People, soil and manioc interactions in the upper Amazon region

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This research was conducted under the auspices of the C. T. de Wit Graduate School for Production Ecology and Resource Conservation

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Thesis
submitted in fulfillment of the requirements for the degree of doctor
at Wageningen University
by the authority of the Rector Magnificus
Prof. Dr A.P.J. Mol,
in the presence of the
Thesis Committee appointed by the Academic Board
to be defended in public
on Wednesday 1 July 2015
at 1:30 p.m. in the Aula.

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People, soil and manioc interactions in the upper Amazon region
210 pages.

PhD thesis, Wageningen University, Wageningen, NL (2015)
With references, with summaries in English and Dutch

ISBN: 978-94-6257-322-2

Abstract

Clara Patricia Peña Venegas (2015). People, soil and manioc interactions in the upper Amazon region. PhD thesis, Wageningen University, The Netherlands, with summaries in English and Dutch, 210 pp.

The presence of anthropogenic soils, or Amazonian Dark *Earths* (ADE), fuels the debate about how pristine the Amazon ecosystem actually is, and about the degree to which humans affected Amazonian diversity in the past. Most upland soils of the Amazon region are very acid, highly weathered, and have a limited nutrient holding capacity; together, these characteristics limit permanent or intensive agriculture. *Várzeas* or floodplains that are periodically enriched with Andean sediments carried and deposited by rivers that cross the Amazon Basin, are moderately fertile but experience periodic floods that limit agriculture to crops able to produce in a short time. ADE patches in uplands usually are more fertile than non-anthropogenic uplands, providing a better environment for agriculture. Most studies about how people manage a broad portfolio of natural and anthropogenic soils come from non-indigenous farmers of Brazil. There is limited information about how indigenous people use a broad soil portfolio, and how this affects the diversity of their staple crop, manioc. With the aim to contribute to the understanding of the role of ADE in indigenous food production, as compared with other soils, and in order to provide information about how indigenous people use and create diversity in Amazonia, research was carried out among five different ethnic groups living in two locations of the Colombian Amazon.

Several social and natural science methods were used during the study. These included ethnography, participant observation, structured and un-structured interviews, sampling of soil and manioc landraces, standardized protocols for the quantification of soil physical and chemical variables, and molecular techniques to assess genetic diversity of manioc and arbuscular mycorrhizal fungi.

Results indicate that ADE patches from the Middle Caquetá region of Colombia are not contrastingly more fertile than surrounding, non-anthropogenic upland soils, except for higher levels of available phosphorus in ADE. Indigenous farmers from the Middle Caquetá region do not use ADE more frequently or more intensively than non-ADE uplands. The swidden agriculture practiced on ADE and on non-ADE uplands is similar. Although ADE patches were not specifically important for swiddens and therefore relatively unimportant for the production of manioc. They were important as sites for indigenous settlements and for maintaining agroforestry systems with native and exotic species that do not grow in soils with low available phosphorus. *Várzeas* were also used for agriculture, whether farmers had access to ADE or not. Differences occurred between locations in the type of floodplains selected and the way they were cultivated. Those differences were not related to differences in soil conditions but were associated with the cultural traditions of the different ethnic groups who cultivate low floodplains, as well as labor availability when organizing collective work (*mingas*) to harvest floodplains.

Manioc diversity among indigenous communities was not predominantly related with differences in soil types. Complete manioc stocks were cultivated equally on ADE, non-ADE uplands or *várzeas*. One issue that could be related with this non-specificity in manioc-soil combinations was the similar arbuscular mycorrhizal fungi diversity of soils and the high number of arbuscular mycorrhizal symbionts associated to manioc roots; these were shown to be independent from the physicochemical composition of the soil or the manioc landrace. Differences in the diversity of manioc stocks among ethnic groups were predominantly related to cultural values attached to different manioc landraces.

This study of indigenous agriculture in environments with natural and anthropogenic soils indicates that people have had an important role in transforming the Amazonian ecosystem through agriculture, with consequences on forest composition and forest dynamics. Pre-Columbian people contributed to this by creating an additional soil- the Amazonian Dark *Earths*. Although ADE are not presently considered to play a major role in indigenous food production, indigenous people believe that ADE have had an important role in the management of the first maniocs cultivated by their ancestors. The domestication of manioc and the creation and maintenance of hundreds of different landraces by indigenous people contributed, and still contributes, to the region's plant diversity.

Table of contents

Chapter 1

General Introduction

The Amazon forest is the biggest patch of continuous tropical forest and also one of the most bio-diverse regions of the world (Peres et al., 2010). The high diversity of the Amazon region is the product of natural events that occurred during the history of Planet Earth such as forest fragmentation during the Pleistocene, marine incursions during the Mid-Miocene and encrustation of Amazonian rivers acting as natural barriers to gene flow (Solomon et al., 2008); human interventions, however, also shaped Amazonian diversity. The Amazon forest has been inhabited for thousands of years by native societies which have been interacting with the environment, changing the floristic composition of the vegetation through agriculture and creating new environments by modifying soils (Balée, 2014). There is a debate among scientists, however, about how much people contributed to shaping diversity in the Amazon region. On the one hand, some scientists affirm that human interventions were heterogeneous and mainly limited to areas near floodplains along the main rivers (Meggers, 2003; McMichael *et al.*, 2012). Therefore, people had little effect on the diversity of interfluvial areas, the diversity there being the product of long-term evolutionary and ecological processes. On the other hand, other scientists affirm that the Amazon landscape was highly impacted by humans. Therefore, many areas of the Amazon region can be considered constructed or 'domesticated' landscapes, constituting 'hotspots' of bio-historical diversity in the Amazon region (Denevan, 1992; Balée, 1993; Heckenberger *et al.*, 2007).

A better understanding of how people use and create diversity would provide important hints to dimension the effect of people in the Amazonian diversity.

1.1. Amazonian landscapes for food production

The Amazon Basin is composed of different environments with a range of conditions and soils (Quesada *et al.*, 2010). Most uplands of the Amazon Basin are dominated by very acid, highly weathered soils, originating from parental materials rich in kaolinite with a naturally limited nutrient holding capacity (Sombroek, 1966; Cochrane and Sanchez, 1982; Ma and Eggleton, 1999; FAO, 2006). Under these conditions indigenous people usually cultivate through swidden agriculture. Swidden agriculture, also known as slash-and-burn or shifting cultivation, consists of a system in which forested areas are "slashed and burnt" to establish polycultures for a short period of time. Cultivation is subsequently followed by a long fallow period. During the fallow, the agricultural field returns into a (secondary) forested area while a new forested area is opened for a new swidden (Hammond *et al.*, 1995; Perreault, 2005;

Bonilla-Bedoya *et al.*, 2013). Consequently, upland landscape is transformed over time into a mosaic of secondary forests varying in age (Junqueira *et al.*, 2011).

Besides uplands with acid, low-fertile soils, in the Amazon region the floodplains known as *várzeas* are also important environments for agriculture. *Várzeas* are enriched with Andean sediments carried and deposited by rivers that come from the Andes and cross the Amazon region (Piedade *et al.*, 2001). Andean sediments deposited on floodplains increase the pH and the cation exchange capacity of the soils and enrich them with calcium and magnesium (Teixeira *et al.*, 2006), resulting in more fertile soils compared with most uplands of the region. Under these conditions floodplain cultivation can be relatively intensive (Shorr, 2000; Fraser *et al.*, 2012), but the crop cycle is limited by floods, and floodplains tend to be covered with younger secondary forests.

The discovery of Amazonian Dark Earths (ADE) or Terra Preta de Índio demonstrated that Amazonian soils could be modified permanently by anthropogenic activities under humid tropical conditions where organic matter degradation rates are usually high and leaching and run-off can be intense. ADE are usually less acid than non-ADE soils, with good cation exchange capacity, good base saturation, and relatively high quantities of organic matter, nitrogen, calcium, and available phosphorus (Glaser and Birk, 2012). ADE not only provide the opportunity for a more permanent agriculture, but also the possibility to introduce, favor or cultivate plant species unable to thrive in other conditions (Junqueira *et al.*, 2011). Therefore, younger secondary forests similar to those observed on floodplains might dominate ADE, but with differences in plant species composition.

Based on archaeological evidence, it has been proposed that - due to the better soil conditions of ADE for agriculture - ADE may have had an important role in the food production of complex societies that emerged in the region (Heckenberger *et al.*, 2007; Arroyo-Kalin, 2010; Schmidt *et al.*, 2014). When ADE were not present, pre-Columbian societies inhabited bluffs near floodplains and cultivated these intensively, using uplands as a complementary environment for food production during flooding (Denevan, 1996, 2012). However, observations on contemporary indigenous groups do not follow previous patterns. The cultivation of ADE has been reported only in Kuikuro communities of Brazil (Schmidt and Heckenberger, 2009), but not in indigenous groups of the Colombian Amazon region where ADE are present (Eden *et al.*, 1984; Torres-Sanabria and Rucaurte, 2013). In indigenous communities where ADE are not present, swiddens are placed more frequently on uplands than on floodplains (Eden and Andrade, 1987; Wilson and Dufour, 2006; Acosta *et* *al.*, 2011).

Why land use by different indigenous groups does not follow a consistent pattern is not clear, but it is also not clear if practices or knowledge of contemporary indigenous groups support hypotheses addressed by researchers. This thesis addresses the indigenous use of ADE in relation to other available soils as well as the indigenous knowledge about ADE formation and the role of ADE in manioc (*Manihot esculenta* Crantz) domestication and diversification.

1.2. Manioc, the Amazonian staple crop

Enhanced by the presence of ADE, the Amazon region offers a broad range of environments with soils that differ in composition allowing cultivation of different crops. However, the main crop cultivated in the region is manioc, which is also the staple crop for most of the native population (Dufour, 1988; Duputié *et al.*, 2009b; Fraser, 2010a). Manioc, usually vegetatively propagated through stem cuttings, dominates the crop fields and is characterized by the cultivation of a high diversity of landraces (Ferguson *et al.*, 2012; Bradburry *et al.*, 2013). Manioc landraces are roughly classified into two groups according to the concentration of cyanide compounds in their roots and related processing as sweet maniocs (those with less than 100 mg cyanogenic compounds per kg of roots) or bitter maniocs (those with more than 100 mg cyanogenic compounds per kg roots) (Dufour, 1988).

The high diversity of manioc in the Amazon region has been attributed to environmental and social factors. It has been stated that sweet maniocs are generally cultivated in the upper Amazon Basin near the Andean foothills where soils are more fertile while bitter maniocs are generally cultivated in the lower Amazon basin where soils are more acid and less fertile (Bradburry *et al.*, 2013). However, this is not always the case (Fraser, 2010b; Fraser *et al.*, 2012), suggesting that a broader portfolio of soils could promote convergent adaptation of manioc which results in the selection of specific manioc landraces for specific environments (Fraser and Clement, 2008; Alves-Pereira *et al.*, 2012), in this way increasing manioc diversity. Additionally, the cultural management of manioc could promote or deplete manioc diversification. On the one hand, the geographical isolation of ethnic groups in the region (Elias *et al.*, 2000), the use of manioc landraces associated to socio-cultural and symbolic values (Emperaire and Peroni, 2007), culinary traditions of each particular group (Wilson and Dufour, 2006), and the domestication of manioc volunteer seedlings into new landraces increase manioc diversity (Pujol *et al.*, 2007). On the other hand, the permanent exchange of manioc landraces among farmers and communities could homogenize the genetic diversity among communities, decreasing manioc diversity in the region. Indigenous farmers are exposed to different environments to cultivate manioc but also to specific cultural and social rules that are reflected in their manioc portfolios. Cultural exchange of manioc stems could break geographical separation of maniocs. As manioc still has the capacity of sexual reproduction, the cultivation together of genetically different maniocs could result in a genetically homogeneous stock of manioc landraces through time. But if cultural exchange is accompanied by a strict maintenance of clones and farmers´ stocks are enriched by the additional selection of volunteer seedlings, the result will be higher manioc diversity in the region. It is not clear how indigenous people manage all these eventualities and how these are reflected in manioc diversity. This thesis addressed how soil variability and cultural patterns act together to explain manioc diversity in the study area.

As the evolutionary selection of manioc favored bulky roots rich in starch as the principal edible part of the manioc plant, the root system has a limited capacity to acquire nutrients from the soil. Manioc copes with this limitation by associating to arbuscular mycorrhizal fungi. Arbuscular mycorrhization is a plant-fungi association between Glomeromycota endo-symbiont fungi and plants (Fitter and Moyersoen, 1996) with an important role in the mobilization of soil phosphate and other nutrients to roots (Helgason and Fitter, 2009). Arbuscular mycorrhizal fungi are affected by plant community composition (Davison *et al.*, 2011) and soil conditions (Entry *et al.*, 2002). Plant communities of floodplains and non-flooding environments and of ADE and non-ADE upland soils are different. Therefore, each field plot could provide different arbuscular mycorrhizal fungal communities with different affinities to establish an association with manioc. But because under swidden agriculture arbuscular mycorrhizal fungal communities are exposed more permanently to native species and transitory to crop species manioc-arbuscular mycorrhizal fungi might be a promiscuous association. A clear specificity between manioc and arbuscular mycorrhizal fungi might not be evident.

Additionally, acidity and phosphate availability also affect arbuscular mycorrhization (Entry *et al.*, 2002). In general, manioc roots cultivated in Amazonian soils with high acidity and low phosphate availability are well-mycorrhized and arbuscular mycorrhizal associations are effective providing the nutrients manioc requires (Howeler and Sieverding, 1983a; Dodd *et al.*, 1990; Ceballos *et al.*, 2013). On the contrary, the arbuscular mycorrhization in environments with high soil phosphate availability is generally inhibited or less efficient (Howeler *et al.*, 1982; Howeler and Sieverding, 1983b; Habte and Manjunath, 1987). It is not clear whether all manioc landraces have the same affinity to establish arbuscular mycorrhizal associations under different environmental conditions. Differences in manioc arbuscular mycorrhization among landraces could affect the way farmers manage manioc in the different environments, and therefore promote or diminish manioc diversification. The frequency and abundance (as percentage of arbuscular mycorrhization per root length) in which manioc roots are colonized by arbuscular mycorrhizal fungi in Amazonian floodplains and ADE have not been reported yet. This thesis compares the arbuscular mycorrhization of the different manioc landraces in environments with different soil fertility to evaluate the effect of the manioc type and the soil composition in this plant-fungi association.

1.3. Studies on Amazonian Dark Earths in Colombia

Studies related to ADE in Colombia were done in the 1980´s with the financial support of the Corporación Araracuara and summarized in a few publications, which are now part of the scientific background of the Instituto Amazónico de Investigaciones Científicas Sinchi. Those publications emphasize the archaeological aspects of ADE (Herrera, 1981; Eden *et al.*, 1984; Herrera *et al.*, 1992; Morcote-Ríos and León-Sicard, 2011) and do not provide information about the use of ADE by contemporary indigenous groups or about differences in land use management and manioc diversity among indigenous groups with and without access to ADE. With the aim to study ADE in more detail and in a broader geographic area, in 2010 the Terra Preta program, funded by the Interdisciplinary Research and Education Fund (INREF) of Wageningen University, was created. This thesis joins the efforts of the Sinchi Institute and the Terra Preta Program to contribute in two ways: to the understanding of indigenous farmers' perceptions and actual use of ADE in Colombia in relation to other Amazonian soils; and to providing information about indigenous knowledge and indigenous land use useful to understand how indigenous people use and create diversity in the region.

1.4. The study area

1.4.1. Geographical and demographic information

This study was conducted in the Amazon region of Colombia, specifically in the Amazonas state. The Amazonas state is the biggest state of Colombia with a total area of 108,700 km^2 (Figure 1.1) which corresponds to 10% of the total area of the country and 23% of the Colombian Amazon region. The Amazonas state has been inhabited by many different ethnic groups. Today, it is inhabited by 25 different ethnic groups, each with its own cultural background and particular cultural pattern to interact with the environment. From the total area of the Amazonas state 9,209,244 ha (around 85% of the state) corresponds to legally recognized indigenous territories known as "*resguardos*". There, about 19,000 indigenous people live, which corresponds to 40.5% of the total population of the Amazonas state (Castro, 2009). There are relatively numerous indigenous people settled in the Amazonas state in *resguardos* which are managed according to their "Plans of life" (own community plans to administrate the portion of the *resguardo* assigned). The *resguardos* are formed by thousands of kilometers which include diverse landscapes with soils with different fertility for indigenous food production. Additionally, *resguardos* in general have low influence of markets. All those characteristics made the Amazonas state an ideal location to study diversity use and diversity creation as a product of indigenous relations with the environment.

In the Amazonas state two locations were included as areas for the thesis field work. One location corresponds to the municipality of Leticia in the southern part of the Amazonas state in the upper course of the Amazon River. There, fieldwork was done in the Tikuna community of San Martín de Amacayacu located in the Tikuna, Cocama and Yagua TICOYA *Resguardo*. This indigenous community was selected to be considered one of the most traditional communities of the study area without access to ADE. Additionally, agricultural fields in Fantasy Island, Puerto Triunfo and the Tacana were included in this study, to evaluate interactions between manioc and soils not affected directly by culture.

The second location corresponds to the northern part of the Amazonas state in the middle course of the Caquetá River (Figure 1.1), in four indigenous communities located in two *resguardos*: The Aduche *Resguardo* where the Andoke community of Aduche and the Uitoto community of Guacamayo are settled; and the Nonuya *Resguardo* where the Muinane community of Villazul and the Nonuya community of Peña Roja are settled. The second location was selected as the presence of ADE has been reported there before (Leon-Sicard, 1983; Mora *et al.*, 1991), and it is also one of the oldest human occupations and one of the oldest evidences of maize cultivation in the Amazon Basin (Mora *et al.*, 1991).

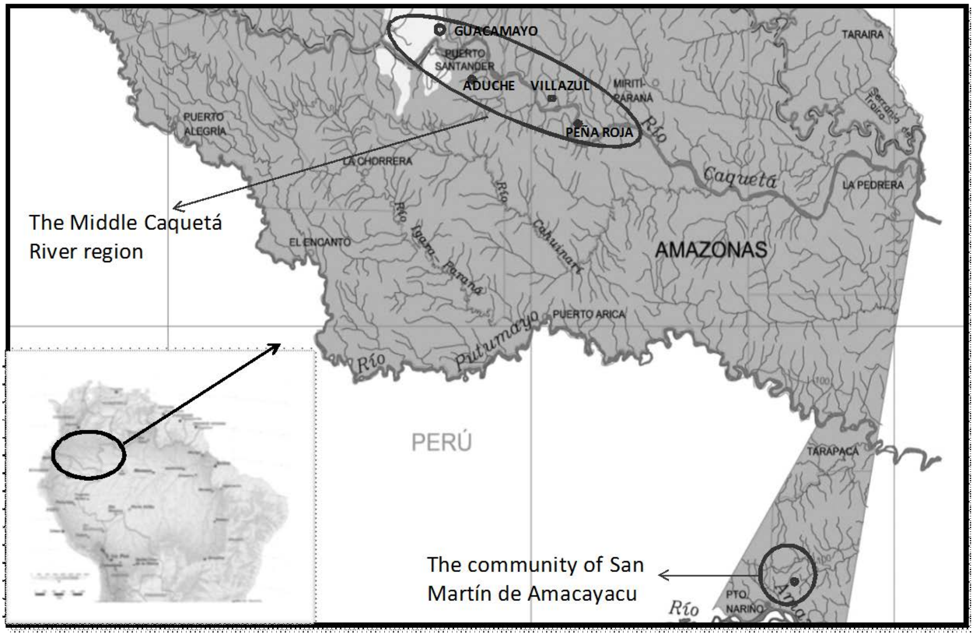

Figure 1.1. Part of the hydrographic map of the Amazonas state of Colombia made by Sinchi (2002); scale 1:500,000, modified to indicate the location of the indigenous communities that participated in this research, as well as other locations referred to in this thesis.

The way in which people relate with their environment – thereby using and at the same time creating diversity – must be seen in its historical context. A historical contextualization of each one of the ethnic groups that participated in this research is therefore important.

1.4.2. History of the study area and its people

In the first location of this research, the Tikuna is the biggest and most representative ethnic group of the area. The Tikuna are today the most numerous ethnic group of the Amazon Basin and distributed in communities in the upper Amazon River in Brazil, Colombia and Peru (Umbarila, 2011). Tikuna means "People of dark skin" because of the Tikuna tradition of staining their bodies in a dark color with the juice of the unripe fruit of the *Genipa americana* tree during celebrations. The Tikuna people maintain this tradition until today. The Tikuna are divided into two main groups of clans, those with feathers and those without feathers. Tikuna communities traditionally corresponded to one or more malokas. In each one a Tikuna clan lived together according to their own political organization (Chapter 4).

Riverine indigenous groups from the Colombian Amazon had their first sporadic contact with Europeans in the 17th century. Those first contacts introduced Old World diseases that resulted in recurrent epidemics that natives could not control, and approximately 95% of the native population had died by 1650 (Dull *et al.*, 2010). After, in the first decade of 18th century, the Portuguese traveled from Brazil upstream along the Amazon River and arrived at the study area looking for indigenous people to take them as slaves to work on the sugar cane plantations along the lower part of the Amazonas River (Rosa, 2000). The most exposed communities to diseases and slavery were those located along the main rivers such as the Omaguas, now extinct. Omagua territories were occupied by the Tikuna in what is roughly the present-day Tikuna territory. After the Portuguese, the Spanish Jesuit mission arrived to evangelize indigenous people and convert them into Christians. At the beginning of the 20th century the Spanish Jesuits forced Tikuna people living in their traditional malokas to live in single houses as nuclear families as the Jesuits considered it immoral to live all together in a single house. Most Tikuna communities lost the tradition to live in malokas in this way but people from San Martín de Amacayacu lost the tradition in a different way. Between 1966 and 1971, Tikuna families abandoned their malokas in the Cotuhé River (a tributary of the Putumayo River near Tarapacá), the Matamatá River (a tributary of the Amazonas River), and a maloka in the middle course of the Amacayacu River to re-organize themselves in a new community. They wanted to receive governmental support to build a school and receive an electric generator but the government did not consider a single maloka as a “community organization” suitable for financial support forcing them to found the community of San Martín de Amacayacu with nuclear family houses.

In the second location of this research, four ethnic groups were selected , the Andoke, Muinane, Nonuya and Uitoto, all part of the “*Gente de Centro*” (People of the Center), were the ethnic groups selected. *People of the Center* is a name adopted by those ethnic groups to indicate their common origin from the interfluvial region between the Putumayo and the Caquetá Rivers (Acosta, 2013). The four ethnic groups share some traditions (Chapters 3 and 4), but identify themselves as different groups with different languages and cultures. The Andoke, known as “People of axes”, have been the traditional inhabitants of the Middle

Caquetá. According to Andoke mythology, "*the daughter of Nenefí* (the Andoke God) *was pregnant. Because she did not have relations with a man, she could not deliver a human baby, delivering a tool: The stone axe"*. (Interview with Fissi Andoke, October 12th of 2012). According to Fissi, the stone axe was given to the Andoke to open swiddens. Because this, the Andoke word BUθKA that means logging could be translated as "to use the stone axe". Andoke introduced stone axes to Uitoto (Henao, 1989) and other ethnic groups of the Colombian Amazon.

The traditional life of indigenous communities of Colombia was deeply disturbed at the end of the 19th century after the Colombian internal war called "The Thousand Day War", when Colombia decided to promote international investments to extract natural rubber from its Amazon forest. The Peruvian Julio César Arana answered to the Colombian invitation and created with British financial support the *Peruvian Amazon Rubber Company.* The main office of the company in London received the rubber collected in *La Casa Arana,* a location set in a place known as La Chorrera on the Igará Paraná River (Figure 1.1) and the traditional territory of the Uitoto, known traditionally as "*the sons of coca, tobacco, and sweet manioc*". There, the company used indigenous slaves captured in the region as the main workers for rubber extraction under conditions that caused thousands of them to die, reducing considerably the indigenous population of the Colombian Amazon (Chapter 3).

Rumors of the inhuman conditions in which native people worked for *La Casa Arana* reached the British government which investigated what was happening in Colombia through its Consul in Brazil. The results of the investigation were published in the *Blue Book* and precipitated the liquidation of the Peruvian-British rubber company. Between 1921 and 1930, Julio César Arana moved to Peru the indigenous slaves he still had and the rubber already collected, crossing the Amazon jungle in South direction from La Chorrera to the Putumayo River, the frontier between Colombia and Peru (Figure 1.1). The weaker people died on the way. Few others arrived to Peru carrying the rubber. Others took advantage of the situation and escaped during the journey into the direction of the Middle Caquetá region. The Andoke who escaped returned to Aduche. People of Andoke clans that survived reconstructed their malokas, one for each clan. Slaves from other ethnic groups organized new settlements and started a new life. Some of those settlements corresponded to the communities participating in this work: the community of Guacamayo (founded by the Uitoto in 1967), and the community of Villazul (founded by the Muinane, traditionally known as "People of River Estuary", in 1956). In the case of the Nonuya known traditionally as "People of Achiote (*Bixa orellana*)" only four men survived and arrived to live in Villazul, adopting the Muinane language and customs (Echeverri and Landaburu, 1995). But in 1990 these Nonuya decided to rescue their own language and customs and founded the community of Peña Roja.

The Tikuna communities were less affected during the rubber boom, as they offered less resistance to slavery. In the Tikuna mythology "white people" would arrive to punish them. Therefore Tikuna accepted slavery as a divine punishment (Rosa, 2000). Slavery of Tikuna communities along the Amazon River was a kind of neo-feudal domination in which indigenous people extracted the rubber exclusively for a patron and the patron allowed them to maintain their own settlements and live according to their traditions.

In 1935 the government of Colombia opened a high security Penal Colony in Araracuara as it is very remote from the main cities of Colombia and as the region has a difficult natural landscape: a rocky plateau surrounded by the Caquetá River rapids (Figure 1.2). In 1938 an improvised airstrip was created at the top of the sandstone plateau to facilitate communications which is until today the main entry port to the area (Figure 1.2). In 1971 the Penal colony was closed, but many of the guardians and prisoners did not leave the place. Together, they organized a small village at the other side of the Caquetá River called Puerto Santander (Figure 1.1) which is the main place for commerce in the area until today. Puerto Santander is also the main place of contact between indigenous people and the market. In 1977 the buildings of the Penal Colony were given to the Corporación Araracuara, the first independent institution for scientific research in the Colombian Amazon region (Franco, 2007) and supported by the Dutch government. Most of the research on ADE in Colombia was done by the Corporación Araracuara (Leon-Sicard, 1983; Eden *et al.*, 1984). This period also coincided with the legal recognition of the traditional territories of Amazonian ethnic groups as "*resguardos*", a kind of indigenous reserve. In 1983, the *resguardo* of Puerto Nariño, a multi-ethnic *resguardo* made up of Tikuna, Cocama and Yagua people and known by its acronym TICOYA was created. The community of San Martín de Amacayacu is part of this *resguardo*. In 1988, the Predio-Putumayo *resguardo* was created. The Predio-Putumayo *resguardo* is the biggest indigenous reserve of Colombia and comprises almost half of the Amazonas state (5,818,702 ha). To facilitate the administration of the Predio-Putumayo *resguardo* it was sub-divided into smaller *resguardos*. Two of them are the Aduche *resguardo* where the communities of Aduche and Guacamayo are located, and the Nonuya *resguardo* where the communities of Villazul and Peña Roja are located.

In 1991, Colombia re-wrote its political constitution and created the Ministry of

Environment and five research institutes to support it. One of them is the Instituto Amazónico de Investigaciones Científicas Sinchi. In 1993, the mission and functions of the Sinchi institute were legally formalized as the main scientific research center for the Colombian Amazon region, inheriting all the goods, scientific and technical patrimony of the former Corporación Araracuara.

Figure 1.2. Landscape of Araracuara, one of the research locations: A. Rapids of the Caquetá River and at the top of the rocky plateau, the location of the airport (Picture by Gerard Verschoor); B. View of the improvised airport of Araracuara over the natural rocky plateau (Picture by Clara Peña).

1.5. This thesis

This thesis aims, first, to contribute to understanding indigenous farmer’s perception and actual use of ADE in Colombia in a context in which ADE and other soils are accessible for their use; second, it aims to provide information about indigenous knowledge and indigenous land use that could help to better understand how indigenous people use and create diversity in the region.

An analytical framework was established (Figure 1.3) to clearly identify the gaps addressed by the thesis. First, the Amazon region is culturally diverse with approximately 420 different ethnic groups (UNEP and ACTO, 2009). Cultural links to environment and differences in traditions could affect people × environment interactions in terms of land use and diversity management. The thesis includes different indigenous ethnic groups (four for Chapter 3 and five for Chapters 2 and 4) to understand these differences.

Second, agriculture is considered the main anthropogenic activity that reflects ecological and social co-adaptation (Altieri, 2002). This thesis documents indigenous agriculture in communities with and without access to ADE. How different environments are managed simultaneously in the landscape. And to investigate how differences in the environment (additionally to culture) could influence the intensity in which each environment is used for food production and the diversity of the crops cultivated.

