

## Amazonian Dark Earth Shapes the Understory Plant Community in a Bolivian Forest

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### ABSTRACT

Amazonian Dark Earths (ADE) are the result of human modification of the Amazonian landscape since pre-Columbian times. ADE are characterized by increased soil fertility compared to natural soils. In the Amazonian forest, soil fertility influences understory herb and fern species composition. However, little research has been done to evaluate the effect of ADE on the composition of the understory community. We evaluated the effects of ADE and soil in 36 plots (150 m × 4 m) established in a Bolivian moist forest (La Chonta). For each plot, we determined soil nutrients, and the composition, richness, and abundance of terrestrial fern, angiosperm herb, and understory palm species. We found that the presence of ADE created a gradient in soil nutrients and pH that affected the understory species composition especially of ferns and palms. Additionally, the higher nutrient concentration and more neutral soil pH on ADE soils caused a decrease of ferns species richness. We therefore conclude that the current composition of the understory community in this particular Bolivian forest is a reflection of past human modifications of the soil.

*Key words:* anthrosols; Bolivia; soil pH; *terra preta*; terrestrial angiosperm herbs; terrestrial ferns; understory palms.

PLANT DIVERSITY AND COMPOSITION ARE DRIVEN BY HISTORICAL EVENTS, DISPERSAL LIMITATION, and biological (Fine *et al.* 2004), environmental (ter Steege 2009), and anthropogenic filters (Ross 2011). These filters determine the locations that are adequate for germination, growth and survival of plants (Fine & Kembel 2011). In Amazonian forest, edaphic characteristics are one of the most important environmental filters, shaping the floristic composition and diversity of understory communities. Several studies have shown that exchangeable base concentration and to some extent clay percentage in the soil influenced the distribution patterns of understory fern, angiosperm herbaceous and palm species (Costa *et al.* 2005, 2009, Poulsen *et al.* 2006, Kristiansen *et al.* 2012, Zuquim *et al.* 2014). It has also been found that exchangeable base concentration positively affected species richness of Marantaceae and ferns (Costa 2006, Tuomisto *et al.* 2014) while it negatively affected palm species richness in western Amazon (Vormisto *et al.* 2004).

Plant distribution is not only shaped by biological and environmental factors, but also by anthropogenic ones. Humans can change the environmental conditions (*e.g.*, light, soil nutrients), and hence plant distribution through disturbance of the vegetation (*e.g.*, shifting cultivation) and soil modification. Humans also may directly impact species distribution by harvesting useful species or deliberately planting them. In Central Amazonia, for example, there is a higher abundance of useful tree and palm species in areas surrounding past human settlements (Levis *et al.*

2012). Pre-Columbian civilizations have strongly affected the environment in several ways: through the presence of roads, moats, and bridges at upper Xingu in Mato Grosso Brazil (Hecckenberger *et al.* 2003); earth works in the province of Beni, Bolivia (Erickson 2010); and the pervasive existence of Amazonian Dark Earths (ADE) in the Amazon basin (Sombroek 1966, Glaser & Birk 2012). In this paper, we focus on ADE or black earth (*'terra preta'* in Portuguese), which is a type of anthrosol characterized by a thick dark or gray top layer with presence of ceramics indicating past indigenous settlements (Sombroek 1966, Woods & Glaser 2004). ADE are the product of kitchen remains, such as garbage deposition, over thousands of years (Schaan *et al.* 2009). ADE patch sizes range between 2 ha to more than 100 ha (WinklerPrins & Aldrich 2010), and possess higher concentrations of total and available P and Ca (from the addition of animal bones to the soil), higher total N (Lehmann *et al.* 2003), and higher concentrations of charcoal and C (Glaser *et al.* 2003) than the surrounding ultisols and oxisols from most of the Amazon region (Falção *et al.* 2009). When ADE soils are present in a given area, they form a gradient of fertility from the center of the ADE patch to the surrounding natural soils (Fraser *et al.* 2011, Costa *et al.* 2013).

Human-induced changes in soil structural, physical, and chemical properties, and soil processes have the potential to have long-lasting effect on the understory vegetation. For example, charcoal addition leads to more stable organic matter, nutrient levels, and probably to higher soil water retention capacity in ADE compared to non-ADE soils (Glaser *et al.* 2002), while the addition of organic waste leads to higher nutrient concentrations

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(P, N, and Ca) (Glaser 2007). Higher Ca concentrations increase the base exchangeable concentration and pH of the soil, which in turn also increases the availability of other cations. In combination, the increased nutrient storage and nutrient availability enhance plant nutrient uptake (Neumann & Römheld 2012). The interplay between nutrient supply and species-specific nutrient demands determine in the end where species occur. At the lower end of the soil fertility gradient an increase in nutrients has the potential to fuel plant growth, and enhance species abundance and richness. At the higher end of the soil fertility gradient, species richness may even decline, when nutrient availability becomes supra-optimal, or when fast growing species dominate and out-compete the others (Grime 1973).

