natural forests, pastures and silvopastoral systems along a rainfall gradient. Data are means and confidence intervals.



Figure 3. Soil microbial biomass carbon and microbial biomass nitrogen concentrations in dry (**a**,**b**) and rainy (**c**,**d**) seasons under natural forests, pastures and silvopastoral systems along a rainfall gradient. Data are means and confidence intervals.

3.2. Soil Basal Respiration and Net Nitrogen Transformations

The soil basal respiration was greater in wetter sites (i.e., sites with 1232 and 1661 mm of MAR) than in the drier counterparts (i.e., sites that receive 711 and 917 mm of MAR) (Figure 4, Table 2). In addition, net N transformations differed considerably among sites reflecting changes in rainfall amount. However, the paired comparisons using the Tukey–Kramer HSD test show that soils from the driest end of the rainfall gradient had the highest N transformations, and net N mineralization and net nitrification rates decreased with increase in rainfall amount. The season did not have a significant effect on soil basal respiration. However, large variation in net N transformations between seasons were observed, with higher net N mineralization and net nitrification rates in the rainy season than in the dry season.

Land-use change from natural forests to extensive pasture and intensive silvopastoral systems increased soil basal respiration (Figure 4, Table 2). However, net N transformations did not change with land-use change irrespective of the livestock production system. No significant changes in these soil C and N fluxes were observed between pasture and silvopastoral systems.



Figure 4. Soil basal respiration, net nitrogen mineralization and net nitrification in dry (**a**–**c**) and rainy (**d**–**f**) seasons under natural forests, pastures and silvopastoral systems along a rainfall gradient. Data are means and confidence intervals.

3.3. Enzyme Activities

The activity of C- and N-acquiring enzymes varied significantly among sites; but changes were not consistently related to rainfall regime (Figure 5, Table 2). Intermediate sites across the gradient (i.e., sites that receive 911 and 1232 mm of MAR) had higher polyphenol oxidase and 4-N-acetylglucosaminidase, or β -1, 4-glucosidase activities, respectively, whereas the wettest site showed the lowest activity for the three enzymes. In contrast, soils from the wettest end of rainfall gradient had the highest acid phosphatase activity, reflecting the low concentration of available P. Rainfall seasonality did not have consistent effect on the activity of C-, N- and P-acquiring enzymes (e.g., on polyphenol oxidase, β -1, 4-N-acetylglucosaminidase, and acid phosphatase) across sites. However, generally the activity of β -1, 4-glucosidase was greater in soils collected in the dry season than in soils collected in the rainy season.

The land use did not affect the activity of C-acquiring enzymes in soils (Figure 5, Table 2). However, there were significant differences in the activity of N- and P-acquiring enzymes between natural forests and intensive silvopastoral systems across sites, with an increase in the ß-1, 4-N-acetylglucosaminidase and acid phosphatase activities under the legume-silvopastoral system. No significant changes in N- and P-acquiring enzyme activities were detected in between extensive pastures and natural forests, or with intensive silvopastoral systems.



Figure 5. Cont.



Figure 5. Activities of β-1, 4-glucosidase, polyphenol oxidase, β-1, 4-N-acetylglucosaminidase and acid phosphatase in soils in dry (**a**–**d**) and rainy (**e**–**h**) seasons from natural forests, pastures and silvopastoral systems along a rainfall gradient. Data are means and confidence intervals.

3.4. Multivariate Analysis and Soil Metric Relationships

The PCA allowed us to observe the effects of rainfall on soil metrics in each land-use system in the dry and rainy seasons (Figure 6). The two firsts principal components explained 61 and 52 percent of data variation for the dry and rainy seasons, respectively (Tables 3 and 4). Across the entire data set, the first principal axis summarized 47 percent of the variation in soil metrics in the dry season (Figure 6a, Table 3). Organic C, total N, NH₄ and acid phosphatase had the highest correlation scores on this axis. Sites found at the negative end of PC1 exhibited the lowest activity of acid phosphatase (pastures and silvopastoral systems at 1232 and 1661 mm of MAR) and the highest NH₄ concentrations (pastures and silvopastoral systems at the wettest end of the rainfall gradient) (Figures 2 and 5). By contrast, sites found at the positive end (natural forests and pastures at the driest end of the rainfall gradient) exhibited the highest organic C and total N concentrations (Figure 1). The second axis accounted for 14 percent of the variation in soil characteristics. Sites found at the negative end of PC2 exhibited resplained variation in soil characteristics. Sites found at the negative end of PC2 exhibited the highest polyphenol oxidase activities irrespective of land use (sites at 917 mm of MAR). By contrast, sites found at the positive end (all land uses at the driest end of the gradient) exhibited low phosphatase activity.