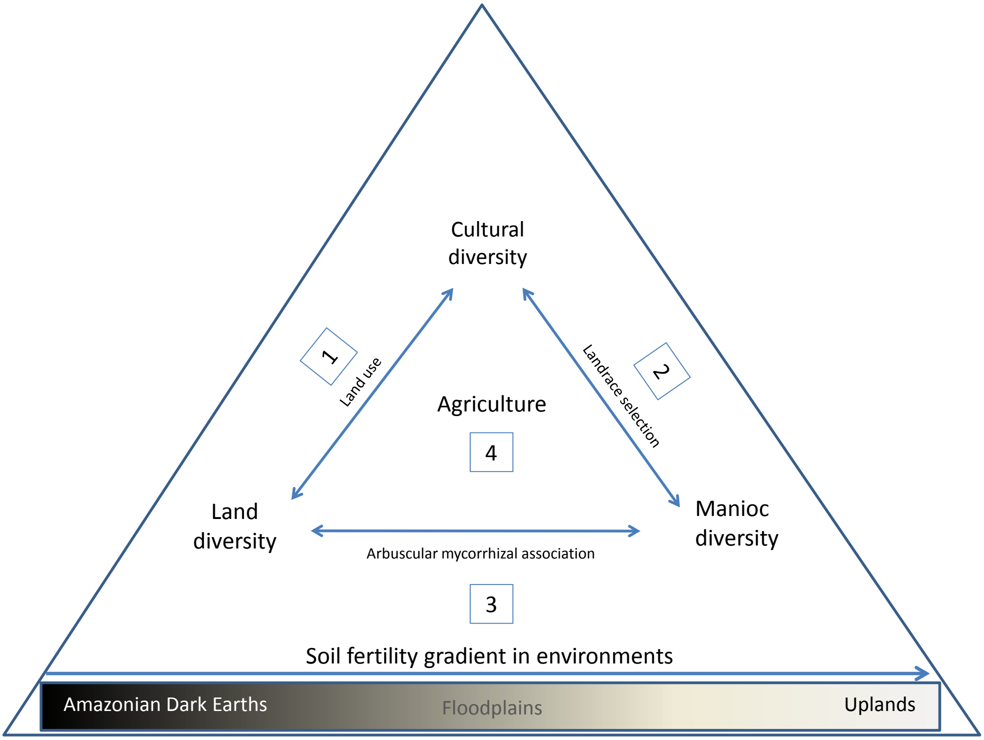

Figure 1.3. Graphic representation of the framework used in this thesis. Numbers indicate the research questions that correspond to each topic studied. The expected soil fertility gradient of environments is indicated by the direction of the arrow and the color gradient from black (the most fertile) to white (the least fertile).

Third, agriculture depends on environmental conditions. The Amazon region has a diversity of landscapes which vary in their soil composition (represented in Figure 1.3 by the bar with the darkest edge for ADE and the clearest edge for non-ADE uplands), vegetation, microbial composition, and in their chance to experience periodical floods. This thesis compares land use in communities with access to floodplains, and with and without access to ADE. Differences among communities might occur as communities with access to ADE would have a broader portfolio of environments for food production than communities without access to ADE. In this context, in the thesis it is proposed to investigate what soils are selected for agriculture, and which ones for other purposes, and how much ADE are preferred by indigenous people in comparison with other soils. Finally this thesis tries to investigate how people´s practices and background support scientific interpretations about ADE creation and the role ADE had in pre-Columbian agriculture and manioc domestication.

Cultural and environmental conditions determine what crops are cultivated. This thesis focuses on the study of manioc for two main reasons: manioc is the staple food of indigenous people in areas with and without access to ADE (Wilson and Dufour, 2006; Fraser, 2010a; Acosta *et al.*, 2011); and manioc diversity has been previously documented in natural and anthropogenic soils of the Amazon region (Arias *et al.*, 2005; Alves-Pereira *et al.*, 2012). In this thesis, it is attempted to investigate how cultural and environmental conditions act together to shape manioc diversity.

Manioc needs an arbuscular mycorrhizal association to satisfy its nutritional requirements. But the arbuscular mycorrhizal association is affected by the floristic composition of vegetation and the soil condition. Floristic composition of flooded and non-flooded forests is different according to plant species' susceptibility to floods and therefore, arbuscular mycorrhizal communities associated with them are expected to differ. When forests are logged for swiddens to cultivate manioc, part of the arbuscular mycorrhizal community colonizes manioc roots, reflecting that arbuscular mycorrhizal community variability. However, not all maniocs are equal and some have more toxic roots than others. In this thesis, it is investigated how arbuscular mycorrhizal community composition of different soils is reflected in manioc roots and how variable manioc arbuscular mycorrhizal association is in relation to manioc diversity (in terms of the manioc types or the landraces cultivated). However, edaphic variables such as pH and phosphorus availability also affect arbuscular mycorrhizal composition of soils. Upland (ADE and non-ADE) and floodplain soil composition differs according to the parental material from which soils originated and the type, quality and quantity of inputs that they received affecting their pH and phosphorus availability and therefore, their arbuscular mycorrhizal community composition. This thesis compares arbuscular mycorrhizal communities and manioc mycorrhization of different manioc types in environments with contrasting soils to provide information on the role and variability of this plant-fungi association in different Amazonian environments. An additional value to the general knowledge on ADE is that in this thesis it is reported for the first time how the arbuscular mycorrhizal community composition of ADE is in comparison with other soils.

The creation of a new environment for food production, such as ADE, could change indigenous people interaction with their environment, changing the biotic and abiotic conditions of uplands for food production and therefore, changing indigenous preferences for cultivating environments, the selection of crops and varieties cultivated (in this case referring to the selection of different manioc types and landraces), and agricultural patterns associated with the species cultivated and indigenous culinary traditions. Differences among indigenous communities with and without ADE in those aspects have not been documented previously as there is limited information about the management of ADE by indigenous people.

To approach the previously described gaps in knowledge, the thesis focuses on the study of indigenous land use for agriculture and on manioc as the crop that exemplifies how people select and transform native crops. Based on these particular topics of study, the knowledge gaps are transformed into research questions to contribute to the debate about how much indigenous people use and create diversity in the Amazon region:

1. Research question to approach cultural diversity and land diversity interaction: How do cultural preferences and conditions of natural and anthropogenic environments determine land use among indigenous people of the Colombian Amazon? (Chapters 2 and 3).
2. Research question to approach cultural diversity and manioc diversity interaction: How do cultural and environmental conditions jointly shape manioc diversity in indigenous communities of the Colombian Amazon? (Chapters 4 and 5).
3. Research question to approach land diversity and manioc diversity interaction: How different are arbuscular mycorrhizal communities of natural and anthropogenic soils of the Colombian Amazon and how much do those differences affect manioc mycorrhization? (Chapter 5).
4. Research question to approach the interaction among culture, land and manioc diversity: Does indigenous agriculture in the Colombian Amazon reflect a co-adaptation between people and environment that has enhanced Amazonian diversity, supporting the scientific hypothesis that people play an important role in the conservation and creation of Amazonian diversity? (Chapters 2, 3, 4 and 5).

To explore and answer the research questions proposed, for Chapters 2, 3 and 4 social science methodologies (ethnography, participant observations, structured and un-structured interviews) and natural science methodologies (composite-soil sampling, extensive sampling for inventories, standardized protocols for the quantification of soil physical and chemical variables) were applied. To answer the research questions proposed for Chapters 4 and 5 in which manioc and arbuscular mycorrhizal fungi diversity are explored, two types of methodologies were applied: First, classical methodologies based on the comparison of morphological features to explore diversity at morphotype level (manioc descriptors developed by world reference collections of manioc (CIAT, 1984; Fukoda and Guevara, 1998), arbuscular mycorrhizal fungi taxonomic classification using the morphological description of arbuscular mycorrhizal fungi spores (Schenck and Perez, 1988)), and molecular methodologies to explore diversity at genotype level (variability of manioc single nucleotide polymorphisms using direct sequencing (Duitama *et al.*, 2014), and variability of the subunit 18S of the ribosomal DNA to estimate arbuscular mycorrhizal virtual taxons in soils and manioc roots (Öpik *et al.*, 2009)). The combination of different field and laboratory methodologies allowed the discussion of results in a transdisciplinary (researcher-indigenous people) and interdisciplinary (natural sciences-social sciences) way. This approach helped to achieve the goal of this thesis: to provide information about indigenous knowledge and indigenous land use in order to understand how indigenous people inhabiting different environments (with and without ADE) use and create diversity in the region.

1.6. Thesis outline

The thesis consists of six chapters. This introduction (Chapter 1) presents the context of the study area, the research questions and the analytical framework (Figure 1.3) of the thesis. The following four chapters (Chapters 2 to 5) address specific knowledge gaps that are addressed through research questions.

There is little information about indigenous agriculture in environments with anthropogenic soils or floodplains. There is no available information about how indigenous people select and manage a landscape with a diverse portfolio of soils with diverse fertility. In **Chapter 2**, indigenous agriculture on natural and anthropogenic soils of the Colombian Amazon is described. The production systems in these environments are also compared among communities with and without access to ADE. Differences among communities and ethnic groups are discussed, addressing the role of soil fertility and other criteria in the selection and use of the different environments for agriculture.

The use of ADE for indigenous agriculture has not been reported before, but other uses of ADE have also not been reported. Indigenous knowledge on the origin and ancient use of ADE has been briefly indicated for the Kuikuro from the Brazilian Amazon but not for other indigenous groups. In **Chapter 3**, indigenous classification of natural and anthropogenic soils by indigenous communities of the Upper Amazon region of Colombia, and indigenous perceptions about their suitability for agriculture and other uses are addressed. Indigenous knowledge about origin of natural and anthropogenic soils, and ancient and contemporary uses is discussed and compared with current scientific knowledge about past Amazonian land use.

As reports of indigenous agriculture on ADE are limited, information about manioc diversity of indigenous stocks cultivated in ADE and manioc diversity in communities with access to natural and anthropogenic soil is not available. Socio-cultural preferences have been reported for single ethnic groups but comparison among different groups is not possible as previous inventories were done in different times and using different methodologies. In **Chapter 4,** differences in manioc diversity among five ethnic groups of the Colombian Amazon are compared. Morphotypic and genotypic manioc diversity is assessed in Amazonian communities with and without access to ADE. Indigenous estimation of manioc diversity through manioc morphotypes is compared with manioc genotypic diversity and discussed. The sources of manioc diversity are also explored, evaluating the role of soil diversity and social differences in manioc diversification. Additional indications of manioc diversity hotspots and for manioc diversity conservation are included.

Arbuscular mycorrhizal fungal communities have not been studied in ADE and reports of arbuscular mycorrhizal fungal communities on floodplains are limited. A comparison of the arbuscular mycorrhization of manioc in Amazonian environments with different phosphorus availability has not been made. There are few reports on how manioc root arbuscular mycorrhization occurs in landraces with different levels of toxicity (due to variations in the root concentration of cyanogenic compounds). In **Chapter 5**, root arbuscular mycorrhization of manioc in natural and anthropogenic soils of the Amazon region is described and compared. The abundance and richness of arbuscular mycorrhizal fungal communities from environments with natural and anthropogenic soils are compared. Root arbuscular mycorrhization of manioc is evaluated in relation to arbuscular mycorrhizal fungal communities of soils, soil pH and phosphorus availability. Differences in manioc mycorrhization in relation to manioc diversity (types of landraces evaluated) are assessed.

In the General Discussion (Chapter 6) a synthesis and a discussion of results are presented. Answers to research questions here presented are provided as the major contribution to the debate about how much people contribute to shape diversity in the Amazon region. The thesis also presents some unsolved issues as suggestions for further research.

In summary, the findings of this thesis indicate that the creation of ADE constitutes a new environment for agriculture, but ADE are not always contrastingly different to non-anthropogenic soils. Indigenous people perceive this similarity between soils as similar conditions for cultivation of manioc, their staple food. Floodplains on the other hand are also important places for manioc agriculture, but the agriculture practiced in floodplains located at different height of the riverside and different frequency of flooding varies. Low floodplains (flooded every year) are used permanently through flood-recession agriculture and harvested by *mingas* (numerous people helping through collaborative work). High floodplains known as *restingas* (which are flooded once every 5 to 10 years) are used through swidden agriculture and harvested through family work. There are no specific manioc landraces for any of the different soil types studied. Indigenous farmers maintain highly diverse stocks of sweet and bitter manioc landraces that move from one field to another, independently of the edaphic or flooding differences among sites. The high affinity of manioc for arbuscular mycorrhizal fungi makes it a promiscuous arbuscular mycorrhizal species always colonized by arbuscular mycorrhizal fungi, independently of the edaphic conditions or the particular arbuscular mycorrhizal fungal community of the different soils. This particular affinity of manioc for arbuscular mycorrhizal fungi explains in part why manioc could be moved from one field to another and successfully cultivated in different sites with contrasting soil fertility as was observed in this study.

In general, manioc diversity in the study area is high but manioc diversity is little determined by environmental conditions. On the contrary, cultural values attached to manioc explained most of the manioc variability found in the study area. People therefore, are considered an important transforming actor in the Amazon region using most of the environments for food production, and affecting forest composition and dynamics.

Additionally, people create a new environment, the Amazonian Dark Earths, not naturally present in the Amazon region before human occupation. People also domesticate native species such as manioc and create cultural values associated with it which results in hundreds of different landraces that contribute to enhance the Amazonian diversity. It is possible to conclude that the human contribution to shape the actual Amazonia diversity is clearly important and exemplified through the cultivation of manioc.

Chapter 2

Challenging current ADE knowledge: Indigenous agriculture in different soils of the Colombian Amazon

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Submitted to Culture, Agriculture, Food and Environment

Abstract

Amazonian indigenous people access different farmlands with different inherent soil fertility. Extensive literature exists on indigenous Amazonian swidden agriculture on low-fertile uplands, but not on fertile Amazonian Dark Earths (ADE) or floodplains. Current literature suggests that ADE are preferred by studied farmer communities for agriculture among other soils due to their fertility and non-flooding risk. It is not clear whether indigenous farmers also prefer ADE and apply the same land-use management practices reported for non-indigenous communities. During two years, we studied indigenous agricultural systems on different soils, through participant observations and interviews with farmers. Contrary to previous literature, ADE and non-ADE were similar except for higher phosphorus availability in ADE. Indigenous agriculture was also similar on both soils as well as the cultivated manioc stocks. Site selection and management of plots in floodplains differed among communities and depended on farmer access to communal labor rather than on floodplain soil conditions.

Key words: Amazonian soils, indigenous agriculture, land-use management, Amazonian Dark Earths, floodplain.

2.1. Introduction

For small farmers living in tropical forests, the soil is the most important resource for agriculture and labor the main required input. Access to a broad portfolio of soils might provide better opportunities for sustained livelihoods (German, 2003; Fraser and Clement, 2008; Arce-Nazario, 2011).

The Amazon basin is commonly divided into two types of farmland: uplands and floodplains. Most Amazonian uplands are considered to have limitations for a permanent and intensive agriculture while floodplains are considered more amenable to intensive agriculture (Meggers, 1954; Denevan, 1996; McMichael *et al.*, 2012). Amazonian uplands generally have very acid, highly weathered soils (Richter and Babbar, 1991), originating from parental materials rich in kaolinite with a naturally limited nutrient holding capacity (Ma and Eggleton, 1999) and thus have a low inherent nutrient availability. However, within low-fertile uplands patches of anthropogenic soil are found, known as Amazonian Dark Earths (ADE). These anthropogenic soils are enriched with ashes, charcoal, plant remains, and specially with animal bones and human faeces which results in a higher nutrient content compared with background soils (Birk *et al.*, 2011; Glaser and Birk, 2012). Typically ADE are less acid than surrounding uplands, leading to a higher cation exchange capacity and base saturation. ADE have higher organic matter content and more pyrogenic carbon (Glaser *et al.*, 2001; Sombroek *et al.*, 2003) which results in a higher nitrogen, calcium and potassium availability (Lima *et al.*, 2002). ADE are also richer in phosphorus and calcium than background soils (Glaser and Birk, 2012) and therefore phosphorus/potassium ratios, and calcium/magnesium ratios are significantly higher than in background soils.

Floodplains also vary in fertility (Junk, 1997) and could be divided roughly into two classes: floodplains with a limited fertility flooded by black water rivers originating in the Amazon basin; and fertile floodplains enriched by white water rivers carrying and depositing Andean sediments (Piedade *et al.*, 2001), locally known as *várzeas*. Researchers usually refer to *várzeas* when mentioning floodplains as fertile environments important for agriculture. *Várzeas* have near-neutral pH values, large amounts of calcium and magnesium (Teixeira *et al.*, 2006) and a better cation exchange capacity due to the texture and mineral composition of Andean sediments resulting in a better fertility compared with uplands. *Várzeas* can be classified in terms of their height in respect to the river water level and related period and frequency of flooding into low floodplains that are flooded every year, and *restingas* (high floodplains) that are not flooded yearly.

Swidden agriculture on Amazonian uplands is well documented (Hammen, 1984; Eden and Andrade, 1987; McGrath *et al.*, 2001; Wilson and Dufour, 2006; Acosta *et al.*, 2011; Thomaz, 2013; Béliveau *et al.*, 2014). Upland swiddens are typically half to one hectare in size (Eden and Andrade, 1987; Perreault, 2005), placed in locations previously covered by mature forests or old secondary forests (Acosta *et al.*, 2011). Manioc is the dominant crop species cultivated in swiddens (Hammond *et al.*, 1995). Manioc is cultivated for one or two long production cycles of about one to three years each (Fraser, 2010b), followed by a fallow period (Wezel and Ohl, 2005) of about 26 years or longer.

Agriculture on other Amazonian soils has been addressed in few papers. Agriculture on ADE has been described for *Caboclo* farmers (with a mixed Amerind-European or Amerind-Euro-African heritage) of the Middle Madeira River in Brazil (Fraser, 2010a; Fraser *et al.*, 2011a). On ADE, *Caboclos* practice a more intensive swidden agriculture than on uplands characterized by smaller swidden areas (Fraser, 2010a) in which manioc is replanted consecutively up to three times (Fraser *et al.*, 2011a) for a shorter growing period (Fraser, 2010a) than in non-ADE upland. Fallow periods on ADE are up to three times shorter than on non-ADE upland (Fraser and Clement, 2008; Fraser *et al.*, 2012) but weed infestation is a larger problem and therefore more labor is required to control them (German, 2003; Hiraoka *et al.*, 2003).

Caboclo agriculture on floodplains is similar to the one described for ADE. Swiddens are smaller than those observed on non-ADE uplands, usually placed in areas previously covered by young secondary forests, and opened after short fallows of 1.6 ± 4 years on average (Fraser, 2010b; Fraser *et al.*, 2012). Because cultivation is limited by floods only a short production cycle is possible and manioc landraces therefore bulk quickly (Fraser, 2010b). Adams *et al.* (2005) found that some *Caboclos* prefer to cultivate manioc on high floodplains rather than on low floodplains to secure a longer growing period and therefore allow more time for root bulking. As on ADE, weed growth on floodplains is also more vigorous and weed control requires more labor than on uplands (Adams *et al.*, 2005).

Limited information about indigenous agriculture on fertile Amazonian soils (such as ADE and floodplains) seems available. The Kuikuro indigenous group from Brazil cultivate nutrient-demanding crops on ADE (Schmidt and Heckenberger, 2009). Uitoto and Andoke indigenous groups with access to ADE (Eden *et al.*, 1984) cultivate mainly non-ADE upland under swidden systems, and rarely cultivate floodplains (Eden and Andrade, 1987), but their article does not mention ADE use. Shorr (2000) described an agricultural system in floodplains practiced by a Tikuna community with recently improved access to markets. In this system, which he called flood-recession agriculture, farmers continuously cultivate low floodplains with watermelon without additional fertilization, restricting the fallow period to the flooding period.

In low input agriculture as practiced by indigenous farmers labor constitutes the main input into the system. Farmers afford the required labor in different ways. Some use mainly family labor (including parents, grandparents, and children) in all agriculture activities, independent of their age. As indigenous farmers do not have capital for hiring labor, they use collaborative labor in activities that require a high labor input such as site opening, weed control or harvesting (Downey, 2010; Takasaki *et al.*, 2014). Collective labor consists of reciprocated work in which different persons outside the direct family are invited to work in exchange for food and drinks (Takasaki *et al.*, 2014). Contributing to collective work also opens the opportunity to ask for labor contributions in return when time comes. It has been documented that in areas where other economic activities exist, the use of collective work is replaced by wage labor (Peroni and Hanazaki, 2002). Today, most indigenous communities participate in regional economies by selling their agricultural surpluses, producing goods for sale (e.g. handicrafts), working in the timber or tourist industry (Hammond *et al.*, 1995) or by engaging in a host of cash generating activities such as mining of alluvial gold (Hammond *et al.*, 2007; Peña-Venegas *et al.*, 2014a, Chapter 2 of this thesis). However, the impact of these activities on the availability of labor for indigenous agriculture in these communities is not known.

Although swidden agriculture on low-fertility uplands is the main production system used by Amazonian indigenous people, there is no information whether indigenous farmers also practice swidden agriculture on more fertile soils or if other production systems (such as flood-recession agriculture) are also practiced by indigenous groups without a strong relation to markets. There is no information either on how indigenous people mobilize labor for different agricultural environments, and how this relates to household labor availability. More information is still required to have a better picture of indigenous agriculture on different Amazonian soils. This paper reports on research conducted among five indigenous communities of the Colombian Amazon to study how agriculture was carried out on different soils. Participatory observation and interviews with indigenous farmers were made in all communities. All communities had access to non-anthropogenic uplands and *várzeas* (low floodplains and *restingas*) and four had access to ADE (Figure 2.1). This paper compares agricultural systems on different soils and relates the differences to soil characteristics, age of fallows, and labor use.

2.2. Material and methods

2.2.1. Study area

Two locations in the Colombian Amazon were selected for this study. The first one was the Tikuna indigenous community of San Martín de Amacayacu, located in the most southern part of the Colombian Amazon, on the upper Amazonas River. The community is located between 03º50'17.3" South and 70º17'57.3" West, at an altitude of 95 m.a.s.l. along the last section of the Amacayacu River, just five kilometers upstream before it joins the Amazon River. The community is inhabited by 153 families (own community census in 2011) and located in the Tikuna, Cocama and Yagua Indigenous *Resguardo* TICOYA which has an approximate extension of 140,000 ha. The community's upland swiddens are, for the most part, located within Amacayacu National Park. The second location comprises a part of the Middle Caquetá region (the portion of the Caquetá River between Araracuara and the island of Maria Cristina). Here, at an altitude of 128 m.a.s.l., four communities were selected: the Andoke community of Aduche (27 families), the Uitoto community of Guacamayo (34 families), the Muinane community of Villazul (17 families), and the Nonuya community of Peña Roja (15 families),[1] which are distributed in two legally recognized indigenous territories. The communities of Aduche (00º39´21" South and 72º17´32" West) and Guacamayo (00º31´25" South and 72º22´38" West) are located in the Aduche *Resguardo*; and the communities of Villazul (00º 40´00" South and 72º16´32" West) and Peña Roja (00º 44´29" South and 72º 05´09" West) are located in the Nonuya *Resguardo*.

Tikuna farmers distinguish two main types of soils on which they carry out agriculture. The first is "*tierra firme*" which are uplands with elevations around 100 m.a.s.l. and slopes between 1-3% composed by soils of denudation origin, formed over old floodplains of the Amazon River but not affected by actual river floods (IGAC, 1979). The second are the "*bajiales*" as they denominated *várzeas* flooded by a combination of water from the Amazon and the Amacayacu River (the first a white water river and the second a black water river).

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[1] Based on community censuses carried out by local authorities in 2011.

Farmers distinguish two types of *várzeas*: those that are located in low areas and are flooded every year (Figure 2.1), and those located in more elevated areas and that are flooded once every five to 10 years. Around the community of San Martín de Amacayacu no ADE were observed and, when ADE were described to them, they did not recall a similar soil in their territory.

Farmers from the Middle Caquetá region distinguish the same two main types of soils. One, the "*tierra firme*" which corresponded to elevated plateaus between 200 and 300 m.a.s.l. with slopes between seven and 25%, and composed of superficial soils of sedimentary origin, originating from the erosion of parental materials from the Paleozoic period (IGAC, 1979). Within the "*tierra firme*" farmers discern the "*arenas negras*" as a more-or-less specific subcategory of uplands (Chapter 3 of this thesis, Peña-Venegas *et al.*, 2015a). "*Arenas negras*" correspond to ADE in the scientific literature. For this study ADE were considered as a specific group of soils due to its anthropogenic origin, which differentiates it from surrounding upland soils (Figure 2.1). Second, the *várzeas* which correspond to those periodically flooded by the Caquetá River (Figure 2.1), and which farmers locally called "*vegas*". Within "*vegas*" farmers distinguish between the "*propia vega*" (low floodplains flooded annually) and the "*restingas*" (high floodplains flooded once every five to 10 years; see Figure 2.1).

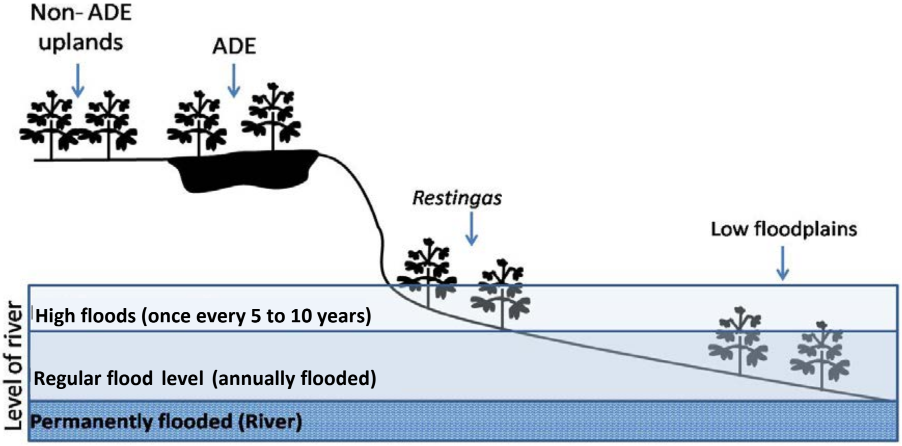

Figure 2.1. Location and nomenclature of soil types used by indigenous farmers in relation to the riverpulse.

2.2.2. Selection of indigenous fields for monitoring and fieldwork

In all communities, the most experienced farmer families were selected; the selection itself was done by the different communities (Table 2.1).

A preliminary inventory was made of the number of fields (64) that selected farmers were using at the time of our research. Since our main purpose was a detailed description of indigenous production systems, only fields that had been opened recently (i.e. no more than 6 months old) were further selected for continuous monitoring; an important reason for this selection was that this allowed for a relatively precise reconstruction of the initial activities in the production cycle. Additionally, fields opened between September and December of 2011 were selected for monitoring and for direct observation of the first steps in the production cycle. In total, 25 fields were monitored continuously from September 2011 until September 2013 to obtain information on agricultural activities and the way these were performed (Table 2.1).

Table 2.1. Number of indigenous families that participated in the research, representativeness in percentage of each community in the farmer´s sample, and number of indigenous fields per community selected for monitoring and direct observation of the production cycle.

Community	**Number of families**	**Percentage respect to total families**	**Number of fields monitored**			
			Non-ADE upland soils	**ADE**	**Low floodplains**	***Restingas***
San Martín de Amacayacu	20	13%	3		3	
Aduche	9	29%		5		
Guacamayo	10	33%	3			
Villazul	8	47%	3	1		1
Peña Roja	6	40%	4			2

2.2.3. Location and soil composition of farmlands

During the first visit to fields, the landscape in which they were located was described and a composite soil sample of about 500 g of the A horizon was collected by mixing five soil sub-samples, one from each one of the corners and one from the center of the field. In cases where two fields were adjacent to each other, only one soil sample was collected to represent the soil of the two fields. A total of 20 soil samples were analyzed: nine from non-ADE uplands (three from the Amazon region and six from the Middle Caquetá region), five from ADE and six from *várzeas* (two low floodplains from the community of San Martín de Amacayacu and four *restingas* from the Middle Caquetá region). Soil samples were analyzed in the National Laboratory of Soils of the Instituto Geográfico Agustín Codazzi-IGAC in Bogotá, Colombia. The analyses included soil granulometry, pH (1:1 in water), percentage of organic carbon (Walkley – Black), cation exchange capacity (with normal and neutral ammonium acetate), DTPA-extractable Ca, Mg, K, Na, percentage of total bases (base saturation with normal and neutral ammonium acetate), and available phosphorus (Bray II). Analyses were executed according to the protocols standardized by the laboratory (IGAC, 2006). The size of agricultural fields was first estimated by the indigenous farmers and then corroborated or adjusted *in situ* with a GPS, taking the length and width of the field and calculating the total area.