To date, few studies have examined the possible effect of ADE and associated human activities on plant distribution and floristic composition. In recently abandoned croplands, there is a higher diversity and biomass of light-demanding weeds on ADE soils than in adjacent non-ADE soils (Major *et al.* 2003, 2005). Young secondary forests on ADE and non-ADE soils shared only 23 percent of woody species (palms and trees with dbh >5 cm) and 46 percent of understory palm species. This low similarity was attributed to differences in soil fertility and to the enrichment with useful tree and palm species at ADE sites (Junqueira *et al.* 2010, 2011). Finally, the only study performed in an old growth forest showed that density of human-used tree species was similar between ADE and non-ADE sites in the Bolivian Amazon (Paz-Rivera & Putz 2009).

We evaluated the effect of ADE soils on the composition and diversity of understory angiosperm herbs (hereafter referred to as herbs), ferns, and palms in an Amazonian Bolivian forest. We tested the hypothesis that the physical and chemical characteristics of soils differ along a gradient from ADE to non-ADE soils. We then tested the hypothesis that floristic composition, species richness and abundance of understory herbs, ferns and palms differ along the gradient from ADE to non-ADE soils. We predict that soil fertility and soil organic matter (and with that indirectly also soil water content) would increase along the gradient from non-ADE to ADE soils; and that species richness and abundance of herbs, ferns and palms would increase with soil fertility and soil organic matter (and thus soil humidity), as has been reported elsewhere in mostly oligotrophic Amazonian forests (Tuomisto *et al.* 2002, 2014; Vormisto *et al.* 2004, Costa *et al.* 2005).

## METHODS

**STUDY SITE.**—We conducted the study in the 100,000 ha forestry concession of Agroindustria Comercial La Chonta, Guarayos province, Bolivia (15°47' S, 62°55' W). Mean annual temperature is 24.3°C and annual rainfall is 1580 mm (data from 2000 to 2006 from La Chonta sawmill) with a dry season (<100 mm/mo) from May through September (Peña-Claros *et al.* 2012). The study site is located on the southwest border of the Brazilian Precambrian Shield (Navarro & Maldonado 2002) and has sandy-loam soils with neutral pH and rich in nutrients (Paz 2003, Peña-Claros *et al.* 2012). A previous study showed that ADE soils in

La Chonta forest cover about 20 percent of a studied area of 216 ha (Paz-Rivera & Putz 2009).

The forest at La Chonta can be classified as a semi-deciduous tropical moist forest (Peña-Claros *et al.* 2012). Floristic comparisons of several lowland forests in Bolivia show that the forest at La Chonta is transitional between the forest of the Northern Amazon region and the Southern Chiquitano dry forest (Toledo *et al.* 2010). The forest canopy has an average height of 27 m, and approximately one-third of the canopy species shed the leaves in the dry season (Markestijn *et al.* 2010).

The forestry concession of La Chonta was established in 1974. Currently, they harvest around 3 trees/ha (7.68 m<sup>3</sup>/ha) belonging to 17–19 tree species. During its first 20 yr, the concession logged only trees of mahogany (*Swietenia macrophylla*) and tropical cedar (*Cedrela odorata*). Before this time, there was no evidence of forest management in the area. Nevertheless, the presence of ADE soil with pieces of charcoal and pottery of 400–300 yr B.P. indicates that there were indigenous settlements in the area (Paz 2003).

We carried out research in twelve large-scale (27 ha) permanent sample plots established by the Bolivian Forest Research Institute (IBIF, in Spanish), hereafter referred as the IBIF-permanent plots, that are part of the Long-term Silvicultural Research Program, LTSRP (Peña-Claros *et al.* 2008). IBIF-permanent plots were distributed throughout three logging compartments, which were harvested by the company between 2001 and 2002, after plot establishment.

**DATA COLLECTION.**—First, we performed a preliminary survey in the IBIF-permanent plots, using the grid system of the 27 ha plots to make an inventory of the presence of ADE soils. At each 50 m × 50 m grid intersection of each plot, a soil sample was cored with an auger, providing 130 sample points per plot, for a total of 1750 points. Presence of ceramics and charcoal was evaluated visually, and the soil color was determined with Munsell Soil Color Charts. Subsequently, we made soil color maps using the Kriging interpolation function of ArcMap software (Klomberg 2012). Based on the soil color maps and the presence of ceramics and charcoal, we established a total of 36 rectangular plots (150 m × 4 m). Fourteen plots were established in areas with dark soil (black or very dark brown color, mainly 7.5YR 2.5/1, 7.5YR 2.5/2 and 7.5YR 2.5/3 in the Munsell system); these plots were considered ADE plots. Fourteen additional paired plots were established on adjacent areas with lighter soil color (brown, yellowish brown or reddish brown, mainly 7.5YR 4/3, 7.5YR 4/4, 7.5YR 5/4, 5YR 5/3); these were considered as non-ADE soil plots. Distance between adjacent plots ranged between 120 and 400 m. Four additional pairs of plots on ADE sites previously determined by Paz-Rivera and Putz (2009) were established outside the IBIF-permanent plots, so that the total sample size was of 36 plots. We took geographical reference points of every transect using a GPS (Garmin *Etrex* Vista HCx, Kansas City, KS, U.S.A.).

