The effect of Amazonian Dark Earths on the composition, diversity and density of understory herbs, ferns and palms

In a Bolivian tropical forest

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ABSTRACT

Soils in the humid tropical lowlands are frequently considered to be of low quality for crop growth. However among these, mostly nutrient poor soils, there is one soil type which is extremely nutrient rich. This anthropogenic soil type, called Terra Preta or Amazonian Dark Earth (ADE), bears testimony to the presence of Amerindian populations in the past. Research on these soils is mainly focused on its characteristics and the effect it has on crops and secondary forest, but currently little is known on the effects it has on old growth forest.

The aim of this research was to evaluate the effect of ADE soils on the composition, diversity and density of 42 species (6 Marantaceae, 6 Heliconiaceae, 2 Costaceae, 3 Poaceae, *Erythrochiton fallax*, 16 fern, 6 palm species and 2 other species) in the moist tropical forest of La Chonta, Bolivia. These species were selected because the majority of them is known to respond to soil fertility, while palm species are likely to have been actively cultivated by Amerindians in the past.

To record where ADE us present in La Chonta, a grid was created in the twelve 27ha permanent sample plots on which soil samples were taken every 50 meters. This resulted in 1725 sample points where soil colour and presence of charcoal and ceramics were recorded. Approximately 25% of the sample points contained dark soils associated with ADE. Only 2.9% of the sample points contained ceramics and only 1.28% had charcoal. Based on the soil colour, soil maps were created with help of an interpolation tool. These maps served as basis for the establishment of 22 paired transects, on ADE and Non-ADE soils, 150m long and 4m wide. Transects were subdivided in 5m subplots where the abundance of the species was recorded and additionally environmental factors (canopy openness, slope, tree and liana cover) were measured. For each transect a pooled soil sample was analysed for nutrients and pH. ADE had significant higher values of N (0.17%), P (10.70 mg/kg), pH (7.08) and Ca (5.17 cmol/kg) compared to Non-ADE soils (N: 0.12%, P: 5.42 mg/kg, pH: 6.62, Ca: 3.47 cmol/kg).

With the help of a Mixed Linear Model we found that ADE does not influence the abundance of the majority of the species found. Furthermore, species richness and diversity did not differ significantly between the two soil types. Only 5 out of 24 analysed species (*Heliconia stricta, Pteris propinqua, Attalea phalerata, Pharus latifolius, Monatagma juranum*) and two out of six species groups (Marantaceae and Poaceae) were significantly influenced by ADE, and they all showed higher abundances on Non-ADE soils. Additional factors such as topography and climate or the high overall background fertility found in La Chonta could be the drivers of the higher abundances of these species. The lower abundance on ADE of *Attalea phalerata* could be caused by overexploitation by past civilizations. Results from an indicator species analysis suggest that *Erythrochiton fallax*, a species which did not show significant influences with the results from the model, can be used as an indicator species for ADE soils.

For the 10 most abundant species of each family, we also evaluated the effect of within-transect variation in environmental heterogeneity (canopy openness, slope, tree and liana cover) on species abundance. Canopy openness had the largest influence on the majority of species. However, the association can be positive (e.g. *Heliconia episcopalis*) or negative (*Erythrochiton fallax*).

Concluding, it is suggested that ADE soils have only a modest impact on the vegetation, affecting 20 % of the species, and 33% of the families evaluated. The high background fertility levels at the La Chonta forest (compared to other Amazonian forests) may have decreased the impact of ADE on species distribution.

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1. Introduction

1.1 Background

1.1.1 Origin of Amazonian Dark Earths

Most soils in the humid tropical lowlands are considered to be highly weathered and to have chemical properties which are unfavourable for plant growth and generally these soils (Laurance *et al.* 1999). When slash and burn agriculture is applied together with the occurrence of high temperatures and rainfall this could result in soil degradation, through erosion or depletion of minerals and organic matter, within only a few years (Barber, 1995). Without continuous inputs of fertilizers, these limitations cannot be easily overcome. The discovery of soils in the Amazon Basin having the attributes of fertile soils, such as high nutrient availability and organic matter contents, were therefore surprising. These Amazonian Dark Earths (ADE) were first described in the scientific community as early as the 1870s (Lehman *et al.* 2003). But locally these soils were already known as “Terra Preta do Índio” (Indian Black Earth), this due to the high carbon content in the soil. Terra Preta has been defined as a type of Latosol, with a carbon content ranging from high to very high (over 13-14% organic matter) in the A Horizon, however without hydromorphic characteristics (Lehman *et al.* 2003)

These soils bear testimony to the presence of ancient human populations in Latin America, and have therefore been studied intensively by archaeologists. Lehman *et al.* (2003) showed that ADEs are more widespread than previously was thought, pointing towards the existence of large civilizations in the Amazon Basin. High population densities and complex societies can only survive with productive agriculture, something hard to imagine given the constraints that the soil environment presents in the Amazonian lowlands. Currently it is a popular belief that areas of fertile Dark Earths were intentionally created by Amerindian populations for agricultural production in order to sustain large populations, however the fact that ADE presents important variants (e.g. close to settlements more nutrient rich areas are found) prevents from clearly determining whether all soils were intentionally created or the lightest variants are the by-product of human habitation (Lehman *et al.* 2003).

1.1.2 Initial research on ADE

Initially the main focus of research was on gaining knowledge regarding the functioning of soil organic matter and nutrients from these anthropogenic soils. Which showed that Anthropogenic Dark Earths have shown to contain abundantly more organic matter and elevated concentrations of nutrients (especially phosphorus, calcium, potassium and sodium; Paz-Rivera and Putz, 2009) than common Amazonian soils, however it is difficult to define clear borders since variation in concentrations have been found in the ADE soils found in Latin America. Secondly researchers wanted to understand how these soils came into existence, to use this information to improve the production potential of the low quality soils present (Lehman *et al. 2003).* However, more recently the scope of studies regarding ADE has been broadened to include vegetation responses. The presence of ADE soils has rejected the notion of virgin or pristine untouched rainforests (Willis *et al.* 2004), resulting in researchers starting to focus more on the imprint left by human populations in the past on these forests.

However, still little research is done on the effect of ADE on patterns of plant distribution. The majority of research done has focused on early successional forest, rather than on mature forest (e.g. Junqueira *et al.* 2010). Major *et al.* (2005) evaluated the diversity and biomass of weeds in abandoned crop lands which are situated on ADE. They found high diversity and biomass on ADE soils when compared with abandoned crop lands on adjacent non-ADE soils. In another study carried out on secondary forest until 30 years after abandonment, plots established on ADE and on adjacent soils (non-ADE) shared only 46% of understory palm species. This might be due to the timeframe. Abandoned crop lands harbour more short lived pioneer species, while in secondary forest long lived pioneers and shade tolerant species are found. Therefore, above results suggest that ADE can influence the distribution of some plant species; however, one could argue whether human activity may have caused these changes by planting useful species (Junqueira *et al*. 2010; Junqueira *et al*. 2011). For example, remains of some palm species have been found in archaeological excavations in the new world suggesting their use by ancient civilizations (Morcote-Rios and Bernal 2001). However recent research in Bolivia by Paz-Rivera and Putz (2009) did not show a significantly higher abundance of 17 useful tree species, including palms, on the ADE sites, which suggests that in this area soil type does not affect the floristic composition of species utilized by man on ADE sites.

1.1.3 Forest selection for research

So far, differences found in studies that compare floristic composition of ADE soils with the less nutrient rich soils of the Amazon have mainly been carried out in forests of early successional stages, but it is currently not well known if these differences still persist in old-growth forest. Furthermore, the studies mentioned above have given special attention to species cultivated by humans and less attention has been given to naturally occurring species that can be responsive to soil fertility. Soils are the primary nutrient base of plants; therefore they are very important for the growth and the characterization of systems. The most striking property of ADEs are their high fertility. However, these soils do not have high availability of all nutrients necessary for optimum plant productivity. Additionally, total contents could be high but not available for plants. An example of this is nitrogen. N contents are significantly higher in ADE soils; however, the availability is only slightly higher or even lower (Lehmann *et al.* 2003).

Early-successional forests on ADE are characterized by higher percentages of vegetation cover, increased weed richness and a relatively higher proportion of annual and leguminous plants compared to non-ADE (Major *et al.* 2005). Local farmers also recognized differing stages of forest regrowth on ADE soils, specific vegetation-structural characteristics associated with ADE, such as more dense understories and lower canopies (Woods and McCann, 1999). Most researches find a positive influence on the vegetation due to these increases in soil fertility associated with ADE soils; however Paz-Rivera and Putz (2009) found no differences in the density of 17 useful tree species when comparing anthropogenic and non-anthropogenic soils. The study by Junqueira *et al.* (2010) gave contrasting results, showing that secondary succession on ADE soils does differ with the formation of a secondary forest that is floristically different due to the soils present.

Although it is known that especially palms, ferns and some herb species do respond to soil fertility (Costa, 2006; Heckenberger *et al.* 2007; Costa *et al.* 2008; Anderson *et* *al.* 2010), it is not certain whether ADE affects the distribution of these groups as well.

1.1.4 Research framework

This research was carried out within the framework of the Terra Preta Programme of Wageningen University-INREF, where my research was part of the PhD project of Estela Quintero Vallejo. We evaluated the effect of ADE on the composition, diversity and density of understory herbs, ferns and on palms in a Bolivian Amazonian forest. Figure 1 shows our hypotheses how composition, diversity and density will be affected by ADE.

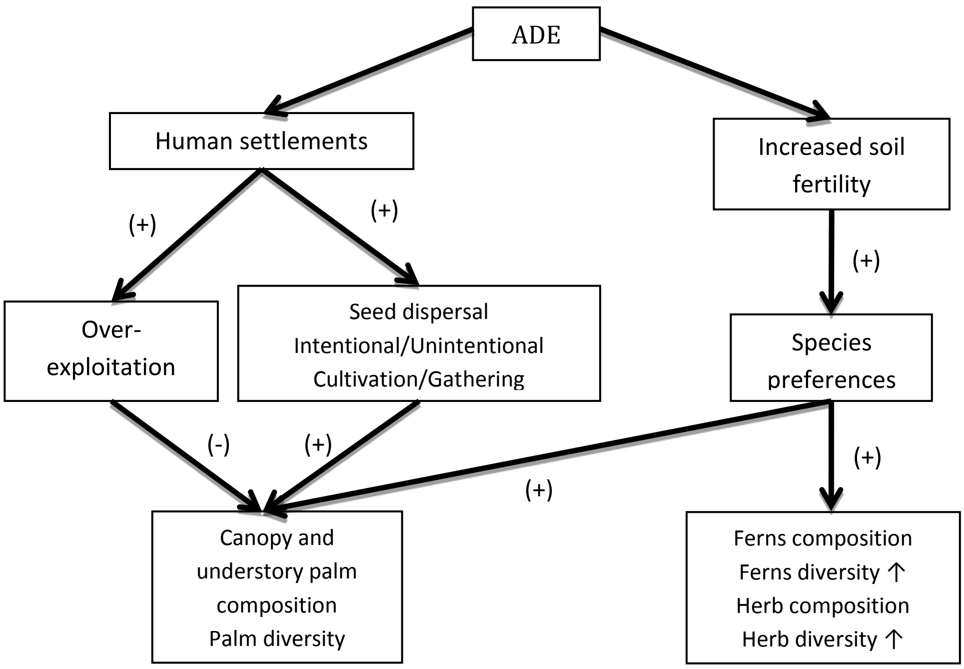

Figure 1 Conceptual diagram showing the hypothesized effects of ADE on composition of ferns, herbs, and palms. The 3 boxes on the top represent ADE and its main characteristics. The next level of boxes represents processes or mechanisms in which the soil fertility or human settlements can influence the presence of chosen species. Boxes on the bottom line represent patterns that we are expecting to find. Solid lines are connecting causes, processes or mechanisms and the outcome in a direct way. Parenthesis and signal represent a positive effect (+) or a negative effect (-) (courtesy of E. Quintero Vallejo).

1.2 Research objectives and research questions

Since in La Chonta forest has been present for several centuries it might be possible to see what the effect is of the established ADE soils on this forest have been. However, prior to focusing on the influence of soils one needs a better understanding of the (a)biotic climate present. Therefore we first wanted to look at differences between the soils, but also look at the influence of environmental variables on the vegetation. From this two questions were formed:

1. Can differences in concentrations of pH, Ca, P and N be found between the two soil types?
2. Are there environmental factors which influence species distribution?

The following two corresponding hypotheses were developed:

1. ADE soils are more fertile and higher P, Ca, N and pH levels are found compared to non- ADE soils.
2. Canopy openness, slope and tree cover positively influence the species distribution, while liana cover has a negative influence.

The objective of this research was to study the possible relationship between soils (ADE and Non-ADE) and the composition, diversity and density of understory herbs, fern and palm species. To answer this the following research question has been formed:

3. What are the effects of Amazonian Dark Earths on the composition, diversity and density of understory herbs, ferns and palms in the tropical moist forest of La Chonta, Bolivia?

As ADE are more fertile than common Amazonian soils and since Marantaceae, Heliconiaceae and Costaceae respond positively to increased soil fertility (Costa *et al.* 2005; Costa 2006), we hypothesise that the floristic composition of these herbs, ferns and palms are positively associated with ADE soils.
ADEs' are closely associated with the presence of human settlements. Henceforth, we are assuming that in these areas there was more intensive use of resources such as palms and other species interesting for consumption. This also includes the presence of more sophisticated agroforestry systems on ADE soils (Clement, 2006; Junqueira *et al.* 2011). Palm species are used widely by humans and are accordingly included in this research. The cultivation of Palm and the gathering of the seeds could increase the density on ADE soils but then again diversity can be poorer due to the selective use of only specific species (Figure 1). Alternatively, the

overexploitation and logging of palm species could also have reduced the density of palms present.

Concluding, the hypotheses for research question three are:

3. The abundance, diversity and density of Marantaceae, Heliconiaceae, Costaceae and ferns are positively linked with ADE soils
4. The abundance, diversity and density of Palms are higher in ADE due to the active enrichment of palms by humans in the past, or alternatively: the abundance, diversity and density of Palms are lower in ADE due to overexploitation by past civilizations

2.Methodology

2.1 Site description

Figure 2 Location of the La Chonta concession in the department of Santa Cruz, Bolivia (Taken from Paz-Rivera and Putz, 2009)

This study was conducted in the 100.000 ha concession of La Chonta, a lowland tropical forest in the Guarayos province Bolivia (15°45’ S, 62°60’ W; Figure 2). Guarayos is a transitional region between the humid forests of Amazonia to the north, the drier forests of Chiquitos and Chaco to the southeast, and the savannas of Mojos to the west. The vegetation of La Chonta is classified as subtropical humid forest. Annual mean precipitation is approximately 1580mm with a dry season between May and October. Mean annual temperature is 24.3°C (Paz-Rivera and Putz, 2009). The study site is located on the border of the Brazilian Precambrian Shield and has sandy-loam soils that are neutral in pH and rich in nutrients (Paz-Rivera, 2003; Peña-Claros *et al.* 2008; Peña-Claros *et al.* 2012). The relatively open forest canopy is semi-deciduous with mature forest heights of 25-30 m. Estimations of the age of the majority of canopy trees is at least 140 years (Paz-Rivera and Putz, 2009).

The forestry concession of La Chonta was established in 1974. During the first 20 years mahogany (*Swietenia macrophylla*) and tropical cedar (*Cedrela odorata*) were harvested. Before this time there is no evidence of forest management in the area. Nevertheless, the presence of ADE soil with pieces of charcoal and pottery of 400 to 300 years B.P., are evidence of indigenous settlements in the area (Paz-Rivera, 2003).

La Chonta is one of the areas where the Long-term Silvicultural Research Program (LTSRP) is carried out by the Instituto Boliviano de Investigacion Forestal (IBIF). The LTSRP plots were established using a randomized block design with three blocks and four silvicultural treatments. The company harvested the compartments after the establishment of the blocks between 2001 (block 1 and block 2) and 2002 (block 3). Each block consists of four 27-ha plots (450m x 600m), which have received different silvicultural treatments, being a control, normal logging, low intensity logging and high intensity logging (Peña-Claros *et al.* 2008). In total there are twelve large-scale permanent sample plots in the area and within these plots tree growth and survival has been monitored 1, 2 and 4 years after establishment (Peña-Claros *et al.* 2008).
To answer the main research question first a detailed soil map has been established to identify the ADE soils in the twelve 27 ha plots, after which the effect of ADE on herbs, ferns and palms were evaluated by measuring the floristic composition, diversity and density of these species in 22 transects established on ADE sites with 22 paired plots on Non-ADE sites. Below the two components of the research will be further elaborated.