2.2.4. Reconstructing the production cycle

Farmers identify different steps and activities in their production systems –from the selection of an area to establish a crop field until the field is abandoned for a fallow period. The most frequently used terms (in Spanish) to refer to each one of the steps were used between researchers and farmers to allow for a common vocabulary. Individual interviews with farmers were held to reconstruct the first steps of the production cycle and to establish (with them) how to record the information in forms. Forms were filled out by farmers at the end of each day a farmer worked in her field; this provided information about the activities undertaken, the date, the number of persons involved and how much time was spent on the activities. To train farmers, the forms were first filled out with the help of the research team, but later farmers filled them out directly. Since some of the older farmers were illiterate or did not speak Spanish, one of their children was trained to fill the forms for their parents. This was not the first time farmers of these communities recorded data as they had participated in different, earlier research projects of governmental institutions, NGOs and universities.

Each time the researchers were in the community a visit to each field was made and the information previously recorded was confirmed, clarified or corrected - thus creating a permanent feedback and form fill-out training cycle. With this purpose, periodic visits were made to each community, with a total of eight visits per community for 2 to 4 days each. The forms collected during each visit were transcribed into an Excel sheet.

2.2.5. Labor estimation of each step of the production cycle

The time farmers spent each day doing a given activity was added to obtain the total time spent on it. Because field sizes and the number of persons who participated in each activity varied between agricultural fields, the data were converted to person hours per hectare. As farmers sometimes recorded they worked “a complete day”, all farmers were asked at what time they started and at what time they finished agricultural activities in their fields when they worked a complete day (excluding the time they spend walking to get to and comeback from the field). The mean number of working hours of a full work day was estimated at 5.6 hours. This value was then used to transform the estimation of labor in the raw data into person hours per hectare.

2.2.6. Statistical analysis

A non-parametric one-way Kruskal-Wallis ANOVA analysis was used to compare soil physicochemical composition within uplands and *várzeas* of the two locations and between ADE and non-ADE uplands for the Middle Caquetá region.

A one-way Kruskal-Wallis ANOVA analysis was also used to compare the size, the vegetation age of sites used to locate agricultural fields, and the field management in labor time among different land and soil types. As some fields were opened on forested areas that, according to farmers’ collective memory, had not been cultivated before, these forests were considered as over 100 years old. The field management was compared among the different land and soil types in terms of the time spent on the different activities, the number of cycles of weed control and the length of the manioc growing cycle before its harvesting started.

Indigenous farmers cultivated a high diversity of maniocs in their fields; a total of 47 landraces were registered in the 25 fields monitored. Manioc harvest started after around one year after planting by digging up a few roots each day in accordance with family requirements - except on *várzeas*. In low floodplains all manioc was harvested at the same time shortly before the arrival of floods. In *restingas* manioc harvest started after 5 months and was finished it in no more than two months, independently if *restingas* harvesting was pushed by the flood or not. To evaluate the differences in manioc plant height (a measure of potential sources of vegetative propagules for new agricultural fields) between soil types, information about the name of the manioc landrace and the height of the longest stem in each manioc plant dug up during harvesting was recorded. As not all farmers and communities cultivated the same manioc landraces, only data of nine manioc landraces which were cultivated on the four different soil types (non-ADE and ADE upland soils, low floodplain and *restinga* soils) were selected for this analysis: *Amarilla* (five registers); *Borugo* (six registers); *Cáscara morada* (seven registers); *Guava* (12 registers); *Pan* (10 registers); *Masatera* (seven registers); *Yucuna* (10 registers); *Ereño Juti* (six registers); and *Lupuna* (six registers).Values of manioc plant height of each manioc landrace were tested against soil types using a non-parametric Kruskal-Wallis ANOVA test with the analytical software Statistix 9.0 (Statistix, 1998), using $p \leq 0.05$ as criterion to denounce differences as significant.

2.3. Results

2.3.1. Soil composition of farmlands

Sampled soils varied in physicochemical composition but all had pH ≤ 4.5 (Table 2.2). Upland soils from the two different locations differed in texture and chemical composition in line with differences in the parental materials from which soils were formed. Upland soils from San Martín de Amacayacu were more clayey ($p = 0.01$), had more calcium ($p = 0.01$) and more potassium ($p = 0.01$) than uplands from the Middle Caquetá region (Table 2.2).

The physicochemical composition of ADE was more variable than that of non-ADE uplands. The phosphorus availability was significantly higher in ADE ($p < 0.01$) than in non-ADE uplands, but none of the other chemical variables differed significantly (Table 2.2). Means of the ratios of available phosphorus (P) and potassium (K), and of calcium (Ca) and magnesium (Mg) however, were higher in ADE than in non-ADE uplands. The ADE P/K ratio (1144.5) was 62 times higher than for non-ADE upland P/K ratio (18.5), and ADE Ca/Mg ratio (2.5) was 3.8 times higher than for non-ADE upland Ca/Mg ratio (0.66), distinctly showing the anthropogenic enrichment of ADE.

Farmers from San Martín de Amacayacu only cultivated low floodplains while farmers from the Middle Caquetá region only cultivated *restingas*. Chemical differences between the low floodplains used by farmers from San Martín de Amacayacu and the *restingas* used by

Table 2.2. Soil characteristics of fields sampled in two locations and separately for soil types. Values are expressed as means with standard deviations between brackets. Means within a land type and column followed by an asterisk are significantly different according to a non-parametric one-way Kruskal-Wallis ANOVA test ($P < 0.05$).

Land type	Location	pH-H_2O	^{a}OC	^{b}CEC	^{c}Ca	^{c}Mg	^{c}K	^{c}Na	^{d}BS	^{e}P
Non-ADE uplands	SM Amacayacu (n=3)	4.1(0.2)	2.8 (1.0)	21.5 (8.1)	3.2 (3.6)*	2.2 (2.4)	0.4 (0.1)*	0.1 (0.0)	23.3 (16.3)	10.7 (2.3)
	Middle Caquetá (n= 6)	3.9 (0.6)	3.3 (3.7)	14.9 (12.2)	0.2 (0.1) *	0.3 (0.4)	0.2 (0.1) *	0.1 (0.0)	7.6 (7.5)	3.7 (6.2)
Floodplains	Low floodplains SM Amacayacu (n=2)	3.7 (0.0) *	2.7 (1.7)	33.5 (16.3) *	0.3 (0.1) *	0.4 (0.3)	0.4 (0.3)	0.1 (0.0) *	3.3 (0.6)*	13.0 (18.1)
	Restingas Middle Caquetá (n= 4)	4.3 (0.2) *	1.4 (0.3)	12.1 (0.5) *	2.4 (1.9) *	1.6 (1.2)	0.2 (0.0)	0.1 (0.0) *	36.1 (27.8) *	9.1 (10.5)
Uplands Caquetá	Non-ADE (n=6)	3.9 (0.6)	3.3 (3.7)	14.9 (12.2)	0.2 (0.1)	0.3 (0.4)	0.2 (0.1)	0.1 (0.0)	7.6 (7.5)	3.7 (6.2) *
	ADE (n= 5)	4.0 (0.3)	1.8 (0.7)	9.5 (4.7)	1.0 (0.9)	0.4 (0.4)	0.2 (0.1)	0.1 (0.0)	16.9 (7.9)	228.9 (313.7) *

[a] Percentage of organic carbon (Walkley – Black); [b] Cation exchange capacity ppm(using normal and neutral ammonium acetate); [c] DTPA-extractable calcium, magnesium, potassium and sodium (ppm); [d] Percentage of base saturation; [e] Available phosphorus (mg kg-1; Bray II).

farmers from the Middle Caquetá region were apparent only for soil acidity (p=0.03) and the related percentage base saturation (p= 0.03) (Table 2.2), but these differences did not explain differences in the selection and use of *várzeas* among farmers of the two locations.

2.3.2. Swidden agriculture on uplands

Sites selected for swiddens were always covered by forest and required previous consultation with forest spirits and forest owners (animals and plants) before opening a field. Indigenous farmers considered this consultation very important to prevent accidents, crop pests and diseases, and to secure a good production. After this first measure indigenous farmers considered three main steps for the opening of a site. First the area was cleaned of annuals, shrubs and small trees with machetes. In the second step larger trees were logged with axes and machetes or with chainsaws (only in 3 of the 19 upland sites). In the third step branches and stems were chopped in smaller pieces to facilitate a faster drying of material. Cleaning, logging and chopping activities followed the annual weather pattern of the region using the dry period so all logged and chopped vegetation would dry properly before burning. After burning, crop planting started. Indigenous farmers planted more than 10 different crops in swiddens (Table 2.3), but manioc was generally planted first, distributed more-or-less homogenously across the swidden area, and occupying around 70% of planting space. When manioc was not planted first, maize (*Zea mays* L.), plantain (*Musa* sp.), watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai), sugar cane (*Saccharum officinarum* L.) or chili (*Capsicum* sp.) were planted first. The main reason to plant these species before manioc was because they require sites with high quantities of ash and charcoal and it is easy to find these sites when manioc is not yet planted.

The length of the manioc growing period (the period between planting and the start of harvesting) in uplands (including ADE) was between 10 and 16 months (Table 2.4). No differences (p> 0.05) were observed in the growing period of manioc in non-ADE or ADE uplands of the Middle Caquetá region. During the growing period farmers weeded the swiddens two to three times, without significant differences in the number of cycles needed on ADE or non-ADE uplands.

Once manioc harvesting started no systematic weeding occurred. Manioc was harvested progressively, selecting each time the number of plants and the landraces required for daily use. Fields therefore acted as an *in vivo* manioc storage place. In four of 19 swiddens

Table 2.3. Crops, fruit trees and palms cultivated in indigenous swiddens of the Colombian Amazon region specified for *restingas*, ADE and non-ADE uplands.

English name	Scientific name	*Restingas*	ADE	Non-ADE
Achira	*Canna indica* L.			X
Avocado	*Persea americana* Mill.	X		
Araza	*Eugenia stipitata* McVaugh			X
Asai	*Euterpe precatoria* Mart.	X		
Bacuri	*Garcinia gardneriana* (Planch. &Triana) Zappi	X		X
Banana	*Musa* sp.			X
Barbasco	*Lonchocarpus nicou* (Aubl.) DC.		X	
Bean	*Phaseolus* sp.			X
Bore	*Xanthosomas agittifolium* (L.) Schott			X
Borojo	*Genipa americana* L.			X
Caimo	*Pouteria caimito* (Ruiz &Pav.) Radlk.		X	X
Cashew	*Anacardium occidentale* L.	X		X
Chili	*Capsicum annum* L.	X	X	X
Coca	*Erythroxylum coca* Lam.		X	X
Cocoa	*Theobroma cacao* L.			X
Copoazu	*Theobroma grandiflorum* (Spreng.) K.Schum.			X
Dale dale	*Pseudolmedia laevigata* Trécul		X	X
Hairstain	*Palicourea triphylla* DC.		X	X
Lemon	*Citrus limon* (L.) Osbeck	X		
Lulo	*Solanum sessiliflorum* Dunal	X	X	
Maize	*Zea mays* L.	X		X
Mafafa	*Xanthosomas agittifolium* (L.) Schott	X		X
Milpeso	*Oenocarpus bataua* Mart.	X		
Manioc	*Manihot esculenta* Crantz	X	X	X
Papaya	*Carica goudotiana* (Triana&Planch.) Solms	X		X
Peach palm	*Bactris gasipaes* Kunth			X
Peanut	*Arachis hypogaea* L.	X		
Pineapple	*Ananas comosus* (L.) Merr.		X	X
Plantain	*Musa paradisiaca* L.	X		X
Saffron	*Curcuma longa* L.	X		
Sugarcane	*Saccharum officinarum* L.	X	X	X
Sweet pepper	*Capsicum annuum* L.			X
Sweet potato (batata)	*Ipomoea batatas* (L.) Lam.		X	X
Indian yam (ñame)	*Dioscorea trifida* L.f.	X	X	X
Tobacco	*Nicotiana tabacum* L.	X		X
Tomato	*Solanum lycopersicum* L.	X		X
Tree grape	*Pourouma cecropiifolia* Mart.	X		X
Ucuye	*Macoubea guianensis* Aubl.	X	X	X
Water melon	*Citrullus lanatus* (Thunb.) Matsum. &Nakai	X	X	X
Zapote	*Conceveiba martiana* Baill.			X

monitored on uplands (one from primary forest and three from secondary forests on non-ADE soils), while harvesting manioc farmers considered the soil of some patches was good enough for a second cycle of manioc production and shortly replanted these patches with stems obtained from the same manioc plants that were previously harvested. Harvesting continued for two to three years (later in replanted fields) until all manioc plants were harvested, after which swiddens were left for a fallow period.

2.3.3. Continuous flood-recession agriculture

The low floodplains were only cultivated in San Martín de Amacayacu through a flood recession system in which fields were left uncultivated during the annual flooding period only. Farmers perceived low floodplains as natural cropping landscapes that do not require special permission (e.g. by spirits) for their use. The sparse vegetation of annuals present after the water receded was cleaned with a machete. Logging and chopping was unnecessary. The cleaned vegetation was sometimes burned and sometimes not. Manioc was the only crop cultivated on these fields. The length of the growing period was never longer than 5 months as it was limited by the flood. Most weed seeds are not tolerant to a prolonged flood and during the short growing period weeds developed poorly; hence weeding was done once or not at all. All manioc plants were harvested in one or two days, shortly before the field was flooded. All manioc roots were peeled after harvesting. Some peeled roots were processed immediately as *farinha* (a fermented and roasted manioc granulate) and others were buried using a traditional technique to preserve manioc roots.

2.3.4. Swidden agriculture on *restingas*

Swidden agriculture on *restingas* mixed elements of swidden agriculture on uplands and flood-recession agriculture on low floodplains. As for uplands, sites selected for swidden agriculture were previously covered by forest and required consultation with forest spirits and forest owners before opening.

Cleaning, logging and chopping activities followed the dynamics of the river, opening the sites when the river started to recede, whether the *restinga* had been flooded or not. Forests on fields opened in *restingas* were significantly younger than in uplands ($p= 0.01$) and dried easier, requiring a shorter period (no more than 4 weeks) without heavy rains to be dry

Table 2.4. Characteristic of field and crop management in different land and soil types for two study areas. Values correspond to means with standard deviations between brackets.

LAND TYPES	Area of fields (ha)	Age of fallows (years)	Cleaning (hours)	Logging (hours)	Chopping (hours)	Time required to open the swidden (hours)	Planting manioc (hours)	Number of cycles for weed control	Time required tocontrol weeds (hours)	manioc growing period (months)	Time required to harvest manioc (hours)*
Non-ADE uplands Amazonas (n=3)	0.7 (1.1)	41.7 (50.6)	69.3 (13.2)	87.3 (42.1)	69.3 (13.2)	226.3 (66.1)	26.0 (14.1)	2.0 (1.0)	646.3 (856.3)	15.7 (4.0)	
Non-ADE uplands Caquetá (n=10)	0.2 (0.4)	47.8 (45.3)	128.4 (104.0)	112.8 (87.2)	8.2 (9.7)	237.2 (182.9)	155.0 (176.9)	2.7 (1.5)	816.6 (778.9)	13.5 (3.9)	
Amazonian Dark Earths Caquetá (n=6)	0.2 (0.4)	39.5 (37.6)	76.0 (42.7)	80.7 (39.6)	42.2 (42.3)	192.5 (106.7)	117.7 (84.0)	3.2 (1.3)	601.2 (546.1)	10.5 (2.1)	
Low floodplains Amazonas (n=3)	0.7 (0.4)	1.0 (0.0)	53.3 (70.2)	8.7 (10.3)	8.7 (10.3)	71.3 (57.8)	179.5 (252.4)	0.7 (0.6)	82.7 (136.3)	4.7 (0.6)	194.0 (252.0)
Restingas Caquetá (n=3)	0.3 (0.6)	15.0 (5.0)	447.5 (253.9)	259.0 (324.1)	7.3 (12.7)	565.7 (630.2)	2200.0 (n.d.) **	2.7 (0.6)	2476.3 (1986.4)	5.3 (1.5)	

* Only possible to record completely during field work for fields on low floodplains.

** n.d. not determined as data of only one swidden are available enough for burning. Manioc was also the main crop planted on *restingas* and occupied more than 70% of the planting space, with a range of others crops planted alongside (Table 2.3). The growing period of swiddens on *restingas* was significantly longer than on low floodplains (p= 0.02), but significantly shorter than in swiddens on non-ADE uplands (p= 0.01), and long enough to require weeding (Table 2.4).

Particularly in *várzeas* a climbing herb from the genus *Mimosa* (with many small spines on its branches) grew in abundance. Farmers called this herb "*cortadera*" (Spanish for cutting herb) as farmers frequently cut their hands when removed it. Although "*cortadera"* is more abundant in *várzeas* than in uplands, fallow periods in *restingas* were longer than in low floodplains and therefore "*cortadera"* was more abundant in *restingas* - taking farmers more time to weed than swiddens on uplands. Harvesting started between four to six months after manioc was planted, and took no more than two months. Harvesting was precipitated when the level of the river started to rise above the regular level (as happened in 2011). Otherwise farmers maintained maniocs for one or two more months for better root bulking - but never prolonged harvesting beyond six months.

2.3.5. Age of vegetation on land selected for agricultural fields and field size

Average vegetation age of sites selected for fields was significantly higher in uplands than in floodplains (p= 0.02), and not significantly different between uplands with non-ADE and ADE (Table 2.4). Swiddens opened on uplands independently of the soil condition were covered by mature forest older than 100 years or secondary forest between five and 70 years of age. Field sizes were not significantly different between uplands and floodplains or among ADE and non-ADE uplands.

2.3.6. Management of farmer´s manioc germplasm

Manioc was planted mainly from stem cuttings between 10 and 15 cm long. However, manioc volunteer seedlings were not generally weeded but left to grow alongside the clonal manioc plants in order to evaluate their root production. Indigenous farmers called manioc stem cuttings "seeds" although these are not seeds in the botanical sense. Manioc stems used for planting a new field were usually collected during the manioc harvesting of a different field. However, manioc stems from the same field were sometimes used to replant parts of a field where manioc was harvested and that farmers considered was still fertile enough for a second production cycle. Additionally, in seven of 25 plots studied, manioc stems were collected from plants of which the roots were not harvested. In this case, farmers collected the longest and thickest stalks of selected manioc plants and left the thinner stems and all roots to continue growing until harvesting at a later stage.

All landraces were planted in all soils in proportions that depended on expected culinary needs and not on any agronomic consideration. Manioc germplasm movement indicated an active flux of manioc among land and soil types (Figure 2.2). In all communities manioc germplasm moved back and forth between uplands and floodplains and, in the communities of the Middle Caquetá, also between ADE and non-ADE uplands. Indigenous farmers indicated that manioc root production is important, but stressed that so is the production of manioc propagules for new fields; they also stated that manioc plants grow taller on floodplains and on ADE than on non-ADE, thus producing more manioc propagule per plant.

This was corroborated by us: in seven of nine manioc landraces tested, plant height was higher in floodplains than in uplands and for some landraces differences between ADE and non-ADE were observed. However, only three manioc landraces showed significant differences in height when planted on different soils: *Cáscara morada* ($p= 0.05$; $n= 7$) with an average height of 210 cm on non-ADE, 252 cm on ADE, and 397 cm on floodplain soils; *Guava* ($p= 0.02$; $n= 9$) with an average height of 290 cm on non-ADE, 317 cm on ADE, and 397 cm on floodplain soils; and *Masatera* ($p= 0.04$; $n= 7$) with an average height of 245 cm on non-ADE, 227 cm on ADE, and 301cm on floodplain soils. Differences indicate that, certainly for some manioc landraces, an extra production of propagules is obtained. Based on the above data, an extra three to nine manioc propagules per plant stem were obtained when they were cultivated on floodplains instead of non-ADE uplands. Differences in propagule production between ADE and non-ADE soils were not so clear as between non-ADE uplands and floodplains.

2.3.7. Labor time

Most labor activities in the field were done by nuclear families but during opening and harvesting fields some families used collective work (locally known as *minga)*. In San Martín

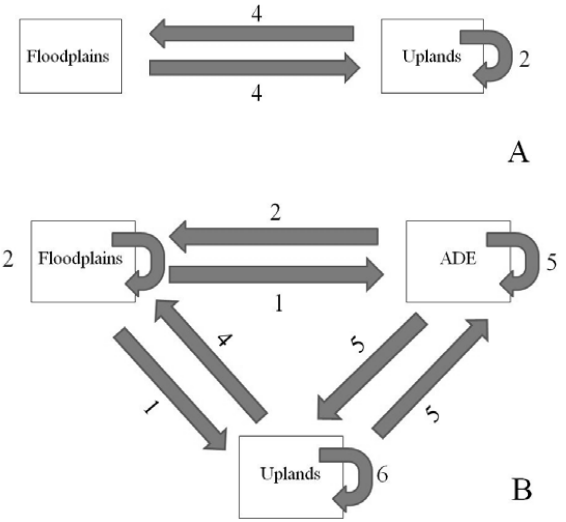

Figure 2.2. Movement of manioc germplasm from old to new agricultural fields planted in 2011 and 2012 according to land and soil type. ADE: Amazonian Dark Earths in uplands. A. the community of San Martín de Amacayacu (n= 10 fields); and B. communities of the Middle Caquetá region (n= 31 fields). Numbers indicate the number of fields from where manioc stocks were moved in the direction of the arrow.

de Amacayacu all three fields in low floodplains were opened and harvested through *minga* and two of three swiddens in non-ADE uplands were opened through *minga*. In the Middle Caquetá region only two swiddens located in non-ADE uplands were opened through *minga,* the other 17 were opened and harvested exclusively with family labor. According to indigenous farmers of the Middle Caquetá region working in *minga* was more common in the past than it is today.

Estimations indicated that opening a 1-ha plot would take one person 13 work days when there is no forest to log and 100 work days for forested sites (Table 2.4). When sites were opened through *minga* the clearing, logging and chopping were finished in a single day. Otherwise, these activities took several consecutive days depending on the family workforce in terms of number and work capacity of family members. Time spent on manioc harvesting could only be assessed in the low floodplains of San Martín de Amacayacu. On average, harvesting a 1-ha plot took 194 person hours (35 person days), because of the flood pressure low floodplains were always harvested through *minga*, harvesting a 1-ha plot in no more than 2 days. At community level, the number of persons for *mingas* and the number of days for harvesting all manioc on low floodplain plots was limited, therefore only few plots were established in low floodplains by prestigious farmers who had the capacity to organize *mingas* and knew the techniques to bury the manioc roots properly.

In *restingas*, the flood water will take more time to reach the fields even in years with high floods, offering farmers more days for manioc harvesting than in low floodplains. In years with regular floods plots would not flood at all and farmers would have months to harvest fields. However, as in *restingas* weed pressure was high and weed control was difficult, farmers did not leave manioc to grow as long as in uplands.

2.4. Discussion

The interviewed indigenous farmers used both fertile and low-fertile soils for agriculture. Sites opened by farmers from the Middle Caquetá region on ADE and non-ADE uplands had similar physicochemical characteristics (Table 2.2), though ADE clearly showed higher available P and higher P/K and Ca/Mg ratios – which is typical of anthropogenic soils. ADE have been reported to contain on average more phosphorus, nitrogen, calcium, potassium, and magnesium, compared with background soils (Hiraoka *et al.*, 2003; Glaser and Birk, 2012). Although peripheral areas of ADE use to be less fertile than the center of ADE (Fraser, et al. 2011b), our results indicate that in the Middle Caquetá region ADE were not consistently more fertile than background soils except for a higher phosphorus availability on ADE. This might explain why the area of swiddens, the age of fallows, the swidden management and the time spent controlling weeds were all similar between ADE and non-ADE uplands; this contrasts with reports from the Central Amazon where striking differences between ADE and non-ADE uplands were reported (Fraser and Clement, 2008).

The age of the vegetation on selected sites was not significantly different between ADE and non-ADE uplands. All fields were opened in very old secondary forests (on average older than 40 years) and mature forests older than 100 years. The old age of forests opened for swiddens can be related to the low population densities which results in low land-pressure. Due to this long recovery period of sites previously used for agriculture, secondary forests can accumulate enough above and belowground biomass to provide crops with the nutrients they require in a new swidden. Swiddens opened in old secondary forests required similar time for weeding to swiddens opened in mature forest; this contrasts with reports about swiddens in younger secondary forests that required more time for weeding than swiddens in mature forests (Awanyo, 2008; De Rouw *et al.*, 2014). These secondary forests, however, were clearly much younger than the ones used by farmers interviewed in this research.

Manioc was the main crop cultivated in all soil types, and the prime reason indicated by indigenous farmers to practice agriculture. According to indigenous farmers, there was no specific match between manioc landraces and land types or soils, and all manioc landraces grew well on all land types and soils. In fact, all landraces were moved between land and soils types - with an important flux between floodplains and uplands and *vice-versa* (Figure 2.2). This contrasts with observations made for C*aboclo* agriculture in which specific landraces are cultivated on specific soil types (Fraser and Clement, 2008; Fraser *et al.*, 2012). Interestingly, farmers indicated that manioc root production is important in floodplains but, in addition, manioc plants also grow taller there thus producing longer stems in a short time. This claim could be proven right only for some manioc landraces that were significantly taller when growing in floodplains compared to uplands and therefore an important source of manioc propagules for upland swiddens. However, a more systematic collection of information on indigenous fields with this purpose in mind is required to more rigorously verify this statement made by farmers.

Floodplain cultivation seems to be an important component of indigenous agriculture as floodplains were cultivated in the two locations (also in those where ADE are present), but floodplains were used differently in different communities. Farmers from San Martín de Amacayacu used low floodplains and practiced a flood-recession system. Low floodplain cultivation requires less time opening sites, burning and controlling weeds when compared to *restinga* cultivation. But *mingas* are needed to secure harvests on time. The flood-recession system practiced by Tikuna farmers from San Martín de Amacayacu is a traditional practice among Tikuna, and is accompanied by technologies of manioc burying to preserve high volumes of harvested roots (Acosta and Mazorra, 2004). The exclusive cultivation of watermelon in low floodplains and an intensification of sweet manioc, banana and maize in *restingas* observed by Shorr (2000) in a Tikuna community might be an adaptation of the traditional Tikuna flood-recession agriculture to markets. Flood-recession systems for manioc production are apparently not so rare in the Amazon region and also occur among *Caboclo* communities as fallows were 1.6 ± 4 years on average (Fraser *et al.*, 2012), but not recognized as a continuous agriculture system by these authors.

Farmers from the Middle Caquetá region in turn used *restingas* and practiced a swidden system there. Cultivation of *restingas* entailed more labor to control weeds; this might explain the infrequent use of floodplains observed in this study and reported previously in the area (Eden and Andrade, 1987). Apparently, agriculture on *restingas* seems not to be a free choice, but a consequence of changes in the organization of labor within the communities. Since *mingas* are reciprocal support institutions (Lyle and Smith, 2014), they require a continuity in reciprocity relations for their survival (Guillet, 1980). But reciprocity relations subside whenever those partaking in it are not available anymore. In the Middle Caquetá region wage labor has become much more common since gold mining and other economic activities exists in the region. Those working in alluvial gold mining (most of whom are indigenous people) are either employee under a verbal agreement or have to surrender a minimum amount of gold per week in order to be able to keep their jobs and can therefore no longer participate in *mingas*. Importantly, young people (who have the best work capacity) prefer to receive cash for their involvement in mining, than food or drinks for participating in *mingas*. This seems to have forced farmers to adjust their agriculture to fit the available work force within the family and cultivate *restingas* instead of low floodplains. Similar changes in the organization of work have been reported by Peroni and Hanazaki (2002) in communities where other economic activities introduce wage labor as replacement of collective work. The benefits however that a salary could provide indigenous families (e.g. compensating for deficiencies in agricultural production by enabling them to buy food on the market) do not materialize as men largely spend the money on alcoholic drinks (Chapter 2 of this thesis, Peña-Venegas *et al.*, 2014a). Family staple support therefore continues to depend mainly on women, through traditional agriculture on uplands and *restingas*, and on forest and river resources.

2.5. Conclusions

Both Amazonian fertile and low-fertile soils are cultivated by indigenous farmers. In contrast to what indicates literature, ADE and non-ADE from the Middle Caquetá region are very similar in their physicochemical composition. Due to this similarity, swidden agriculture on both soils is also similar in opposition to literature on systems elsewhere in the Amazon basin that reports important differences in the agriculture practiced on natural and anthropogenic Amazonian soils. Similarities of natural and anthropogenic soils might also explain why there is no difference in the portfolio of manioc landraces grown on the different soil types as reported for Central Amazonia. Therefore, the agriculture practiced by indigenous farmers from the Colombia Amazon on ADE differed from previous reports in the literature. Additionally, selection and use of floodplains is not related to the soil conditions or market pressures for agricultural products but responds rather to cultural traditions and labor availability for *mingas*.

Acknowledgements

To Camilo Torres from the Universidad Jorge Tadeo Lozano (Colombia), James Fraser from Lancaster Environment Centre, Lancaster University (United Kingdom), Ignacio Piñeros, Fissi Andoke, Aurelio Suárez, José and Elías Moreno, and Adriano Paky, leaders of the indigenous communities for their help and support during field work. We wish to express our gratitude to the indigenous women, owners of the swiddens, for their hard work and active participation in the research.