In each plot we counted individuals belonging to fern species and species of the Marantaceae and Arecaceae families, as

these have been shown to respond to soil fertility (Costa 2006, Poulsen *et al.* 2006, Andersen *et al.* 2010a). We also included other families that were easy to recognize and abundant in the understory of La Chonta, such as the Commelinaceae, Costaceae, Heliconiaceae, Poaceae, and Zingiberaceae (Table S1). For species with smaller individuals, such as most ferns, we were able to distinguish separately individuals. However, several species grow in clumps, hampering the identification of individual plants. Stems of small clump-forming species (*e.g.*, *Bolbitis serratifolia*) located within 20 cm of each other were counted as part of the same clump; otherwise, they were counted as separate individuals (*cf.* Costa 2006). For large-sized species, such as *Bactris major* and *Heliconia* spp., we determined clump formation by excavating the roots and checking for underground connectivity. We identified the species in the field when possible using field guides for ferns, Marantaceae and Zingiberales (Zuquim 2008, Costa *et al.* 2011a, b). For all species, we also collected specimens to confirm their identity at the Herbario del Oriente Boliviano in Santa Cruz, Bolivia.

To determine soil properties we collected seven soil samples of ~250 g each at intervals of 25 m within each plot; we sampled mineral soil to a depth of 40 cm. We created a compound soil sample per transect, from which we characterized soil color using the Munsell System. Soil samples were further analyzed at the Centro de Investigación Agrícola Tropical (CIAT) in Santa Cruz, for measurement of the following chemical and physical variables: concentrations of N, P, exchangeable  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{K}^+$ ,  $\text{Al}^{3+}$ ; pH; organic matter content (OM); total exchangeable bases (TEB); cation exchangeable capacity (CEC); base saturation; acidity; and soil texture. Soil texture (percentage of sand, silt, and clay) was measured using a Bouyoucos hydrometer; pH and electric conductivity was determined in 1:5 distilled water equilibrating for 90 min.; concentrations of exchangeable  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{K}^+$ , and  $\text{Na}^+$  were determined in 1 M ammonium acetate at pH 7. After extraction,  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  were measured with an Atomic Absorption Spectrophotometer; concentrations of  $\text{K}^+$  and  $\text{Na}^+$  were measured with a flame photometer; exchangeable aluminum ( $\text{Al}^{3+}$ ) was measured in 1 M hydrochloric acid (HCl). Total P was determined by Olsen method; OM was determined by Walley-Black method, and total N was measured using the Micro-Kjeldahl method (Barber & Cochrane 1993). TEB was defined as the sum of the most important exchangeable cations ( $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{K}^+$ , and  $\text{Na}^+$ ). CEC was calculated as the sum of TEB plus acidity. Base saturation was computed as the percentage of exchangeable cations or bases relative to total CEC.

We measured canopy openness to account for influence of light intensity on species distribution. Canopy openness was determined with a convex spherical densiometer at four cardinal points by two independent observers that held the densiometer at ~1 m aboveground level. Measurements were strongly correlated between observers ( $R^2 = 0.83$ ;  $P < 0.001$ ). Canopy openness was measured every 5 m in each transect, and the 25 points were then averaged to give one estimate per plot (Englund *et al.* 2000, Paletto & Tosi 2009).

**DATA ANALYSES.**—We explored overall variability across our plots using Principal Component Analysis (PCA) based on eight chemical variables (pH, concentrations of P, exchangeable Ca, Mg, K, Na, Total N, and OM content) and three physical variables (percentage of sand, silt, clay), using the values from all 36 plots. Because variables had different measurement units, we standardized them by subtracting from the mean and dividing by the standard deviation. PCA was based on a correlation matrix.

*Environmental effects on species composition.* To evaluate the effect of ADE soils on species composition we selected a subset of edaphic variables considered as indicators of the presence of ADE soils (Glaser & Birk 2012). These variables, hereafter called ADE variables, are: pH, concentration of P and Ca, OM content, total N and presence of ceramics. To determine which factors drove understory species composition, we performed Redundancy Analyses (RDA) using the six ADE variables as well as UTM coordinates, light availability (canopy openness), and plot elevation as explanatory variables; and species composition with their abundances on each transect as dependent variables. Geographical UTM coordinates were included to account for the spatial distances among plots, given that the distance between plots varied from 0.25 to 8 km. Light availability was included, as light can vary among plots due to logging and application of silvicultural treatments (Peña-Claros *et al.* 2008); plot elevation accounted for topographical differences in La Chonta. RDA is a constrained ordination method, in which the ordination axes are linear combinations of all explanatory variables. RDA constrains the variability in the data set (species composition per transect) to these ordination axes, and tests the significance of this ordination with Monte Carlo Permutation tests. Two Monte Carlo Permutation tests were performed: the first one was used to determine the significance of the species composition variability explained by all canonical axes; the second was used to test for the significance of the contribution of each explanatory variable (Lepš & Šmilauer 2003). The latter analysis allowed us to select those independent variables that significantly explained species composition in the plots. We did four RDA analyses: one for the complete dataset (all 37 species); one for herbs (Comelinaceae, Costaceae, Heliconiaceae, Marantaceae, Poaceae, and Zingiberaceae); one for ferns; and one for palms. We evaluated these groups separately as they may respond differently to soil fertility (Costa 2006, Andersen *et al.* 2010a).