2.2 Soil mapping

On each of the twelve 27 ha plots a grid of 50x50 m was established and on each corner of the grid a soil sample was cored using an auger, giving a total of 130 sample points per plot. The criterion for the size of the grid is based on the smallest size of ADE patches that Paz-Rivera and Putz (2009) found at La Chonta (0.3ha); hence, with such a grid system also the smallest ADE patches can be identified. Luckily in these 27ha plots such a grid was already more or less in place. Since ADEs are known for its characteristic black colour this sampling scheme could help in the mapping process (Paz-Rivera and Putz 2009). The colour was determined using the Munsell Soil Colour Charts. 7.5YR2/1 in the Munsell soil colour system is considered as the primary colour for ADE (Glaser and Woods, 2004). From this data collection maps were created using the Ordinary Kriging function with a spherical semi-variogram model within the Interpolation box of the Spatial Analyst Tool in ArcMAP.

2.3 Data collection

2.3.1 Herbs, ferns and palms

With the established soil maps we were able to define the areas where ADE were present. On these ADE sites 22 transects (150m long and 4m wide each) were established in each ADE patch and 22 paired transects (150m long and 4m wide each) on non-ADE areas adjacent to the ADE plots were established at least 50 metre away from the border of the ADE patch, distributed in the treatments where ADEs were present. This method was chosen due to the large variability found in the soils. With these transects we tried to include this soil and vegetation heterogeneity within our results. Establishment of ADE transects was based on the darker soil colours in the transects and the presence of ceramics. However some plots were established solely based on soil colour due to the absence of ceramics. Furthermore several transects have been located on points described by Paz-Rivera and Putz (2009) since there was a lack of good ADE sites in the 27ha plots. Each transect was subdivided in 5x5m subplots in which presence/absence of all species of the families: Marantaceae, Costaceae, Heliconiaceae, Arecaceae, and Pteridophyta species above 20cm height were recorded (For a full list of species found see Appendix 2). Additionally some more common Poaceae species and *Erythrochiton fallax* have been recorded due to their presence in the La Chonta forest. Botanical collections were made to confirm the exact identity of these species. The abundance of palms, herbs and ferns were recorded by counting the number of individuals present. This data supports the determination of composition of species, diversity, and density.

2.3.2 Soil properties

From each transect seven soil samples at fixed intervals of 25m were taken to create a compound sample to analyse the soil chemical features such as N, P, Ca, Mg, Al, K, C, pH, organic matter content and the physical properties of the soil like the soil texture. The samples were analysed at the Centro de Investigación Agricola Tropical (CIAT) in Santa Cruz, Bolivia. For an extensive explanation of the methodology used see Peña-Claros *et al.* (2012)

2.3.3 Canopy openness

Canopy openness was measured in every 5x5m subplots mentioned above. Canopy openness was measured to see whether light influences the species distribution, as it is commonly to be considered to be the most limiting factor for plant establishment, growth and survival in tropical rainforests. With help of a convex spherical densiometer that was held at waist height of the observer measurements were taken. The spherical densiometer is a simple instrument for estimating canopy openness comprising a convex mirror etched with a grid of 24 squares (Englund et al. 2000). The observer then counts the number of dots up to a total of 96 (24 squares subdivided into 4 smaller squares; Paletto and Tosi 2009). The data was divided by 96 to calculate the average canopy cover per point. The final measure for every plot is the average of every point collected in all 25 (5X5 m) subplots.

2.3.4 Other variables

Additional factors are considered as co-variables. Records of the slope were taken to see whether this influences the species presence. Therefore slope was measured using a Clinometer in every 5x5m subplot. Estimations of the understory cover by lianas and trees were also done for every 5x5m subplot. The cover (or absence of cover) could also affect species presence in the plots, therefore it is important to get an idea of the cover.

2.4 Data analysis

2.4.1 Transect variability

Due to the heterogeneity of the forest long transects were established, to see the impact of this we analysed the variability of the most abundant species of each group within the transect with the help of ANCOVA's. Transect was a fixed factor, while the environmental variables (Canopy openness, slope, tree and liana cover) were included as co-variables. Furthermore the interaction between transect and covariable has also been included in the test in order to get a better understanding of the differences between the covariable within the transects and the influence it has on the species distribution. Since both *Bolbitis serratifolia* and *Adiantum diogoanum* are extensively present in the area both fern species were analysed. The most abundant species analysed here are: *Bolbitis serratifolia, Pharus latifolius, Adiantum* *tetraphyllum, Costus scaber, Heliconia episcopalis, Erythrochiton fallax and Astrocaryum murumuru.*

2.4.2 Soil data

A t-test has been done to test for differences between ADE and non-ADE for single soil variables. Only the most important soil variables in accordance with Lehmann *et al.* (2003) were chosen, being P, Ca, N and pH.

2.4.3 Vegetation data

The effect of ADE on diversity and density of herbs, ferns and palms was first depicted by creating species area curves, with on the X-axis the 22 paired transects and on the Y-axis number of species found for three groups: All species, ferns and palms. Furthermore the effect of ADE on the species was tested by using Mixed linear models in which soil type and block are fixed factors and large plots (27ha) and plot pairs (ADE and non-ADE small plots) are random factors. For the transects which were established outside the blocks and plots were assigned to a specific block which was in the vicinity of the transect. All transects outside the blocks were added as transects where a normal treatment took place, since the normal treatment is most similar to the logging taking place outside the blocks. Notice that ADE patches are nested inside the plots and plots are nested inside the blocks. Mixed linear models release the assumption of independence among experimental units. Furthermore, canopy openness was included as co-variable (Table 1). Species area curves were drawn to get a better understanding of the influence of ADE on species.

Table 1 Summary of the statistical tests used for analysing data. Compared/fixed factors, dependent variables, number of replicates per comparison (n), total number of samples (N), and models to be used. (E(y) =expected value of dependent variable, μ=average of dependent variable, β= common slope for patch size covariable, β_1= common slope for canopy openness covariable, ε = model error).i=1,2; k=1,2,3; j=1,2,3,4; l=1,2,...,12 (Courtesy of E. Quintero Vallejo)

Factors and covariables	**Dependent variable**	**n**	**N**	**Model**
2 Soil types (ADE and non-ADE)(**S**); 3 blocks (**B**); 4 Plots (random factor) (P); 12 Pairs (**Pa**) covariable: Canopy openness (**L**).	ADE/ Non-ADE Diversity Density	12	48	$E(y)=\mu + S_i + B_k + P_{jk} + Pa_{jkl} + \beta_1 L + \varepsilon$

3. Results

3.1 Soil analysis

3.1.1 Soil mapping

It was very difficult to identify borders of ADE sites, therefore no specific patches were distinguished and transects were made on areas where grid points in a 150 meter range showed to have a dark colour class (ranging from very dark brown to black).Analysing the surface area of a specific patch of ADE soils is, in practice, impossible because of insufficient sampling intensity and furthermore, the exact borders of the patches have been interpolated with Arc Map, therefore we cannot conclude with certainty that these borders are accurate. With an increased intensity in the field one could be able to find borders. However we found no clear borders in La Chonta. Rather than having clear patches of ADE soils we found vague coalescences of different soil colours. Every patch of ADE soils we found differed in size and form, however we did find a gradient in soil colour within the plots from ADE points to Non-ADE points. Grid point analysis showed that approximately 25% of the grid points in this research are on the very dark soils which are indicators for ADE sites. The presence of ceramics and charcoal are less common (respectively 3% and 1% of the grid points; Table 2). Furthermore looking at the presence of ADE, one can see that block 1 has the least amount of ADE while block 3 has the most.

Table 2 the grid point analysis, showing per treatment the amount of grid points with dark soils, "normal" lighter soils, ceramics and charcoal. The lower rows also depict the total per variable and the percentage of the total amount of grid points measured this variable consists of.

Block	Dark soils	Normal soils	Ceramics	Charcoal	Total grid points
1 Intensivo	14	117	2	1	131
1 Mejorado	5	125	0	0	130
1 Normal	0	146	5	6	146
1 Testigo	0	129	0	1	129
2 Intensivo	69	76	7	4	145
2 Mejorado	4	138	0	0	142
2 Normal	32	104	7	0	136
2 Testigo	0	148	1	2	148
3 Intensivo	68	87	5	2	155
3 Mejorado	79	56	0	1	135
3 Normal	91	83	13	3	174
3 Testigo	63	91	10	2	154
Percentage	**24,64**	**75,36**	**2,90**	**1,28**	
TOTAL	**425**	**1300**	**50**	**22**	**1725**

The resulting maps from the analysis of the grid points can be found in appendix 1. An example is shown below (Figure 3). In this example one can see three patches of dark ADE soils. But even outside these colour zones ceramics or charcoal have been found (e.g. bottom right corner). The map shows that no clear forms or sizes can be found among ADE sites.

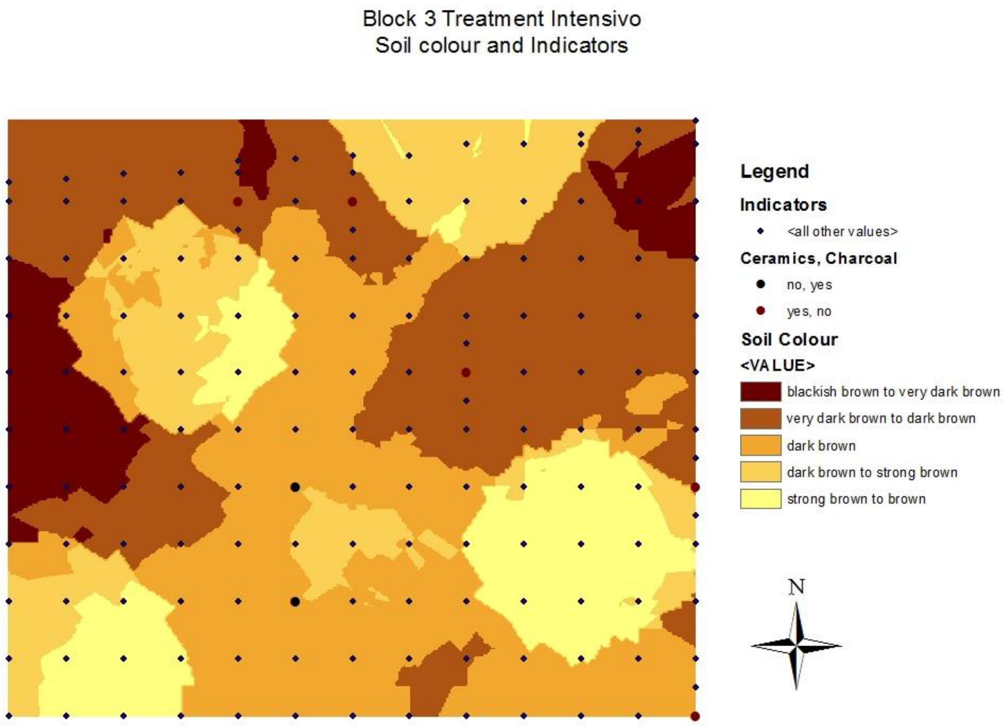

Figure 3 an example of a soil map based on five colour classes (as described in the Munsell Soil Colour Charts). This map shows Block 3, treatment Intensivo where both charcoal and ceramics are present. The grid point system used is established by the IBIF, star starting in the bottom left corner with the point 0, 0 and at the bottom right corner 600,0 (Note: not all transects are exactly a rectangle). The map was created using the kriging interpolation function in Arc Map.

3.1.2 Soil properties

Figure 4 depicts the differences in soil properties between ADE and Non-ADE soils. Although the differences are significant (table 3), the depiction in the figure does not show this clearly. One can see that higher values (Table 3) are recorded for all soil properties measured. Meaning that ADE are a richer soil type.

Table 3 T-test showing the differences between the two types of soil (ADE and Non-ADE) and soil characteristics (pH, Calcium, Phosphorus, Nitrogen). N=44.

	Mean			
	ADE	**Non-ADE**	**F**	**P**
pH	7,08	6,62	11,621	,001
Ca	5,17	3,47	4,537	,039
P	10,70	5,43	8,785	,005
N	0,17	0,12	10,752	,002

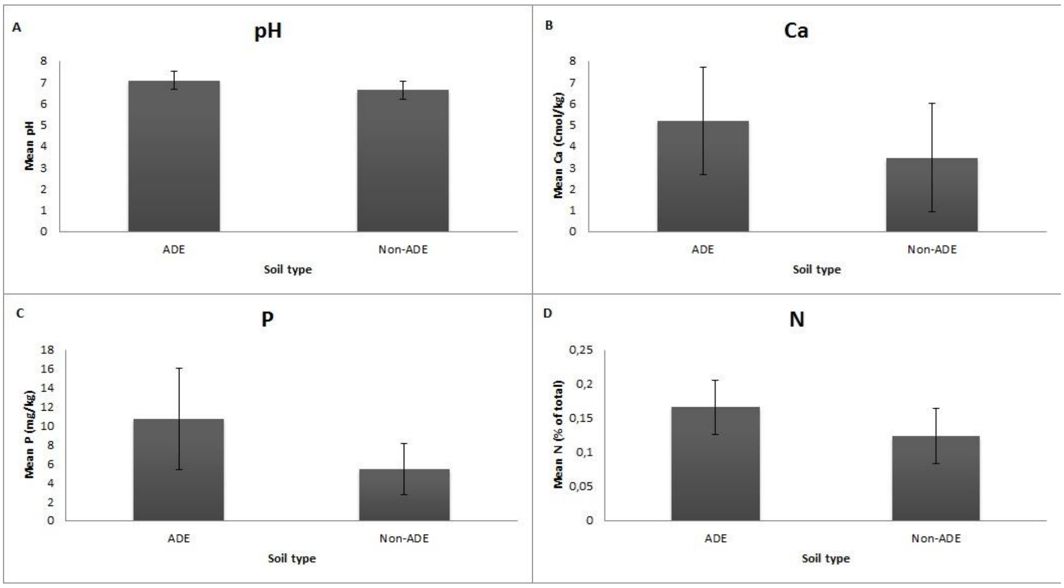

Figure 4 Nutrient differences between ADE and non ADE soils, with mean and standard deviation. N= 44. Bars represent the Standard Deviation A: pH, B: Ca (Cmol/kg), C: P (mg/kg), D: N (Percentage of total).

3.2 Species distribution

A list of the species found within the transects can be found in appendix 2. In total we found 42 species. Of these species six are Heliconiaceae, six Marantaceae, two Costaceae, six Arecaceae (Palms), sixteen fern species and 6 other species. The presence of these species and their abundance among subplots have been recorded in appendix 3. One can see for instance that a species such as *Erythrochiton fallax* can be found in relative high numbers, but only occurs in approximately 15% of the subplots. The most abundant species by far is *Bolbitis serratifolia*, followed by *Adiantum tetraphyllum,* a still unknown Poaceae species, *Costus scaber* and *Heliconia episcopalis*. The list of five most frequent species are rather similar, only *Astrocaryum murumuru* is slightly more common than *Heliconia episcopalis.*

4.3 Variability within transects

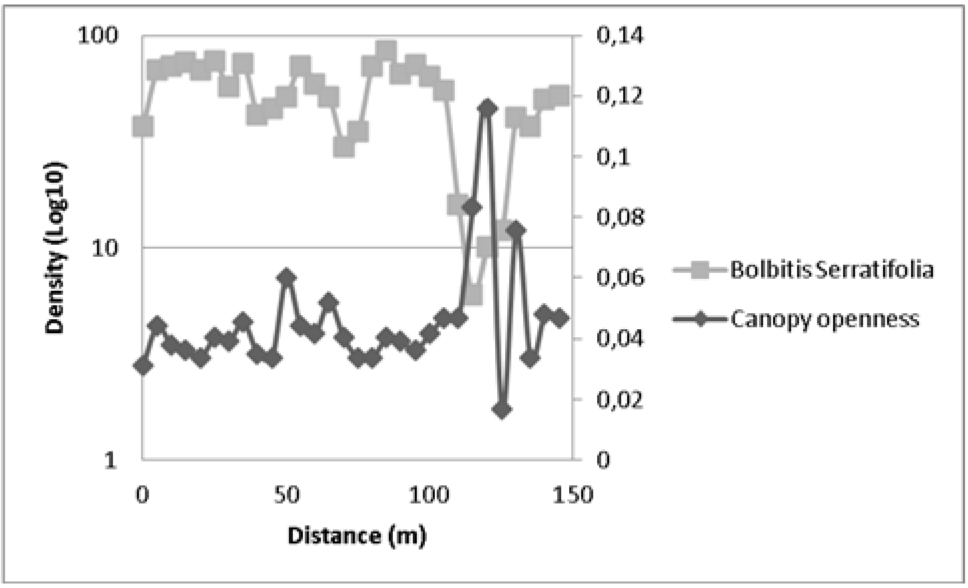

Figure 5 Spatial variation in canopy openness (right y-axis, in proportions) -and the abundance of the fern *Bolbitis serratifolia*(left y-axis) along line transect 1. The data on the y axis is Log10 transformed.