On the other hand, in the rainy season, the first principal axis summarized 34 percent of the variation (Figure 6b, Table 4). The importance of organic C, total N and acid phosphatase detected in the soils of the dry season was also observed in the first PC of the rainy season soil samples. Sites found at the negative end of PC1 exhibited high values in acid phosphatase activities under livestock production systems (the wetter sites; i.e., extensive pastures and silvopastoral systems at 1232 and 1661 mm of MAR). Furthermore, the positive end of the PC1, reflect the highest organic C and total N concentrations in soils under the natural forests at the 711 mm of MAR. The second

axis accounted for 17 percent of the variation. Polyphenol oxidase and microbial biomass C and N explained the second-largest fraction of the explained variation in soils. Sites found at the negative end of PC2 exhibited the highest concentrations of microbial biomass C and N under extensive pastures and intensive silvopastoral systems at the driest end of the rainfall gradient. By contrast, sites found at the positive end of this spectrum exhibited the highest polyphenol oxidase activity under extensive pastures and intensive silvopastoral systems, but in sites at 917 mm of MAR.



Figure 6. Principal components (PC) analyses biplots of the soil metric data for sites along a rainfall gradient in dry (**a**) and rainy (**b**) seasons. Red circles 711-mm of mean annual rainfall sites; green triangles 917 mm of mean annual rainfall sites; blue squares 1232 mm of mean annual rainfall sites; lilac symbols 1611 mm of mean annual rainfall sites.

	PC1	PC2	PC3
Eigenvalue	7.045	2.091	1.440
Cumulative percent variation	46.9	60.8	70.4
Eigenvectors			
Organic C (OC)	0.94	0.06	0.14
Total N (TN)	0.91	-0.26	0.12
NH_4	-0.64	0.20	0.12
NO ₃	-0.52	-0.13	0.58
Total P (TP)	0.84	0.06	-0.14
Available P (AP)	0.44	0.63	0.49
Microbial biomass C (MBC)	0.80	-0.14	0.001
Microbial biomass N (MBN)	0.68	0.27	0.31
Soil basal respiration (SBR)	0.43	-0.61	-0.41
Net N mineralization (MIN)	0.84	0.39	-0.15
Net nitrification (NIT)	0.87	0.35	-0.13
ß-1, 4-glucosidase (BG)	0.08	0.21	-0.43
Polyphenol oxidase (POX)	0.21	-0.74	0.34
ß-1, 4-N-acetylglucosaminidase (BNA)	0.70	-0.11	0.17
Acid phosphatase (PHO)	-0.67	0.46	-0.29

Table 3. Eigenvalues, cumulative percent variation, and eigenvectors of the first three principal components (PCs) for the soil metrics in the dry season.

Table 4. Eigenvalues, cumulative percent variation, and eigenvectors of the first three principal components (PCs) for the soil metrics in the rainy season.

	PC1	PC2	PC3
Eigenvalue	5.174	2.601	2.025
Cumulative percent variation	34.4	51.7	65.2
Eigenvectors			
Organic C (OC)	0.89	0.10	0.11
Total N (TN)	0.90	0.23	0.22
NH_4	-0.26	-0.28	0.74
NO ₃	0.16	0.49	0.22
Total P (TP)	0.82	-0.21	-0.04
Available P (AP)	-0.04	-0.03	-0.14
Microbial biomass C (MBC)	0.56	-0.74	0.01
Microbial biomass N (MBN)	0.34	-0.63	0.03
Soil basal respiration (SBR)	-0.72	0.35	0.30
Net N mineralization (MIN)	0.53	0.38	0.58
Net nitrification (NIT)	0.63	-0.14	0.46
ß-1, 4-glucosidase (BG)	-0.61	-0.20	0.51
Polyphenol oxidase (POX)	0.27	0.77	0.29
ß-1, 4-N-acetylglucosaminidase (BNA)	-0.01	0.51	-0.50
Acid phosphatase (PHO)	-0.84	-0.21	0.34

The correlation matrix (Pearson's correlation test) across the rainfall gradient show a relevant pattern among soil C, N and P metrics impacted by the rainfall regime (Tables S1–S4). Consistently, two groups of interacting soil metrics appeared. The first group was composed by the sites at the driest and the wettest ends of the gradient with more significant associations between soil metrics (44 in the case of the site that receive 711 mm of rainfall, and 48 in the case of the site that receive 1661 mm of rainfall). The second group was composed by sites at the intermediate range of the rainfall gradient, that show a lower number of significant associations among soil metrics (20 and 35, for sites at 917 mm and 1232 mm of MAR, respectively).