*Environmental effects on species richness and abundance.* Species richness per transect was modeled as a function of the six ADE variables, spatial location, plot elevation, and light intensity using multiple regression analysis based on generalized linear models (GLM). These models allow for not having linear combinations between expected values of response and explanatory variables, by including a non-linear link function. In our case, we used the logarithm as a link function for count data. We used backward multiple regression to evaluate significance of the explanatory variables that were standardized with mean 0 and variance 1, to be able to compare parameters estimated in the

model. Regressions were performed for species richness of the whole community (all group of plants combined), for herbs (all families combined), and ferns, but not for palms, as only a total of six palm species were found. GLM were also used to assess the effect of ADE variables, spatial location, plot elevation, and light intensity on the abundance of individuals per transect for herbs (all families combined), ferns and palms. Palm abundance was included in the analysis because there were enough individuals in the plots to do the analyses.

Finally, to evaluate the response of individual species to ADE soils we analyzed species response curves. For each species that occurred in more than six plots (*i.e.*, >15% of sample units: 11 herbs, 9 ferns and 5 palms) we determined response curves to pH, concentration of Ca and canopy openness. We tested only for pH and Ca because they are good indicators of the presence of ADE soils at La Chonta and those variables most influenced species composition, richness, and abundance (see Results). We fitted linear and quadratic regressions for each explanatory variable, and selected for each species and for each variable the model with the lowest Akaike Information Criterion (AIC).

RDA and response curves of individual species were done using CANOCO 5 software (Ter Braak & Šmilauer 2012); paired *t*-tests and GLM were performed using Genstat 15.1 (VSN International Ltd., Hemel, Hempstead, U.K.).

## RESULTS

**NUTRIENTS AND TEXTURE OF ADE SOILS.**—The ADE soils were generally more fertile than non-ADE soils, as indicated by the PCA based on soil chemical and physical characteristics which explained 82 percent of the variation among plots. The first axis, which explained 60.9 percent of the variance, separated plots with high concentration of P, Ca Total N, and high pH (with positive score values) from plots with lower quantities of these elements (with negative score values). ADE and non-ADE plots distribute continuously along the first PCA axis, indicating that there is a gradient of fertility between ADE and non-ADE soils (Fig. 1). The second axis explained 22.4 percent of the variance, but ADE and non-ADE plots were intermixed along this axis (Fig. 1).

**GENERAL FLORISTIC OBSERVATIONS.**—The studied groups consisted of 37 species: 14 ferns, 6 palms, and 17 species of herbs with 6 Heliconiaceae, 5 Marantaceae, 2 Costaceae, 2 Poaceae, 1 Zingiberaceae, and 1 Commelinaceae (see Table S2). Total abundance was 48,458 individuals, with 36,108 ferns, 10,194 herbs, and 2156 palms. Among herbs, Heliconiaceae was the most abundant family with 6747 individuals, whereas the most abundant species were the ferns *Bolbitis serratifolia* (29,386 individuals) and *Adiantum cf. pulverulentum* (6152 individuals).

**EFFECT OF ADE VARIABLES ON PLANT COMPOSITION.**—Plant species composition was significantly influenced by soil and spatial variables (Fig. 2). RDA for all species combined and for each of the groups (herbs, ferns and palms) showed a consistent pattern. The

first axis that explained a higher percentage of variation in all combined species, herbs, and palms was associated with spatial variables, elevation or light, depending of the group that we evaluated, but this axis did not separate ADE from non-ADE plots (Figs. 2A, B and D). The second axis was associated with pH and variables related with fertility, such as concentration of soil exchangeable bases and total N. Interestingly, this axis dispersed ADE and non-ADE, suggesting that there is a gradient of fertility along ADE and non-ADE soils, mainly determined by differences in pH and Ca concentration, which are significantly associated with changes in the floristic composition of the plots (Table 1; Figs. 2A, B and D). Fern composition was better explained by soil variables, and ADE and non-ADE plots showed an intermingled distribution along the main axes (Fig. 2C).

The RDA showed that, when all species were combined, species composition was significantly explained by differences in pH, Ca concentration, spatial location and canopy openness (Table 1). When species groups were analyzed separately, we found that canopy openness and concentration of Ca consistently explained the variance in all cases, but their contribution differed among groups. For ferns Ca and soil pH explained 52 percent of the variation and for palms 20 percent of the variation in species composition. For herbs, Ca in the soil only accounted for 12 percent of the total variation. Spatial location significantly explains species composition of herbs and palms, whereas plot elevation significantly explained species composition of palms (Table 1).

**EFFECT OF ADE VARIABLES ON RICHNESS AND ABUNDANCE.**—Species richness decreased when soil pH increased, both when all species were combined, and for the fern species alone (Table 2). Abundance of individuals was explained by soil variables only in the case of herbs and palms. Herb abundances significantly increased with Ca concentration and canopy openness. Palm abundance was negatively affected by pH and positively affected by Ca concentration. Finally, fern abundances were negatively affected by canopy openness and spatial location (Table 2). These results are consistent with the RDA, which also indicated that spatial location, canopy openness, pH and concentration of Ca are the most important variables explaining species composition, richness and abundance.