Within transects, there is substantial spatial variation in canopy openness and fern abundance, particularly for the common species, and the two variables could be associated. In transect one (Figure 5), for example, one can see that at the same place were changes in canopy openness occur also changes in the density of *Bolbitis* are found, with an extreme alteration around the 125m mark; a huge increase in canopy openness and a decline in the density of *Bolbitis*. Relationships between species abundance and abiotic conditions were formally analysed for the 10 most abundant species, with a series of ANCOVA's, with each time another environmental condition (i.e. canopy openness, slope, tree and liana cover) as the covariate (Table 4). The environmental variables do show influences on species abundance, although some play a larger role than others. The understory tree cover (significant for 5 species) has a negative influence on the species, while canopy openness (significant for 6 species) shows a positive influence. Increased tree densities could result in a decrease in canopy openness, which in turn could negatively affect a light demanding species. Other way around this also is the case. Decreased tree densities lead to increased canopy openness, resulting in favourable conditions for light demanding species.

Slope, however, does not play a significant role in the presence of the majority of the common species in the transects, with only one species, a Heliconiaceae reacting to slope positively. Stiles (1975) stipulates that besides the fact that slope, with other factors, do play a role in Heliconia distribution the main factor still is light availability. Liana cover seems to only influence *Heliconia* species and *C. scaber* negatively. By forming dense liana stands these species lose the competition for resources or are damaged by these lianas. Heliconiaceae and *C. scaber* are rather fragile plants and could therefore be easily damaged by lianas.

There is for 7 out of the 10 evaluated species an interaction between transect and canopy openness, which indicates that in the different transects species do react differently to canopy openness. To visualize this, the canopy openness per transect has been related to the presence of *Bolbitis serratifolia* (Figure 6). In most of the transects a negative relationship was found, however in three transects there was a positive relationship. To clarify these results transects which show a correlation coefficient higher than 0,3 or lower than -0,3 are only depicted. This threshold was chosen to include both positively and negatively influenced transects in sufficient amounts to show this relation.

Table 4 the influence of different biotic/abiotic variables on the 10 most common species in the transects, calculated with multiple ANCOVA's. T= Transect, C=Covariable (i.e. the variable mentioned in the adjacent column), TxC= the interaction between the transect and the covariable, F= the F-value given by the ANCOVA, P= the significance value given, R^2= the proportion of variability accounted for by the statistical model used (N=44).

	Canopy openness							**Slope**							**Tree cover**							**Liana cover**						
	T		C		TxC		*R²*	T		C		TxC		*R²*	T		C		TxC		*R²*	T		C		TxC		*R²*
	F	P	F	P	F	P		F	P	F	P	F	P		F	P	F	P	F	P		F	P	F	P	F	P	
Bolbitis serratifolia	4,8	**,000**	5,8	**,017**	1,9	**,000**	0,47	9,4	**,000**	0,3	,592	1,2	,146	0,45	14,6	**,000**	3,4	,066	1,6	**,006**	0,46	19,2	**,000**	0,1	,800	1,4	**,044**	0,45
Heliconia episcopalis	3,4	**,000**	7,7	**,006**	2,9	**,000**	0,58	4,7	**,000**	1,5	,224	1,6	**,015**	0,56	27,5	**,000**	18,7	**,000**	2,8	**,000**	0,59	31,1	**,000**	4,4	**,036**	0,8	,785	0,55
Adiantum tetraphyllum	1,2	,217	0,0	,910	0,9	,625	0,36	9,4	**,000**	0,2	,642	1,2	,223	0,37	12,5	**,000**	7,6	**,006**	0,7	,932	0,36	11,9	**,000**	0,5	,466	1,0	,561	0,36
Pharus latifolius	3,5	**,000**	2,0	,156	1,4	,056	0,60	18,2	**,000**	0,5	,497	1,0	,532	0,59	21,3	**,000**	4,7	**,031**	0,7	,959	0,59	31,9	**,000**	0,2	,664	0,9	,668	0,59
Costus scaber	2,7	**,000**	7,3	**,007**	1,4	**,032**	0,31	4,6	**,000**	0,0	,831	1,1	,325	0,30	6,8	**,000**	6,4	**,012**	1,1	,349	0,30	10,0	**,000**	10,0	**,002**	1,5	**,027**	0,32
Erythrochiton fallax	13,6	**,000**	10,3	**,001**	2,9	**,000**	0,78	20,1	**,000**	1,5	,227	1,9	**,000**	0,78	10,3	**,000**	12,7	**,000**	8,6	**,000**	0,83	85,8	**,000**	1,4	,230	0,5	,997	0,76
Astrocaryum murumuru	2,0	**,000**	3,5	,060	1,4	**,047**	0,18	2,4	**,000**	0,5	,474	1,4	**,049**	0,17	2,5	**,000**	0,9	,343	0,9	,727	0,16	3,5	**,000**	0,1	,725	1,1	,346	0,16
Bactris major	3,3	**,000**	4,5	**,034**	2,193	**,000**	0,29	3,2	**,000**	0,4	,533	1,2	,173	0,26	4,5	**,000**	1,1	,285	2,2	**,000**	0,29	7,9	**,000**	0,1	,718	1,6	**,007**	0,27
Heliconia stricta	1,8	**,001**	0,3	,562	1,351	,066	0,33	6,5	**,000**	0,3	,557	1,3	,122	0,33	7,7	**,000**	0,2	,690	1,1	,308	0,32	12,8	**,000**	5,6	**,018**	1,3	,118	0,33
Heliconia metallica	3,8	**,000**	3,9	**,050**	2,602	**,000**	0,57	10,3	**,000**	4,2	**,040**	0,7	,955	0,54	23,3	**,000**	2,6	,108	1,3	,120	0,55	32,5	**,000**	8,7	**,003**	1,6	**,010**	0,55

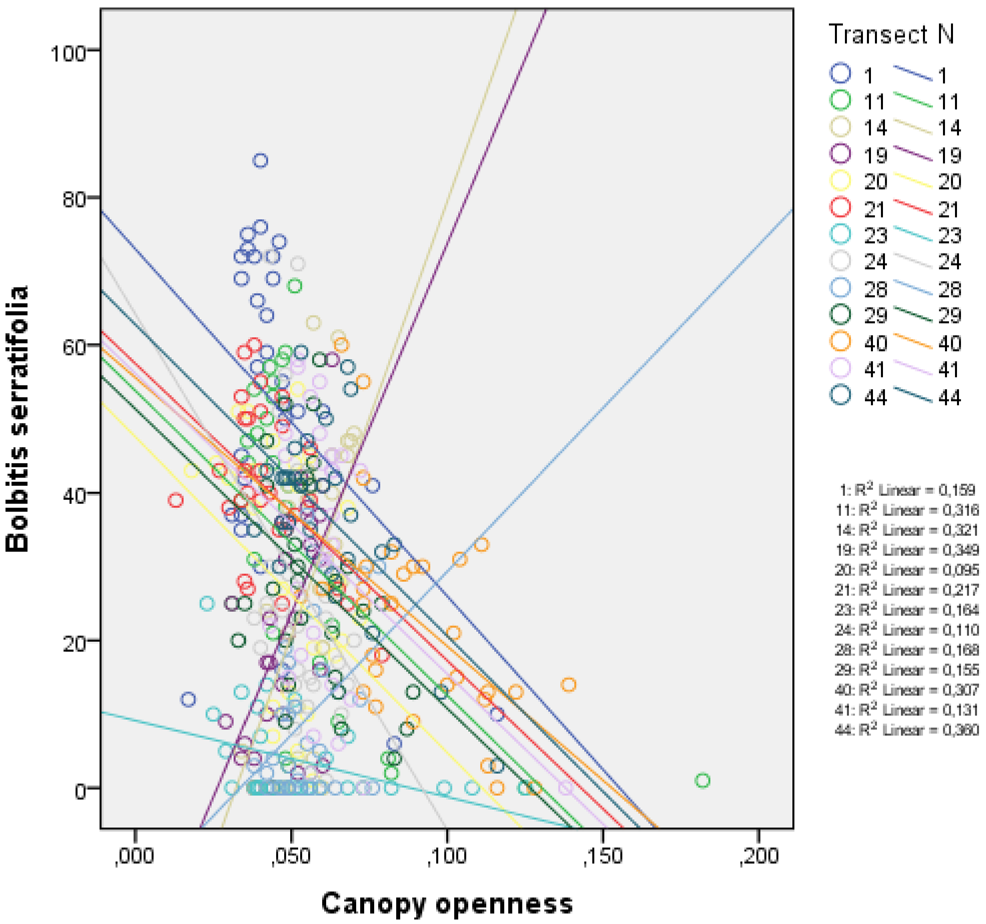

Figure 6 the relation between the abundance of *Bolbitis serratifolia* and canopy openness, for 13 individual transects. Regression lines, and coefficients of determination are given. In this graph the majority of transects has been removed due to the fact that their correlation coefficient was insufficient. A threshold of correlation coefficients of < -0,3 and >0,3 has been used.

3.4 Influence of ADE soils

3.4.1 Species area curves

The species are curves drawn for all species, ferns and palms (Fig. 7). This gives a first impression in the fact that differences between soil types are found with an increase in species richness. Both soil groups are overlapping, however it seems dependent on the species present, e.g. palms do not show a clear difference, but fern diversity seems higher in non-ADE soils, however it still falls within the 95% confidence intervals.

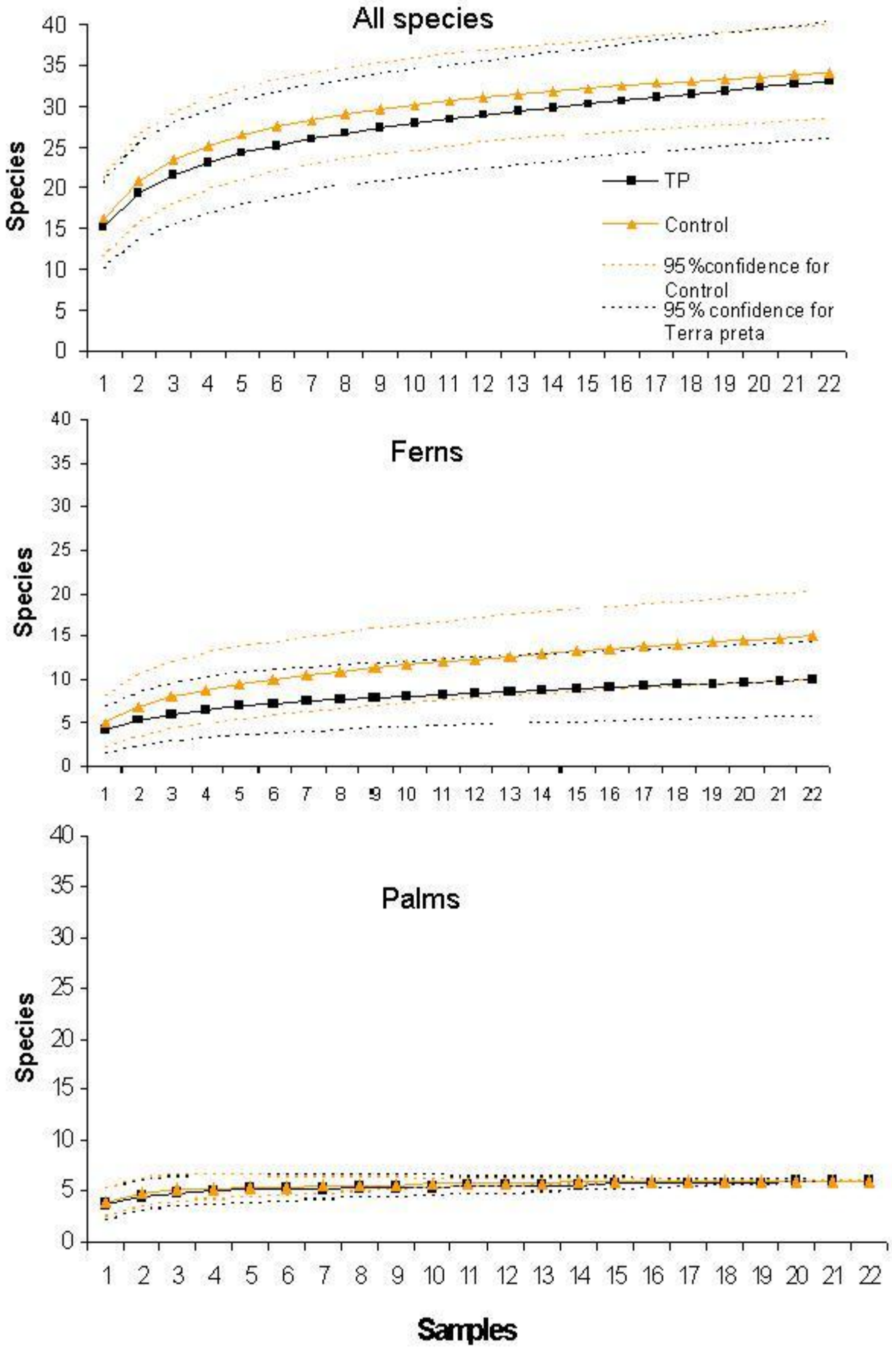

Figure 7 Species Area curves. A: Curve for all species, B: Curve for the group of ferns, C: Curve for the group of palms

3.4.2 Influence on abundance, diversity and richness

The abundance of five out of 10 species evaluated was significantly affected by soil type (ADE or non-ADE), while two species groups (Arecaceae and Marantaceae) also show an influence by soil type. However, all these species and groups are primarily found in areas with no ADE soils. Therefore these results suggests that these species are negatively influenced by ADE soils. The most abundant species of these five is *Pharus latifolius*(F= 9.22, P = 0,007; table 5). The influence of canopy openness to the presence of *Bolbitis serratifolia* as shown previously is also depicted in this analysis (F = 5.22, P = 0.032). As a group, the Poaceae and Marantaceae were also significantly less abundant on ADE than on non-ADE. Looking at the richness and diversity no differences can be found, this matches the results shown in the species area curves given above. Looking at the ferns however, this model suggests no differences between the two soil types, while the species area curves do show a tendency towards more ferns on Non-ADE soils.

Table 5 Influence of ADE or non-ADE soils on species presence using a generalized linear model. From this table species which did not show a significant relationship with one of the variables were removed. The complete table can be found in appendix 4 Soil= ADE or Non-ADE, treat*soil = Treatment * soil type. Significant values are shown in bold.