Chapter 3

Classification and use of natural and anthropogenic soils by indigenous communities of the Upper Amazon region of Colombia

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Accepted for publication in Human Ecology

Abstract

Outsiders often oversimplify use of Amazon soils by considering abundantly available natural soils poorly suitable for agriculture and sporadic anthropogenic soils agriculturally productive. Local perceptions about potentials and limitations of available soils might be different but information on these perceptions is scarce. We examined how inhabitants of the Colombian Amazon classify and use natural and anthropogenic soils. The study was framed in ethnopedology: local classifications, preferences, rankings, and uses of soils were recorded through interviews and field observations in four indigenous communities of the Middle Caquetá region. Indigenous groups recognized nine soils varying in suitability for agriculture. They identified anthropogenic soils as most suitable for agriculture but only one group used it predominantly for their swiddens. As indigenous groups did not perceive soil nutrient status as limiting, they did not base site selection on soil fertility or on the interplay between soil quality and performance of manioc genetic resources.

Key words: Soil, Amazonian Dark Earths, manioc, indigenous communities.

3.1. Introduction

About 70% of the Amazon basin is mainly composed of very acid, highly weathered natural soils with poor availability of the most important plant nutrients (Richter and Babbar, 1991). There are, however, small patches of anthropogenic soils known as Amazonian Dark Earths (ADE) with completely different characteristics: ADE are usually less acid with better cation exchange capacity and base saturation than natural soils (Glaser *et al.*, 2001). ADE also contain more nitrogen, calcium, available phosphorus (Lima *et al.*, 2002), and organic matter; the higher organic matter content results in better moisture-holding capacity and lower rates of nutrient leaching than in natural soils (Glaser and Birk, 2012).

Several archaeologists alleged that the poor fertility of Amazonian soils was an environmental limitation to socio-cultural development in the region (Roosevelt, 1999; Meggers, 2003; McMichael *et al.*, 2012). In contrast, other archaeologists posited that about 2000 year ago, Amazonian societies coped with this apparent environmental limitation when ADE emerged; these soils permitted them to increase food production and to develop complex societies (Heckenberger *et al.*, 1999; Denevan, 2003; Heckenberger *et al.*, 2008).

Soil is an important resource directly related to sustainability, especially in societies that largely depend on subsistence agriculture for their food security, such as the indigenous groups in Amazonia. Understanding how indigenous groups perceive, distinguish, classify and use soils would help us to understand from the local perspective the potentials and limitations of soils for community development. The perception of Amazonian soils might have been oversimplified and therefore the potentials and limitations of Amazonian soils might have been wrongly interpreted. Local perceptions of Amazonian soils might be different and even more complex than expected (Balée, 2003; Barrera-Bassols *et al.*, 2006), but information about how indigenous people perceive natural and anthropogenic soils is limited.

Earlier reports about how indigenous people in Amazonia identify and classify soils have merely described indigenous soil classes (Wilshusen and Stone, 1990; WinklerPrins and Barrera-Basols, 2004; Sánchez *et al.*, 2007) but not the soil uses or people's preferences. Most recent studies on Amazonian soils focused on how indigenous and *Caboclo* (with Amerind-Euro or Amerind-Euro-Afro heritage) people recognize and describe ADE, not taking into account surrounding natural soils or merely making brief references to them (German, 2004; Schmidt and Heckenberger, 2009; Fraser *et al.*, 2012) .

In the Colombian Amazon region, ADE have been reported along the Caquetá River (Herrera *et al.*, 1992; Mora, 2003), along some small tributaries of the Amazon River (Morcote-Ríos and Sicard, 2012) and along the Putumayo River (J.A. Echeverri, unpublished data). Most of the area of the Colombian Amazon basin is inhabited by indigenous groups which have access to both natural soils and ADE. For the Middle Caquetá region where most studies on ADE have been conducted, reports show that indigenous people recognize ADE as the soils most suitable for agriculture (Galán, 2003; Andoque and Castro, 2012). Studies on native production systems, however, reported that indigenous people use uplands on Oxisols and alluvial soils (floodplains) but did not report the use of ADE (Hammen, 1984; Eden and Andrade, 1987; Calon and Kuiper, 1993; Verkleij and Nederveen, 1998). Reported uses of ADE in the Brazilian Amazon basin indicated that wherever human settlements were located near ADE, people used ADE for subsistence or market-oriented production (Hiraoka *et al.*, 2003; Fraser *et al.*, 2011a). There are no reasons to think that indigenous people from the Middle Caquetá region might be the exception.

The research question, therefore, is: How do indigenous people from the Middle Caquetá region of Colombia classify and use natural and anthropogenic soils? To answer this question, semi-structured interviews with open-ended questions, participatory observations and field observations were undertaken with four ethnic groups that inhabit the Middle Caquetá region of Colombia. An ethno-pedology approach (Wilshusen and Stone, 1990; WinklerPrins and Barrera-Basols, 2004) was used to assess, understand, and interpret the way indigenous people classify and use soils based on their own understanding and preferences.

3.2. Material and methods

3.2.1. Study area

The research was conducted in the Middle Caquetá region, on the border between the Colombian states of Amazonas and Caquetá. The area is located between 00°22´14.9” S and 00°55´11”S and between 72°06´36.3” W and 71°26’18.3” W (Figure 3.1). This region is formed by the intersection of sedimentary plains of Tertiary origin (dissected terraces and hills), with rocky outcrops of Paleozoic origin running to the north creating elevated plateaus, and crossed by the alluvial planes of the Caquetá River and its tributaries. Elevation ranges between 200 and 300 m, with slopes between 7 to 25%, and average annual rainfall is 3,000 mm (Duivenvoorden and Lips, 1995), December, January, and February being the driest months of the year with 150 mm of rainfall per month on average.

At the two sides of the river there are two small semi-urban municipalities: Araracuara at the northern border of the Caquetá River with a population of 1,637 inhabitants (60% of them indigenous people), and Puerto Santander at the southern border of the Caquetá River with a population of 2,373 inhabitants (67% of them indigenous people) (López, 2009). The two municipalities have basic infrastructure for health care, education and commerce. In addition, Araracuara has a basic airport infrastructure where weekly flights constitute the main connection between the region and the rest of Colombia. With the exception of these two municipalities, the study area was situated in indigenous *resguardos* (legally recognized indigenous territories). The field work was done in four indigenous communities: Aduche, Guacamayo, Peña Roja, and Villazul (Figure 3.1).

The communities of Aduche and Guacamayo share the Aduche *resguardo* with an area of 62,178 ha, located at the two river sides of the Caquetá River excluding Puerto Santander and Araracuara municipalities. The community of Aduche is located mainly on transitional soils between the coluvio-alluvial valleys of Caquetá and Aduche Rivers and the denudation surfaces. These soils are found in plane, well-drained areas with slopes of 1 to 7%, in which recently coluvio-alluvial sediments were deposited (IGAC, 1979). The community of Guacamayo was founded in 1967 and it is located at the back side of Araracuara. The landscape is rich in rocky formations from sedimentary origin, some of them with petroglyphs. Soils are superficial and limited by the bedrock. The presence of quartz gravy developed soils with sandy textures and clayey soils in deeper strata (IGAC, 1979). In addition, Caquetá´s River sides provide Aduche and Guacamayo with extensive areas of floodplains.

The communities of Peña Roja and Villazul share the Nonuya *resguardo* with an area of 59,840 ha, which was created by the communities after their arrival in the Middle Caquetá region. The communities of Peña Roja and Villazul are located on elevated terraces of the Tertiary plateau, facing the Caquetá River. Both have access to islands and extensive areas of floodplains from the Caquetá River. The community of Villazul was founded in 1956 and is located about 50 km from Araracuara down river. Peña Roja is the youngest community. It was founded in 1990 when Nonuya people living in Villazul decided to establish a Nonuya community to rescue their tradition (Echeverri and Landaburu, 1995).

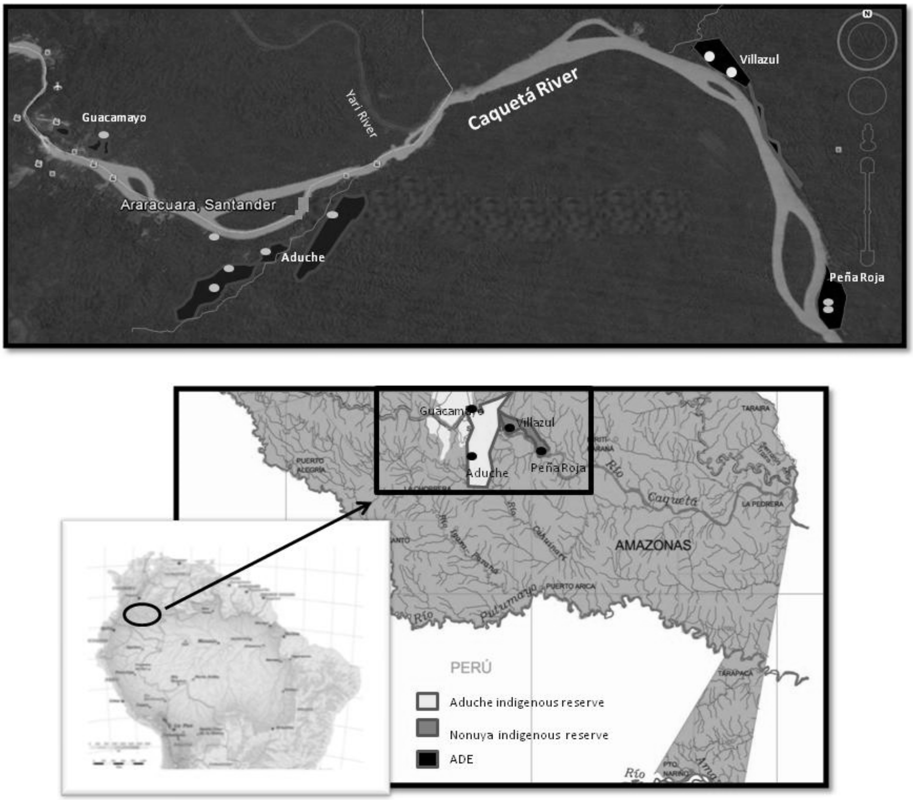

Figure 3.1. Map of the study area including the location of Aduche (the big one) and Nonuya (the small one) *resguardos*, indigenous communities, anthropogenic soils (areas in black) and malokas of communities (clear dots). Illustration is based on the map of the Amazon basin elaborated by the Amazon Cooperation Treaty Organization-ACTO (2008), the hydrographic map of the Colombian Amazon region was elaborated by the Instituto Amazónico de Investigaciones Científicas Sinchi (2002) and the image of the study area taken from Google Earth (2014).

3.2.2. Population

Indigenous communities of Aduche, Guacamayo, Peña Roja, and Villazul are inhabited by Andoke, Uitoto, Nonuya, and Muinane ethnic groups with a common origin. They denominate themselves as *Gente de Centro* (People of the Centre) in reference to their interfluvial origin between the Caquetá and Putumayo Rivers. The study area corresponded traditionally to the Andoke´s territory and has been occupied by them since before the 18th century (Franco, 2002), with an occasional migration forced by the rubber boom between the

1900s and 1930s. The other three ethnic groups were displaced from their original territories by the rubber boom and arrived in the Middle Caquetá region around the 1950s.

Indigenous settlements along the Middle Caquetá region are composed of individual family houses and one or more malokas[1]. The community of Aduche is inhabited by 128 persons belonging to 27 Andoke families, living in small habitational sub-nuclei around six malokas (one for each remaining Andoke clan). The community of Guacamayo is inhabited by 153 persons belonging to 34 families, living in houses distributed across Araracuara. The single maloka that exists is managed by a Uitoto man, son of one of the founders of the community. The community of Peña Roja is inhabited by 71 persons belonging to 15 families living in houses distributed along the banks of the Caquetá River. There are two malokas, each one managed by one of the sons of the community founder. The community of Villazul is inhabited by 77 persons belonging to 17 Muinane families organized in a unique small habitational nucleus with two malokas managed by the sons of the founder of the community.

Populations of these ethnic groups were strongly diminished by the rubber boom at the beginning of the 19th century. Estimations of their populations before the rubber boom were about 10,000 Andoke, 15,000 Uitoto, 1,000 Nonuya, and 2,000 Muinane inhabitants, according to the records taken by Thomas Whiffen during his journey in the region between 1908 and 1909 (Andrade, 1986). After the rubber boom, their populations decreased to about 30 Andoke, 300 Uitoto, 4 Nonuya, and 10 Muinane inhabitants, according to estimations made by members of the communities. In the Nonuya and Muinane ethnic groups where only few men survived, ethnic groups broke the tradition to only marry between clans of their own ethnic group and made new agreements to marry women of other ethnic groups (Orlando Paky, personal communication). This allowed them to increase the number of inhabitants in their ethnic groups and perpetuate their cultures. Although these communities became more multiethnic for outside observers, communities followed men´s tradition and recognized themselves as mono-ethnic communities.

For this research, each community was asked to suggest farmer families who knew well their territory, knew most about soils and were active farmers. Nine families from Aduche, ten from Guacamayo, six from Peña Roja, and eight from Villazul (33%, 29%, 40% and 47% of community´s total population respectively) were selected, conserving the representativeness of each ethnic group in the sample.

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[1] Communal indigenous houses with round shape made of wood and with a roof of palm leaves where traditional leaders live and teach the culture to other community members.

3.2.3. Permissions

This project was part of the free prior informed consent agreement between the Instituto Amazónico de Investigaciones Científicas Sinchi and the communities associated to the indigenous organization Consejo Regional Indígena del Medio Amazonas-CRIMA to work together on traditional food production as part of the process developed by the Sinchi Institute to build up the institutional politics with indigenous communities (Acosta and Mendoza, 2006). Soil sampling was done by the Sinchi Institute in the frame of the new legislation for research institutes associated to the Ministry of Environmental Issues of Colombia (Decreto 1376 of 2013), in which the Sinchi Institute does not need permission for genetic resources assessment when the material collected is only for research without a commercial interest.

3.2.4. Field work

From September 2011 to September 2013, communities were visited eight times to collect information, discuss preliminary results and make field observations in the swiddens. Visits to the study area were for 1 or 2 weeks, working with each community between 2 to 4 days during the day and the night, for a total of 90 days. Because in indigenous communities men and women have different roles and manage different but complementary information, during field work members of the research team participated and assumed the corresponding gender role to access male and female information. Interviews and field work were planned together with local people according to the progress of the research. Participatory observations occurred during field work and during daily community activities in the course of our visits.

3.2.5. Natural and anthropogenic soils in the study area

As a starting point for the research, an initial discussion between communities and the research team took place about what indigenous people understand by soil. After this discussion, communities elaborated maps of their territories localizing the soils they distinguished. They named soils in their native language, in Spanish (their second language) or in both. In most cases, native names corresponded to words that define soil texture and/or color, but in other cases soil names were words with no direct correspondence in the Spanish language. In such cases, linguistic interpretation or translation of names was included. Uitoto and Nonuya translations could be made by Juan Alvaro Echeverri, co-author of this paper who speaks Uitoto and has been working in the study area for many years. Expert academic linguists for Muinane and Andoke languages were not found. Therefore native Muinane and Andoke persons fluent in both their language and in Spanish helped. Orlando Paky, health promoter of the area who was educated by the Instituto Linguístico de Verano and participated in the translation of the Holy Bible into Muinane helped with the interpretation and translation of Muinane words. Fissi, the leader of the Andoke ethnic group who is expert on the Andoke language and culture helped with the interpretation and translation of Andoke words.

Based on the maps produced by the communities, field trips with farmer families were planned to visit and describe each soil. In the field, an Edelman auger was used to collect a 90-cm deep core sample of the soil profile. GPS coordinates were taken where soil samples were collected and a participatory description of soils was made. Soil description included the profile observation and horizons description by features observable in the field such as texture and color (using a Munsell soil color chart). Information about the soil's recent use history, its suitability for agriculture, and crops, trees or palms that might grow well in each soil was also collected.

About 500 g of A horizon was collected from each soil for physicochemical analyses. At the end a total of 30 soil samples were obtained for physicochemical analyses that corresponded to a unique soil sample of a soil type or duplicate samples of the same soil type collected in different communities (Table 3.1). Soil samples were analyzed in the National Soil Laboratory of the Instituto Geográfico Agustín Codazzi - IGAC in Bogotá, Colombia. Physicochemical analyses included: texture, pH (1:1 in water), Al saturation (exchangeable Al with KCl), organic carbon (Walkley – Black), cation exchange capacity (with normal and neutral ammonium acetate), minor elements (Ca, Mg, K, Na) by DTPA, percentage of total bases, base saturation (with normal and neutral ammonium acetate) and available phosphorus (Bray II).

After the complete soil inventory was finished in each community, each farmer ranked soils from very good (with the number 1) to very poor (with the number 5) according his or her perception of the suitability of the soil to establish swiddens. After the evaluation was finished in all communities, the 30 evaluations were grouped for a final ranking of soils. The final ranking was discussed with farmers to confirm that the soil ranking represented the view

Table 3.1. Classification of Amazonian soils by indigenous communities of the Middle Caquetá region, soil ranking for swidden suitability and indigenous perception of soil productivity.

LANGUAGE	SOIL TYPES									
	Soils unsuitable for cultivation	Soils suitable for cultivation								
English	Clays for ceramics; Rocks and white clays to draw; *Mauritia flexuosa* patches; soils of stone to make fire; soils for swidden of the sun	Red clay Oxisols with coarse ferric stones	Red clay Oxisols	Yellow clay Oxisols	White clay Oxisols	Oxisols with a top layer of more than 20cm of litter	White sandy soils	Sandy Ultisols with a top layer with more than 20 cm of fine roots	Alluvial Entisols	Anthrosols; Amazonian Dark earths (ADE); Black Earth or Black Sand
Muinane	No native names recorded	Not found in their territory[b]		T+fatyije jinije		Tataga junije	Nógañu junije	Not found in their territory	Without a local name	Nógañu junije
Uitoto	Nogonie; ziz+nie; Za+core; Kaiyanɨe; Jetekore	Without a local name[a]		Ed+ké		++kan+e	Koniy+ño	Tapire	Todaire/ Jirueñŧe	Ji+k+no
Nonuya	No native names recorded	Not found in their territory	Doxegi nokea	Boxarro nokea	Joctegi nokea	Jinoouŧ nokea	Nichoɨ nokea	Not found in their territory	Jibubui nokea	Jitɨrɨnichoɨ nokea
Andoke	No native names recorded	Fxedeθfosí	Pefíí	Poθmaí	Doθmaí	Without a local name	Po´sxafθsí	Sañeifosí	θnpoafosí	Ñesxaθ

Soil ranking for swidden suitability	Do not apply	5	5	3	5	4	4	5	2	1
Indigenous perception of soil productivity[c]	Those are not suitable for cultivation. Some are used for other activities and other ones must be conserved in their natural stage.	It is used only once for a swidden. Thereafter, it is only useful to crop fruit trees.	It is a bad soil for agriculture. It is used only when it is well burnt.	At the beginning the soil is good for swiddens, but with the time soil becomes too hard to cultivate it.	It is not used for agriculture. The soil is very poor in nutrients.	It is not often used because crops including manioc do not produce well.	Manioc production is regular. It is not good for plantain and corn and crops only produce making local burnings.	It is not commonly used. It is only used to crop pineapple and ucuye (a traditional fruit tree)	It is a good soil. Good to crop manioc, plantain, corn, red pepper and peanut.	It is the best soil for agriculture. Only plantain and corn not always grow well here.

[a] The soil was not observed during the field trips for soil description in the territory of the community;

[b] Indigenous people recognized and described the soil but they did not recall a native name for it;

[c] Indigenous perception of each soil productivity was based on the answers given by the farmers that distinguished each one of the soils listed.

of the majority.

Field trips around communities were also undertaken to localize ADE and to estimate the surface area of ADE. During field trips, soils were checked superficially for color and presence of anthropogenic materials. Information about the type of vegetation (natural or cultivated species), its age (mature forest, secondary forest, young fallow, swidden in different stages or grassland), and the area of each patch of ADE was recorded. Areas of ADE were estimated *in situ* with a GPS. The correct area estimation of ADE was difficult because they were discontinuous and had irregular shapes. To improve estimations of ADE areas, GPS information was compared with maps indigenous people made of their territories, maps of Indigenous Reserves provided by the Instituto Colombiano de Desarrollo Rural-INCODER, and graphs of local ADE published by Herrera *et al.* (1992) and Andrade (1983). The result is presented in Figure 3.1.

3.2.6. Indigenous narratives about origin of soils and their ancient use

Most of the information about origin and ancient uses of soils and myths referring to these aspects was collected from traditional leaders at night in the *mambeadero*[2]. Discussions were always joined by *mambe* (coca powder) and *ambil* (tobacco paste) as the essential elements for dialogue. Pre-structured trigger questions were prepared but the research team always adopted a flexible approach about the order in which questions were asked or the order in which topics were addressed to let the traditional leaders feel comfortable answering. Because of that, not all the *mambeadero* sessions provided relevant information for the research and more *mambeadero* sessions were required than originally expected to obtain the reported information.

3.2.7. Swidden location, estimations of soil productivity and indigenous perceptions of soil productivity

Based on the soil maps elaborated in each community, farmers indicated the number of swiddens they had, where they were located and on which type of soil. Information for 2011

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[2] The space in the maloka for knowledge exchange

and 2013 was recorded.

A preliminary research on the swidden production system in the study area was done to understand the particularities of it. The information collected helped to identify variables used to estimate soil productivity. Three variables were used to estimate soil productivity in the three main groups of soils indigenous farmers ranked: fallow duration, swidden area, and time between planting and harvesting manioc (*Manihot esculenta* Crantz). Variables were evaluated in 20 swiddens (5 from Peña Roja, 8 from Guacamayo, 5 from Aduche and 2 from Villazul) from which 9 were located on Oxisols and Ultisols, 4 on Alluvial Entisols, and 7 on ADE Anthrosols.

Fallow period starts when swiddens are abandoned after a cropping period when labor effort is no longer compensated by production due to the increased presence of weeds and soil nutrients depletion. The fallow duration reflects the removal of nutrients from soil during the cropping period and the time required to restore nutrient stocks to a minimum to allow production of a new crop. In soils with limited nutrients it is expected that long periods are needed to restore them without human intervention. In more fertile soils, on the other hand, nutrient depletion is less and fallows might be shorter. Fallow duration was estimated in years based on local farmer´s knowledge about when the place was used before, for how long and how many years the soil rested before a new swidden was established. In cases people indicated the patch was a primary forest never logged before, it was assumed the area had a fallow period of at least 100 years.

A relationship between swidden size and soil fertility is expected. Larger fields will be needed on less fertile soils with lower productivity than more fertile soils. The swidden area (in square meters) was estimated in the field with a GPS.

A better plant nutrition is reflected by a faster plant growth. Manioc as the main crop planted in swiddens is a good indicator to evaluate the relation between plant growth and soil productivity. In manioc, a better plant nutrition results in a more active nutrient translocation to roots and therefore in an early root bulking (Alves, 2002). When root bulking is early farmers can harvest manioc early, thus shortening the crop cycle of manioc. A short cycle could be advantageous for certain product preparations that are produced in large quantities. The months between manioc planting and harvesting was estimated from 20 swiddens permanently monitored since manioc was planted until when it was ready for harvesting according to indigenous criteria. Because swidden harvesting on floodplains is biased by flood, swiddens located at *restingas* (Alluvial Entisols on high floodplains that are only reached by high floods) were monitored, hoping farmers could make the manioc harvesting decision based on manioc root bulking and not on the flooding regime. Indigenous farmers cultivated around 12 different manioc landraces per swidden. Those manioc landraces were cultivated indistinctively on Oxisols, Alluvial Entisols or ADE Anthrosols. Consequently, the moment of manioc harvesting was determined by a specific manioc landrace or by multiple manioc landraces farmers considered ready for harvesting.

Field trips to swiddens were also used to ask and observe swidden productivity according to indigenous perceptions. Indigenous perceptions included expectations in relation to swidden production as well as problems faced in the swidden in relation to productivity.

3.2.8. Manioc inventories

Inventories of manioc landraces managed by each community were done during field trips to swiddens. Portfolios of landraces of communities were compared in relation with the type of soil on which swiddens were located. A manioc landrace was defined as a unique combination of morphological characteristics clearly recognized by local people and identified by a local name. Landraces were classified by indigenous people into three main groups: sweet maniocs (those with non-toxic roots that can be consumed after being cooked without a previous treatment of detoxification), white bitter maniocs also known as maniocs "to grate" (toxic landraces, white to very pale yellowish colored roots, used to obtain starch after having grated them) and yellow bitter maniocs (toxic maniocs with yellow pulp colored root of which their complete biomass is used in different preparations). In addition to field trips, during research team visits to communities, researchers shared meals or were involved in the preparation of those, being important opportunities to observe culinary traditions.

3.2.9. Statistical analysis

A one-way ANOVA Kruskal-Wallis test for non-parametric data was done for the twenty registers obtained for fallow duration, swidden area and number of months between manioc planting and harvesting in the three groups of soils indigenous farmers ranked. A Chi-square test was done to assess differences in manioc inventories among ethnic groups. Differences were considered significant at $p \leq 0.05$. All statistical analyses were performed with the analytical software Statistix 9.0.

3.3. Results

3.3.1. Indigenous classification of soils

Indigenous people of the Middle Caquetá region have a complex view on the world. They understand that living and non-living elements are composed of physical and spiritual components. All elements, including humans themselves, are equally important parts of a unique unit, the world. Because all components are equally important, they cannot be isolated from each other. In this way, the soil does not exist *per se*. It is part of a “place” that includes also other elements such as vegetation, water sources, landscape and animals that live there in an integral way.

Although different elements exist and interact in the world, each element has particular characteristics that confer to the place attributes to be used for specific purposes. Soils of places are classified by indigenous people into two main groups: soils suitable for cultivation and soils not suitable for cultivation (Table 3.1). Soils not suitable for cultivation commonly show cultural (taboos), physical or chemical constraints for agriculture. In any case, they have important roles in the maintenance of the environmental equilibrium. Examples of these soils according to Uitoto people are the *Kaiyan ɨe* or “soils of stone to make fire”; the *Jetekore* or swiddens of the sun in which wild animals find fruits to eat; and the *Za+core* which are soils permanently swamped and covered by broad patches of *Mauritia flexuosa* palm whose fruits are an important source of food (mainly proteins and oil) for wild animals.

Soils suitable for cultivation have two distinct layers (horizons) indigenous people of the Middle Caquetá region recognized: one formed by the litter layer and the first layer of dark earth (A horizon for soil scientists) that indigenous people denominate the *workable soil*. The second layer is formed by the deeper soil and the bedrock (B horizon, deeper mineral horizons and bedrock for soil scientists) indigenous people denominate the *dead soil*.

In the research area, indigenous people recognized nine different soils suitable for cultivation, although the quality of some of them restricts their use to sporadic occasions (Table 3.1). Indigenous soil classifications were based on soil texture, soil color and the presence of other easily observable features in the field. Each ethnic group classified soils differently. Muinane people had the simplest soil classification mainly based on texture; they recognized two main groups of soils: clayey and sandy soils. Uitoto people also classified clayey soils in one group, but recognized differences among sandy soils grouping them separately and using specific words to name each one of them. Nonuya people based their soil classification on both texture and color. Nonuya native names referred to texture and color characteristics followed by the word *nokea* which means soil (*tierra* as they translate it into Spanish). Nonuya people distinguished differences between clayey soils but grouped all soils with sandy texture into a unique group. Andoke people particularly recognized each soil individually. The Andoke language does not use a specific word for "soil" and named each soil using a specific word.

All indigenous groups recognized ADE. They called it *Tierra negra* or *Arena negra* in Spanish (black earth or black sand in English), but they also had native names for it. For the Nonuya and Muinane ethnic groups ADE were classified as one of the soils into the group of sandy soils using a common word to denominate sandy soils in general (*Nógañu jiin ɨje* as in Muinane language) or adding a word to highlight the dark color of ADE (as in Nonuya language in which they added the word black, *jitɨrɨ*, to the words *nichoɨ nokea* that mean sandy soil).

Soil native names provide information beyond merely its texture or color. The Uitoto word *++kan+* used to denominate a soil with a thick layer of litter also means fish odor according to the *n+pode* dictionary developed by Griffiths et al. (unpublished manuscript) that might be related to the production of volatile substances during organic matter decomposition easily perceived by the amount of litter in this soil. The *Tapire* (or *Zafire*) soils as Uitoto people denominate sandy soils with a thick upper layer of fine roots indicate the particular short and thin forest that grows on these soils. More interesting meanings have the words used by Uitoto and Andoke people to denominate ADE. The Uitoto word *Jí+k+no* can be analyzed as *Jɨi-* "small", *-kɨ* both mean "fire" or "generation", and *–no* (*nɨe*) is the suffix for "place (soil)" so the name could be translated as "soil with small particles due to fire or use by former generations". Andoke people called ADE *ÑesxaΘ* that means textually black soils, but the term indicates that black color origin is burning.