**INDIVIDUAL SPECIES RESPONSES.**—We evaluated the response of the most frequent species to pH, Ca and canopy openness, as these variables consistently had significant effects on species composition, richness and/or abundance. Remarkably, of the 25 species evaluated all but one (*Pharus latifolius*) showed a significant, although weak, response to pH and Ca (Table S3). Some palm species, *e.g.*, *Astrocaryum murumuru*, which was the most abundant palm in our study site (1246 individuals), showed a type of bimodal response to Ca concentration and pH (Table S3; Fig. 3F). More species responded to pH (12 of 25 species) than to Ca concentration (seven species) (Figs. 3A–F) or canopy openness (six species; see  $R^2$  values in Table S3). Many species were more frequent at lower pH, which could explain the negative relationship between pH and overall species richness (Table 2).

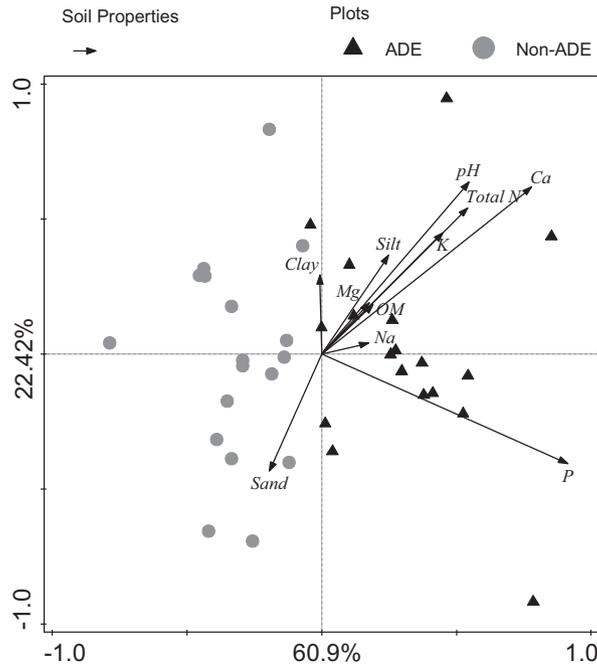


FIGURE 1. Results of Principal Component Analyses of soil parameters for Amazonian Dark Earth (ADE, 18 plots, black triangles) and non-ADE plots (18 plots, gray circles) in La Chonta, Bolivia. Arrows represent the environmental variables used in the analyses and their magnitude of importance in the ordination.

TABLE 1. Results of a Redundancy Analyses (RDA) evaluating the effect of explanatory variables in species composition of all species together, and separately for angiosperm herbs (Marantaceae, Costaceae, Heliconiaceae, Poaceae), palms, and ferns. Data presented are the variation explained,  $R^2$ , followed by the P-value (in parenthesis). The P-value is associated with Monte Carlo permutation test that evaluated the null hypothesis of no correlation between the species composition and environmental variables. The level of significance for the individual environmental variables was  $\alpha = 0.05$ . Significant relations are shown in bold.

	Groups			
	All Species	Herbs	Ferns	Palms
All explanatory variables	<b>53.8 (0.002)</b>	<b>53.7 (0.002)</b>	<b>42.8 (0.012)</b>	<b>52.6 (0.002)</b>
Individual variables				
pH	<b>9.3 (0.002)</b>	2.6 (0.19)	<b>7.1 (0.016)</b>	<b>5.3 (0.03)</b>
Total N (%)	3.6 (0.05)	3.0 (0.14)	2.7 (0.30)	<b>7.4 (0.01)</b>
P (mg/Kg)	1.9 (0.36)	1.0 (0.81)	3.5 (0.16)	2.9 (0.17)
Ca (cmol/Kg)	<b>4.8 (0.02)</b>	<b>6.5 (0.006)</b>	<b>15.0 (0.002)</b>	<b>5.2 (0.04)</b>
OM (%)	1.5 (0.65)	2.1 (0.31)	1.7 (0.58)	2.1 (0.32)
Ceramics	1.5 (0.59)	1.6 (0.50)	1.0 (0.9)	2.0 (0.38)
Canopy openness	<b>7.3 (0.004)</b>	<b>4.8 (0.03)</b>	<b>6.0 (0.02)</b>	<b>6.7 (0.02)</b>
X Coordinates	<b>18.6 (0.002)</b>	<b>25.9 (0.002)</b>	2.1 (0.48)	<b>6.9 (0.01)</b>
Y Coordinates	2.4 (0.16)	2.6 (0.20)	1.4 (0.71)	1.5 (0.58)
Plot elevation	2.8 (0.11)	3.4 (0.09)	2.4 (0.36)	<b>12.6 (0.006)</b>

## DISCUSSION

We evaluated whether ADE soils have an effect on the understory plant community through changes in soil properties. Along the gradient from non-ADE to ADE soils in La Chonta, soil cations, P and total N increased as did soil pH. Species composition also carried along this gradient, with species

distribution associated with soil pH, Ca concentration and, to a lesser extent, total N. In general, species richness decreased with pH and abundance increased with nutrient levels. Consequently, we found that gradients in soil pH and Ca concentration generated by ADE presence were significantly related to gradients in composition, diversity, and abundance of the understory community.