Species	**Block**		**Treatment**		**Soil**		**treat *soil**		**Canopy openness**	
	F	P	F	P	F	P	F	P	F	P
Individual species										
Heliconia episcopalis	0	0,97	0	0,974	3,75	0,07	14,83	**0,001**	0,35	0,565
Heliconia stricta	0,01	0,936	6,95	**0,019**	10,75	**0,004**	1,02	0,326	1,78	0,199
Bolbitis serratifolia	15,17	**0,001**	0,02	0,882	0,83	0,372	0	0,974	5,22	**0,032**
Pteris propinqua	1,21	0,289	0,06	0,813	7,98	**0,015**	1,13	0,72	1,21	0,284
Astrocaryum murumuru	4,41	**0,049**	0,83	0,373	0,61	0,443	0	0,972	0	0,962
Bactris major	4,46	**0,05**	1,69	0,213	2,35	0,143	2,42	0,138	0,21	0,652
Attalea phalerata	0,8	0,39	2,31	0,157	13,55	**0,003**	3,74	0,076	1,04	0,323
Syagros sancona	0,3	0,59	0,93	0,347	1,18	0,291	0,02	0,901	8,43	**0,008**
Pharus latifolius	0,04	0,836	0,84	0,373	9,22	**0,007**	0,74	0,401	0,5	0,483
Monotagma juranum	10,22	**0,028**	5,39	0,058	17,72	**0,005**	5,17	0,066	0,01	0,937
Species groups										
Fern	16,26	**0,001**	0,16	0,692	0,85	0,366	0,11	0,747	6,22	**0,02**
Arecaceae	8,6	**0,009**	4,48	**0,048**	2,44	0,134	0,03	0,861	0,54	0,469
Poaceae	0,13	0,724	0,58	0,457	8,48	**0,009**	0,85	0,369	0,64	0,428
Marantaceae	16,46	**0,001**	10,66	**0,004**	6,05	**0,023**	7,3	**0,014**	0,12	0,728
Diversity and richness										
Shannon diversity	7,189	**0,011**	0,06	0,812	1,83	0,191	0	0,945	0,54	0,468
Richness	1,12	0,302	4,53	**0,047**	2,59	0,123	1	0,33	1,49	0,235

4. Discussion

In order to answer the main research question, what are the effects of Amazonian Dark Earths on the composition, diversity and density of understory herbs, ferns and palms in the La Chonta Forest in Bolivia, first it was important to look at the influence of spatial variation and environmental variables on species abundance. In the second part of the discussion the focus will be on the influence of ADE on the species found within this research.

4.1 Anthropogenic Dark Earths and nutrient contents

I hypothesized that ADE soils would be more fertile than non-ADE soils, especially in terms of P and Ca. We indeed found that ADE soils had significantly higher P, Ca, N and pH than non ADE soils. However differences were not that high (fig. 4). There is a high variation among the different transects were soil samples were taken. Furthermore, the La Chonta forest seems to show smaller differences due to the fact that the background fertility levels are already quite high (Teixeira, personal communication 2011). Looking at the typically components which are enriched by anthropogenic soils due to the addition of bones (Calcium and phosphorus) we do find a clearer differentiation among the two soil types. However, Lehmann *et al.* (2003) stipulates that this increased numbers of Ca and P are mainly caused by chemical dynamics in the soils (e.g. relationship of organic carbon with Ca and P) and not on different inputs during habitation by past populations.

There is no clear field-definition of ADE soils around Latin America to define our soils as ADE. This is the case because the composition seems to differ in the region (as shown in Lehman *et al.* 2003). Sombroek *et al.* (2002) concluded that current knowledge on ADE does not yet permit a field-relevant detailed classification scheme. However they did list some criteria for improvement of classification, being: thickness of dark layer, colour ranges; higher organic C content and CEC; range of extractable P content; levels of Mn and Zn; presence of charcoal; krotovinas; soil texture; and base saturation. An effort by Kämpf *et al.* (2003) in creating a classification system did not result in a system which is easy to use in the field. A further step could be to compare the characteristics of these soils with ADE soils in other regions to test for similarities and be certain our soils can be classified as ADE.

4.2 Influence of Spatial and environmental variation

Our second research question was: are there environmental factors which influence species distribution at small spatial scales? We hypothesised that canopy openness, slope, tree and liana cover cause the variability in the vegetation. There is small-scale spatial variation in the abundance of the species (as shown in Figure 5), which can be explained by small-scale variation in environmental conditions (specifically tree cover and canopy openness), by transect, and their interaction (Table 4). Within this section we will try to analyse how these variables influence the presence of species.

In almost all cases the location of the transects itself significantly influences the presence of a species within. This could be caused by several factors. Montagnini and Jordan (2005) name elevation, soil fertility, environmental conditions and dispersal as factors influencing species diversity. Dispersal limitation is an important factor in species presence in a forest, but also other factors such as disturbances (e.g. fire or tree gap formation) and historical land use can play a role in forest composition (Whitmore, 1998; Primack, 2006). Nevertheless, the four most important measurable environmental variables (being canopy openness, slope, tree cover and liana cover) also explain some of the spatial variation, however this differs per species. For example *Bolbitis serratifolia,* the most common species found within this research, is negatively influenced by transect and canopy openness, since an increased canopy openness leads to a drying out of the lower forest layers, while ferns prefer humid conditions. *B. serratifolia* is the most abundant species found, occurring in over 80% of the subplots. This species forms a sort of carpet in the understory which could have implications for the other species found. The formation of these carpets could indirectly be caused by silvicultural treatments. Our data did not find this relationship, however, van der Heide (2007) found that ferns were more common in the control treatment compared to the other treatments. Furthermore, fern cover was influenced by soil type and topography. However, the dense understory created influenced seed removal negatively. With understories of Heliconia spp. and ferns seed removal was over 50% (Van der Heide, 2007). This could influence the succession of the forest significantly.

The fact that the cumulative effect of the transects and one other variable significantly influence the presence or absence of a species within a transect shows that there is variation in abundance at a larger spatial scale. This could be influenced by for example soil types present, local disturbance history, topology and hydrology of the area. However, it was not the scope of this research to investigate all these additional factors. This interaction shown, does mean that the transects differ in their range of environmental conditions and hence, the influence of the different measured variables and the effect it has on the species could differ per transect. Some environmental variables do not even have an influence on specific species. For instance slope, this variable did not influence 90% of the most common species (table 4).
The majority of the results are in line with the common knowledge. An example could be *Costus scaber,* whose abundance increases with a lower cover of trees and thus also increased openness. Swenson (2009) indicates that *C. scaber* is a light-demanding species, which is in line with the findings of this research. However as shown in table 4 the relationship between openness and cover is influenced by the interaction of the environmental factor with the transects, so spatial variation on a landscape scale could also be of importance for the establishment of *C. scaber* in the region.

Two of the three *Heliconia* species show a (positive) influence from canopy openness and *H. episcopalis*, was positively affected by tree cover, and occurs therefore supposedly in more shaded conditions. There is a common conception that the different *Heliconia* species are found at different positions along the light gradient (from shade tolerant species to different light demanding species), but the intensity of some species are significantly higher in areas with increased light availability (e.g. forest gaps; Stiles, 1975; Van der Heide, 2007; Swenson, 2009). All three *Heliconia* species are negatively affected by liana cover; liana cover may reduce light cover or increase competition for space, with the liana's physically crushing the fragile *Heliconia* with its tangles, which negatively affects the presence of Heliconiaceae.

In areas where there is a huge variation in slope a significant influence of slope can be recorded (Harms *et al.* 2001), however in our research area there is only very modest topographic variation (Klomberg, personal observation). Due to this, slope did not affect the majority of species found, only *Heliconia stricta* seems to be related to slope. Furley (1996) suggest that slope and drainage influence the availability of moisture, resulting in a differentiation of vegetation. For Heliconiaceae temperature, slope, moisture and soil type is also mentioned as being important, however, the extent of its importance differs per species (Stiles, 1975).

4.3 Influence of ADE on species

The main research question is whether species are influenced by the presence or absence of ADE soils. With this question three hypotheses were formulated. 1) The abundance, diversity and density of Marantaceae, Heliconiaceae, Costaceae and ferns are positively linked with ADE soils. 2) The abundance, diversity and density of Palms is either higher on ADE due to the enrichment of palms by humans in the past, or lower on ADE due to overexploitation by past civilizations. All two hypotheses were rejected by our results.

Approximately One fifth of the evaluated species (5/24)(*Attalea phalerata, Heliconia stricta, Pteris propinqua, Pharus latifolius* and *Monatagma juranum;* Appendix 4), and one third of the evaluated family groups (Marantaceae and Poaceae; 2/6)showed a significant preference for non-ADE soils, thereby suggesting a negative link with ADE soils. Looking at these species we can already conclude that Costaceae, Shannon diversity and richness are not influenced by ADE soils, since none of the species and groups as a whole showed significant results. All the other families researched have at least one species which was negatively influenced by the ADE soils. This is in line with the indicator species analysis done by Quintero Vallejo *et al.* (2012) with the same dataset. This analysis showed that *Attalea phalerata, Heliconia stricta, Adiantum argutum* and *Pteris propinqua* are indicators for Non-ADE soils. The other two species which were not included in this indicator species analysis are generally distributed more on the Non-ADE transects (*Pharus latifolius* 61,3% of the measured individuals and *Monatagma juranum* 80,3%). This means that the suggested link between Marantaceae or Heliconiaceae and ADE soils is negative, thereby rejecting the first hypothesis. However, other research, found that fertility (with increased fertility in ADE soils) is an important factor in the occurrence of Marantaceae (Costa, 2006) and Heliconiaceae (Stiles, 1975). Therefore one needs to look at other factors which might have influenced the distribution of these families associated with high

fertility. Competition with a fast growing pioneer species could have caused the absence of these species on these more fertile soils. Still, other mechanisms related to ADE development could have played a role in the absence of these species. For instance the successional stage of the forest. It could be that species currently avoid ADE or they are still in the process of recolonizing it. The results found by Junqueira *et al.* (2010; 2011) suggest that in secondary forest some palm species (including *A. Phalerata)* are positively associated with ADE soils. Given the fact that his secondary forests are “younger” than the La Chonta forest, this could indicate that the palm species *A. phalerata* eventually was outcompeted and now occurs less on ADE soils. Therefore it could be possible that the effects of ADE are only found in early successional stages, while in later stages influences from surrounding areas reduce the effects of ADE. However due to the different characteristics between these forest types it is difficult to assign a change of influence solely to soils. As was shown above other environmental factors play a significant role in the distribution of species.
The indicator analysis (Quintero Vallejo *et al.* 2012) also found that *Erythrochiton fallax* was the only species which could act as an indicator for ADE soils. The statistical model we conducted however, did not show the result for *E. fallax* (Appendix 4). This could be due to the fact that *E.* fallax prefers, besides sandy soils, low light environments and furthermore, the absence of disturbances such as logging could have triggered the creation of these vast patches of *E. fallax* (Van der Heide, 2007) and therefore we cannot conclude with certainty that soil type is the main driving factor of the presence or absence of *E. fallax* in this area.

Of all the palm species found in the transects only one species showed a significant response to ADE. The reduced abundance of *Attalea phalerata* on ADE soils is in contradiction with a study done by Paz-Rivera and Putz (2009)in the same area. They found that *A. phalerata* occurs mostly on terra mulata soils, an intermediate soil type in the gradient of ADE to Non-ADE. Junqueira *et al.* (2011) however suggest that this species could act as an indicator for ADE in Brazil. More recently Clement (co-author of Junqueira *et al.* 2011; personal communication 2012) stated that this species is usually found in less fertile soils. Thereby supporting the findings of our research. Generally, researchers suggest that palm distributions are commonly associated with human settlements (as shown by Clement 1999; Morcote-Rios and Bernal 2001; Paz-Rivera and Putz, 2009), while environmental factors also play a role in their distribution at different scales (McPherson and Williams 1998; Anderson *et al.* 2010; Eiserhardt *et al.* 2011). A different human population density or usage intensity of palms could therefore (together with environmental variables) be the explaining factor for the occurrence or absence (due to over usage) of *Attalea phalerata* in these forests. We can conclude that no clear direct relationship between palms and ADE can be found. Therefore one can reject the second (The abundance, diversity and density of Palms is positively linked with ADE due to the role of palms in past civilizations) and third hypothesis (The abundance, diversity and density of Palms are negatively linked with ADE due to overexploitation by past civilizations). However as suggested above there is a possibility that human settlement (which was the basis ADE development) influences the palm distribution negatively through overexploitation (e.g. Morcote-Rios and Bernal, 2001).

The big question remains why these species which were associated with soil fertility actually do not prefer these richer sites. So what drives these species? As already explained in 4.1 it could be that the high background soil fertility already is of a sufficient extent to address the needs of these species. Furthermore, additional factors could have influenced the composition of the species we included in this research. Van der Heide (2007) found that the silvicultural system and topography significantly influences the presence of ferns and heliconia species in the research plots at La Chonta. However our data only found the link with treatment for 1 species of Heliconia and for the family groups Arecaceae and Marantaceae. Furthermore, our data suggests for 4 species, 3 families (Arecaceae, Marantaceae and ferns) and the Shannon diversity index (table 5) that the block they were found in played a role. So topography could have influenced these species and groups as well. Eiserhardt *et al.* (2011) looked at the drivers of palm distribution, with climate being the most important factor at landscape and broader scales. Soil, topography, vegetation and hydrology only at landscape and local scales, while dispersal plays a role at all scales, however according to Costa *et al.* (2008) the effect of dispersal limitation with palms does not explain the composition. Fraser *et al.* (2011a) found that crop species and landrace populations deviate on anthropogenic and non-anthropogenic soils as a result of the interaction between selection and management, soil physical and chemical properties and plant responses over time. Therefore, we can conclude that many additional factors influence the composition of these species in the forest and no clear explanation of the factors influencing the presence or absence can be given.

4.4 Strengths and limitations of the current research

This research tried to fill in a niche within the current knowledge on ADE research. Research of effects of ADE on vegetation has mainly been on previously abandoned agricultural lands (e.g. Major *et al.* 2005) and secondary forests (e.g. Junqueira *et al.* 2010). To our knowledge, only one study evaluated the ADE effects on vegetation in “old” Amazonian forest, where the influence was very small (Paz-Rivera and Putz, 2009). Another research done in a Cameroonian forest however suggests that species composition in this forest still shows signs of historical disturbances caused by land use between three and four centuries ago.
However the lack of a clear classification system made it difficult to specifically classify the soils as ADE. Variations in soil colour were recorded, so it could be possible that within this research ADE transects were partially situated on more *terra mulata* (intermediate) like soils. However, the presence of ADE soils has been determined in combination with laboratory research on its chemical composition. Therefore the data on ADE soils are rather reliable. On the other hand we found out, that the boundaries between ADE and non-ADE were rather vague and not always clearly to be determined.

The present research helps in a limited way to detect the presence of ADE-soils in the La Chonta tropical forest. As we showed, *Attalea phalerata, Heliconia stricta, Adiantum argutum* and *Pteris propinqua* are rather indicators for Non-ADE soils.
Moreover it has become clear that other factors, like canopy also play a role in the presence of some species. Therefore this study shows the complexity of the relationship between soil composition (ADE or non-ADE) and presence of the species studied in this research.

4.5 Recommendations for further research

I do believe that these soils can alter the aboveground system due to the increased fertility available for the plants. However, to see changes would either need an enlarged timeframe or presses the need for more research on the small scale influences of these soils, such as effects on functional traits. Currently E. Quintero

Vallejo is busy taking a second step and looking at specific plant/seedling responses, by analysing seedlings and soils within a greenhouse. Looking at functional trait level could show influences in growth strategies of plants. Soil type could affect the trade-off between root or leaf development. With this approach also a wider range of species is used which could be influenced by ADE.

Furthermore I believe that ADE and Non-ADE soils found in Latin America are to be classified along a gradient instead of now as two categories, this is in line with research done by Fraser *et al.* (2011b). This gradient approach could show the small scale implications of increased fertility and soil components on species presence, while with the current lumped approach differences could be lost.

Additionally comparisons between ADE sites across Latin America could help to get a better idea of the gradient in which ADE soils are found and could help in the formation of a classification system for ADE soils.

4.6 Conclusion

With certainty I can conclude that Anthropogenic Dark Earths did not have a strong lasting effect, with only 5 out of 24 species showing a negative influence, on the understory species found in the La Chonta forest. Nevertheless, the results do show some interesting findings regarding influences of certain species to factors (See table 6). However some contrasting data has been recorded and according to the test there is one species which could act as an indicator species for ADE in this region. In the indicator species analysis done by Quintero Vallejo *et al.* (2012) with the same dataset *Erythrochiton fallax* was seen as a good indicator for anthropogenic soils. However the Generalized Mixed Linear Model did not show this relationship. As shown before this species is influenced by soil type, however, looking at these two tests, one could argue that it is not ADE type that influences it, but a mixture of several factors (light, soil and disturbance). Therefore I would discourage the use of this species as an indicator. Both tests did show some species (e.g. *Attalea phalerata*) which can be used more safely as an indicator for non-ADE soils.