3.3.2. Indigenous understanding of the origin and ancient use of soils

Indigenous people of the Middle Caquetá region agreed that natural soils were formed naturally but had a different perception of ADE origin. In local indigenous understanding

ADE have a mythical origin in which fire is an important element. The mythical Andoke tale for *ÑesxaΘ* formation talks about a fest in the sky organized by Pepái, the son of the Andoke god Nenefí, to which only the good persons who lived in The Earth at that time were invited. During the fest, people threw away bones of the cooked animals that opened springs of hot water which burnt The Earth. Bones of eaten animals and bodies of bad people in The Earth amended the soil and gave to *ÑesxaΘ* their characteristics. The Uitoto version of ADE creation also talks of a time in which the world was burnt. The evidence of that episode according to Uitoto people are the black patches *that have small parts of animals or animal forms we don`t know today*.

On the more recent history indigenous people indicate that ADE, formed in mythical times, provided good agricultural soils. Aurelio, the traditional leader of the Guacamayo community said that *Ji+k+no were the favorite soils of ancient people. So, when ancient people found those black patches of soil, they settled there*. Fissi, leader of the Andoke people, indicated that *in ancient times people pulled the woods up from the soil* (removed the litter and decaying wood lying on the soil) *to check the soil color. When they found ÑesxaΘ, they settled their communities there*. The practice of locating indigenous settlements on ADE is still maintained. Muinane, Nonuya and Uitoto ethnic groups that did not live in the Middle Caquetá region traditionally established their communities on ADE.

The Middle Caquetá region was traditionally inhabited by the *Cacambra* (a local bird species) and the *Cucarrón* (beetle in English) Andoke clans which are now extinct. Actual indigenous people, however, know who lived there and how much those soils were appreciated for food production. Muinane people indicated that *Carijonas* (an almost extinct ethnic group of the Colombian Amazon region) were the oldest inhabitants of the area while Nonuya people indicated that both *Cacambras* and *Carijonas* were the oldest inhabitants there. Aurelio, leader of Uitoto people, indicated that *ancient people selected on ADE because the production was good and those soils could be used after short fallows without problem* (without compromising crop production). Fissi pointed out that "*Andoke used to fight against Carijona people for those patches of dark soil. Carijona people looked for those places because they knew they were good for manioc cropping. During Andoke and Carijona fights for ÑesxaΘ, people were killed, their goods were destroyed, their malokas were burnt and the winner took the territory. Andokes also fought against Carijona to recuperate their territories and so on for many generations. The broken ceramics and artefacts are found where ancient malokas and houses existed and they are the remains of those wars"* (Fissi's interview, May

18th of 2012).

Andoke people believe those artifacts are not only burnt household waste but also remains of broken utilities of malokas and houses intentionally destructed. Then, places where ADE were formed were exposed to frequent small burnings and also to periodical big burnings when complete communities were destroyed. Community destruction could lead to high amounts of organic matter in the soil that with burnings might produce higher amounts of charcoal and ashes than regular burnt household waste. High amounts of charcoal and ashes might change the environmental conditions of soils for ADE formation or potentiate the initial beginnings of the ADE process formation, but this is an element for further discussion among scholars.

In summary, indigenous mythology indicates soil creation before human existence. Indigenous groups currently living in the Middle Caquetá region do not recognize themselves as the creators of ADE. Their historical memory expressed through their narratives goes to a time in which ADE already existed, the region was densely inhabited, ADE had a key role in food production, they were not able to recreate it, and they needed to fight for its use. That picture does not correspond to what we find today.

3.3.3. Today's use of natural and anthropogenic soils in the study area

Most natural soils of the study area are covered with primary and secondary forest indigenous people use for different purposes:

Fruit collection: Not all species indigenous people consume are cropped. An important number of edible plants were never domesticated or their domestication was truncated at some point in the human history (Clement, 1999) and indigenous people go regularly to forested areas to collect them.

Extraction of materials for construction: All materials used for house or boat constructions, for the elaboration of house artifacts, furniture, and tools for food processing are mainly obtained from the forest, except metal artifacts and modern tools for hunting and fishing.

Collection of medicinal plants: As is the case for some edible species, some natural medicines are wild plants. Medicines include complete wild plants or parts of them such as roots, leaves, bark or resins. Most of the medicinal plants are not cultivated or not maintained

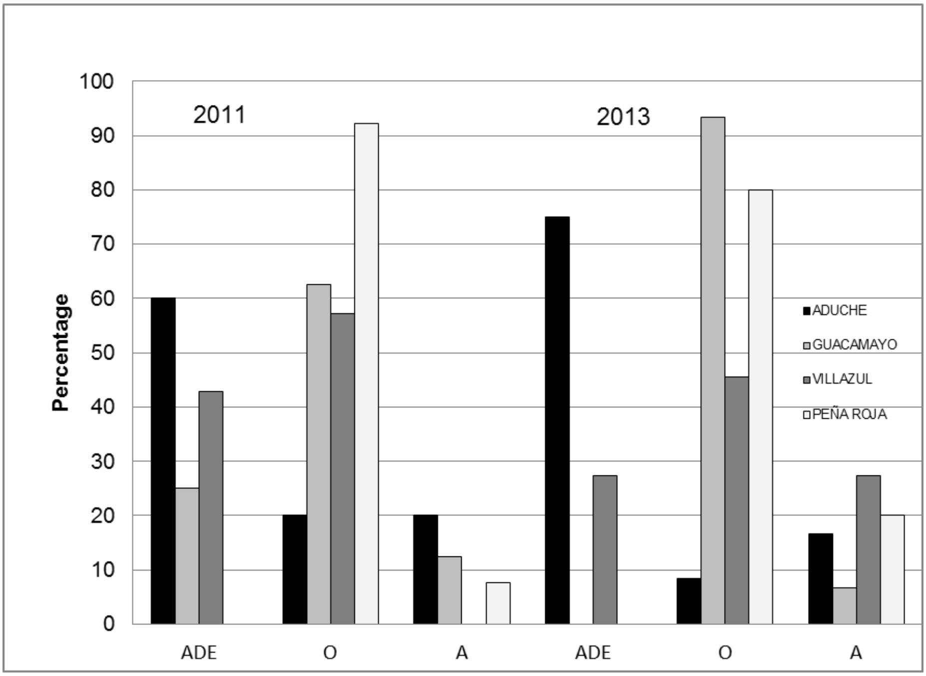

Figure 3.2. Percentage of farmers' swiddens located on Amazonian Dark Earths (ADE), Oxisols (O) or Alluvial Entisols (A) during 2011 and 2013 in the Andoke community of Aduche, the Uitoto community of Guacamayo, the Muinane community of Villazul, and the Nonuya community of Peña Roja, Middle Caquetá region of Colombia.

in anthropic environments and people depend on forested areas to obtain them.

Areas for hunting: Most of the hunting events occur in secondary forests where there are palms and fruit trees still producing. Additionally, there are specific places to hunt specific animals such as *salados* (soils with a high concentration of salts wild animals visit periodically to restock minerals) were most of the big mammals are hunted or patches of the *Mauritia flexuosa* palm where big rodents are hunted.

Swidden establishment: Between 50% and 90% of the indigenous swiddens were located in natural soils (Figure 3.2).

Common uses of ADE observed in the indigenous communities were:

Settlement: Most of the *malokas* and houses of the communities of Aduche, Peña Roja and Villazul were located on ADE (Table 3.2). Indigenous people appreciate places on ADE as they are plane landscapes with good soils with often natural streams of fresh potable water in the proximity.

Agroforestry systems: Swiddens observed in all types of soils were mainly of transitory

Table 3.2. Percentage of settlings (number of houses), agroforests, grasslands and swiddens located on Amazonian Dark Earths (ADE) in each one of the communities visited. Estimates are based on observations during field trips in 2013 and reflect a relative frequency of uses and not absolute values.

Use of ADE	Aduche	Guacamayo	Peña Roja	Villazul
Settling	93	6	60	100
Agroforest	100	10	100	100
Grassland	100	0	100	100
Swidden	75	0	0	27

crops and almost no palms or fruit trees were planted there. Most palms and fruit trees were planted around *malokas* and houses on ADE, producing agroforestry systems. Agroforests not only included native trees and palms but also exotic plants such as citrus trees, coconut palms and mangos. Farmers from Villazul indicated that "*we plant fruit trees and palms in a swidden if we want to abandon and transform it into a fruit tree garden. After that, we will not log the fruit trees anymore. We will not use that place for a swidden anymore. Those places are for hunting and for fruit collecting"* (Ana Rita Andoke's interview November 27th of 2012).

Grasslands: In the communities of Aduche, Villazul and Peña Roja some of ADE or parts of them near or in the settlements were covered by non-native grasses (Table 3.2) such as star grass (*Cynodon nlemfuensis* Vanderyst) and humidicola grass (*Brachiaria humidicola* (Rendle) Schweick). None of the communities raised cows or other domestic animals that could feed on those grasses. Periodically and especially when grasses became dry, people burnt it to stimulate its re-grow. Interviews with local people indicated that grassed patches were planted by men as they like grassed landscapes. Women however, indicated that they would prefer to use ADE for crop production but they consented men´s decisions.

Swiddens: Soil ranking for swiddens indicated that by consensus indigenous farmers considered ADE as the best soils for food production (In the case of Muinane people, sandy soils in which ADE are included were ranked in first place as very good soils) (Table 3.1). Common expressions people used to refer to ADE included "*These soils are always preferred"*; *"they are so good"; "they have a lot of nutrients"; "The best soils"; "Very good soils for manioc and fruits"; "they produce good manioc".* The soil ranked in second place was Alluvial Entisol. Other soils listed were considered as soils with limitations for agriculture but which are suitable to cultivate.

Chemical composition and soil fertility measures reported in Table 3.3 were not part of the environment conceptualization indigenous people make. They used soil color, soil texture, and vegetation as indicators of potential productivity. They understood the importance of organic matter in soil nutrient supply. From their experience they knew that a dark soil holds more nutrients. They also recognized which trees and which type and age of vegetation provided more and better organic matter that would confer to the soil a deeper and better *workable soil* for their crop production. An old vegetation, with a deep *workable soil* that produced well before would be the main criteria to select a place for a new swidden.

Every year each indigenous family opens a new swidden on uplands. Swiddens are cropped mainly with manioc which occupies about 70% of the total cropped area; other non-staple crops such as plantain (*Musa paradisiaca* L.), pepper (*Capsicum annuum* L.), pineapple (*Ananas comosus* Merr.), and corn (*Zea mays* L.); ritual species such as coca (*Erythroxylum coca* Lam.) and tobacco (*Nicotiana tabacum* L.); and some medicinal and cosmetic plants. Crops with short production cycles while manioc harvest starts a year after planting and continues for another two years until manioc finished. This means, each family had three to four swiddens on uplands in growing or harvesting stages and 18% of the families additionally had one or two swiddens on floodplains.

Because mainly ADE and Alluvial Entisols had a *workable soil* with good conditions for food production, their frequently selection for swiddens was expected. Swidden inventories made in 2011 and 2013 indicated that Uitoto, Nonuya, and Muinane farmers used predominantly Oxisols while Andoke farmers used predominantly ADE for their swiddens in the same period (Figure 3.2).

It could be assumed that because of the relative abundance of ADE in their surroundings, *Caboclos* of the Central Amazon have been more exposed and have more access to ADE, explaining why ADE are used more in the Brazilian Amazon than in other regions. Limited access to ADE was therefore explored as a reason for the results described above.

3.3.4. Accessibility to ADE use

It is known that indigenous farmers will not open swiddens farther than 5 km from their community, because of human-limited physical capacity to transport harvested products from far away. All ADE registered were less than 5 km from the communities, therefore ADE were available for swiddens. Total ADE area in the Aduche reserve was estimated to be 115 ha (86 ha in the Andoke territory and 29 ha in the Uitoto territory), and in the Nonuya reserve to be

Table 3.3. Physicochemical composition of nine Amazonian soils recognized by indigenous communities from the Middle Caquetá River region of Colombia. Texture is presented as a range and the other variables are expressed as the average and its standard deviation (SD) in parenthesis (for soils with more than one sample) according to the number of soil samples collected from each soil.

Soil name	No. Soils	Texture	pH[h]	E.A.[i]	E.A.S.[j]	% O.C.[k]	C.E.C.[l]	Ca[m]	Mg[n]	K[o]	Na[p]	T.B.[q]	% B.S.[r]	P[s]
Red clay Oxisols with coarse ferric stones	1	LCS[a]	4.0	4.0	78.0	2.0	14.0	0.4	0.3	0.3	0.1	1.0	7.0	ND[t]
Red clay Oxisols	2	LC[b] to LS[c]	3.9 (0.2)	5.0 (1.4)	89.6 (1.3)	2.0 (0.7)	13.0 (4.3)	0.2 (0.0)	0.1 (0.0)	0.2 (0.1)	0.1 (0.0)	0.6 (0.1)	4.5 (0.1)	ND
Yellow clay Oxisols	5	S[d] to SL[e]	4.0 (0.1)	5.5 (1.5)	77.3 (16.1)	3.5 (1.4)	18.5 (3.8)	0.7 (0.7)	0.0 (0.3)	0.3 (0.1)	0.0 (0.0)	1.5 (0.1)	8.3 (5.0)	18.5 (25.1)
White clay Oxisols	1	LC	4.4	5.4	89.0	2.1	12.1	0.1	0.1	0.2	0.1	0.7	5.5	15.7
Oxisols with a top layer of more than 20cm of litter	3	LCS to SL	3.8 (0.5)	4.7 (4.0)	70.0 (37.5)	4.0 (2.7)	20.0 (14.1)	1.2 (1.9)	1.2 (2.0)	0.4 (0.3)	0.1 (0.1)	2.9 (4.2)	11.1 (11.7)	2.0 (3.3)
White sandy Oxisols	6	LS to SL	3.6 (0.2)	3.8 (1.3)	82.8 (7.6)	2.3 (1.3)	12.6 (7.4)	0.2 (0.1)	0.3 (0.3)	0.2 (0.1)	0.0 (0.0)	0.8 (0.4)	6.8 (3.0)	6.0 (7.4)
Sandy Ultisols with an top layer with more than 20cm of fine roots	1	LS	3.3	7.5	93.6	10.6	39.2	0.1	0.1	0.2	0.0	0.5	1.3	ND
Alluvial Entisols	5	CL[f] to L[g]	4.4 (0.3)	3.0 (2.0)	42.1 (30.6)	2.5 (1.0)	16.4 (4.2)	3.3 (3.0)	1.4 (1.0)	0.3 (0.1)	0.1 (0.1)	5.1 (3.7)	32.8 (24.2)	4.6 (7.8)
ADE Anthrosols	5	SL to LS	3.8 (0.1)	2.5 (1.3)	60.5 (22.2)	1.7 (0.6)	9.3 (4.2)	1.1 (0.9)	0.3 (0.2)	0.2 (0.1)	0.1 (0.0)	1.7 (1.1)	17.2 (7.7)	88.6 (157.2)

Texture: [a]Loamy clayey sandy soils; [b] Loamy clayey soils; [c] Sandy loamy soils; [d] Sandy soils; [e] Sandy loamy soils; [f] Clayey loamy soils; [g] Loamy soils.

[h] pH (1:1 in water); [i] Exchangeable acidity with KCl; [j] Exchangeable acid saturation with KCl; [k] Percentage of organic carbon (Walkley – Black); [l] Cation exchange capacity using normal and neutral ammonium acetate; [m] Calcium by DTPA; [n] Magnesium by DTPA; [o] Potassium by DTPA; [p] Sodium by DTPA; [q] Total bases; [r] Percentage of base saturation using normal and neutral ammonium acetate; [s] Available phosphorus by Bray 2 in parts per million.

[t] Phosphorous availability not detected by Bray 2 (Minimum phosphorus concentration detected by the method is 0.1ppm).

70 ha (distributed in almost equal areas of 35 ha for the Nonuya and Muinane groups). Land tenure in indigenous reserves is collective and all community members have equal access to land. Then when ADE hectares were equally divided over the families of each group, each Andoke family had access to 3.18 ha; each Uitoto family to 0.85 ha; each Nonuya family to 2.33 ha; and each Muinane family to 2.05 ha. ADE access for Uitoto families could be less because some ADE were also part of the Araracuara municipality and were used by families that were not part of the community of Guacamayo. Results indicated that all ethnic groups had access to ADE, although some ethnic groups had access to more ADE land than others (Andoke farmers for example). However, ADE accessibility did not explain the results as ADE use did not correspond to the accessibility to it.

3.3.5. Estimation of soil productivity and its indigenous perception

There was a high variability in fallow duration (Figure 3.3A), swidden area (Figure 3.3B) and time between planting and harvesting manioc (Figure 3.3C), independently of the soil in which swiddens were located. Kruskal-Wallis one-way ANOVA test showed no significant differences in the duration of fallows (p= 0.34) or in swidden areas (p= 0.41) on different soils. Differences in the time between planting and harvesting manioc among soils were significant (p= 0.03). Manioc grown on Alluvial Entisols was harvested earlier than manioc grown on uplands but there were no significant differences between Oxisols and ADE, despite differences in their chemical composition. Indigenous farmers estimated swidden productivity based on manioc production. From 33 interviewed farmers, 64% were satisfied with their swidden production independently of the soil selected. Only four farmers declared being dissatisfied with swidden production. Two farmers with swiddens on ADE indicated that swiddens were not burnt properly and nutrients did not liberate properly into the soil affecting swidden production. Two other farmers with swiddens on non-ADE indicated that strong rains on soils with poor drainage capacity and groups of capybara (*Hydrochoerus hydrochaeris*) spoiled a good portion of the cultivated manioc.

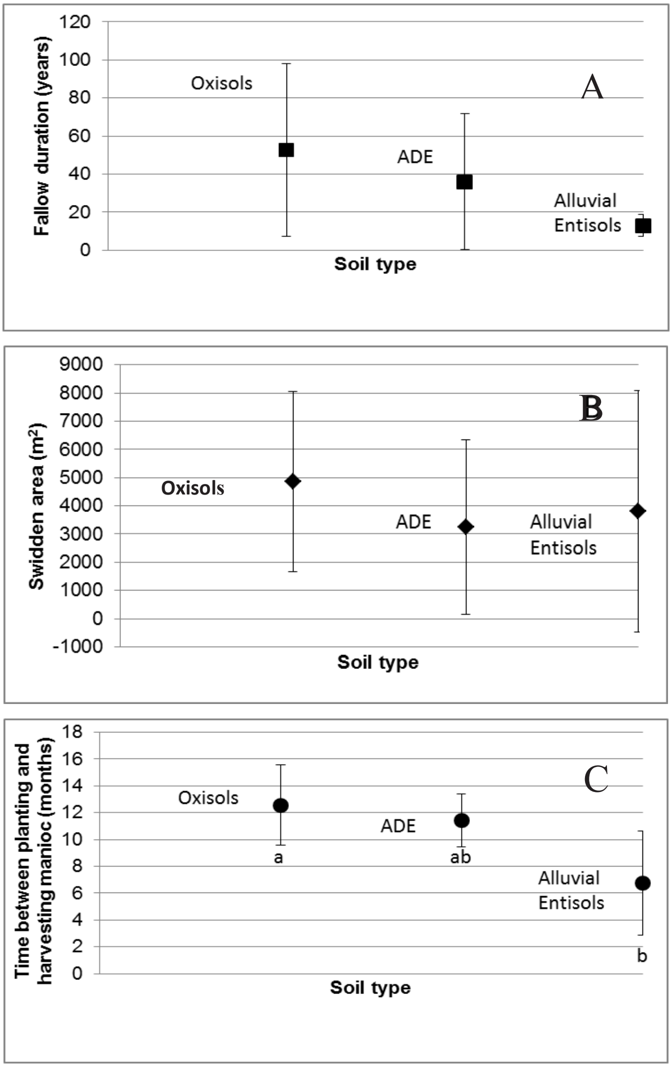

Figure 3.3. Average and standard error of fallow duration, swidden area and time between planting and harvesting manioc in swiddens on Oxisols (O), Amazonian Dark Earths (ADE) or Alluvial Entisols (A). A. Fallow duration (in years) of places where swiddens were established; B. Swidden area in square meters; C. Time between planting and harvesting manioc in months (letters under each soil correspond to test results of pair-wise comparison).

3.3.6. Cultural values associated to soil selection

Indigenous communities maintained very diverse manioc inventories of sweet, white and yellow bitter manioc landraces (Figure 3.4). When the proportion of sweet, white and yellow bitter maniocs was compared among communities, significant differences in the number of

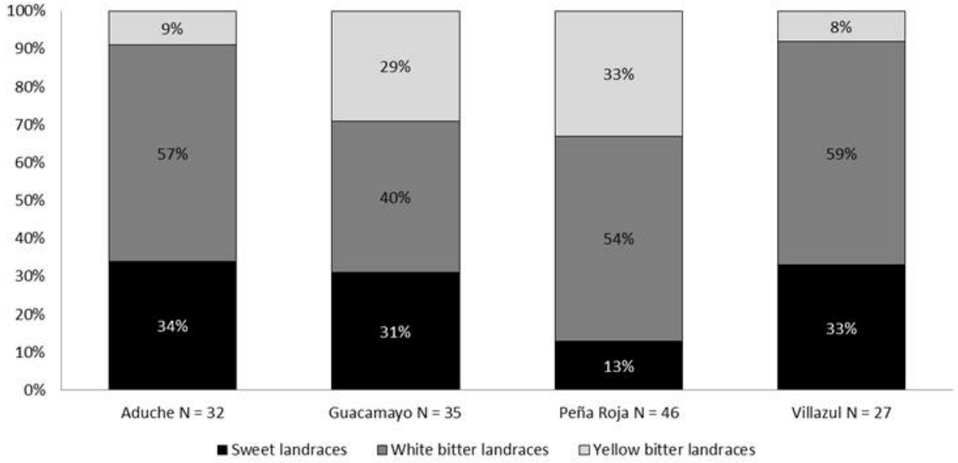

Figure 3.4. Manioc inventories (N) and percentages of sweet, white bitter, and yellow bitter landraces cultivated in the Andoke community of Aduche, the Uitoto community of Guacamayo, the Nonuya community of Peña Roja, and the Muinane community of Villazul, Middle Caquetá region of Colombia.

sweet and yellow bitter manioc existed (10.5 and 25.8 respectively compared to a Chi-square table value of 7.82). Andoke and Muinane communities cultivated the lowest numbers of yellow bitter maniocs and they were also the communities that used ADE predominately for swiddens. The Nonuya community on the other hand, cultivated the highest number of yellow bitter maniocs and was the one that did not use ADE for their swiddens, neither in 2011 nor in 2013.

Differences in manioc inventories among ethnic groups were related to their culinary preferences. Nonuya and Uitoto people traditionally consume *casabe de masa* (round flat breads made with the whole fermented yellow bitter manioc root biomass) as the main way to consume manioc. As bitter maniocs grow well on Oxisols (Eden and Andrade, 1987; Wilson and Dufour, 2006), Nonuya farmers do not require ADE for swiddens and prefer ADE for cropping agroforests with exotic species they appreciate and that cannot be grown on non-ADE. On the other hand, Andoke and Muinane people traditionally consume manioc mainly as *casabe de almidón* (round flat breads made from starch obtained from white bitter manioc roots).

3.4. Discussion

3.4.1. Composition of Amazonian soils

According to the standard soil quality indexes for Colombian soils used by the Instituto Geográfico Agustín Codazzi-IGAC (IGAC, 1979) and the soil study done in the Middle Caquetá region by Duivenvoorden and Lips (1995), soils of the research area do not have physical problems for agriculture as all of them are loamy to sandy soils. The main constraint is their high acidity which causes high levels of exchangeable aluminum toxic to plants, low Ca availability and low base saturation which results in a reduced fertility. Most of Amazonian parental materials from which soils originate are rich in kaolinite which has limited nutrient holding capacity (Ma and Eggleton, 1999). Soil organic matter therefore plays an important role in cation exchange capacity (Glaser and Birk, 2012). In environments with high temperatures and high humidity as common in the Amazon region organic matter decomposition is rapid. Nutrients liberated after organic matter decomposition are rapidly leached due to the frequent strong rains and the low nutrient-holding capacity of soils, resulting in a limited fertility of most natural upland soils of the region.

Results of this research indicated that upland soils have a pH of 4 and an exchangeable acid saturation over 70%, independently whether they were natural or anthropogenic soils. Alluvial Entisols on the contrary have an exchangeable acid saturation around 40% (Table 3.3) explained by the sediment enrichment that is experienced every year when the Caquetá River floods them (Piedade *et al.*, 2001) and deposits sediments from the Andes with different mineral composition.

Rather than the high soil acidity (Table 3.3), other edaphic variables determined the conditions for agriculture. Soils with more organic carbon have higher cation exchange capacities. Soils with better conditions for agriculture were generally those with higher Mg and K availability, a higher total base saturation and a higher percentage of base saturation (Table 3.3). When ADE and Alluvial Entisols were compared, alluvial soils had higher Ca amounts and a better chemical composition for agriculture than ADE, but indigenous farmers ranked Alluvial Entisols in the second place. Periodical floods that limit the number of crops that can be produced on alluvial soils were the main factor in indigenous soil ranking. Corn and plantain that are usually cropped in Alluvial Entisols are complementary to the staple-food manioc, and farmers do not need to crop them permanently or in large amounts to satisfy their requirements. Hence advantages for these crops are generally not major determinants in indigenous appreciation of soils.

Indigenous description of soil layers were in concordance with the scientific knowledge of soils. Indigenous discrimination of *workable soil* and *dead soil* corresponded well with the activity and function each layer has in relation to plant nutrition, resource capture and agricultural practices as seen by natural sciences. The *workable soil* for indigenous people is the one in which people work to produce food and it is also the fertile portion of soils. For soil scientists it is the layer where organic matter transformations occur and it is susceptible to degradation or improvement by human agency. In soils with high turnover rates of organic matter, such as most of the natural Amazonian soils, generally the topsoil plays an important role in plant nutrition (Serna-Chavez *et al.*, 2013). Microbial activity is also found to be mainly restricted to the first 20 cm of these soils (Peña-Venegas *et al.*, 2007). The term *dead soil* on the other hand, describes well the almost inexistent biological activity in soil layers below the A horizon where very old and leached materials coming from a predominant kaolinite bedrock with low natural cation exchange capacity hardly provides nutrients to plants.

3.4.2. Origin of Amazonian Dark Earths and other soils

Soil scientists agree that natural soils are formed by the natural erosion of bedrock, the action of weather on those materials and the decomposition of organic matter. On the other hand, scientists accepted that ADE are anthropogenic soils created by inhabitants of the Amazon region between 2000 and 500 years ago (Neves *et al.*, 2004), easily distinguished from natural soils by their chemical properties and other naked-eye observable features such as their dark color, their deep A horizon with presence in most cases of potsherds, lithics and charcoal pieces that were left by ancient anthropogenic activities (Kämpf *et al.*, 2003). Therefore, ADE are classified as Anthrosols (according to soil science nomenclature) or as anthropogenic soils (a term used by researchers of both natural and social sciences). For indigenous people all soils (including ADE) were created by nature. However, indigenous people recognized a relationship between ancient people and ADE in which human activities and fire were important elements associated to ADE. It is interesting that native words used to denominate ADE approach the currently accepted definition of ADE among scholars. Those words enclosed information of two major elements related with ADE formation: fire and human activity. A similar understanding of the ADE formation is shared with *Caboclos*. *Caboclos* of the Middle Madeira River also associate ADE with old sites of indigenous residences and recognize the importance of burning processes in ADE formation (Fraser *et al.*, 2011a). However, a new element about ADE formation is provided by indigenous knowledge. While scholars explain the presence of ceramics and human artifacts in ADE as waste deposits of ancient settlements (Schmidt *et al.*, 2014), indigenous narratives included other sources as the remains of the complete destruction of communities.

3.4.3. Actual indigenous use of Amazonian Dark Earths

Indigenous narratives about the ancient use of ADE is not the one they have today and the picture recalls more pre-Columbian times when the region was densely inhabited (Dull *et al.*, 2010) and ADE were used intensively.

Today, indigenous people from the study area did not use ADE primarily for food production. It is remarkable that instead of using ADE for swiddens, some indigenous people preferred to keep ADE covered with grasses for aesthetic reasons. On the contrary, studies from the Brazilian Amazon on how local farmers used ADE indicated that C*aboclos* and indigenous communities chose predominantly ADE for agriculture. Some communities could face limitations to access ADE as Kuikuro people who had to walk about 10 km to cultivate ADE (Schmidt and Heckenberger, 2009) but despite that constraint they continued cultivating it. In the Middle Caquetá region some indigenous farmers could have restrictions to cultivate ADE, but this did not explain why farmers without restrictions to use ADE were inclined to cultivate Oxisols. Indigenous soil selection of swiddens therefore was not based on soil fertility as the main condition and other conditioning aspects drove this selection. In the case of Aduche where ADE were used more for swiddens than in the other communities studied, a cultural issue might be related with this difference. Burgos and Cerón (2012) found that maniocs cultivated in sandy soils with high phosphorus availability accumulate more starch. In natural soils of the Middle Caquetá region most phosphorus is present as Al-P or Fe-P with a low availability (Souza *et al.*, 2009). The higher phosphorus availability in ADE and long periods of manioc growth (ADE do not experience periodical floods as floodplains do) could allow a larger accumulation of root starch in white bitter maniocs that particularly Andoke and Muinane people appreciated, encouraging them to use ADE more frequently for their swiddens.