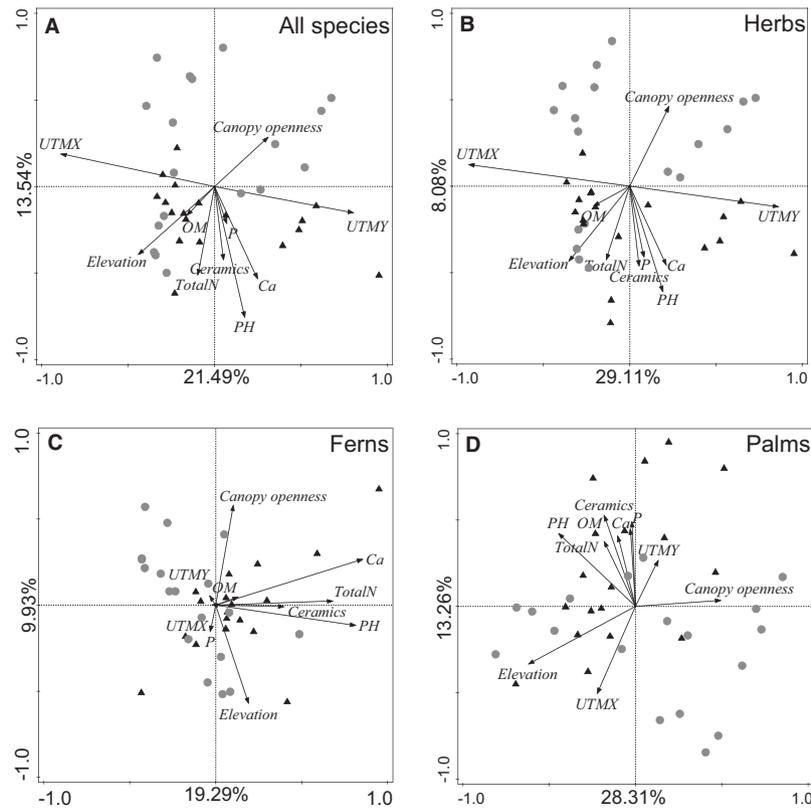


FIGURE 2. Biplots produced after the redundancy analyses, representing the distribution of the plots based in species composition and restricted to soil and environmental explanatory variables (Table 1). ADE plots are represented with black triangles and non-ADE plots are represented with gray circles. Arrows represent explanatory variables. Biplot of all understory species (A); of herbaceous species (B); of fern species (C) and of palms (D).

**NUTRIENTS AND TEXTURE OF ADE SOILS.**—We hypothesized that past anthropogenic enrichment activities would have led to a higher fertility of ADE soils compared to non-ADE soils. We indeed found that 10 of 12 chemical variables related to soil fertility were higher in ADE than non-ADE soils (Table S1). Most studies in the Amazon region have found large differences between ADE soils and surrounding soils in soil color, pH, organic matter content, CEC and concentrations of nutrients, such as P, Ca, N, Mg, K and Zn (Glaser & Birk 2012). Particularly, P and Ca concentrations are 100 times higher in ADE soils compared to the surrounding soils; however, variability in the concentration of P among and within ADE sites can be high (Lehmann *et al.* 2003, Falcão *et al.* 2009). Interestingly, in La Chonta P and Ca concentrations were only 2.6 and 1.6 times higher in ADE compared to non-ADE soils, respectively. Similar results have been found in other regions of the Bolivian Amazon (Hastik *et al.* 2013). These smaller differences between ADE and non-ADE are likely the result of higher background soil fertility levels in the study site. Given the geological history of this region (Southern Amazon basin) that includes the pre-existing Brazilian Shield and geological processes of sedimentation and erosion originated by the uplift of the central Andes in the Quaternary (Latrubesse *et al.* 2010), La Chonta soils vary widely in age.

We hypothesized that ADE and non-ADE soils are not so much two distinct groups but that they form the extremes of a continuum in soil fertility, which was indeed confirmed by the ordination analysis (Fig. 1). In several sites in Central and South Amazonia it has been suggested that inside archeological ADE sites, variation in soil characteristics is better described by a fertility gradient that goes from the darker ‘center’ region with higher fertility to lighter areas in the surroundings ending in the natural adjacent less fertile soils (Fraser *et al.* 2011, Schmidt *et al.* 2014).

**EFFECT OF ADE AND OTHER EXPLANATORY VARIABLES ON SPECIES COMPOSITION AND SPECIES RESPONSES.**—We hypothesized that understory floristic composition is shaped by the presence of ADE soils. Our findings partially supported these hypotheses: understory floristic composition indeed responded to below-ground resources that were indicators of ADE presence. However, to a lesser extent they also responded to aboveground resources (canopy openness) and were affected by spatial distribution of the plots (Table 1; Fig. 2). We found that, among the ADE variables, Ca concentration and pH accounted for around 25 percent of the total variation in species composition (Fig. 2). This was especially the case with fern species composition. Several studies on distribution patterns of ferns have shown the importance of soil exchangeable bases (Ca, Mg, K,

TABLE 2. Results of backward multiple regression models evaluating the effect of explanatory variables on species richness and abundance of individuals on each transect for all species combined, angiosperm herbs (*Marantaceae*, *Costaceae*, *Heliconiaceae*, *Poaceae*), palms, and ferns. Regression coefficients (a) of each explanatory variables that significantly fitted the model. For each model we present  $R^2$ , intercept (b) and significance level (p). Slopes (a) and intercepts (b) are represented in log scale given that a logarithmic function was used as the link function to fit the model ( $\text{Ln}Y = b + a_1x + a_2x + \dots + a_nx$ ).