Forest age could play a role in finding a reason for the absence of Ade indicators. There is a possibility that the influence of ADE on the vegetation decreases along the successional gradient. In the early developmental stages the increased soil fertility favours specific species, while over time it could be that on a small scale the competition between species and the presence of dispersal sources are more important in forming the species composition than the influence of these soils.

Furthermore, the background fertility of La Chonta could have weakened the effects of the ADE on the presence of species in this forest. In the case of larger differences in soil fertility between soil types alternating species compositions are found (e.g. Major *et al.* 2005; Junqueira *et al.* 2010).

Acknowledgments

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Reference list

Anderson, K.M. Turner, B.L. and Dalling, J.W. 2010. Soil-based habitat partitioning in understory palms in lower montane tropical forests. *Journal of Biogeography* **37**: 278–292.

Barber, R.G. 1995. Soil degradation in the tropical lowlands of Santa Cruz, eastern Bolivia. *Land Degradation &Rehabilitation* **6:** 95-107.

Clement, C. 2006. Fruit trees and the transition to food production in the Amazon. *In*: Balee, W. and Erickson, C.L. (eds.) 2006. *Time and Complexity in Historical Ecology: Studies from the Neotropical Lowlands*. New York: Columbia Univ. Press. 165–185.

Costa, F.R.C. 2006. Mesoscale Gradients of Herb Richness and Abundance in Central Amazonia. *Biotropica* **38**(6): 711–717.

Costa, F.R.C. Magnusson, W.E. and Luizao, R.C. 2005. Mesoscale distribution patterns of Amazonian understory herbs in relation to topography, soil and watersheds. *Journal of Ecology* **93**: 863–878.

Costa, F.R.C. Guillaumet, J. Lima, A.P. and Pereira, O. 2008. Gradients within gradients: The mesoscale distribution patterns of palms in a central Amazonian forest. *Journal of Vegetation Science* **20**.

Eiserhardt, W.L. Svenning, J. Kissling, W.D. Balsley, H. 2011. Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. *Annals of Botany*, Oxford University Press.

Englund, S.R. O'Brien, J.J. and Clark, D.B. 2000. Evaluation of digital and Wlm hemispherical photography and spherical densiometry for measuring forest light environments. *Canadian Journal of Forestry Research* **30**: 1999–2005.

Fraser, J.A. Junqueira, A.B. Kawa, N.C. Moraes, C.P. 2011a. Crop Diversity on Anthropogenic Dark Earths in Central Amazonia. *Human Ecology 2011.*

Fraser, J. Teixeira, W. Falcão, N. Woods, W. Lehmann, J. and Junqueira, A.B. 2011b. Anthropogenic soils in the Central Amazon: from categories to a continuum. *Area 2011.*

Furley, P.A. 1996. The Influence of Slope on the Nature and Distribution of Soils and Plant Communities in the Central Brazilian *Cerrado*. *In:* Anderson, M.G. and Brooks, S.M. 1996. *Advances in Hillslope processes, Volume 1.* Wiley publishers, New York. 327-346.

Glaser, B. and Woods, W.I. 2004. *Amazonian Dark Earths: explorations in space and time.* Springer-Verlag, New York.

Harms, K. E. Condit, R. Hubbell, S. P. and Foster, R. B. 2001.Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology* **89**: 947–959.

Heckenberger, M.J. Russell, J.C. Toney, J.R. and Schmidt, M.J. 2007. The legacy of cultural landscapes in the Brazilian Amazon: implications for biodiversity. *Philosophical Transactions of the Royal Society B* **362**: 197–208.

Junqueira, A.B. Shepard, G.H. and Clement, C.R. 2010. Secondary forests on anthropogenic soils in Brazilian Amazonia conserve agrobiodiversity. *Biodiversity and Conservation* **19**(7): 1933-1961.

Junqueira, A.B. Shepard, G.H. and Clement, C.R. 2011. Secondary Forests on Anthropogenic Soils of the Middle Madeira River: Valuation, Local Knowledge and Landscape Domestication in Brazilian Amazonia. *Economic Botany* **65**(1): 85–99.

Kämpf, N. Woods, W.I. Sombroek, W. Kern, D.C Cunha T.J.F. 2003.Classification of Amazonian Dark Earths and other ancient anthropic soils. *In:* Lehman, J. Kern, D.C. Glaser, B. and Woods, W.I. (Eds) 2003. *Amazonian Dark Earths: Origin, Properties and Management.* Kluwer Academic Publishers, New York.

Laurance, W.F. Fearnside, P. M. Laurance, S. G. Dela-monica, P. Lovejoy, T. E. Rankin-de Merona, J. M. Chambers, J. Q. and Gascon. C. 1999. Relationship between soils and Amazon forest biomass: a landscape-scale study. *Forest Ecology and Management* **118**:127-138.

Lehman, J. Kern, D.C. Glaser, B. and Woods, W.I. (Eds) 2003. *Amazonian Dark Earths: Origin, Properties and Management.* Kluwer Academic Publishers, New York.

Major, J. Steiner, C. Ditommasso, A. Falcao, N.P.S. and Lehman, J. 2005. Weed composition and cover after three years of soil fertility management in the central Brazilian Amazon: Compost, fertilizer, manure and charcoal applications. *Weed Biology and Management* **5:**69–76.

Montagnini, F. and Jordan, C.F. 2005.*Tropical Forest Ecology, the Basis for Conservation and Management*. Springer, Berlin – Heidelberg, Germany.

Morcote-Ríos, G. and Bernal, R. 2001.Remains of palms (Palmae) at archaeological sites in the new world: A review. *The Botanical Review* **67:** 309–350.

Paletto, A. and Tosi, V. 2009. Forest canopy cover and canopy closure: comparison of assessment techniques. *European Journal of Forestry Research* **128**: 265–272.

Paz-Rivera, C.L. 2003.*Forest-use history and the soils and vegetation of a lowland forest in Bolivia.* M.Sc. Thesis. University of Florida, Gainesville, FL, USA.

Paz-Rivera, C.L. and Putz, F. E. 2009.Anthropogenic Soils and Tree Distributions in a Lowland Forest in Bolivia. *Biotropica* **41**: 665–675

Peña-Claros, M. Fredericksen, T.S. Alarcón, A. Blate, G.M. Choque, U. Leaño, C. Licona, J.C. Mostacedo, B. Pariona, W. Villegas, Z. And Putz, F.E. 2008*.* Beyond reduced-impact logging: silvicultural treatments to increase growth rates of tropical trees*. Forest Ecology and Management* **256:**1458–1467*.*

Peña-Claros, M. Poorter, L. Alarcón, A. Blate, G. Choque, U. Fredericksen, T.S. Justiniano, M.J. Leaño, C. Licona, J.L. Pariona, W. Putz, F.E. Quevedo, L. and Toledo, M. 2012. Soil effects on forest structure and diversity in a moist and a dry tropical forest. *Biotropica* **44**: 276–283.

Primack, R.B. 2006 *Essentials of Conservation Biology, fourth edition*. Sinauer Associates, Sunderland, MA.

Quintero Vallejo, E.M. Klomberg, Y.G. Bongers, F. Poorter, L. Toledo, M. Peña-Claros, M. 2012. Effect of Amazonian Dark Earth on the composition, diversity and density of herbs, ferns and palms. Poster presented on 19-06-2012 at the ATBC Conference, Bonito, Brazil.

Sombroek, W. Kern, D. Rodrigues, T. Cravo, M.S. Cunha, T.J. Woods, W. and Glaser, B. 2002. Terra Preta and Terra Mulata: pre-Columbian Amazon kitchen middens and agricultural fields, their sustainability and their replication. Paper no. 1935. Bangkok, Symposium 18 - Anthropogenic factors of soil formation, *17th World Congress of Soil Science*.

Stiles, F.G. 1975.Ecology, Flowering Phenology, and Hummingbird Pollination of Some Costa Rican Heliconia Species. *Ecology* **56**(2): 285- 301.

Swenson, N.G. 2009. Herbaceous monocot plant form and function along a tropical rainforest light gradient: a reversal of dicot strategy. *Journal of Tropical Ecology* **25**(1): 103-106.

Van Der Heide, G. 2007. Dense understory patches in a tropical moist forest in La Chonta: occurrence and effects on seed removal. *MSc thesis Wageningen University.*

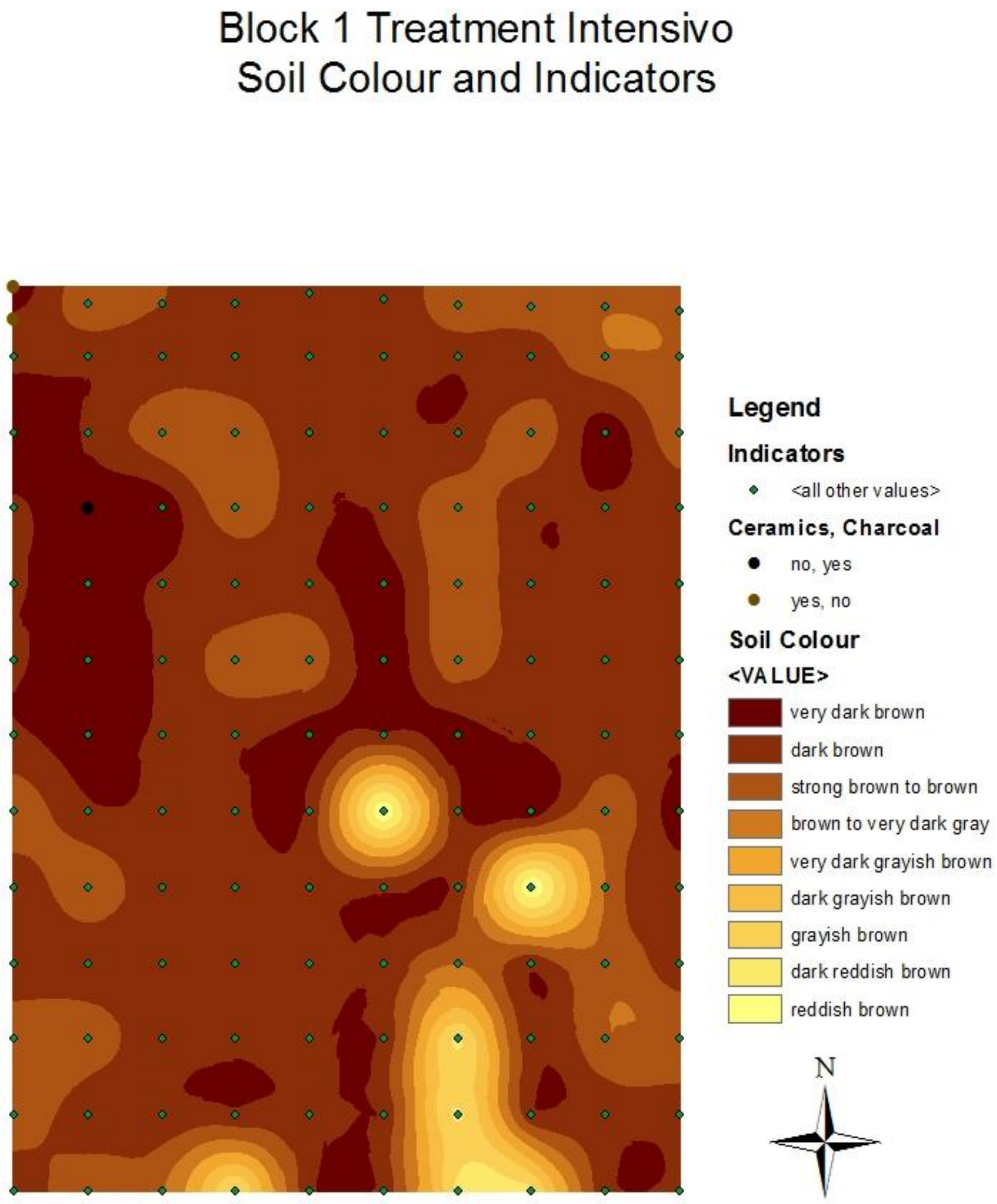
Van Gemerden, B.S. Olff, H. Parren, M.P.E. and Bongers, F. 2003. The pristine rain forest? Remnants of historical human impacts on current tree species composition and diversity. *Journal of Biogeography* **30**: 1381-1390.

Whitmore, T.C. 1998. A*n Introduction to Tropical Rain Forests.* Oxford University Publishers, Oxford, UK.

Willis, K.J. Gillson, L. and Brncic, T.M. 2004. How “Virgin” Is Virgin Rainforest? *Science* **304**: 402-403.

Woods, W.I. and McCann, J.M. 1999. The anthropogenic origin and persistence of Amazonian dark earths. *In:* The yearbook of the conference of Latin Americanist Geographers, **25**. Southern Illinois University, Edwardsville: 7–14.

Appendix 1 Soil maps



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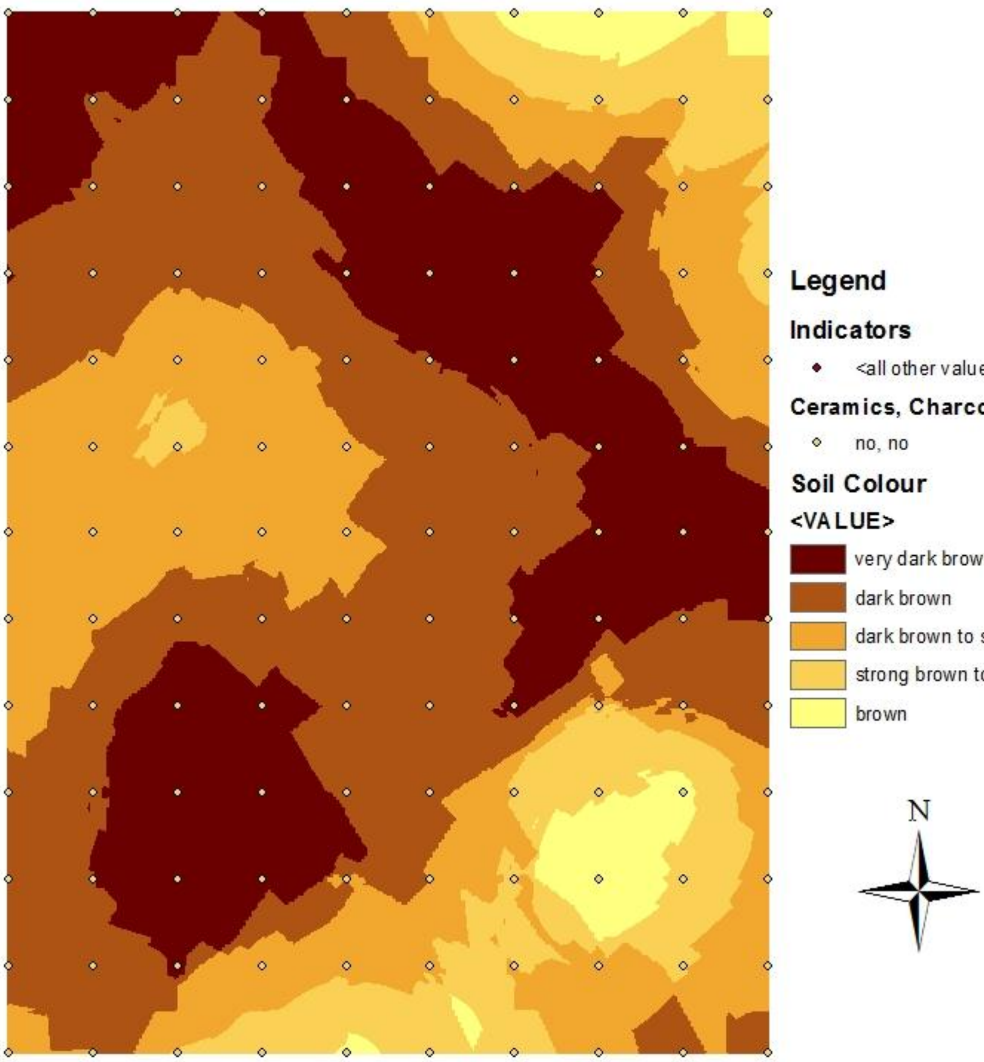