3.5. Conclusions

Soil classification by indigenous groups of the Middle Caquetá region reflected their knowledge about local soils, and their perceptions about their potential and limits for cultivation. Indigenous people recognized ADE as the best soils and agreed that ADE provide good conditions for most of the crops, palms, exotic and native fruit trees, but their higher appreciation for ADE production did not lead to a more frequent use. Contrary, other contemporary Amazonian farmers used ADE for food production more often than other soils (Fraser *et al.*, 2011a). Those farmers produced food for their subsistence but also to supply local markets. Under those conditions, soils such as ADE played an important role in food production. Contemporary uses of natural and anthropogenic soils by indigenous communities of the Middle Caquetá region contrasted with their historical narratives in which ADE had a predominant role in food production. Drastic declines of these ethnic groups' population could change the way ADE were perceived. Today, Andoke, Uitoto, Nonuya and Muinane remain as small ethnic groups living in a region with low population densities where abundant forested areas exist with conditions good enough to guarantee their food security based on manioc, becoming exceptional cases of how ADE are perceived and used.

From all Amazonian soils, ADE were the only one with a clear legislation regarding their use due to their anthropogenic origin, classifying them also as archaeological sites (both in Brazil and in Colombia). Although most ADE had been reported in the Brazilian Amazon, they have been reported in several other countries of the Amazon Basin as well. The frequent use of ADE for agriculture in Brazil by groups traditionally occupying these soils to some extent limits their potential as archaeological sites as this agricultural use may have largely disturbed the sites. Archaeological studies of ADE in Colombia and other Amazonian countries different from Brazil are scarce. However, these countries at the fringe of the Basin may in fact contain more undisturbed ADE and more indigenous communities who preserved their traditions. Such sites and communities with similar perceptions of Amazon soils as those presented in this paper, might constitute an important opportunity to obtain information about Amazonia's history and better understand the origin of those anthropogenic soils.

Acknowledgements

To Fissi and Yua Andoke, Aurelio Suárez, José and Elías Moreno, Adriano Paky, and their communities for their active participation, help and for sharing information with the research team.

Chapter 4

Differences in manioc diversity among five ethnic groups of the Colombian Amazon

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Published in Diversity 2014, 6, 792-826.

Abstract

Manioc is an important root crop in the tropics and the most important staple food in the Amazon. Manioc is diverse but its diversity has not yet been clearly associated with environmental or social factors. Our study evaluates how variation in edaphic environments and in social factors influences manioc diversity among five ethnic groups of the Amazon region of Colombia. Inventories of landraces, genetic analysis of manioc diversity, visits to farmers' swiddens and interviews with farmers were carried out during two years of field work. Morphotypic and genotypic diversity of manioc were large. The different ethnic groups of our study cultivate different sweet and bitter manioc landraces which they select and maintain in accordance with their ancestral rules and norms. Differences in available environments among indigenous communities (such as the presence of different soils) did not markedly affect manioc morphotypic or genotypic diversity, while social factors considerably influenced observed manioc diversity. Manioc diversity was explained by two parallel processes of manioc diversification: volunteer seedling selection and manioc propagule exchange. We argue that, for a full understanding of manioc diversity, indigenous knowledge, as well as morphological and genetic variation should be taken into account.

Keywords: Amazon; indigenous farmers; manioc diversity; manioc classification; morphological diversity; genetic diversity; volunteer seedling; germplasm exchange.

4.1. Introduction

Manioc (*Manihot esculenta* Crantz), a crop domesticated in Central Amazonia around 8000–10,000 years ago (Olsen and Schaal, 1999), is currently the sixth most important crop in tropical and sub-tropical areas of Africa, Asia and America (El-Sharkawy, 2004).The main world collection of manioc is located at the Centro Internacional de Agricultura Tropical (CIAT) in Colombia with more than 5000 accessions. CIAT classifies and conserves this publicly accessible manioc germplasm with an aim to improve crop performance, increase yields under different conditions, and adapt the crop to global climate change (El-Sharkawy, 2006).

World crop collections maintain a core set of germplasm which is considered the minimum number of specimens that represent the genetic diversity of a crop and its relatives (Brown, 1989). However, in the case of manioc, core collections apparently do not represent the diversity present in highly diverse regions such as the Amazon region (Elias *et al.*, 2000; Elias *et al.*, 2001; Elias *et al.*, 2004) and therefore do not necessarily represent the complete diversity of this crop. A way to improve the selection of specimens for their conservation from areas such as the Amazon region is by understanding how manioc diversity is generated and preserved there and what factors affect its diversification. This information is partially available from previous studies conducted in particular areas (Elias *et al.*, 2001; Emperaire and Peroni, 2007; Fraser, 2010a) or among particular ethnic groups of the Amazon Basin (Boster, 1986; Salick *et al.*, 1997), but comparison of results between different locations or ethnic groups has so far not been attempted.

The general consensus among manioc geneticists is that manioc diversity is complex and varies depending on whether or not it is assessed by the number of genotypes or morphotypes (Elias *et al.*, 2001). A genotype is a specific arrangement of genes that confer morphological and physiological characteristics to a particular group of plants. A morphotype is the outcome of the genetic expression that results in a particular arrangement of morphological features that can be recognized in a group of plants. In the field, populations of autochthonous manioc morphotypes (product of natural and artificial selection) are denominated landraces (Zeven, 1998; Villa *et al.*, 2006). At least three reasons can be given why the number of genotypes or morphotypes distinguished in a sample differs. One is that manioc is highly heterozygous (bi-allelic state for most important variable sites). It is monoecious (separate male and female reproductive organs on the same plant) and out crossing rates are thus high, making it difficult to interpret manioc variability (Rabbi *et al.*, 2012). A second reason is that the next-generation molecular markers (with high discrimination power) have become available only recently, making it possible to improve the discrimination of genotypes with respect to the number of morphotypes assessed (Ferguson *et al.*, 2012). A third reason is that manioc, although commonly reproduced clonally, also maintains the capacity to reproduce sexually, thus producing seedlings from a recombination of clonally maintained landraces and causing new genotypes that continuously emerge — genotypes that could (or could not) heretofore be distinguished as different manioc landraces (McKey *et al.*, 2010a). In this paper, we call these seedlings volunteer seedlings (Pujol *et al.*, 2007).

Manioc is the most important staple crop in the Amazon region and exhibits a particularly high diversity there. Manioc diversity is distributed unevenly across different Amazonian environments (Alves-Pereira *et al.*, 2011; Fraser *et al.*, 2012) and ethnic groups (Boster, 1986; Salick *et al.*, 1997; Heckler and Zent, 2008). On alluvial soils from the Madeira River (Brazil), for example, a higher manioc genetic diversity was observed than on highly weathered soils or anthropogenic soils of that region (Alves-Pereira *et al.*, 2011). This difference was partially attributed, on the one hand, to the presence of diversity of soil types apt for manioc cultivation. On the other hand, the distribution of manioc diversity has been explained by the indigenous farmers' practice of collecting naturally occurring volunteer seedlings (Heckler and Zent, 2008) and of cropping, maintaining and exchanging different manioc landraces (Emperaire and Peroni, 2007). Volunteer seedlings are incorporated in farmers' portfolios, thus increasing the number of landraces each farmer holds (Pujol *et al.*, 2007), but also increasing the genetic diversity by inbreeding (Pujol *et al.*, 2005; Duputié *et al.*, 2009b). The selection and maintenance of volunteer seedlings in farmers' portfolios have been attributed mainly to farmers' practices through directional selection in accordance to the agronomic performance of the volunteer seedling and through ideotypic selection when the volunteer seedling is similar to a landrace a farmer already recognizes (Duputié *et al.*, 2009b). However, since volunteer seedlings initially produce a single root (McKey *et al.*, 2010b) and therefore are less productive than maniocs propagated clonally, it is not clear how farmers select and why they maintain volunteer seedlings to propagate them clonally. Manioc exchange usually occurs among kin and reflects a particular farmer's social network (Boster, 1986); sometimes, however, key individuals specialize in the breeding and maintenance of manioc germplasm—as is the case of Amuesha shamans of the Peruvian Amazon (Salick *et al.*, 1997). New landraces increase farmers' manioc portfolios; these in turn are exchanged with other farmers—in this way increasing the number of landraces at community level.

Amazonian societies consider manioc to be much more than only a crop, and attribute to it a variety of symbolic meanings that are part of their wider cultural patrimony (Emperaire and Peroni, 2007). For the Piaroa ethnic group of the Venezuelan Amazon, for example, manioc is considered cultural heritage and is used as a mediator of social relationships (Heckler and Zent, 2008). The social aspects of manioc might thus encourage or restrict its exchange among ethnic groups and in turn affect manioc diversity of a specific area or region. With the aim to contribute to the understanding of manioc genotypic and morphotypic diversity in the Amazon region, interdisciplinary research was carried out to study manioc diversity at the community level, indicating what factors affect manioc diversity, how manioc diversity at community level contributes to manioc diversity at regional level and, finally, what information associated to manioc landraces must be considered to select and conserve manioc diversity *in situ* or *ex situ*. The main question guiding our research was: How is manioc diversity shaped by edaphic and social differences among indigenous communities of the Colombian Amazon? To answer this question, manioc morphological and molecular diversity was evaluated in areas inhabited by different ethnic groups. Soil differences and social factors were analyzed to assess their importance for manioc diversification.

4.2. Materials and methods

4.2.1. Study area

Throughout our research we studied two elements that affect manioc diversity: soil diversity and socio-cultural arrangements. For the study, we selected the Colombian Amazon region, part of upper Amazonia, where manioc diversity has been poorly studied. In the case of soil diversity we were particularly interested in the way Amazonian Dark Earths (ADE) affect manioc cultivation, as the use of these soils by indigenous people has been poorly documented. For this, and with an aim to compare two locations with contrasting soils, we selected an area in the southern part of the Colombian Amazon in which ADE have not been reported, and an area in the Middle Caquetá region in which ADE have been reported. To assess the relation between socio-cultural aspects and manioc diversity we selected the most representative ethnic groups and the most traditional communities of each area of study.

Accordingly, research was carried out among five ethnic groups (Figure 1.1, General Introduction). The first are the Tikuna living in the community of San Martín de Amacayacu, located in the lower section of the Amacayacu River, a tributary of the Amazon River. A second cluster of four ethnic groups (the Andoke community of Aduche, the Uitoto community of Guacamayo, the Muinane community of Villazul, and the Nonuya community of Peña Roja) is located in the Middle Caquetá region.

San Martín de Amacayacu (03°50′17.3″ South and 70°17′57.3″ West) lies within the limits of the Amacayacu National Park and is part of the Tikuna, Cocama and Yagua TICOYA *resguardo* (a legitimate recognized indigenous territory) which covers approximately 140,000 ha. The area is characterized by flat plains of ancient, low alluvial terraces with superficial soils as a result of the high phreatic level of the area. Elevation is around 100m above sea level with slopes between 1% and 3%. The average annual rainfall is 2800mm.The area is covered by a mature dense forest most in a mature stage with abundant epiphytes (IGAC, 1979) with moderate anthropic intervention.

The area of the Middle Caquetá region embraces two *resguardos* of which the communities of Aduche, Guacamayo, Villazul and Peña Roja are a part. The Aduche *resguardo* (approximately 62,000 ha) includes the communities of Aduche (00°39′21″ South and 72°17′32″ West) and Guacamayo (00°31′25″ South and 72°22′38″ West) and the Nonuya *resguardo* (approximately 59,840 ha) includes the communities of Villazul (00°40′00″ South and 72°16′32″ West) and Peña Roja (00°44′29″ South and 72°05′09″ West). The area is formed by the intersection of sedimentary plains of Tertiary origin with rocky outcrops of Paleozoic origin, creating elevated plateaus. The area also includes alluvial plains of the Caquetá River and its tributaries. Elevation ranges between 200 and 300m above sea level with slopes between 7% – 25%. The average annual rainfall is 3000mm (Duivenvoorden and Lips, 1995). The area is covered by a mosaic of vegetation types ranging from mature dense forest to small herbs and bromeliads on the rocky formations (IGAC, 1979), with moderate anthropic intervention.

All the indigenous communities that participated in this research project have access to highly weathered soils and alluvial soils for manioc production (Eden and Andrade, 1987; Shorr, 2000; Adams *et al.*, 2005). Highly weathered soils classified as Oxisols and Ultisols (USDA, 1999) are acid (pH 3–5.5) soils, characterized by prolonged periods of weathering and leaching during their formation, resulting in soils with a low cation exchange capacity, limited amounts of cations and a very low phosphorus availability. Alluvial soils (classified as

Alluvial Entisols) originate from the enriched Andisols sediments from the flooding of the Caquetá and Amazon rivers and their tributaries (Piedade *et al.*, 2001).

The community of San Martín de Amacayacu is the only one without ADE. ADE are very fertile soils with good physical and chemical properties and very suitable for agriculture (Denevan, 1996; Glaser and Birk, 2012). They hold large amounts of organic matter and are less acidic than the Oxisols or Ultisols from which they were formed, resulting in a better cation exchange capacity and base saturation compared to background soils (Glaser *et al.*, 2001). ADE not only have more available nitrogen, calcium, and phosphorus (Lima *et al.*, 2002) but are also less affected by leaching, resulting in a longer-term nutrient availability as compared to background soils (Glaser, 2007).

4.2.2. Fieldwork

The research we undertook was based on a free, prior informed consent agreement between the Instituto Amazónico de Investigaciones Científicas Sinchi and the communities associated to the indigenous organization Asociación de Comunidades Indígenas del Trapecio Amazónico (ACITAM) which includes the community of San Martín de Amacayacu and the indigenous organization Consejo Regional Indígena del Medio Amazonas (CRIMA—which includes the communities of the Middle Caquetá region) to work together on all aspects of traditional food production (Agreement between Sinchi Institute and the AZICATCH, CRIMA and ACITAM indigenous organizations of June 2004) (Acosta and Mendoza, 2006). The activities carried out also obeyed the two main missions of the Sinchi Institute (Colombia, 1993): First, to support the Ministry of Environment in carrying out their commitments and the development of activities stemming from Colombia's participation in international treaties and agreements (such as its support to article 8j of the Convention on Biological Diversity); second, to encourage the development and dissemination of knowledge, values and technologies related to the management of natural resources of ethnic groups of the Colombian Amazon through participatory action research.

Field work was carried out between September 2011 and September 2013. Each community was visited eight times for two to four days, for a total of 20 days per community. For a better understanding of manioc diversity, both morphological and genetic diversity was estimated. Morphological diversity was assessed in the field together with indigenous farmers in 2011, while genetic diversity of the landraces that were recognized by indigenous people was estimated in the laboratory in December 2013. Cultural elements associated to manioc diversity were recorded in all communities between 2011 and 2013. All the information obtained was discussed and analyzed by the authors of this paper.

4.2.3. Populations

Five ethnic groups of the Colombian Amazon region participated in this research: Tikuna, Andoke, Muinane, Nonuya and Uitoto.

The Tikuna people are originally from the upper Amazon Basin; their language (Tikuna) stems from an independent linguistic family. Tikuna people can be divided into two main groups of clans, those with feathers and those without feathers; marriages generally only occur between members of opposed clans, thus promoting exogamy (Rosa, 2000). During the rubber boom at the beginning of 1900s, the Tikuna were less affected than the ethnic groups from the Middle Caquetá region, as the former apparently offered less resistance to slavery than other groups. At present the Tikuna number approximately 35,500 individuals distributed across the Amazon region of Brazil (71%), Colombia (23%) and Peru (6%) (Umbarila, 2002). The community of San Martín de Amacayacu is inhabited by 440 inhabitants (153 families; community census of 2011) who live on one side of the Amacayacu River. Despite having had long contact with white people throughout their recent history, the community of San Martín de Amacayacu maintains its traditional culture.

Uitoto, Andoke, Muinane and Nonuya people presently living in the Middle Caquetá region identify themselves as ethnic groups with a common geographic origin encompassing the area between the Putumayo and the Caquetá rivers. Because of this they call themselves "*Gente de Centro*" (*People of the Center*). Therefore, Uitoto, Andoke, Muinane and Nonuya share different cultural aspects such as the common origin of their languages (rooted in the Wuitoto linguistic family), the construction and use of *malokas* (large houses where traditional leaders are consulted and where they pass on their knowledge) and the use of the coca leaves and tobacco as elements required to establish dialogue within the *malokas*. Between 1908 and 1909 Thomas Whiffen visited the area between the Putumayo and the Caquetá rivers and estimated the number of Uitoto at 15,000, of Andoke at 10,000, of Muinane at 2000 and of Nonuya at 1000 (Andrade, 1986).

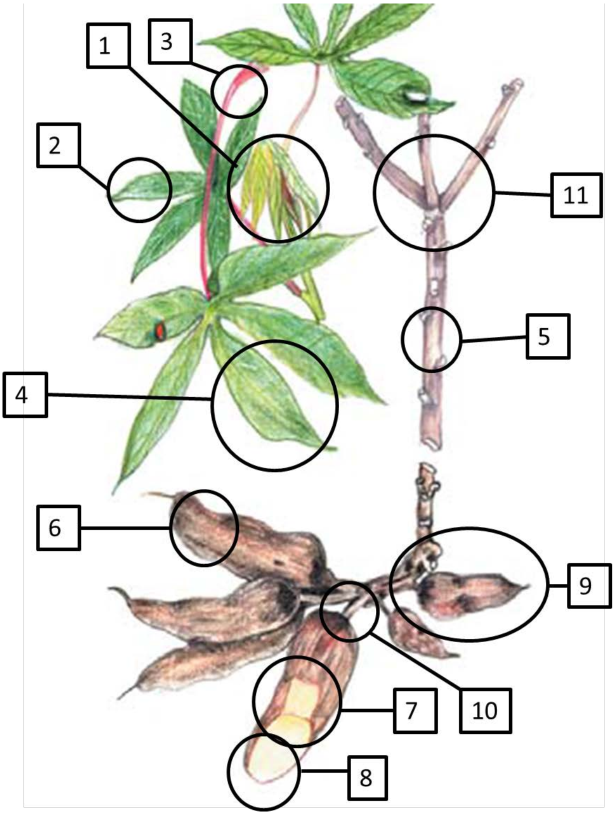
The population of *People of the Center* was strongly diminished by the rubber boom. In some cases (e.g., the Nonuya and Muinane) only few men survived. Therefore, these groups broke with the tradition to marry only between clans of their own ethnic group and made new arrangements to marry women of other ethnic groups (Orlando Paky, personal communication). This allowed them to increase their numbers and perpetuate their particular cultures—at the expense of creating multiethnic communities. The present Uitoto population is estimated to be 8400 inhabitants, with 77% living in Colombia and 23% in Peru where they arrived as slaves during the rubber boom. According to the 2011 community census, the Uitoto community of Guacamayo consists of 153 persons (34 families). Aduche is the only Andoke community that exists today. This community is located on Andoke ancestral territory and inhabited by 128 persons (27 families). The community of Villazul is one of two Muinane communities that remain today. The community of Villazul is inhabited by 77 persons (17 families).The community of Peña Roja is the only Nonuya community that exists today. It is inhabited by 71 persons (15 families).

After explaining the participatory approach of the project and the activities our research would consist of each community selected what they considered to be the most experienced and active farmer families to work with us in this project. Twenty families from San Martín de Amacayacu (13% of the population), ten from Guacamayo (29% of the population), nine from Aduche (33% of the population), eight from Villazul (47% of the population), and six from Peña Roja (40% of the population) were selected. The selected families were composed of couples or elder people and their daughters or sons. Because not all the families were of the same ethnic origin, information about the ethnicity of men and women was recorded. Because women are directly responsible for planting and cooking manioc, it was also assessed whether they followed the cultural traditions of their husbands or their own traditions when cultivating or cooking manioc.

4.2.4. Ethnobotanical data

4.2.4.1. Manioc inventories

An inventory of manioc landraces managed by each community was made to determine manioc morphotypic diversity. Morphotypic diversity was understood as the number of different manioc morphotypes conserved per community and across communities. With each of the communities separately an inventory of their manioc landraces was made to determine manioc diversity. At the start, a preliminary list of the names of the manioc landraces present in the community was elaborated through a group discussion with women farmers. This was followed by visits to swiddens starting with the swiddens local people considered to be the most diverse. In the field, the farmers discussed which plant represented which landrace and jointly a description was made. Whenever new landraces were found, these would be added to the list. When no more new landraces were found on a swidden, the group went to the next swidden to look for other landraces. This procedure was repeated until the people indicated there were no further manioc landraces in their community. This ensured that most landraces



1) Color of apical leaf ; 2) Color of mature leaf 3) Color of petiole; 4) Shape of the leaf lobule; 5) External color of the stalk; 6) External color of bulking root; 7) Color of bulking root cortex; 8) Color of bulking root pulp; 9) Shape of the bulking root; 10) Presence of root stem; and 11) Plant branching.

Figure 4.1. Morphological features used to describe manioc morphotypes. The illustration is a modification (with permission of the Sinchi Institute) of one of the drawings elaborated by Luis Angel Ramos del Águila describing a Tikuna manioc landrace (Arias *et al.*, 2004).

present in the village were recorded, although there is a possibility that some landraces may have been left out from these inventories. The same procedure was repeated in all communities.

The description of manioc landraces was based on morphological characteristics used by indigenous people of the communities and made them equivalent to the morphological indices developed by CIAT (CIAT, 1984) and EMBRAPA (Fukoda and Guevara, 1998). The descriptors of manioc plants included: apical leaf color, mature leaf color, leaf branch color, shape of the leaf lobule, color of the stalk exterior, color of the bulking root cortex, color of the bulking root pulp, shape of the bulking root, presence of a root stem, and architecture of the plant (Figure 4.1); a photographic record of each landrace was taken. The overlap between the descriptors used by indigenous farmers and the descriptors used by CIAT and EMBRAPA is included in Appendix Table A 4.1.

Complementary information collected on manioc landraces included: common name, traditional name, type of manioc according to indigenous classification, type of soil in which the landrace grows best, origin of the landrace (sexual when the landrace was recognized by the farmer as a volunteer seedling or propagated from a volunteer seedling; clonal when the farmer obtained the landrace from a stem cutting), location from where the landrace was obtained, and its uses. Complementary information was used to assess volunteer seedling frequency in indigenous swiddens and their management by farmers.

In order to triangulate the individual inventories of each community and to look for duplicates, after completing the community inventories group discussions were held with farmers who participated in the description of the manioc landraces. To this purpose, the pictures and the description of each landrace were used.

4.2.4.2. Inventory of ethnic manioc dishes

Women from the different ethnic groups were interviewed to list all recipes they knew in which manioc was the main ingredient; and to assess the frequency with which those recipes were prepared. They were asked about all types of preparations including fermented and non-fermented drinks, main meals, snacks, condiments and any preparation they considered were important to include in the list.

In this way an inventory of recipes was obtained. The research team often helped in the preparation of meals and to share these with members of the communities; these were important opportunities to observe culinary traditions and learn about the manioc landraces frequently used in them.

4.2.5. Genetic data

From each one of the landraces described by indigenous people in the field, one to three samples of apical sprouts were collected in paper bags with silica gel as dehydrating agent. Upon arrival at the laboratories of the Sinchi institute in Leticia (Colombia) the samples were completely dried with silica gel and preserved at −20°C.

Plant molecular analyses were carried out within the framework of the new legislation for research institutes associated with Colombia's Ministry of Environment (Decreto 1376 of 2013) (MINAMBIENTE, 2013), and in which the Sinchi institute does not need permission for genetic resources assessment when the material is collected without a commercial interest and for research purposes only. The samples were processed in the Manioc Genetics Laboratory of CIAT, Palmira (Colombia). Upon arrival the samples were lyophilized overnight using an Alpha 2-4LDplus Martin Christ Freeze-dryer (Germany). From lyophilized samples DNA was extracted using Qiagen (Venlo, The Netherlands) DNeasy Plant 96-well extraction kits.

Genetic diversity of manioc has generally been assessed by the study of single sequence repeats (SSRs). However, only a limited number of SSR markers are polymorphic, limiting the power to assess genetic variability in manioc (Kawuki *et al.*, 2009). On the other hand, single nucleotide polymorphisms (SNPs) are the most abundant type of DNA polymorphisms in eukaryotic genomes. For manioc, one SNP can be found per 121 nucleotides. A total of about 2954 SNPs have been found for manioc from which 1190 have been technically and biologically validated for manioc (Ferguson *et al.*, 2012) making them much more abundant than SSRs (Kawuki *et al.*, 2009). Additionally, SNPs are bi-allelic (homozygous or heterozygous), generally stable to mutations, locus specific and co-dominant (Oliveira *et al.*, 2014). SNP information is easily available from generally expressed sequences tags (ESTs) on gene databases (Ferguson *et al.*, 2012), with a low genotyping error rate compared to other markers (Oliveira *et al.*, 2014), and therefore ideal for genetic studies and especially for assessing diversity (Kawuki *et al.*, 2009). For this study 93 SNPs were used (Appendix Table A 4.2) to assess manioc diversity, tested previously by the team of the Manioc Genetics Laboratory of CIAT (Duitama *et al.*, 2014).

Samples were processed using the protocol for SNP genotyping with the EP1™ system and SNP type assays of Fluidigm® version S.01 following instructions from the manufacturer. The SNP assay is based on an allele-specific Polymerase Chain Reaction (PCR) SNP detection chemistry using a Biotium Fast Probe Master Mix, hybridizing SNPs at end-points and attaching signal bases that emit specific fluorescent patterns according to the DNA base that is read (Li *et al.*, 2010a).

Prior to performing allele-specific PCR, a standard amount of manioc DNA (60 ng) per sample was amplified in a three-step procedure to obtain the sample assay. In step one a Specific Target Amplification (STA) with the manioc DNA was done in a thermocycler through 15 min at 95°C for Taq polymerase activation, followed by 14 extension cycles of 95°C for 15 s and 60°C for 4 min. This is called the sample mix. In step two, the sample mix was diluted 1:100. In step three the diluted sample mix was combined with an assay mix which contained the ASP1, ASP2 primers and the locus-specific primer (LSP); the sample assay thus obtained was placed in the sample inlet of the chip of an IFC Controller HX. In the detector inlet a Fluidigm SNPtype™ custom assay based on a core set of 93 manioc SNPs was placed that was previously reported by Ferguson *et al.* (Ferguson *et al.*, 2012) and validated at CIAT's Manioc Genetics Laboratory. After the sample assay and the SNPtype custom assay were placed in the chip, and the IFC Controller HX automatically set up reaction chambers. The 96.96 IFC was placed on the FC1™ cycler and run using the following program: 95°C 5 min then 4 cycles of 95°C for 15 s, 64–61°C for 45 s decreasing by 1°C/cycle, then 72°C for 15 s, followed by 34 cycles of 95°C for 15s, 60°C for 45 s, 72°C for 15 s, and finally 10 s at 25°C.

SNP variability-data were captured in the EP1™ fluorescent reader at cycle 28 and 33 to be able to discriminate between homozygous and heterozygous SNP-allele calls. A direct detection of products was obtained as they emitted peaks at 495, 520, 538 and 554 nm that were read by a BioMark™ System for genetic analysis. Both data sets collected in the EP1™ (at 28 and 33 cycles) were analyzed using the Fluidigm SNP Genotyping Analysis software (Spurgeon *et al.*, 2008).

Sequences of samples collected in the field were compared with sequences from 99 samples of the CIAT's manioc world collection obtained with the same methodology. Samples of CIAT's manioc world collection included samples from South and Central America (71), Africa (1) and Asia (9), 3 hybrids and 15 landraces of unknown origin. Manioc DNA samples from the America's included: 5 from Argentina, 2 from Bolivia, 4 from Brazil, 26 from Colombia, 3 from Costa Rica, 3 from Cuba, 3 from Ecuador, 5 from Guatemala, 5 from Mexico, 2 from Panama, 2 from Paraguay, 5 from Peru, 1 from Puerto Rico, and 5 from Venezuela. The manioc DNA sample from Africa was from Nigeria. Manioc DNA samples from Asia included: 2 from China,3 from Thailand, 2 from Indonesia, and 2 from Malaysia. The three samples of manioc hybrids were ICA-CIAT hybrids obtained by open or controlled pollination. The 15 samples from unknown origin were identified by the codes AM206-5, AM560-2, FLA 21, FLA61, FLA 19, GLA8, GM905-52, GM905-57, GM905-60, SM301-3, TMS60444, C18, SG107-35, GUT64, and JAC3. Results of manioc diversity of the CIAT core collection and samples of this study are presented as Figure 4.2.

4.2.6. Statistical analysis

Chi-square tests were used to assess differences in manioc inventories and differences in the classes of manioc landraces cultivated among ethnic groups. The statistical analyses were performed with the Analytical Software Statistix 9.0.