	Diversity			Abundance		
	All species	Herbs	Ferns	Herbs	Ferns	Palms
Model parameters						
$R^2$	0.17	0.07	0.44	0.40	0.51	0.52
$b$	2.72	1.95	1.40	5.57	6.82	4.01
$p$	0.007	0.069	<0.001	<0.001	<0.001	<0.001
Coefficients (a) of explanatory variables						
pH	-0.07		-0.21			-0.36
OM (%)						
Ca (cmol/Kg)				0.13		0.17
X Coordinates					-0.32	-0.59
Y Coordinates					-0.36	-0.29
Canopy openness				0.23	-0.42	
Plot elevation				-0.19		

Na) in explaining local (Costa *et al.* 2005, Tuomisto 2006) and regional (Zuquim *et al.* 2012, 2014) fern species composition, indicating that ferns specialize for, and partition, the exchangeable bases gradient (Tuomisto & Poulsen 1996, Costa *et al.* 2005).

We also found that Ca concentration, soil pH, and total N had a significant effect on palm species composition (Fig. 2D; Table 1). Similarly in Western and Central Amazon, palm composition was associated with exchangeable base concentration in the soil, both at local and meso-scales (Vormisto *et al.* 2004, Poulsen *et al.* 2006, Costa *et al.* 2009, Kristiansen *et al.* 2012), while in Panama palm species composition was most strongly associated with inorganic soil nitrogen (Andersen *et al.* 2010b). As for herbs, the effect of pH was not significant, and Ca in the soil had only a weak effect on species composition (Table 1). This result is in agreement with another study in Central Amazonia, where exchangeable base concentration in the soil explained a low percentage of the variance of herb species composition (Costa *et al.* 2005). In general, in the soil fertility gradient ranging from non-ADE to ADE soils, we found species of ferns and palms represented mainly by *Adiantum cf pulverulentum*, *Adiantum argutum* and *Attalea phalerata* in the least fertile extremes and herb species such as *Heliconia episcopalis* and *Heliconia metallica* in the most fertile extremes (Fig. 3).

Even at the restricted spatial scale of this study (<10 km<sup>2</sup>), geographical location of the plots had an effect on palm and herb species composition but not on fern composition (Table 1). The spatial effect on composition could be related to dispersal limitation, past human disturbance, and other environmental variables that we did not measure but that have a spatial pattern. Palms and herbs have probably a spatial component in their distribution because large palm seeds tend to disperse closer to the parent trees and many herb species studied here are clonal. On

the other hand, fern spores are light and can disperse larger distances, and therefore a spatial effect on fern composition is not to be expected at this scale. Spatial location was also significantly correlated soil texture (sand:  $r = -0.39$ ,  $P = 0.01$ ; silt:  $r = 0.40$ ,  $P = 0.01$ ). Therefore, it is possible that herbs follow these differences in soil texture, as do species of the *Marantaceae* family in Central Amazon (Costa *et al.* 2005), which may also help explain the spatial structure in herb composition.

EFFECT OF ADE AND ENVIRONMENTAL FACTORS ON SPECIES RICHNESS AND ABUNDANCE.—We predicted that the increase in soil fertility of ADE soils would increase nutrient availability and plant growth, and hence species abundance and richness. We based our predictions on studies from relatively nutrient-poor sites in the Central and Western Amazon, where an increase in exchangeable bases concentration led to a higher density of fern species (number of species/area) and higher fern diversity (Tuomisto & Poulsen 1996, Costa 2006). In contrast, we found that species richness was not directly related with nutrients, but that it decreased with an increase in pH. We think of two possible, not mutually exclusive, explanations for this pattern. First, increases in soil pH are probably the result of Ca addition through human activities (bones) in our study area, as these two variables are highly correlated (Fig. 1; Pearson correlation,  $r = 0.75$ ;  $P < 0.001$ ). These changes are rather recent, preventing a high fern diversity in these relatively ‘novel’ environmental conditions. Second, competition with herbs and palms might affect fern diversity. In our plots, an increase in Ca concentration significantly increased the abundance of palms and herbs (Table 2): species such as *Astrocaryum murumuru* (Fig. 3F), *Heliconia episcopalis* and *Heliconia metallica* (Fig. 3B) increased in abundance toward the more nutrient-rich extreme of the gradient whereas ferns such as *Adiantum argutum* and *Adiantum cf pulverulentum* decreased with