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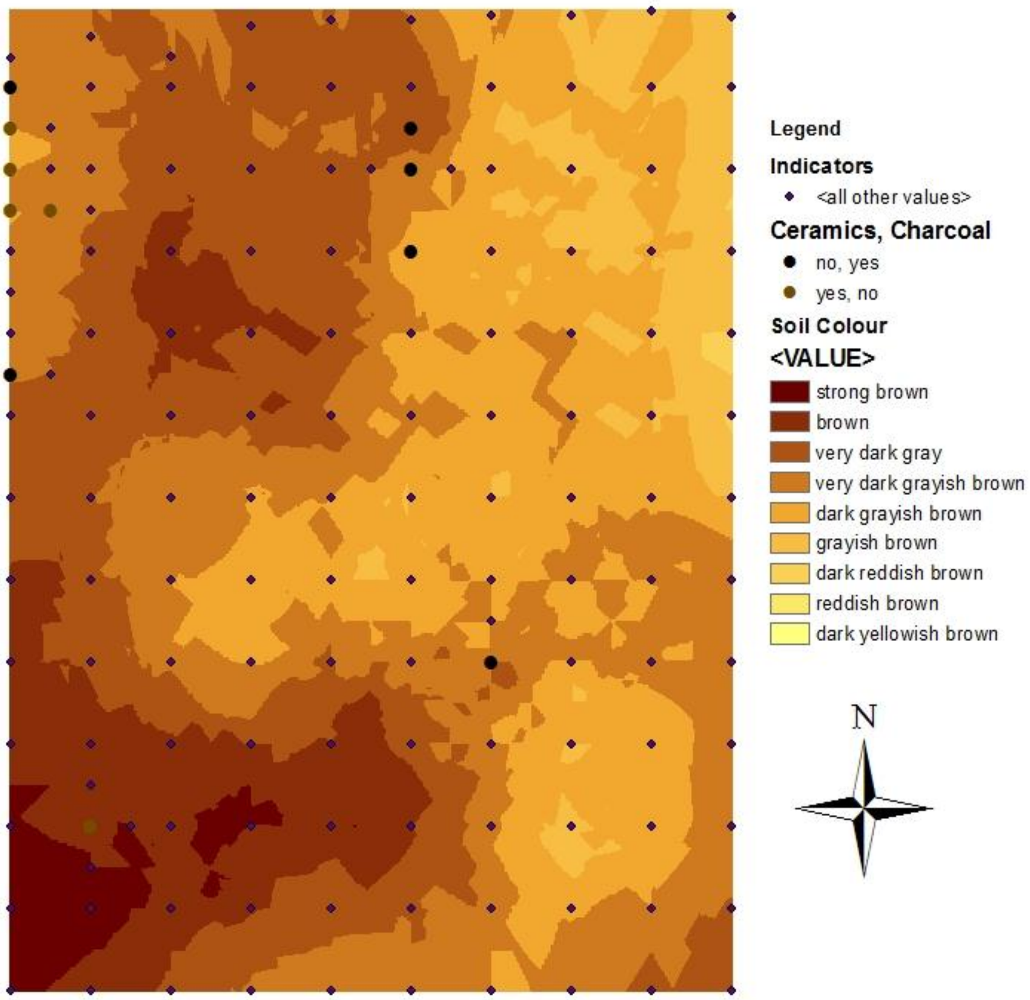

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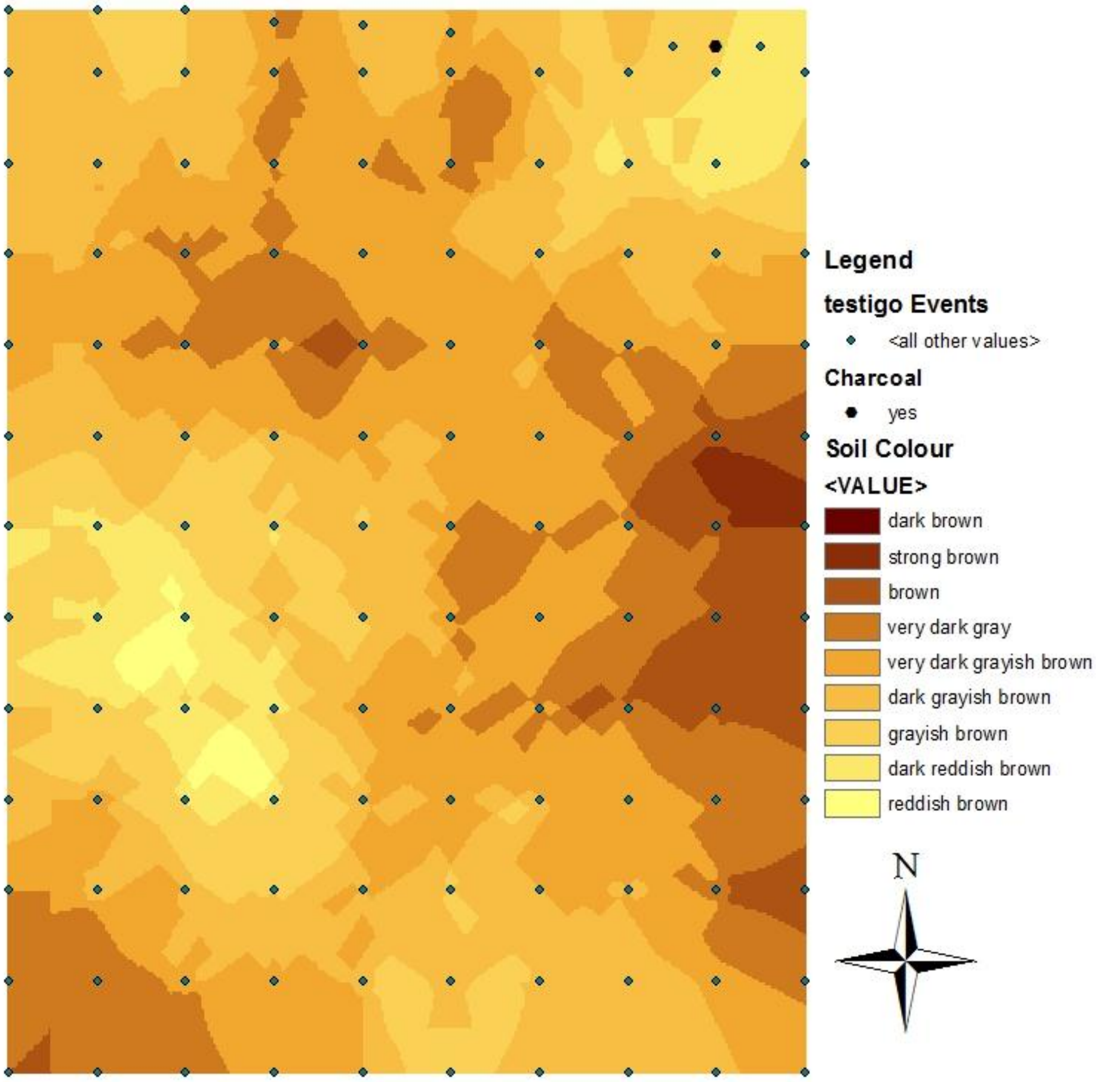

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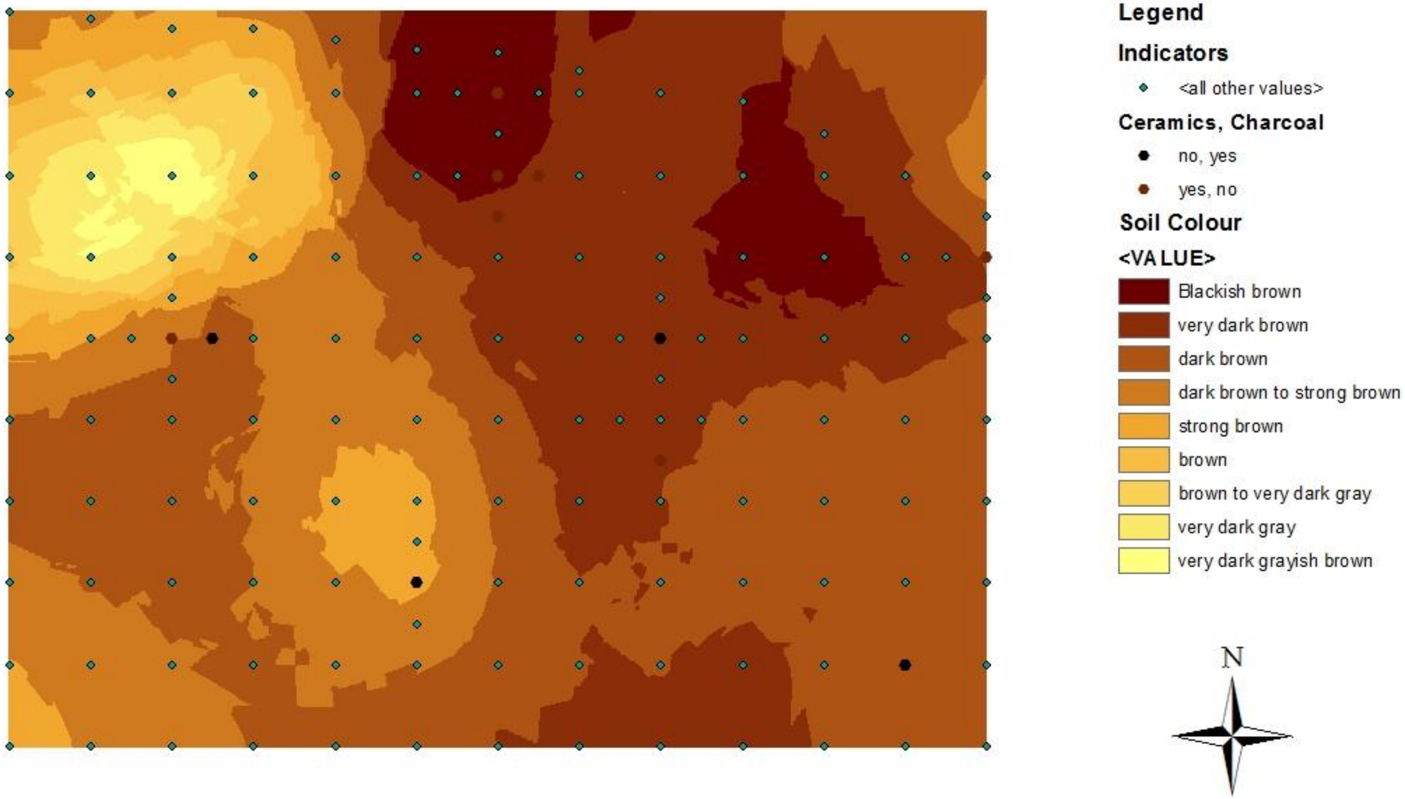

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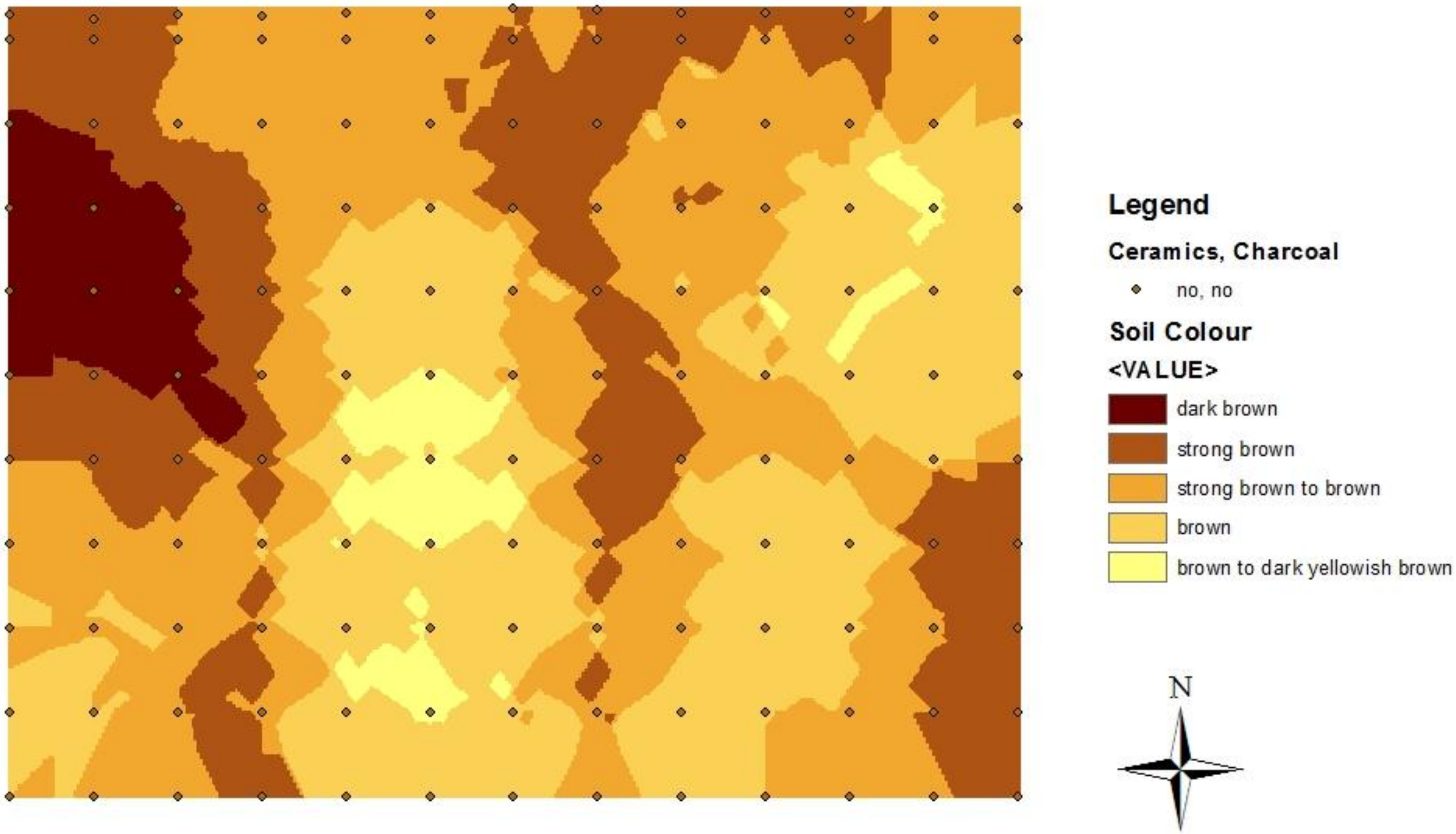

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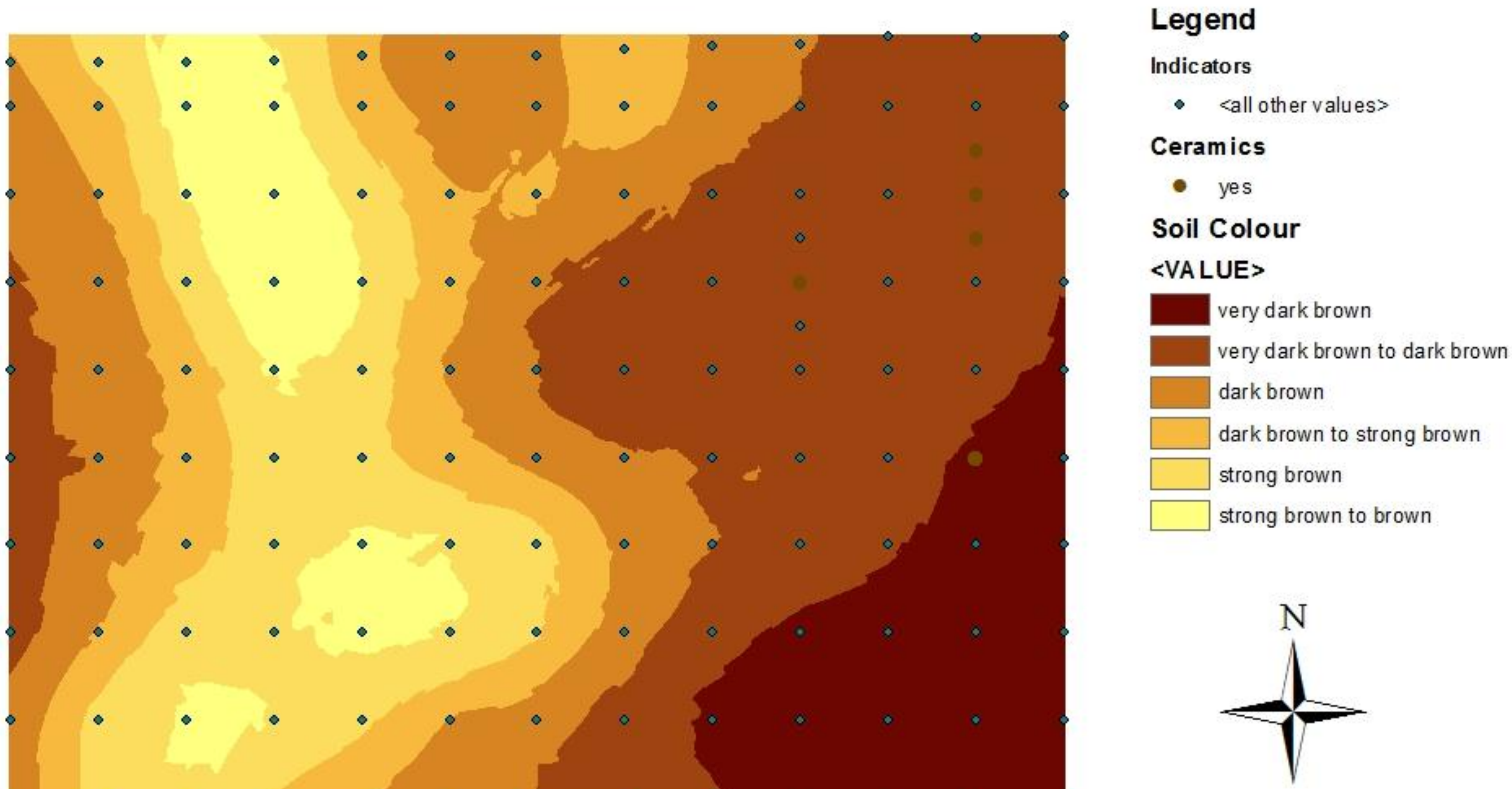