A z-test was used to assess which morphological variables distinguished as different morphotypes plant pairs that were considered duplicates in the genomic analysis. The morphological description obtained for each variable was transformed into binary data (1 = when the morphological description of the variable matched between genotype duplicates, and 0 = when the morphological description of the variable did not match between genotype duplicates). Z was then calculated as:

$$z = \frac{p - \pi}{\sqrt{\pi(1 - \pi)/n}} \tag{1}$$

where *p* was the number of times a variable chosen matched between genotype duplicates; π was the null hypothesis value that in this case was 0.5 as each variable has the same possibility to match or not between duplicates; and *n* was the sample size which corresponded to the number of genotype duplicates tested (21). The test considered that, when the values obtained for each variable were greater than the z-value from the table, the variable was significantly different among the 21 genotype duplicates compared. The variables that obtained the highest values were the variables that matched in most of the duplicates compared while variables with low scores could be potential morphologic discriminators of genotypes.

The sequences obtained from each manioc landrace through its genetic analysis were read, organized and analyzed to obtain the genetic structure of the population of the samples collected. The genetic structure was obtained using a Bayesian model approach (Kawuki *et al.*, 2013) with the STRUCTURE 2.2 software (Pritchard *et al.*, 2000). This Bayesian analysis determines the minimum number of populations (K) that could have generated the observed diversity using an admixture model and assumes that each individual inherited some portion of its ancestry from each one of the K populations determined. The number of K populations is based on the rate of change in the log probability of the data between successive K values. To estimate it, a ΔK method (Evanno *et al.*, 2005) was implemented in the STRUCTURE software to ascertain the most likely value of K in this data set, using 1 to 10 populations. The length of the burn-in period was set on 100,000 and the number of MCMC Reps after burn-in on 200,000. After the value of K was determined, each sample was compared with each one of the K populations to discriminate samples into defined groups that segregate similarly. Information was used to elaborate Neighbor-Joining dendrograms of genetic diversity. The observed heterozygosity (Ho) of each SNP was calculated according to Nei (Nei, 1973) and Shete *et al.* (Shete *et al.*, 2000) using PowerMaker software.

STRUCTURE outputs were processed using CLUMPP v1.1.2 (Jakobsson and Rosenberg, 2007) to account for the variability in individual membership probabilities across the different runs, and to find optimal alignments of independent replicates on each K. Neighbor-Joining dendrograms were elaborated with the data obtained with K=3 and K=6, calculated to be the number of populations that best explained the genetic data obtained (Evanno *et al.*, 2005). Samples that, after being compared with three or six populations (K=3 and K=6) obtained membership coefficients (Q) higher than 0.9 for one of the populations with which they were compared, were considered samples with low genetic variability. On the contrary, samples that obtained membership coefficients (Q) between 0.9 and 0.3 in relation with all of the populations with which they were compared, were considered samples with high genetic variability; that is, the samples with the lowest values were the ones with the highest genetic variability.

4.3. Results

4.3.1. Manioc diversity in the study area

4.3.1.1. Morphotypic manioc diversity

Indigenous descriptions of manioc landraces were based on homolog morphological parameters comparable to those proposed by CIAT and EMBRAPA (*cf.* Figure 4.1 and Table S 4.1) as colors and shapes are morphological characteristics easily recognizable by manioc farmers around the world. All farmers recognized volunteer seedlings as plants that do not grow from stem cuttings, produce only a single bulking root, and appear spontaneously in swiddens on soils where manioc had been grown previously. When CIAT's and EMBRAPA's morphological features for manioc description were discussed with indigenous farmers, they

Table 4.1. Local manioc classification and diversity (number of landraces and between brackets percentage within a community) in five indigenous communities of the Colombian Amazon. T= Total number of manioc landraces per class. EI= Number of manioc landraces associated to ethnic identity in each class; NE= Number of manioc landraces not associated to ethnic identity in each class.

Manioc inventory San Martín de Amacayacu (Tikuna)			**Manioc inventory communities "*People of the Center*"**						**Total**
					Aduche (Andoke)	**Guacamayo (Uitoto)**	**Peña Roja (Nonuya)**	**Villazul (Muinane)**	
Maniocs "*to eat*"	Total	23 (70%)	*Manicuera*	Total	2 (6%)	3 (9%)	2 (4%)	2 (7%)	60
				EI	2	3	2	21(1)	
	EI	10		NE	0	0	0	0	
			Maniocs "*to eat*"	Total	9 (28%)	8 (23%)	4 (9%)	7 (27%)	
				EI	8	0	0	1(1)	
	NE	13		NE	1	8	4	6	
Bitter maniocs	Total	10 (30%)	Maniocs "*to grate*"	Total	18 (57%)	14 (40%)	25 (54%)	16 (59%)	113
				EI	14	0	5(2)	2(1)	
	EI	0		NE	4	14	20	14	
			Yellow bitter maniocs	Total	3 (9%)	10 (28%)	15 (33%)	2 (7%)	
	NE	10		EI	3	1	2(2)	1(1)	
				NE	0	9	13	1	
Total		33			32	35	46	27	173

(1) Of these one *Manicuera*, one manioc "*to eat*", one manioc "*to grate*", and one yellow bitter manioc were identified by informants as landraces originating from the Bora ethnic group. (2) Of these two maniocs "*to grate*" and one yellow bitter manioc were identified by informants as landraces originating from the Miraña ethnic group.

disagreed that the presence/absence of a root stem (Figure 4.1) might be used as a parameter for manioc classification.

Farmers considered that all manioc landraces had a root stem, and that only volunteer seedlings (which have a single root attached directly to the stalk) lacked this. Although among these ethnic groups the presence or absence of a root stem was not considered an appropriate morphological feature to classify manioc, it has been observed that presence or absence of a root stem provided a relevant morphological characteristic to classify manioc landraces cultivated by Makushi people of Guyana (Elias *et al.*, 2001).

In addition to morphological characteristics of manioc, indigenous people also considered toxicity and use as important features to classify manioc landraces. All five ethnic groups used morphological, toxicity and use parameters to classify manioc landraces, but classifications differed in complexity among ethnic groups (Table 4.1). Tikuna people classified manioc landraces into two main groups (Table 4.1): Maniocs "*to eat*" composed of manioc landraces with low root toxicity that can be cooked and eaten directly without a detoxification pre-treatment, and bitter maniocs composed of high toxicity manioc landraces that require a process of detoxification before they can be eaten. On the other hand, Andoke, Muinane, Nonuya, and Uitoto people classified manioc landraces into four main groups (Table 4.1). One group was composed of non-toxic *Manicuera* landraces used to prepare their traditional drink called *Manicuera* (a very sweet juice prepared after grating manioc roots and cooking the squeezed juice in water).

The second group was composed of low toxicity "*to eat*" landraces with white or very pale yellowish roots. The third group was composed of high toxicity "*to grate*" landraces with white to very pale yellowish roots usually used to obtain starch through grating. The fourth group was composed of high toxicity landraces with clearly yellow roots used for different recipes.

From the 173 manioc samples collected and described, 165 came from clonal stems while eight were volunteer seedlings. Among the 173 samples 60 landraces were recognized by local people as non-toxic maniocs which included "*to eat*" and *Manicuera* maniocs (35%) with low toxicity and 113 as toxic maniocs which included "*to grate*" and yellow bitter maniocs (65%) with high toxicity. Manioc inventories included between 27 and 46 different manioc landraces per community (Table 4.1). The average number of manioc landraces per swidden was 12, without significant differences among indigenous communities. After a detailed review with local farmers of samples from their own community and samples collected across all communities of the Middle Caquetá region, only three duplicates were identified by them.

Differences among communities in the total number of manioc landraces were not significant (chi-square value = 4.5, d.f. = 4; α = 0.05), but there were significant differences in the number of low toxicity and high toxicity manioc landraces cultivated among ethnic groups (chi-square values of 10.99 and 21.19, respectively, for low toxicity and high toxicity landraces; d.f. = 4; α = 0.05). The Tikuna community maintained more low toxicity manioc landraces than the *People of the Center* communities. On the other hand, the *People of the Center* communities maintained more high-toxicity manioc landraces (Table 4.1). Although the Tikuna do not themselves make the distinction between bitter manioc landraces with different color of bulking root pulp, we observed that, from the 10 bitter manioc landraces they maintained, eight were yellow bitter maniocs and one had pink root pulp.

When the number of maniocs "*to eat*", maniocs "*to grate*", and yellow bitter manioc landraces were compared among indigenous communities of the *People of the Center*, significant differences in the number of landraces "*to eat*" and yellow bitter manioc landraces were found (chi-square values of 10.5 for landraces "*to eat*" and 25.8 for yellow bitter manioc landraces, respectively; d.f. = 4; α = 0.05).

4.3.1.2. Genotypic manioc diversity

Most of the single nucleotide polymorphisms (SNPs) used discriminated manioc samples well after 28 cycles, and only few samples required 33 cycles to obtain proper discrimination. On average observed heterozygosity was 0.39 across the 93 SNPs, with values between 0.04 and 0.69. Around 20% of SNPs had an observed heterozygosity below 0.30 (Table S 4.2).

When the 173 collected morphotypes were compared genetically with genotypes from the CIAT collection, three of the morphotypes collected that corresponded to one genotype (duplicate 2 in Table 4.2) matched to one of the CIAT genotypes. From the remaining 170 morphotypes 41 corresponded to 20 genotypes as these were duplicates or triplicates (Table 4.2). These differed morphologically in some features (Table 4.2), but the manioc class in which the landraces were classified (z-table value of 0.999), the color of bulking root pulp (z-table value of 0.974), and the uses (z-table value of 0.939) were the characteristics the duplicates mostly shared. Morphological comparison of genotype duplicates indicated that different morphotypes could have identical genotypes based on genetic analyses.

Table 4.2. Comparison of genotypic duplicates indicating which morphological variables indigenous farmers considered equal (value = 1), and which morphological variables they considered different (value = 0) between samples, and differences discriminating between duplicates (by a Z-test). Variables: 1. Class of manioc; 2. Color of bulking root pulp; 3. Uses; 4. Soil in which the landrace grows better; 5. Preferred character to maintain the landrace; 6. Color of petiole; 7. Color of mature leaf; 8. Plant branching; 9. Color of apical leaf; 10. Color of bulking root cortex; 11. Shape of leaf lobule; 12. Root shape.

VARIABLE	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
z-value obtained	3.27	1.96	1.52	1.09	1.09	−0.21	−0.65	−1.09	−1.52	−1.96	−2.40	−2.40
z-value expected (two-tailed 95% C. I.)	0.99	0.97	0.93	0.87	0.87	0.40	0.25	0.12	0.60	0.02	0.00	0.00
DUPLICATES	DUPLICATES AMONG COMMUNITIES											
1.(ADU10, GUO18, GUO22)	1	0	0	0	0	0	0	0	0	0	0	0
2. (ADU16,GUO6, AMA1)	1	1	1	1	0	1	0	0	0	0	0	0
3. (ADU1, GUO29)	1	1	1	0	1	0	1	0	0	0	1	0
4. (ADU11, GUO13)	1	0	1	0	0	0	1	1	0	0	0	0
5. (ADU18, GUO4)	1	1	0	0	1	0	1	0	0	0	1	0
6. (ADU23, GUO8)	1	1	1	0	0	1	1	1	0	0	1	0
7. (ADU30, GUO10)	1	1	0	1	0	1	0	0	0	0	0	0
8. (AMA28, GUO9)	1	1	0	1	0	1	1	1	0	1	0	0
9. (GUO31, PRO23)	1	1	1	1	1	0	1	0	1	1	0	0
10. (PRO2, VA12)	1	1	1	1	1	1	0	0	1	1	0	1
11. (PRO21, VA24)	1	1	1	1	1	0	1	0	0	0	0	0
12. (PRO40, VA19)	1	1	1	0	1	0	0	0	0	1	0	0
13. (PRO42, VA11)	1	1	1	1	1	1	1	1	1	1	0	0
14. (PRO8,VA23)	0	0	1	0	1	0	0	1	1	0	0	0
DUPLICATES	DUPLICATES WITHIN COMMUNITIES											
15. (ADU32, ADU27)	1	1	0	1	0	0	0	1	1	0	0	0
16. (ADU3,ADU4)	1	1	0	1	1	0	1	1	0	0	0	0
17. (AMA7, AMA17)	1	1	1	1	0	1	0	0	1	1	1	1
18. (AMA3, AMA30)	0	0	1	1	1	0	0	0	1	0	1	1
19. (AMA31, AMA32)	1	1	0	1	1	1	0	0	0	0	0	1
20. (PRO9, PRO47)	1	0	1	0	1	1	0	1	0	0	0	0
21. (VA13,VA15)	0	0	1	1	1	1	0	0	0	0	0	1

Codes: ADU: Samples from Aduche; AMA: Samples from San Martín de Amacayacu; GUO: Samples from Guacamayo; PRO: Samples from Peña Roja; VA: Samples from Villazul.

Duplicates were partly collected in different communities with different names and characteristics (30 manioc landraces) and partly collected in the same community (14 manioc landraces). Excluding known genomes (in CIAT´s collection) and duplicates, we obtained a total of 150 unique genotypes that were genomic material new and different from the CIAT core collection, in fact largely grouping into a different cluster (Figure 4.2).

When the genomes of morphotypes collected in this project were compared with genotypes from the CIAT core collection, manioc genotypes from the Tikuna community of San Martín de Amacayacu (AMA) appeared to be closely related to Peruvian manioc genotypes (PER).

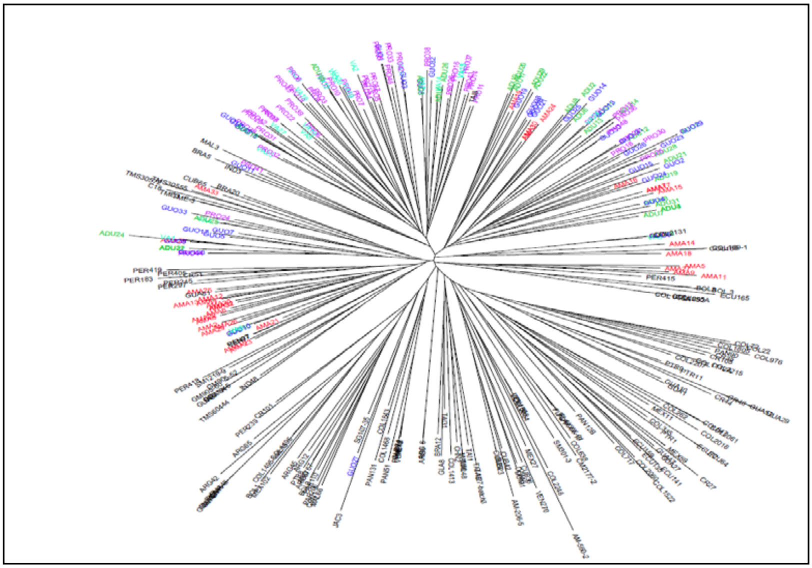


Figure 4.2. Neighbor-Joining dendrogram comparing the molecular diversity of 99 samples of the CIAT manioc core collection (in the bottom of the graph) and 150 manioc landraces from the Colombian Amazon (in the upper part of the graph) collected in this study.

Manioc genotypes from the communities of the *People of the Center* formed a cluster apart from the bulk of the genotypes provided by CIAT (Figure 4.2). When a genetic analysis of manioc samples was done according to their toxicity, "*to eat*" maniocs formed a cluster apart from bitter maniocs ("*to grate*" and yellow bitter maniocs), except for few samples (Figure 4.3). *Manicuera* maniocs on the other hand were genetically more related to high toxicity maniocs than with low toxicity maniocs (Figure 4.3). With K= 3 and K= 6, one cluster (in red in the first STRUCTURE graph and red and pink in the second STRUCTURE

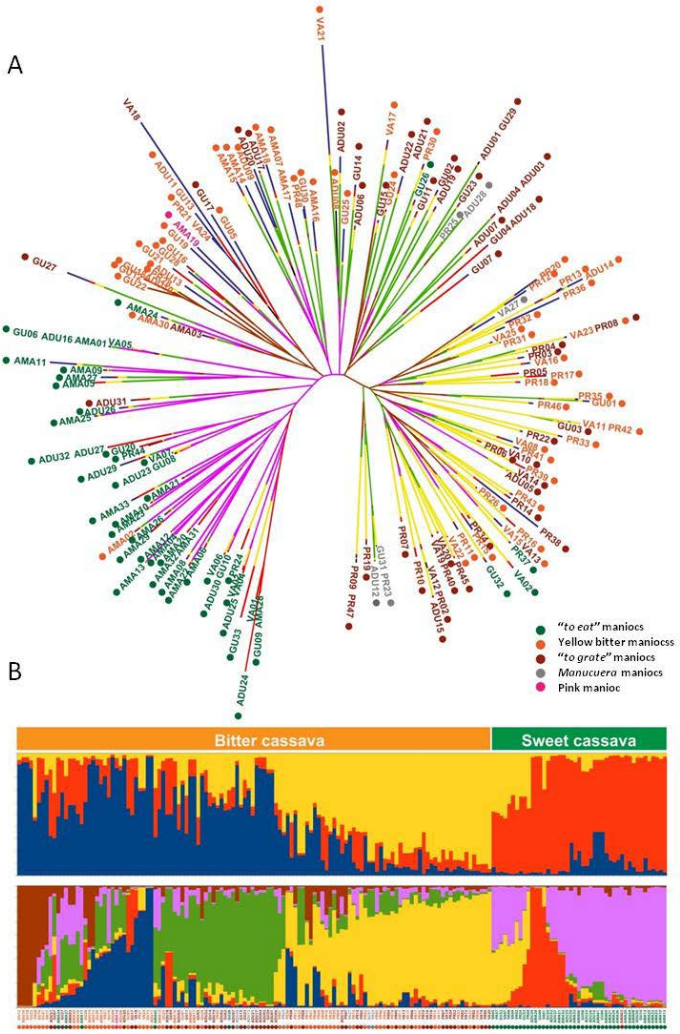


Figure 4.3. Genetic distribution of manioc landraces according to their toxicity.(**A**) Neighbor-Joining dendrogram showing the genetic relation of the different manioc types identified by indigenous people;(**B**) STRUCTURE outputs of the molecular diversity of sampled maniocs according to their toxicity as sweet (low toxicity) and bitter (high toxicity) maniocs obtained with the most likely number of clusters (K=3 and K=6). Each vertical colored bar represents one genotype and the colors indicate the extent to which a genotype genetically belonged to the 3 or 6 clusters.

graph) in Figure 4.3 combined most of the "*to eat*" maniocs. Although some of the "bitter" maniocs were placed in the "sweet" manioc cluster and *Manicuera* maniocs were placed in the "bitter" manioc cluster, indigenous morphotypic and toxicity organization into "*to eat*" and bitter maniocs corresponded largely with the clustering based on genomic information.

From the 150 new genotypes, 74% had high genomic variability indicating they were the product of mixing of several genomes. The remaining 26% of the samples had low genomic variability with single population membership coefficients (Q) higher than 0.9 (Figure 4.4). The proportions of landraces with high/low genomic variation were comparable across communities: 73%/27% for San Martin de Amacayacu, 72%/28% for Aduche, 77%/23% for Guacamayo, 78%/22% for Peña Roja, and 81%/19% for Villazul.

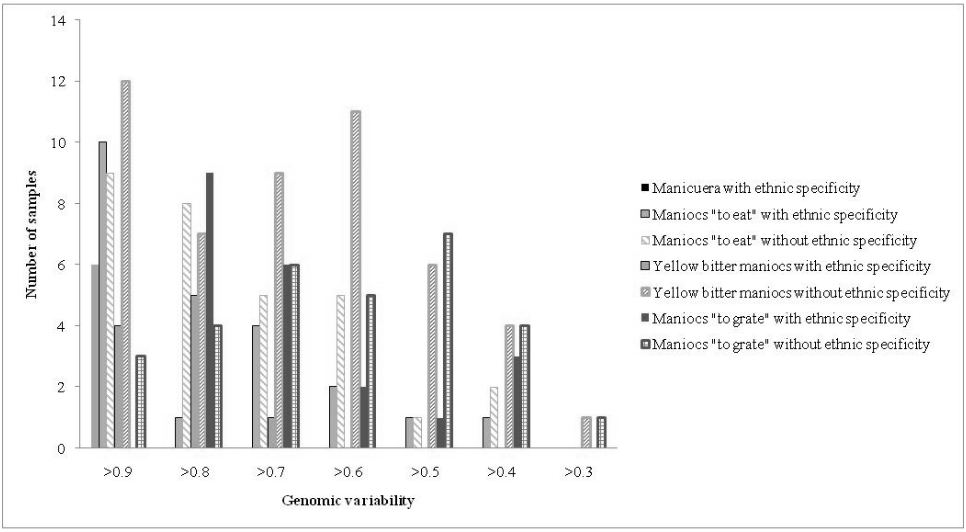


Figure 4.4. Genomic variability as expressed by the single population membership coefficient or Q-value of manioc landraces collected in five indigenous communities of the Colombian Amazon region; a distinction is made between landraces grouped according to ethnic classification (*cf.* Table 4.1) and whether or not they are with/without ethnic specificity.

4.3.2. Sources of manioc landraces

4.3.2.1. Mythical accounts of the origin of manioc use

Ethnic groups from the Amazon region of Colombia consider manioc as a native species. Manioc domestication is attributed to mythical beings and this knowledge is passed on orally from generation to generation.

In Tikuna narratives, manioc came from the mythic "tree of abundance". The maintenance and preparation of this mythic manioc were in the hands of an ancient woman and her husband, a bird that was the owner of fire (Acosta and Mazorra, 2004). Manioc was the food that allowed the mythic twins Yoi and Ipi to procreate and feed their off-spring. According to these narratives, the origin of the Tikuna was directly related to manioc: when Yoi went fishing, he used different baits to fish different animals, but when he used a piece of sweet manioc to fish at the Eware River, he fished the Tikunas (Camacho, 1995). That is why the Tikunas know how to cultivate sweet manioc—their main food.

According to narratives of the *People of the Center*, manioc existed before humans as a Paempa tree (Paempa is the name Andoke people use to refer to *Manicuera* manioc). According to Yua Andoke, one of the students of Yiñeko, the Andoke leader that rebuilt Aduche after the rubber boom, "*the first Manicuera landrace as we know it today originated from a branch of the Paempa tree that fell down and stuck into the ground*" (Interview with Yua Andoke, November 22, 2012). All the ethnic groups of the *People of the Center* agree that *Manicuera* was the first manioc. Andoke people consider it their initial food. In Muinane words, *Manicuera* is "*the breast of Mother Earth and our first food*". An Andoke mythical tale recalls that "*after The Flood*, *DidanAikA*, *the wife of the Andoke God also identified as Mother Earth*, *took branches of the Paempa tree and cut them into small sticks. From each stick originated a new manioc landrace*" (Interview with Fissi Andoke, August 15, 2012).

All *People of the Center* received *Manicuera* but each particular ethnic group received different manioc landraces. This manioc distribution was further explained to us through a mythical tale shared by all *People of the Center*, and told by an elder Uitoto woman:

> "When God started to distribute the manioc landraces among the *People of the Center*, he first distributed *Manicuera* among all groups. Then he distributed maniocs "*to grate*" to Andoke, Muniane and Bora people. It was getting late and there were still other groups waiting for maniocs. He finally gave to Uitoto and Nonuya people yellow bitter maniocs. Because it was too late to grate them, Uitoto and Nonuya women put the roots into the water. That is why Uitoto and Nonuya women don't know how to grate manioc" (Interview with Virgelina Moreno, April 25, 2013).

The Andoke also recount that after Nenefi, the Andoke God, gave them the manioc stalks, he recommended people to search for a burnt, soft soil called *ÑesxaΘ* to cultivate them. In the case of the Uitoto, they were instructed to plant manioc on *Juk+no* soils. *ÑesxaΘ* and *Juk+no* are Andoke and Uitoto terms for ADE (Chapter 3 of this thesis, Peña-Venegas *et al.*, 2015). The use of ADE for manioc cultivation is also referred to in Muinane history. According to an elder woman who was present at the establishment of Villazul at the beginning of the 20th century: "*the community was located on these black soils* [ADE]. *The first swiddens were done there* [on ADE] *because those soils are good for manioc growth*" (Interview with Alicia Kumimarima, November 27, 2012).

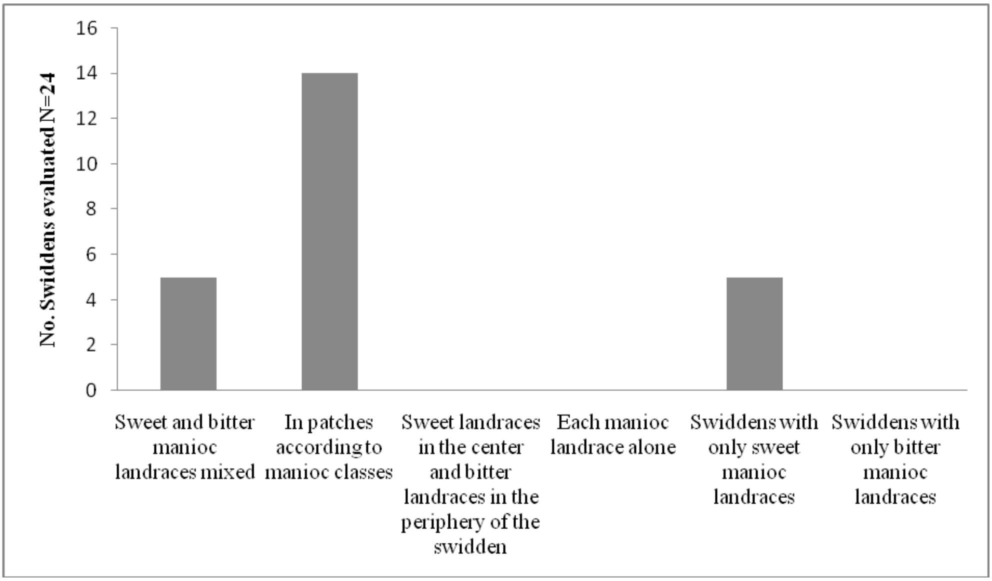
4.3.2.2. Sources of today's manioc inventories

According to the indigenous people participating in our study, the manioc landraces they presently cultivate come from three different sources: landraces received in mythical times (and that provide them with their distinct ethnic identity); landraces obtained throughout their history and which furnish clans with their particular identity; and landraces obtained through exchange with farmers from outside the community.

Mythical narratives indicate that some manioc landraces were given to indigenous people as ethnic identity markers (*Manicuera* for example), yet these are not all the manioc landraces that today bestow an ethnic group with its identity. Tikuna and Uitoto people for example share a common historical event in which other manioc landraces appeared at the time clan differentiation within the ethnic group took place. Tikuna narratives point to a time when individuals were undifferentiated and nobody knew who their relatives were. To avoid this situation, the Tikuna started to use different manioc landraces to create differences between clans (families not bonded by consanguinity). Uitoto people specify that clan differentiation strengthened their identity by selecting particular landraces. According to Uitoto narratives, before a clan was formed people prayed asking for manioc landraces that could grant them identity as a clan. Then they searched for new manioc landraces from those that grew spontaneously (volunteer seedlings) and selected some as their own.

In addition to the manioc landraces that people maintained as ethnic identity markers, other landraces were obtained through exchange. According to our respondents, from the 173 manioc landraces collected in our study, 116 (67%) were obtained through exchange (mainly with neighboring communities), but some landraces came from very distant places—including places outside the Amazon Basin (11% of the total inventory of manioc morphotypes). The remaining 57 landraces (33% of the total inventory of manioc morphotypes) were manioc landraces identified by indigenous farmers as landraces that characterized them as members of a particular ethnic group (including mythical and clan-specific landraces). These 57 landraces also included four Bora manioc landraces introduced by a Bora woman living in Villazul as well as three Miraña landraces introduced by a Miraña woman living in Peña Roja. These landraces are now part of the manioc portfolio of the Muinane and the Nonuya communities respectively (see Table 4.1).

When these landraces that bestow ethnic identity were analyzed genetically, 100% of the *Manicuera*, 53% of maniocs "*to eat*", and 40% of yellow bitter landraces turned out to be genotypes with low genomic variability and thus with a high single population membership or Q-value (Figure 4.4). For landraces without a specific ethnic association, the percentage of genotypes with low genomic variability was between 10% and 30%. None of the "*to grate*" maniocs had a Q-value higher than 0.9, but 43% of the maniocs "*to grate*" with ethnic specificity had a Q-value higher than 0.8 (Figure 4.4).



Note: The pattern of sweet landraces in the center and bitter landraces in the periphery of the swidden was reported earlier by Van der Hammen for the Middle Caquetá region (Hammen, 1984) and also observed elsewhere by McKey and Beckerman (Jakobsson and Rosenberg, 2007).

Figure 4.5. Manioc planting patterns in swiddens of indigenous communities.

When patterns of manioc planting in swiddens were evaluated, the most frequent patterns did not prevent manioc sexual recombination between toxic and non-toxic varieties or within manioc groups (Figure 4.5). In swiddens manioc landraces are commonly organized randomly or grouped in patches according to manioc group, so manioc landraces are never truly separated from others. Therefore, each swidden creates opportunities for crossing among manioc landraces.