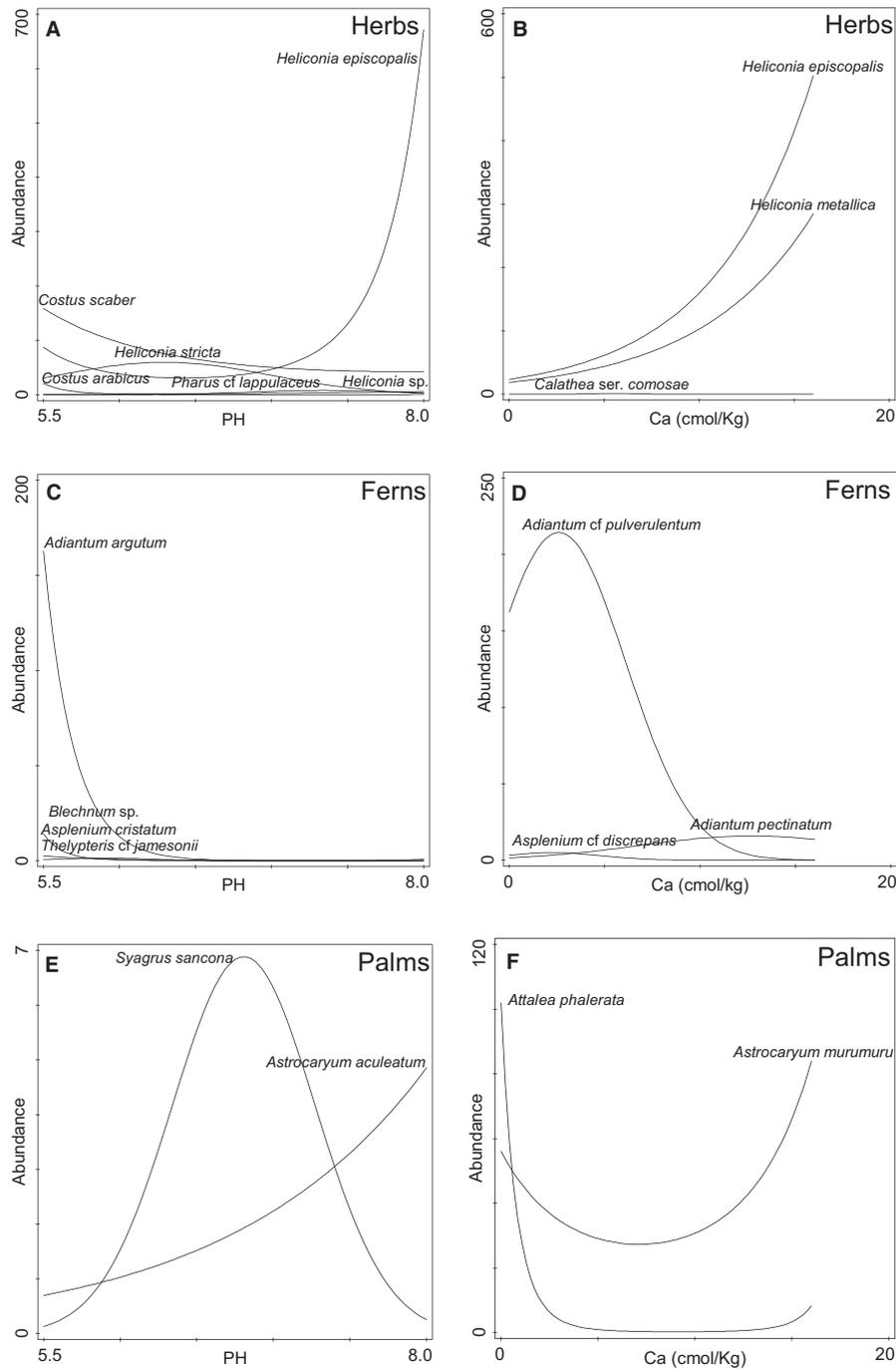


FIGURE 3. Responses of selected forest understory species to soil pH and Ca concentration in the soil at La Chonta, Bolivia. Modeled abundance values are shown for plots of 600 m<sup>2</sup>. (A) herb species with the highest R<sup>2</sup> when soil pH was used as the independent variable, (B) herb species with the highest R<sup>2</sup> when Ca concentration in soil was used as the independent variable, (C) fern species with the highest R<sup>2</sup> when evaluated with soil pH as the independent variable, (D) fern species with the highest R<sup>2</sup> when Ca concentration in soil was used as the independent variable, (E) palm species with the highest R<sup>2</sup> when soil pH was used as the independent variable, and (F) palm species with the highest R<sup>2</sup> when Ca concentration in soil was used as the independent variable. The values of R<sup>2</sup> are shown in Table S2.

fertility (Figs. 3C and D). Polypod ferns, such as those found in our plots, can absorb N and P when they grow in fertile environments as some herbs do. However, their absorption of cations, particularly Ca, is significantly lower than in herbs (Amatangelo

& Vitousek 2008). This could imply that in environments with increased amount of exchangeable bases in the soil, ferns would be able to take less advantage of the improved conditions compared to other group of species.

## CONCLUSIONS

We found that soil fertility differed along a gradient ranging from non-ADE to ADE soils, but that these differences were not as large as those found in other studies in Central Amazonia. Even on the relatively fertile natural soils at La Chonta, the presence of ADE (with increase in Ca) extends the available natural soil fertility along a gradient that influences the understorey species composition, especially of ferns and palms. Past human modifications of the soil probably led to changes in the amount of exchangeable bases in the soil and in soil pH, which increased the abundance of some herbs and palms, and decreased fern diversity. We therefore conclude that ADE soils shape the forest understorey community in this Bolivian forest.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Soil characteristics of Amazonian Dark Earths and non-Amazonian Dark Earths found in a moist semi-deciduous forest in lowland Bolivia.*

TABLE S2. *List of herbs, palm and fern species and families found in the research plots of this study in 'La Chonta' forestry concession, Guarayos Province, Bolivia.*

TABLE S3. *Results of models fitted on species abundance with frequencies higher than 15 percent of the plots.*

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