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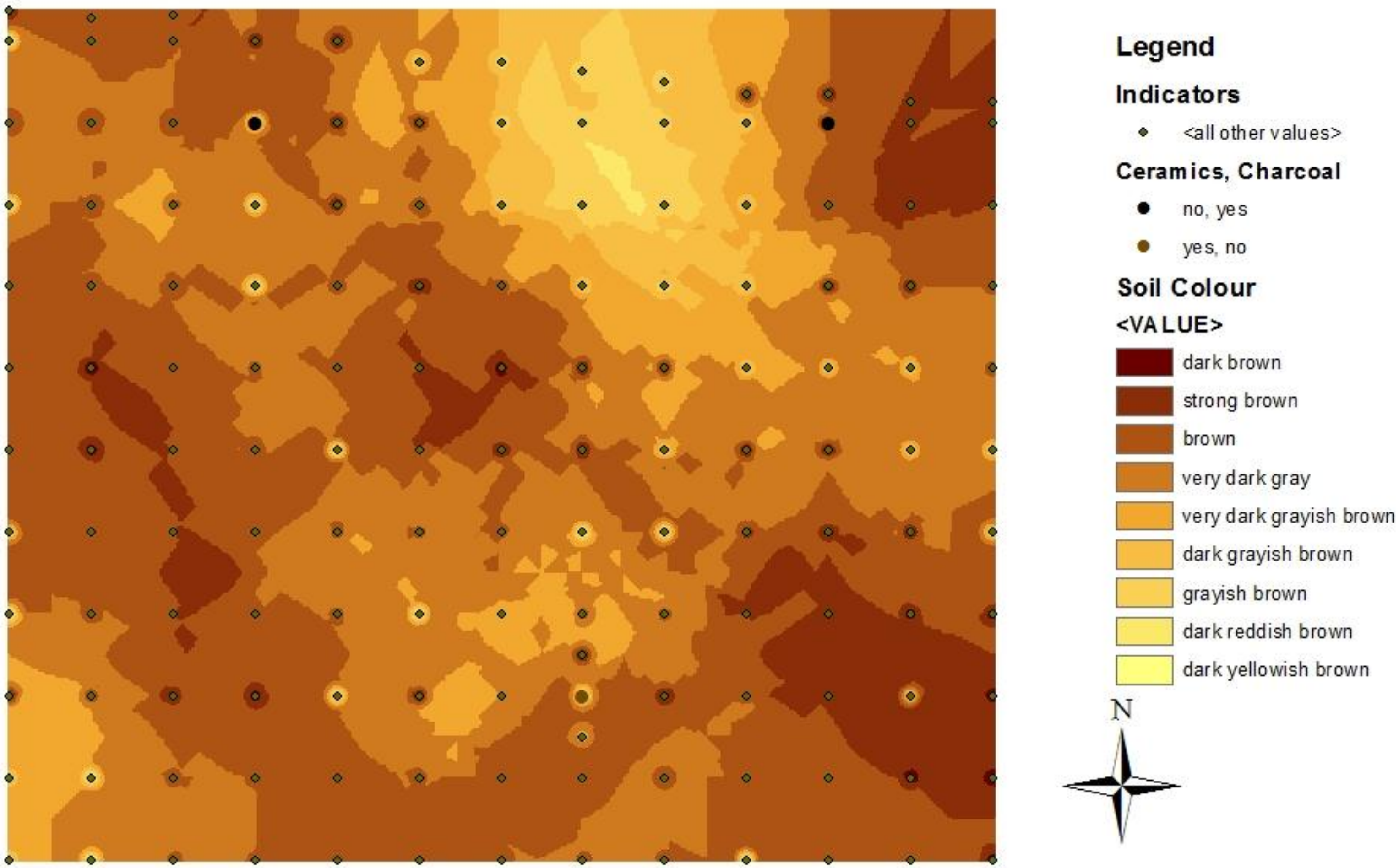
Soil Colour and Indicators



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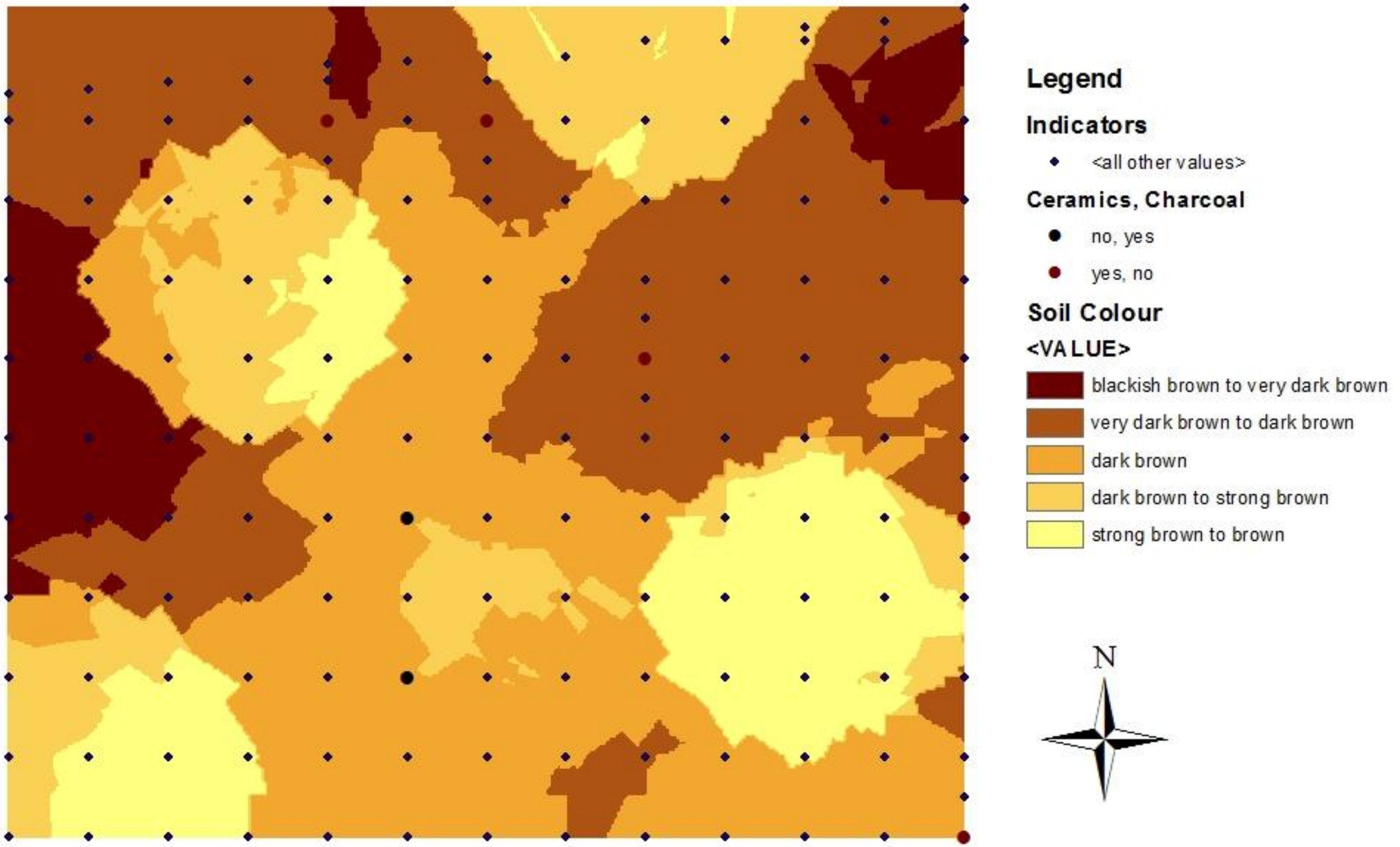
Soil colour and Indicators



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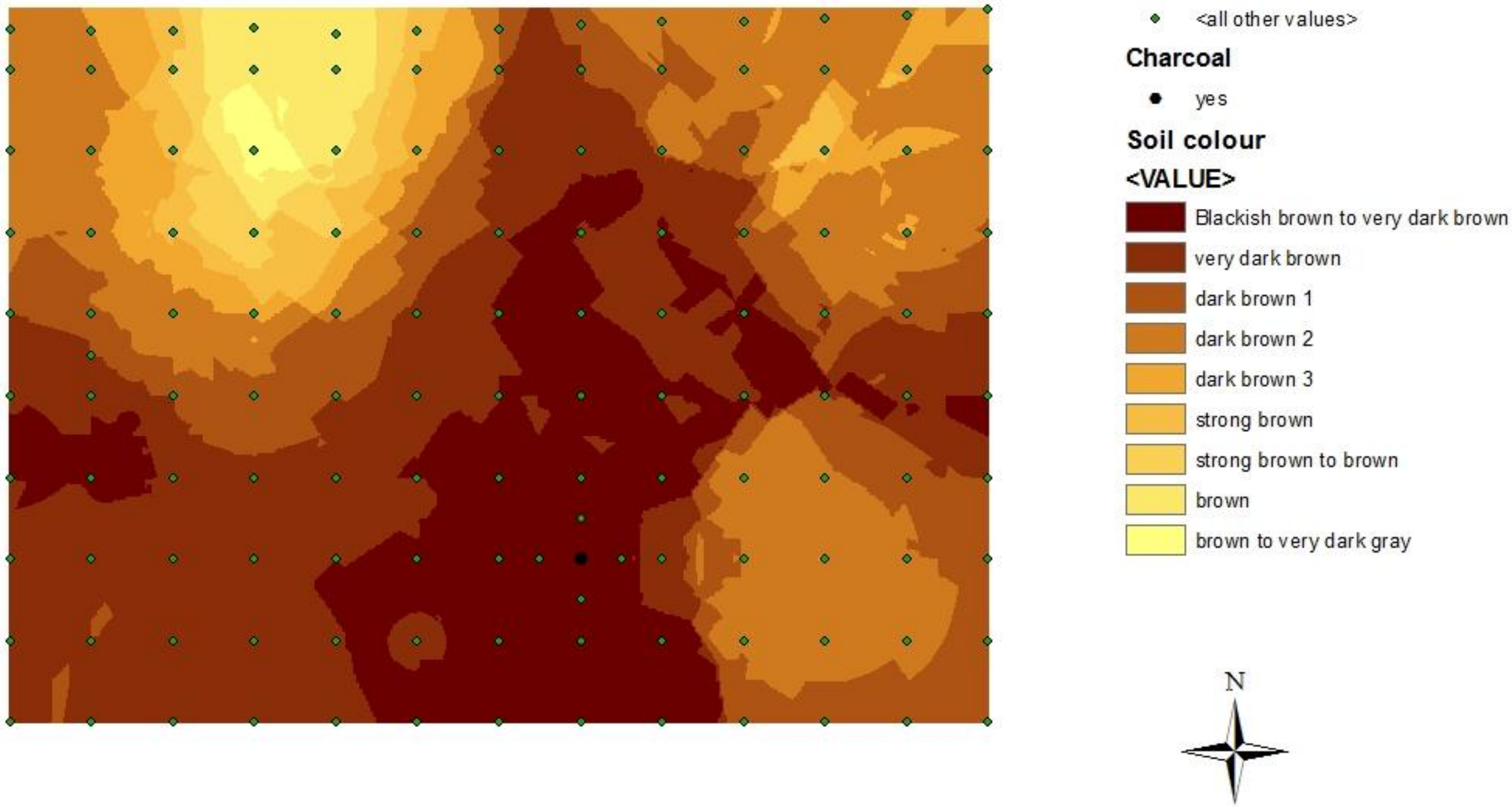
Soil Colour and indicators



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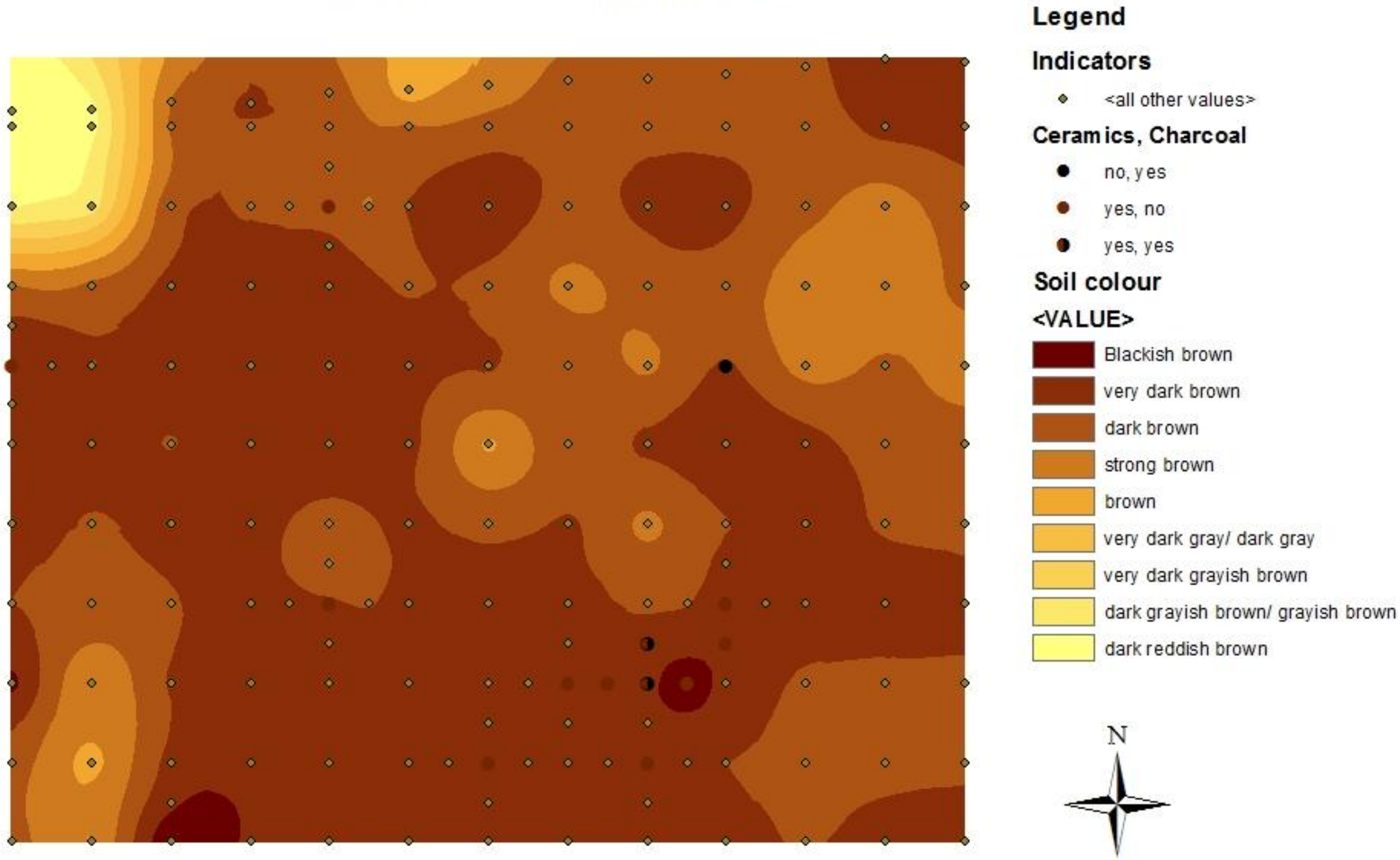