4. Discussion

The present study provides a quantitative overview of C, N and P concentrations, and metrics of their fluxes in the upper mineral soil layer under natural forests and converted livestock lands across the southeast of Mexico. First, we found a loss of organic C, total N and available P with land-use change. Although this organic C trend is consistent with the meta-analysis of Guo and Gifford [57], who reported that the accumulation of organic C in the mineral soil is altered with the conversion of forest cover to pastures, the significant variation in C values across sites following the conversion from natural forests to livestock production systems was probably due to differences in soil type and vegetation, and effects of land-use disturbance on soil parameters. Nonetheless, our study still suggests that land-use change alters the C-holding capacity of soil as regards short C retention capacity, and that intensive management practices (e.g., clear-cutting and slash burning for site preparation and pruning) and rainfall conditions could favor increased soil C losses [58]. On the other hand, the loss observed in the total N is unexpected, considering the inputs of N with the animal excreta in both livestock production systems. Moreover, although biological N fixation is the primary source of N input in tropical lands [59], the observed loss in soil total N at study sites after the conversion to intensive silvopastoral system indicates that land-use change did alter significantly the balance between N input and loss, with consequences for N retention in this agricultural ecosystem.

The significant differences in C and N observed at study sites due to forest conversion could be related to differences in both quantity and quality of C and N inputs through litter and different management practices between native forests and livestock production systems. Plant species differ in their C sequestration potential, and land-use change by changing woody tree species covers with recalcitrant C compounds [60] to non-woody pasture species or leguminous trees, would be expected to alter the sequestration potential of C. Besides the expected large differences in litter inputs to the soil between natural forests and N-rich litter in silvopastoral systems, forest floor mass and nutrients under the natural forests species had a large quantity of organic materials poorly decomposed that would be incorporated into the mineral soils, as has been observed in these forest ecosystems [61], while a high rate of litter decomposition is expected in silvopastoral systems due to high N concentration and low content of recalcitrant compounds in litter from leguminous trees [62].

Soil basal respiration has been used as a powerful index to evaluate the alterations of soil C cycle [63]. In the present study, land-use change increased the soil basal respiration suggesting a higher ratio of labile soil organic C (i.e., soil organic C pool with "fast" decomposition [64,65]) to the total soil organic C under pastures and *Leucaena* plantations than under natural forests, probably reflecting the expected differences across land uses in the quantity and/or quality of the C inputs. It is known that it is the ratio of labile soil organic C to total soil organic C, rather than the total soil organic C content itself, that influences soil quality [66], due to its key role for metabolically active microbes [67] and nutrient supply to growing plants [68]. These expected differences in the contribution of labile soil organic C to soil total organic C among land uses could be related to the chemical recalcitrance of root tissue in the studied native forests [60]. On the other hand, management involving no-till in livestock production systems allows the accumulation of labile forms of organic C in soil surface layers [69,70], while more stable organic C accumulates under native forest soils [71]. In addition, inputs of dung-derived C and N often induce microbial priming effects, promoting soil organic matter decomposition [72]. Aside from these possible drivers of changes in soil organic C mineralization, the observed differences in CO₂ fluxes between natural forests and livestock systems could persist for an extended period considering that organic C stabilization in soil is relatively long-lasting (between 20 and 60 years; [73]).

Additionally, we observed a generalized loss in soil available P values after land-use change, despite the fact that dung is rich in P [74]. Moreover, the activity of the acid phosphatase under silvopastoral systems increased relative to its activity under natural forests, with largest changes in the

wettest end of the rainfall gradient. We cannot determine whether such increase in P-acquiring enzymes under intensive silvopastoral systems resulted from an increase in P-demand by *Leucaena* plantations (thus exacerbating the possible direct nutrient limitation to soil microbes). Generally, P supply limits ecosystem function in tropical zones [12] and in the study region [74]. The land-cover change of native forests to extensive pasture systems maybe does not change this situation. However, the intensive silvopastoral systems maybe makes P-limitation worse, as indicated also by the low availability of P in the soils. Although this hypothesis of pervasive P limitation in silvopastoral systems could be verified with a study of primary production at the ecosystem level, because microbial biomass C:N:P ratios are relatively invariant across ecosystems [75], differences in microorganism efforts to acquire P should be expected between ecosystems that differ in nutrient supply in order to maintain microorganism homeostasis [76], (i.e., soils poor in P have high levels of activity of P-acquiring enzymes, as was observed in the intensive silvopastoral systems).