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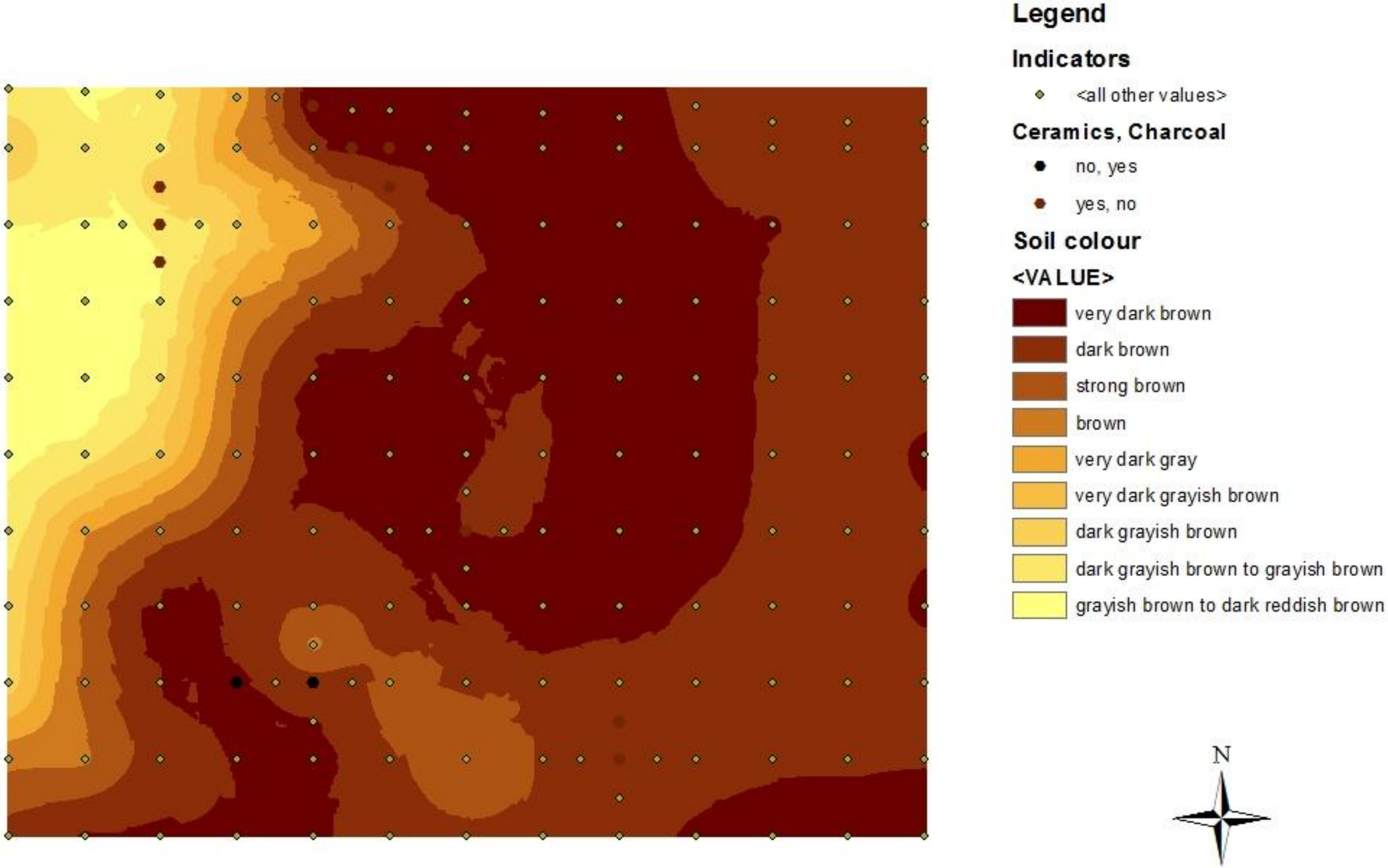
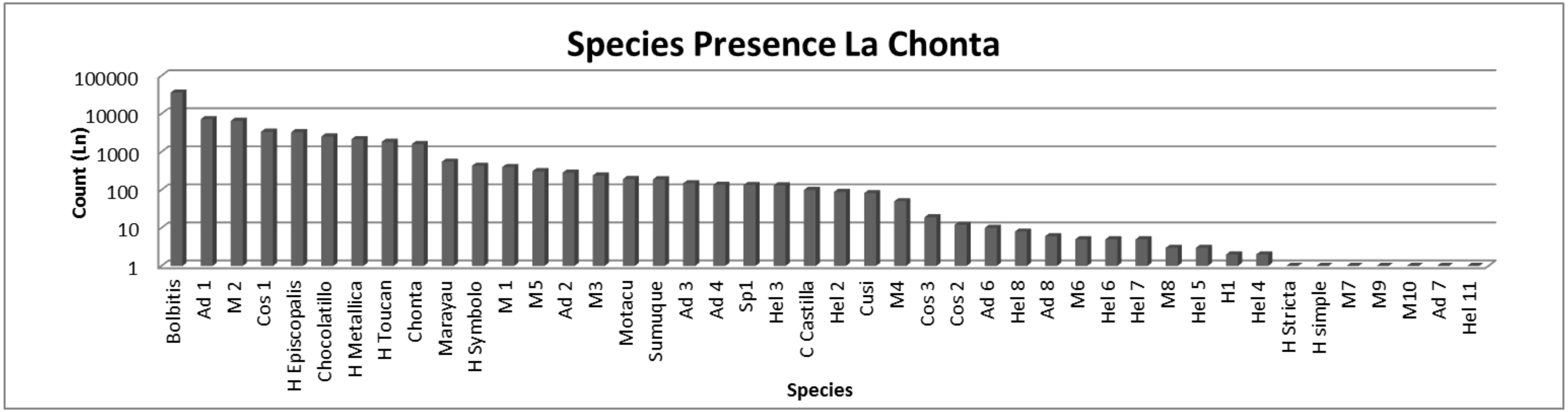
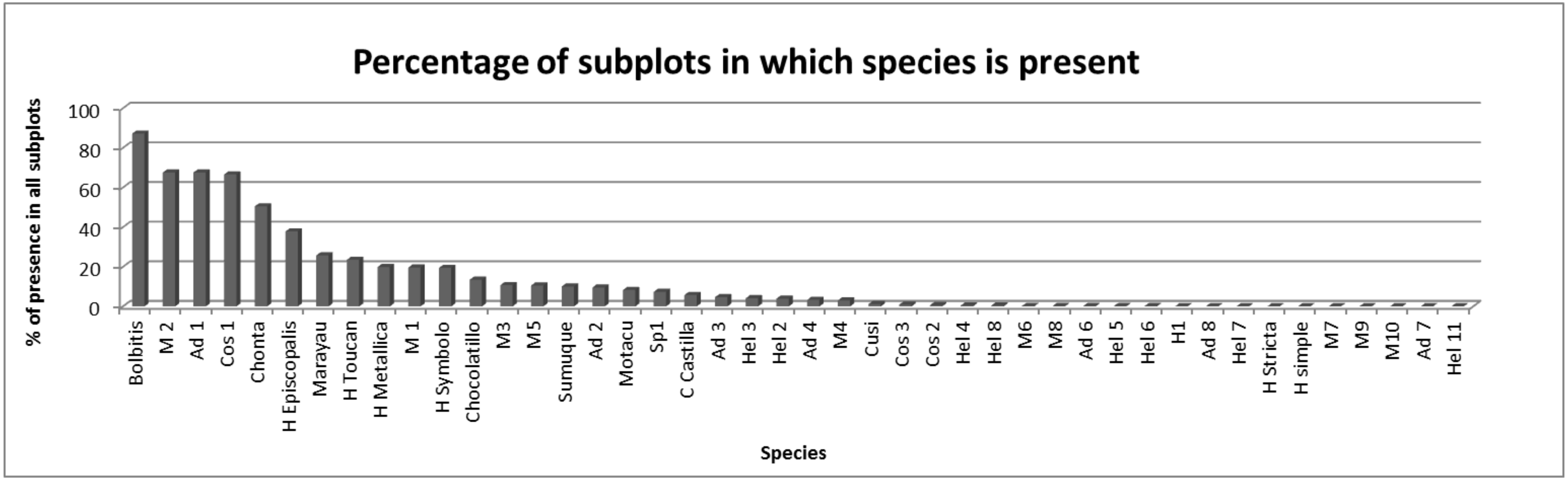


Appendix 2 List of species found

Field name	Scientific name	Family
H Episcopalis	Heliconia episcopalis vell.	Heliconiaceae
H Symbolo	Heliconia rostrata Ruiz & Pav.	Heliconiaceae
H Toucan	Heliconia stricta Huber	Heliconiaceae
H Metallica	Heliconia metallica Planch. & Linden ex Hook.	Heliconiaceae
H Stricta	Heliconia x flabellata Abalo & G. Morales	Heliconiaceae
Sp1	Heliconia sp1	Heliconiaceae
Chocolatillo	Erythrochiton fallax Kallunki	Rutaceae
M 1	Pharus latifolius	Poaceae
M 2	Poaceae sp1	Poaceae
M3	Pharus cf. lappulacens	Poaceae
M4	Calathea ser comosae	Marantaceae
M5	Monotagma juranum	Marantaceae
M6	Cf Ischnosiphon	Marantaceae
M7	Calathea sp3	Marantaceae
M8	Renealmia breviscapa	Zyngiberaceae
M9	Calathea sp1	Marantaceae
M10	Calathea sp2	Marantaceae
Cos 1	Costus scaber	Costaceae
Cos 2	Dichorisandra hexandra	Conmelinaceae
Cos 3	Costus arabicus	Costaceae
Chonta	Astrocaryum murumuru	Arecaceae
Motacu	Attalea phalerata	Arecaceae
Marayau	Bactris major	Arecaceae
Cusi	Attalea glassmanii	Arecaceae
C Castilla	Astrocaryum aculeatum	Arecaceae
Sumuque	Syagrus sancona	Arecaceae
Bolbitis	Bolbitis serratifolia	Dryopteridaceae
Ad 1 =Ad 5 = Ad 3	Adiantum cf tetraphyllum	Pteridaceae
Ad 2	Adiantum pectinatum	Pteridaceae
Ad 4	Adiantum argutum	Pteridaceae
Ad 6	Adiantum latifolium	Pteridaceae
Ad 7	Adiantum plathypyllum	Pteridaceae
Ad 8	Adiantopsis radiata	Pteridaceae
Hel 2	Pteris propinqua	Pteridaceae
Hel 3	Asplenium cf discrepans	Aspleniaceae
Hel 4	Asplenium cristatum	Aspleniaceae
Hel 5	Tectaria incisa	Tectariaceae
Hel 6	Thelypteris sp1	Thelypteridaceae
Hel 7 = Hel 10	Blechnum sp	Blechnaceae
Hel 8	Thelypteris cf jamesonii	Thelypteridaceae
Hel 9	Asplenium cristatum	Aspleniaceae
Hel 11	Indet 3	

Appendix 3 Species presence





Appendix 4 Full results from Generalized Mixed Linear Model

Species	Block		Treatment		Soil		treat *soil		Canopy openness	
	F	P	F	P	F	P	F	P	F	P
Individual species										
Heliconia episcopalis	0	0,97	0	0,974	3,75	0,07	14,83	**0,001**	0,35	0,565
Heliconia rostrata	2,63	0,12	0	0,955	0,76	0,394	0,1	0,757	3,25	0,08
Heliconia stricta	0,01	0,936	6,95	**0,019**	10,75	**0,004**	1,02	0,326	1,78	0,199
Heliconia flabellata					Not Available					
Heliconia metallica					Not Available					
Heliconia sp 1	0,15	0,7	0,12	0,736	0,2	0,657	0,01	0,917	0,06	0,811
Bolbitis serratifolia	15,17	**0,001**	0,02	0,882	0,83	0,372	0	0,974	5,22	**0,032**
Adiantum tetraphyllum	1,17	0,293	0,52	0,479	0	0,996	1,01	0,328	0,97	0,333
Adiantum pectinatum	3,63	0,079	0,47	0,506	3,57	0,078	0,3	0,59	0,09	0,771
Adiantum argutum	0,01	0,908	0,02	0,897	2,86	0,147	0,02	0,896	0,54	0,48
Adiantum latifolium					Not Available					
Adiantum plathypyllum					Not Available					
Adiantopsis radiata					Not Available					
Pteris propinqua	1,21	0,289	0,06	0,813	7,98	**0,015**	1,13	0,72	1,21	0,284
Asplenium discrepans	0,13	0,723	2,02	0,182	0,99	0,339	1,71	0,213	0,01	0,905
Asplenium cristatum					Not Available					
Tectaria incisa					Not Available					
Thelypteris sp 1					Not Available					
Blechnum sp1					Not Available					
Thelypteris jamesonii					Not Available					
Indet 3					Not Available					
Costus scaber	1,07	0,314	0,04	0,851	2,98	0,1	0,23	0,635	0,03	0,87
Dichorisandra hexandra	6,59	0,055	2,01	0,243	2,9	0,149	0,03	0,874	1,42	0,285
Costus arabicus	0,74	0,455	0,03	0,868	3,21	0,156	3,19	0,158	0,76	0,418
Astrocaryum aculeatum	0,5	0,492	3,15	0,097	0,72	0,41	0,76	0,395	3,1	0,098
Astrocaryum murumuru	4,41	**0,049**	0,83	0,373	0,61	0,443	0	0,972	0	0,962
Attalea glassmanii					Not Available					
Bactris major	4,46	**0,05**	1,69	0,213	2,35	0,143	2,42	0,138	0,21	0,652
Attalea phalerata	0,8	0,39	2,31	0,157	13,55	**0,003**	3,74	0,076	1,04	0,323
Syagros sancona	0,3	0,59	0,93	0,347	1,18	0,291	0,02	0,901	8,43	**0,008**
Poaceae 1	0,28	0,602	2,69	0,118	0,02	0,877	0,52	0,479	1,18	0,286
Pharus latifolius	0,04	0,836	0,84	0,373	9,22	**0,007**	0,74	0,401	0,5	0,483
Pharus lappulacens	3,24	0,092	3,86	0,072	1,87	0,193	0,93	0,352	0,6	0,447
Calathea ser comosae	0	0,959	0,53	0,597	0,43	0,56	0,69	0,47	0,27	0,68
Monotagma juranum	10,22	**0,028**	5,39	0,058	17,72	**0,005**	5,17	0,066	0,01	0,937
Ischnosiphon					Not Available					
Calathea sp3					Not Available					
Renealmia breviscapa					Not Available					
Calathea sp1					Not Available					
Calathea sp 2					Not Available					
Erythrochiton fallax	0,86	0,372	0,06	0,804	3,19	0,098	0,04	0,854	2,73	0,114
Species groups										
Heliconiaceae	2,55	0,127	1,84	0,193	1,05	0,318	3,17	0,092	1,47	0,235
Fern	16,26	**0,001**	0,16	0,692	0,85	0,366	0,11	0,747	6,22	**0,02**
Costaceae	1,13	0,301	0,03	0,871	3,14	0,092	0,27	0,607	0,04	0,852
Palm	8,6	**0,009**	4,48	**0,048**	2,44	0,134	0,03	0,861	0,54	0,469
Poaceae	0,13	0,724	0,58	0,457	8,48	**0,009**	0,85	0,369	0,64	0,428
Marantaceae	16,46	**0,001**	10,66	**0,004**	6,05	**0,023**	7,3	**0,014**	0,12	0,728

				Diversity and richness						
Shannon diversity	7,189	**0,011**	0,06	0,812	1,83	0,191	0	0,945	0,54	0,468
Richness	1,12	0,302	4,53	**0,047**	2,59	0,123	1	0,33	1,49	0,235