4.2. Effects of Rainfall Regime on Soil Carbon, Nitrogen and Phosphorus Dynamics

Climatic variables have strong impacts on soil organic C, N and P contents and fluxes in tropical and extratropical soils [5,77], and previous studies suggested that rainfall is the primary factor controlling soil C, N and P dynamics in water-limited tropical ecosystems [15,78]. Our study indicates that organic C, total N and available P, and microbial biomass C and N concentrations increased with decreased rainfall in both natural forests and livestock production systems. This result is in line with those obtained by Burke et al. [79] who reported that rainfall clearly has a direct role regionally and globally in the amount of soil C and nutrients stored. These patterns indicate that C and nutrient accumulation reflect a strong decrease in decomposition rate with the decrease in MAR reflecting also enrichment in organic matter recalcitrance with decrease in rainfall amount [60,80]. Moreover, the soil basal respiration rates decreased with the decrease in rainfall amount, suggesting a moisture limitation for soil C mineralization. In addition, the net N transformations differed considerably among sites with changes in rainfall amount. However, in contrast with the pattern observed for the C mineralization across sites, the observed highest N transformations in soils from the driest end of the gradient, with the largest values in samples taken in the dry season, suggested that there is a large potential of N losses when the rainy season starts. Thus, the expected reduction in rainfall in the southeast of Mexico [81] could open the N cycle irrespective of land use. Thus, our study also suggests that climate change could affect moisture-sensitive biogeochemical processes, and a N limitation could occur in native forests and livestock production systems if drought intensity increases.

Overall, our study demonstrated that soils (both under native forests and livestock systems) at the driest end of the rainfall gradient had C, N and P accumulation during the dry season, probably due to the decrease in decomposition [62] and soil leaching during the rainless period. These large pools of resources in the dry season could be a large input of C and nutrients to microbial biomass and vegetation demands when the rainy season starts. Correlation analysis allowed us to identify variations in the interaction among soil C and nutrient dynamics across sites affected by both the amount and seasonality of rainfalls. In line with Finzi et al. [82], and Delgado-Baquerizo et al. [83] who propose that drought increase would uncouple the C, N and P cycles, our study indicates that the strength of relationships among soil metrics for C, N and P cycles decreased with the decreases in MAR from the 1661 mm rainfall site to the 917 mm rainfall site, indicating that the cycles of C, N and P in the soil are less coupled with drought. A recent study in Texas found that greater soil water content favored soil bacterial communities [84]. Contrary to this trend, the association between soil variables increase below 917 mm of MAR. This could be due to more intense and prolonged seasonal drought that limits soil leaching and favors the microbial control of soil C and nutrient dynamics [85–87].

Regarding the sustainability of the livestock sector in the southeast of Mexico, our study on the consequences of the land-use change and climatic variation in soil nutrient dynamics allows us to conclude that the regulatory mechanisms of soil fertility in these two grazing livestock systems will vary, depending on the details of the site's nutrient limitations and the expected drought intensification.

Aside from these short- and long-term scenarios, the large extension of degraded land in the region [88] creates the opportunity for scaling up tropical forest restoration plans [89] or even the use of intensive leguminous tree plantations, which could be a positive contribution to reduce the massive impact of land use on tropical ecosystems, increase the landscape ecosystem services [8], and limit the

5. Conclusions

The analysis derived from our soil biogeochemical measurements provides an estimate of the response of tropical forest ecosystem and the sensitivity of land-use-change effects to increase in drought in the tropical region of Mexico. Our study indicates that expected climate change could impact moisture-sensitive biogeochemical processes, altering future carbon, nitrogen and phosphorus balances in soils under natural forests, and also in agricultural ecosystems, with potential negative consequences for the sustainability of livestock production systems in these tropical regions. Achieving the agricultural sustainability in these regions depends on limiting drought effects on soil carbon and nutrient losses with a better understanding of their biogeochemical dynamics as well as of the interactions among their cycles.

Supplementary Materials: The following are available online at http://www.mdpi.com/2071-1050/12/20/8656/s1, Table S1: Pearson correlation coefficients for soil metrics in sites that receive 711 mm of total annual rainfall, Table S2: Pearson correlation coefficients for soil metrics in sites that receive 917 mm of total annual rainfall, Table S3: Pearson correlation coefficients for soil metrics in sites that receive 1232 mm of total annual rainfall, Table S4: Pearson correlation coefficients for soil metrics in sites that receive 1661 mm of total annual rainfall

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contribution of the livestock sector to national N emission [90].

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