4.3.3. The effect of different soil environments on manioc diversity

From the five communities studied, San Martín de Amacayacu was the only one without access to ADE. However, as mentioned above, there were no significant differences in the number of manioc landraces between communities, so the presence of ADE did not increase the number of landraces in communities of the Middle Caquetá region. Moreover, from the 173 manioc landraces indigenous people identified, 119 (70%) were classified by them as landraces that grow well in any kind of soil. Among manioc landraces that, according to our respondents, performed better in highly weathered soils (six landraces), alluvial soils (19 landraces) or ADE (29 landraces) there were landraces from all the four different classes. In the cases in which indigenous farmers indicated that some landraces grew better in highly weathered soils, these landraces were not cultivated in ADE; we were also told that these same landraces did not tolerate soils with high moisture content and the roots rotted easily when cultivated in floodplains. In the case of landraces that performed better in alluvial soils, our respondents indicated that these landraces quickly developed bulking roots and could be harvested early (one manioc landrace from San Martín de Amacayacu, for example, takes 3 months on average to be ready for harvesting). In the case of landraces that performed better in ADE, farmers indicated that these landraces produce big roots rich in starch.

4.3.4. The effect of manioc exchange on manioc diversity

Indigenous farmers readily exchange manioc landraces on different occasions. Important exchanges occur primarily between mothers, grandmothers and daughters when the latter get married. Because all communities studied are patrilocal, when a woman marries, she leaves her community and/or home and goes to live at her husband's community and/or home, adopting her husband's ethnic traditions. Before she leaves a cross-generational exchange of manioc landraces occurs, and the newly-wed receives landraces from her mother and grandmother as part of her dowry. As soon as she arrives to her husband's community/home, her mother-in-law introduces her to the husband's traditions. One of the first activities the new couple has to do is to open a swidden to produce their own food. At that moment, the mother-in-law gives her daughter-in-law the manioc landraces that are specific to her son's ethnic group. She will plant them, but mix them with the manioc landraces given to her by her family. Over time, she will exchange with her mother-in-law (and other women in her husband's community) her own manioc landraces, increasing in this way family manioc inventories and, when partners come from different communities, community manioc inventories.

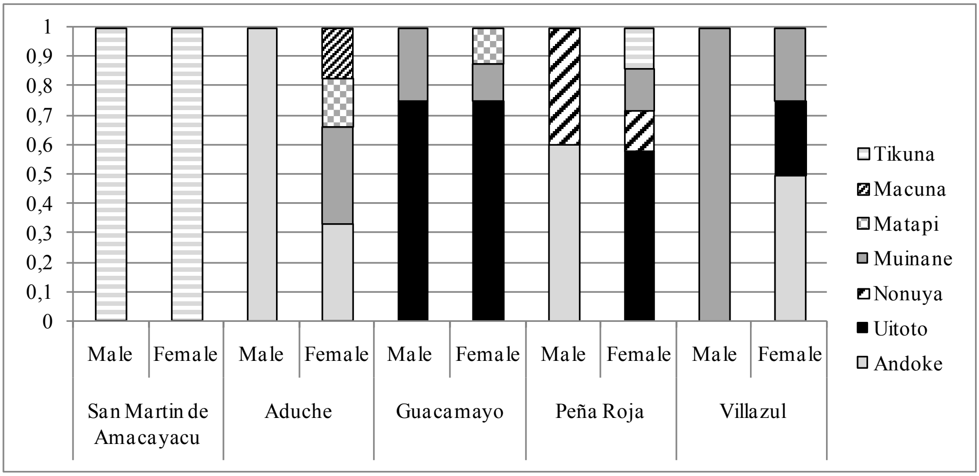


Figure 4.6. Ethnic composition (in fractions) of the group of family farmers in each community who participated in this project.

Traditionally, in most indigenous groups of the Amazon region, men were not allowed to marry women from other ethnic groups. Because of this, manioc stocks of different ethnic groups could develop into distinct clusters. During the last century, however, marriage rules have considerably changed. In the case of the *People of the Center*, for example, interethnic marriages offered patrilocal groups in danger of extinction a chance for cultural survival (Figure 4.6). Nowadays, the ethnic composition of *People of the Center* communities is a mix of ethnic groups but where variation is always larger for women than for men. These changes are reflected in the arrangement of genotypes of manioc landraces in which there are no clear clusters formed by a community (Figure 4.3). In the case of San Martín de Amacayacu, in which most of the marriages are between Tikuna partners (in fact, in our sample all the couples were 100% Tikuna; see Figure 4.6), manioc landraces form a more compact cluster than the landraces of the *People of the Center*.

Apart from manioc exchanges mediated by marriages, opportunities for manioc exchange that are not marriage dependent also occur. Often, women who travel outside the region bring back with them landraces from the places visited (for example, the landrace GUO27 in Figure 4.2 which was brought in from the Vaupes region in the northeast of the Colombian Amazon).This eagerness to increase manioc inventories was also apparent during our collective visits to swiddens to describe and classify manioc landraces. Farmer visitors commonly asked a swidden' owner for stalks of varieties they did not yet possess. This was also observed during collective manioc harvesting of swiddens. The practice of free manioc exchange is part of being an indigenous farmer. In fact, from an indigenous point of view a good farmer is one who maintains a high number of different landraces (and not necessarily the one who produces more per unit of land). In our case, the farmer families that each community selected to participate (*i.e.*, the most appreciated farmers) in the study were also those with the most diverse swiddens (in terms of the number of landraces held by each family).

4.3.5. Indigenous culinary traditions

According to indigenous mythical tales, since not all manioc landraces were equally distributed over all ethnic groups, their culinary traditions also differed (Table 4.3). The composition of manioc inventories of each community therefore, also reflects the culinary traditions of each ethnic group.

Seventy percent of the manioc landraces found in San Martín de Amacayacu were "*to eat*" landraces. Tikuna culinary tradition is therefore based on sweet maniocs mainly. People from San Martín de Amacayacu affirmed that they did not possess bitter maniocs until recently—about 50 years ago or so, when yellow *farinha* was first prepared for sale. They also stated that they traditionally knew the technique to prepare *farinha* from sweet manioc landraces and that they still prepare it for household use, but that they produce yellow *farinha* for cash. *People of the Center* cultivate *Manicuera* landraces exclusively and indeed *Manicuera* landraces grouped together—with the exception of one sample (VA27) which is a *Manicuera* landrace of the Bora ethnic group. They use *Manicuera* landraces to prepare their traditional drink (*Manicuera*) which in their mythical tales is considered as their food and identity symbol. Excluding *Manicuera*, each particular ethnic group recognized other manioc landraces as their own. The Uitoto and Nonuya communities of Guacamayo and Peña Roja held the highest number of yellow bitter manioc landraces. At the same time, these ethnic groups claimed that recipes elaborated with yellow bitter manioc were their own traditional

Table 4.3. Traditional ethnic recipes based on manioc. A stands for Andoke, M for Muinane, N for Nonuya, T for Tikuna and U for Uitoto. Recipes which are not exclusive to any one group are identified with an X.

Ethnic Preparations	**A**	**M**	**N**	**T**	**U**
Based on *Manicuera* maniocs					
Manicuera (Manioc grated and boiledfor a sweet manioc juice)	A	M	N		U
Based on maniocs “*to eat*”					
Arapata (Manioc cooked and mixed with banana)				T	
Colada (Manioc starch cooked with water and sugar)				X	
Dry casabe (Round bread made from the manioc root)				X	
Farinha (A fermented and roasted manioc granulate)				T	
Jutiroi (Juice of fermented manioc leaves boiled)					U
Manioc juice boiled with fish	X	X	X		X
Masato (Manioc beer obtained from a mix of mashed manioc and sweet potatoes)				T	
Monegú (Boiled manioc and kneaded with fish)				T	
Payavarú (Boiled manioc, mixed with toasted manioc leaves and squeezed)				T	
Payavarú wine (Fermented Payavarú)				T	
Pururuca (Masato with banana)				T	
Starch casabe (Round bread made of manioc starch)				X	
Tapioca (A granulate of toasted manioc starch)				T	
Unchará (Manioc bread)				T	
Based on maniocs “*to grate*”					
Arepa (Baked round bread)	X	X	X		X
Caguana (Boiled starch and mixed with fruit juice)	A	M	X		X
Colada				X	
Farinha	X	X	X		
Manioc juice boiledwith fish	X	X	X		X
Starch casabe	A	M			
Tamal (Manioc root packed in banana leaves and steamed)	X	X	X		X
Tapioca				X	
Based on yellow bitter maniocs					
Arepa	X	X	X		X
Caguana	X	X	N		U
Colada				X	
Dry casabe			N		U
Manioc juice boiled with fish	X	X	X		X
Farinha	X	X	X	X	X
Tucupí (Source made cooking the fermented bitter manioc juice with hot chilies)	X	X	X	X	U
Jukui (Tucupí with fish and/or shrimps)					U
Mingao (*farinha* mixed and water)					X
Starch casabe				X	
Tapioca				X	
Tamal	X	X	X		X

preparations (Table 4.3).

The *farinha* that is commonly associated with the use of yellow bitter maniocs was not a traditional preparation of Uitoto and Nonuya people. According to them, they learned how to prepare *farinha* from their yellow bitter maniocs during the rubber boom—when this storable product was used as the main food to feed indigenous slaves. Andoke and Muinane people on the other hand claim to have the tradition to use maniocs “*to grate*” and claim that *caguana* and starch *casabe* are traditional preparations of theirs.

However, maniocs "*to grate*" are also commonly used by other ethnic groups and in fact they form the dominant group of manioc landraces in the manioc inventories of indigenous communities of the Middle Caquetá region. The Tikuna are also starting to use bitter maniocs to prepare traditional recipes that require starch (*colada* and *tapioca*), thus moving away from their more traditional sweet manioc use.

Against our expectations, when complexity in the preparation of recipes (in terms of number of steps and time required) was taken into account, no direct relation between complexity and toxicity was found. There are Tikuna recipes made of non-toxic maniocs that take several days to prepare such as *farinha*, *masato* (manioc beer), *payavarú*, *payavarú* wine, and *tapioca*, and the *People of the Center* use toxic maniocs that also take days to prepare such as dry *casabe* and *tucupí*. However, when complexity in terms of the time spent to prepare recipes made of "*to grate*" or yellow bitter manioc landraces was compared, we found that the preparation of recipes from maniocs "*to grate*" took less time than those prepared with yellow bitter maniocs. Maniocs "*to grate*" are used mainly to obtain the starch of the roots by grating and washing them with water to eliminate cyanogenic compounds and precipitate the starch.

On the other hand, preparations made of yellow bitter manioc required root fermentation in water to liberate cyanogenic compounds, followed by the grating and squeezing of the root biomass to eliminate the cyanogenic compounds before cooking. Differences in the time required for bitter manioc processing might explain why the use of manioc "*to grate*" in communities that traditionally use mainly yellow bitter for their dishes is becoming more popular.

On the other hand, and according to the Tikuna, the use of yellow bitter maniocs among indigenous communities was promoted by outsiders for the elaboration of *farinha* as a non-perishable cash product, and so were new products indigenous people highly appreciate (such as *tucupí*). In this latter case, the toxicity of bitter maniocs is related with other organoleptic characteristics that are perceived by indigenous people as culinary advantage.

Indigenous people know the danger of consuming bitter maniocs when not properly prepared, yet they are not concerned about bitter manioc toxicity as they do not perceive this as a limitation to consume them. In fact, what we observed is that, presently, indigenous people from the communities we included in our study increase the use of bitter maniocs instead of, as we expected, increasing the use of sweet maniocs.

4.4. Discussion

4.4.1. Manioc diversity and manioc classification in indigenous communities of the Colombian Amazon

A total of 173 manioc landraces were collected and distinguished based on morphological parameters. Manioc diversity in study areas of comparable size ranged between 100 and 204 different morphotypes (Boster, 1986; Salick *et al.*, 1997; Heckler and Zent, 2008). This means that the methodology we used (*i.e.*, to assess community manioc diversity through a small group of experienced farmers) gave results comparable to earlier studies.

The numbers of distinguished morphotypes and genotypes differed in our inventory, as also observed in earlier studies (Elias *et al.*, 2000; Elias *et al.*, 2001; Vieira *et al.*, 2008). In some cases, morphological variations of identical genotypes can be attributed to genotype by environment interactions that cause unique morphotypes of the same genotype which local people classify as different landraces (Salick *et al.*, 1997). In other cases, morphologically similar landraces growing together are the result of an ideotypic selection of volunteer seedlings mixed with an already known landrace, resulting in more than one genotype per morphotype (Pujol *et al.*, 2007). In this study, 87% of the morphotypes indigenous farmers distinguished were also considered genetically different; this indicates that farmers recognized more variability in the morphological features of the landraces than the genomic assay did. The high coincidence between morphotypic inventories and genotypic inventories indicates that the descriptors used by indigenous farmers to discriminate different manioc landraces were rather accurate, and that they are experts in discriminating landraces in the field. This expertise has been developed through permanent contact with the different manioc landraces in their swiddens and the efficient transmission of this body of knowledge to other women.

The 93 SNPs selected to discriminate manioc genetic diversity allowed to differentiate different locations and communities (Figure 4.3A) and manioc groups (Figure 4.3B). The average observed heterozygosity across the 160 genotypes was 0.39, similar to heterozygosity reported for samples from Brazil (Oliveira *et al.*, 2014). Using SNP genotyping to discriminate samples genetically, 22 duplicates of genotypes were obtained among 173 samples. These duplicates matched landraces with morphological differences in one or more features (Table 4.2). However, most of the duplicates were consistently classified into the same manioc class according to their toxicity and use, or consistently identified by the color of the bulking root pulp. These two variables define the main characteristics indigenous farmers want to see in a landrace and this in the end will define the way in which a given landrace can be used.

Among scientists, manioc variability is classified in different ways, but toxicity (expressed in terms of the content of cyanogenic compounds) is by far the main feature for manioc classification (Aristizábal *et al.*, 2007; Silva *et al.*, 2008). Manioc landraces with less than 100 mg/kg of cyanogenic compounds are classified as sweet or of direct culinary quality, and manioc landraces with more than100 mg/kg of cyanogenic compounds are classified as bitter or of industrial quality (Wilson and Dufour, 2002; Aristizábal *et al.*, 2007), implying a major processing step is required. The concept of industrial quality is alien to indigenous classifications but by and large they follow the same major distinction of maniocs (Table 4.1) as needing a major processing step or ready to eat after minor processing. In addition, they add the color aspect as of major (culinary) importance.

Accidents of manioc poisoning are extremely rare in Amazonian indigenous communities; apparently, a biocultural co-evolution between people and manioc occurred (McKey *et al.*, 2010a). We evidenced no constraints whatsoever in the use of high toxicity maniocs among indigenous farmers, even though we observed an increase in the use of high toxicity maniocs. The use of low toxicity and high toxicity maniocs encourages indigenous farmers to maintain both types of maniocs in their production systems and thus a potential source of manioc variability that would, of course, be limited in regions where bitter maniocs are not appreciated for human consumption. However, farmers outside the Amazon Basin (as in some African countries) also find advantages in the cultivation of bitter maniocs (Fresco, 1986; Chiwona-Karltun *et al.*, 1998) and are increasingly including high-toxicity landraces in their productive systems (McKey *et al.*, 2010a).

It has been proposed that sweet and bitter maniocs were domesticated in different historical moments, and that these maniocs were distributed unevenly throughout the Amazon region—even though they are presently cultivated together in fields (Mühlen *et al.*, 2013). Our results show a clear genetic clustering for both sweet and bitter maniocs; this might support arguments in favor of a different origin of these two manioc classes. It has been proposed that sweet manioc landraces were domesticated in what is today the state of Rondônia in Brazil (Arroyo-Kalin, 2010) and that from there they spread along the main rivers of the Amazon Basin. This might explain why in Tikuna communities (such as San Martín de Amacayacu) located on the Amazon River and its main tributaries the use of sweet manioc varieties is dominant, while among ethnic groups living in the interfluvial region bitter maniocs dominate. Results also indicate the importance of interethnic marriages among neighboring ethnic groups. This implies a relatively high propagule exchange rate between neighboring groups that also exchange brides as compared against propagule exchange with far away communities, e.g., between San Martín de Amacayacu and the communities of the Middle Caquetá region. This propagule exchange through marriage between neighboring groups has also been observed in other communities (Coomes, 2010; Delêtre *et al.*, 2011; Pautasso *et al.*, 2013; Samberg *et al.*, 2013). The lack of exchange over longer distances strengthens geographical isolation, thus increasing overall manioc diversity in the Amazon region.

When the genomic composition of the morphotypes collected in this study were compared with the genotypes provided by CIAT's world collection most of the samples form a cluster apart from CIAT's genotypes. This indicates that although some of the genomic variability of maniocs from the Colombian Amazon is represented in CIAT's core collection, there is a substantial genetic diversity that is not contained by it. Similar findings were obtained when the germplasm of some Amazonian maniocs was compared with CIAT's core collection using microsatellites (Elias *et al.*, 2001; Elias *et al.*, 2004). The current study also showed clear that potentially diversity available in Colombian Amazon is poorly represented in CIAT's collection.

4.4.2. Sources of manioc variability among ethnic groups

Propagule exchange mechanisms are important sources to increase and maintain crop agrobiodiversity in the Amazon (Coomes, 2010), and manioc exchange is most likely to occur among nearby communities. However, manioc exchange can reduce diversity as active out-crossing of the different landraces exchanged may homogenize crop diversity (Dyer *et al.*, 2011). Our dendrograms show that there exist differences in manioc diversity among groups geographically separated by hundreds of kilometers; these differences however also appear in the cluster of the Middle Caquetá region where communities exist relatively close to one another. Delêtre *et al.* (2011) found that, in areas where ethno-linguistic boundaries are present, particular manioc groups are formed (and which they attribute to differences in marriage rules and therefore manioc exchange). Notwithstanding the differences in marriage rules between the communities studied by Delêtre *et al.* and the communities we researched (where, until recently, manioc exchange was limited by ethnic boundaries), the effect of marriage rules on manioc diversity seem to be comparable.

In our case, social rather than geographical exclusion allowed for the emergence of a relation between particular manioc landraces and ethnic identity; this in turn possibly strengthened the bond within, and the differentiation between, ethnic groups. For indigenous groups of the Colombian Amazon, manioc is not merely a crop; it also constitutes a symbol of identity. There are maniocs that identify ethnic groups with a common origin (*Manicuera* for *People of the Center*) as well as maniocs that identify particular ethnic groups (maniocs "*to eat*" for the Tikuna, yellow bitter maniocs for the Nonuya and Uitoto and maniocs "*to grate*" for the Andoke and Muinane). This link between ethnicity and manioc apparently occurs elsewhere as well, as is the case with the Miraña and the Bora (see above) or the Piaroa of the Venezuelan Amazon (Heckler and Zent, 2008). This particular segregation of maniocs among the different ethnic groups constitutes a source of manioc variation in the region.

Some of the maniocs that provide ethnic groups with their identity must have been obtained from volunteer seedlings selected long ago (so long ago that indigenous people consider them to be of a mythical origin), those that provide clan identity clearly showed that they were obtained through the selection of sporadic volunteer seedlings. These historical moments of volunteer seedlings selection are clear examples of a directional selection of volunteer seedlings. What most probably started as a selection for agronomic performance (Duputié *et al.*, 2009b) could later have led to the selection of a manioc landrace for distinctive features that could help clans to claim it as their own. Volunteer seedlings constitute an important source of manioc variability and are important for the selection of manioc landraces as ethnic identity markers. Today, indigenous farmers continue to incorporate volunteer seedlings into their manioc pools as 5% of the landraces they described were obtained from recently selected volunteer seedlings.

The fact that 33% of the total manioc inventory of landraces constituted a symbol of identity, and that from these *Manicuera*, more than 50% of the "*to eat*" maniocs and 40% of yellow bitter maniocs also have low genomic variability indicates that these landraces have been conserved without major modification to their genomes (that is: without significant recombination). The importance (in terms of historical memory) of these landraces for each one of the ethnic groups studied warrants the special treatment they receive. This fact notwithstanding, all manioc landraces (whether they are or are not attached to ethnic identity) are managed in the same way and planted in patterns that do not prevent possible sexual recombination of landraces.

In contrast to other ethnic groups in which shamans play an important role in the conservation of manioc landraces, in the communities we studied, women are wholly responsible for the management of manioc inventories and their conservation. Results indicate that indigenous women have a deep knowledge of these landraces and furthermore partake in effective knowledge transfer networks involving young women to perpetuate their conservation. This is why ethnic groups that have production systems based on swidden agriculture, have been less affected by outside interventions, and are still able to pass on the knowledge required to manage, conserve or otherwise increase manioc inventories. Swiddens can be considered effective *in situ* reservoirs of landraces with low genomic variability.

Duputié *et al.*(2009b) indicated that the incorporation of volunteer seedlings that had a too high level of inbreeding could reduce agronomic quality, while volunteer seedlings that had a too high level of outbreeding could blur highly appreciated landrace features. Apparently, the indigenous people we studied handle these probabilities appropriately through their intimate knowledge of the morphological characteristics that distinguish important landraces from others, by reproducing them clonally, by planting different landraces in clusters to maintain landraces' most important characteristics, and by testing volunteer seedlings for two or three production cycles before deciding whether to maintain them or not; the latter practice was also observed in the Wayãpi indigenous group (Duputié *et al.*, 2009b). These practices effectively help avoid the negative effects of cross-breeding in clonal populations.

As we show, the use of low toxicity or high toxicity maniocs was directly associated to ethnic culinary traditions (and which in turn provided a specific ethnic or clan-specific identity). Wilson and Dufour (2006) also found a direct relationship between the manioc inventories of the Tukano of the Colombian Vaupés and their culinary traditions. McKey *et al.* (2010a) propose that the use of particular manioc landraces among ethnic groups might be the result of the type of society. Accordingly, high toxicity maniocs would be most favored in large, sedentary societies along floodplains of major rivers where fish supply is abundant and a good part of the time could be used for high toxicity manioc processing. On the other hand, the use of low toxicity maniocs might be favored in smaller and more mobile societies where the main activities are based on hunting and gathering and where there is not enough time for processing manioc or for making or transporting the tools needed for it to a new settlement.

The hypothesis of McKey *et al.* (2010a) however does not hold for the case of the indigenous communities of this study. *People of the Center* who do have a tradition to use high toxicity maniocs do not originate from the floodplains of major rivers but rather from the interfluve between the Caquetá and the Putumayo rivers where the supply of fish is also limited (Pereira, 2011). Although they have moved out of their ancestral territories to areas with fertile floodplains, their tradition to use mainly high toxicity maniocs has not changed. On the other hand, the Tikuna, a much less mobile society than the ethnic groups of the Middle Caquetá region, adopted high-toxicity maniocs only recently and mainly as a way to obtain some cash for goods they cannot themselves produce. We therefore found that the preference for low toxicity or high toxicity maniocs was unrelated with the ease of processing and hence, according to our respondents, not an important reason to select or grow landraces.

4.4.3. Sources of manioc variability among communities

Fraser and Clement (2008) and Fraser *et al.* (2012) suggested that ADE could constitute a different edaphic environment for manioc cultivation which might drive an artificial selection of manioc landraces that perform better in those soils—thus increasing manioc diversity at the community level. However, the number of manioc landraces in our community inventories did not differ significantly between communities with or without access to ADE. Although according to indigenous farmers a few manioc landraces performed better in certain soils, most of the manioc landraces they cultivate grow well in any soil. These indigenous communities have not encouraged soil-manioc specificity, moving their manioc stocks indiscriminately between soils. Having manioc landraces that easily adapt to soil variations allows farmers to harvest enough manioc to satisfy their requirements independently of the soil characteristics of the swidden. Our respondents showed little interest in increasing manioc yields and seemed more concerned in preserving a variety of landraces to satisfy their culinary traditions, thereby maintaining what they deem to be a good quality of life. Our findings match those of Hastik *et al.* (2013) who also found no preference for the use of anthropogenic soils in an Amazonian region with low land use pressure. The favoring of a soil-manioc specificity might be an important aspect in Amazonian societies that are more integrated in the market and more interested in cultivating manioc as a cash crop, showing a proclivity to select specific soils such as ADE in order to improve yields as in the case of *Caboclos* from the Madeira River (Fraser, 2010a). Although manioc-soil specificity was not found in the communities we studied, Andoke and Uitoto narratives attribute an important role to ADE in the conservation of the first maniocs indigenous people manipulated. This is in agreement with the hypothesis that manioc is a native species of Amazonia (McKey *et al.*, 2010a; Arroyo-Kalin, 2012) and that ADE might have played an important role in manioc domestication (Arroyo-Kalin, 2010).

One factor that affected manioc diversity at community level was manioc exchange. The common inclination of farmers to maintain high numbers of manioc landraces can be explained through their concept of life-quality which is based on the notion of abundance of landraces and products. For indigenous people, the good life is “to eat well and live well” which basically means continuous access to a variety of foods which in turn will secure good health, harmonious relationships with the family and the other members of the community, as well as a prolific progeny (Acosta, 2013). Essential to this purpose is to secure an abundance of products and landraces that may serve as a buffer in difficult times.

Manioc exchange among indigenous communities of the Middle Caquetá region could be appreciated in the dendrograms of manioc genetic diversity. Dendrograms also showed a close relation between Tikuna manioc landraces and landraces from Peru (Figure 4.2). This latter relation could be explained by the geographical position of the community of San Martín de Amacayacu and the distribution of the Tikuna ethnic group in the region: the Tikuna’s traditional territory corresponds to the upper part of the Amazon River which includes parts of the Brazilian, Colombian and Peruvian Amazon (Acosta and Zoria, 2012). For the Tikuna, borders within what they consider to be their territory do not exist, and therefore sharing and exchanging manioc landraces with other Tikuna communities of the three countries is common. Finally, manioc exchange has also been induced by external pull factors such as the recent cultivation of high toxicity landraces to prepare yellow *farinha* as a cash product which is easily sold within the community and in close-by urban centers.

Apparently, instead of an erosion of manioc diversity due to outside interventions, manioc diversity has been maintained in the last century and, in some cases, increased by the interplay of three different factors. First, the continuity of local culture which has encouraged indigenous people to maintain manioc landraces with low genomic variation. Second, the continuous experimentation with volunteer seedlings in the field. Third, the willingness of indigenous farmers to maintain highly diverse inventories of manioc in their swiddens as a symbol of a good quality of life. From our perspective, as long as the relationship between indigenous people and manioc continues, the conservation of a high manioc diversity in the region is possible. In this sense, manioc could be considered more than just a crop in the Amazon region: it also needs to be seen as cultural heritage of Amazonian societies.

However, the permanent threats to the conservation of the Amazon Basin, together with the pressure to integrate indigenous people in currently prevailing economic models severely increases the risk of loss of indigenous crop diversity (Salick *et al.*, 1997; Steward, 2007). For this reason, it is expedient to understand the drivers of current manioc diversity and to locate manioc variability hotspots. Information about these issues might be important for those interested in maintaining and increasing public manioc collections, and for those interested in the conservation of manioc diversity, to help develop strategies to conserve these materials *in situ*. There are already some experiences showing that it is possible to protect both crop diversity and the collective knowledge indigenous people have of crops by way of geographical indications or denominations of origin (Acosta and Zoria, 2009) in which the use of molecular tools such as SNPs to discriminate landraces from specific localities or ethnic groups is accurate (Kawuki *et al.*, 2009; Li *et al.*, 2010b; Ciarmiello *et al.*, 2011). Since it is difficult to maintain a real representation of diversity in worldwide crop collections, the possibility to acknowledge and incorporate local farmers in the conservation of diversity could be a real alternative for crop conservation and the preservation of independent cultures. Unfortunately, initiatives to do so are still in their initial stages (Dulloo *et al.*, 2010).

4.5. Conclusions

Inventories of manioc of communities were both morphotypically and genotypically different, with a good correspondence between the two. The high manioc diversity observed in the five indigenous communities of our study is the result of different social factors that have historically affected manioc since its domestication. These social factors have played a more important role than for example e.g., differences in edaphic environments. The main reason for this is that manioc, the staple food for indigenous communities of the Amazon region, is a symbol of identity. Manioc variation is intimately related with ethnicity or clan membership and with local culinary traditions that express this identity. Manioc diversity is therefore linked to cultural aspects and it explains the importance and conservation of each one of the manioc landraces that today exist in our area of study. These aspects are lost when manioc landraces are conserved outside the communities that shaped these people-manioc relationships.

We sampled only five communities in the Colombian Amazon; since the Amazon Basin is inhabited by hundreds of different ethnic groups—each with its distinct people-manioc relationship—the number of manioc landraces in this Basin can be expected to be high and diverse. The knowledge indigenous farmers and, particularly, women have of the characteristics of the manioc landraces they manage, constitutes an important factor for the conservation of particular manioc landraces with low genomic variability. In addition to the particular manioc landraces conserved by each ethnic group, the incorporation of volunteer seedlings into farmers' portfolios and manioc exchange mechanisms are two important and permanent sources of manioc variability in the region.

Swidden agriculture provides indigenous people the opportunity to continue managing highly diverse stocks of toxic and non-toxic maniocs, as well as to select and conserve volunteer seedlings that spontaneously appear in their swiddens. Nevertheless, the production system of the indigenous communities from our study is not any more commonplace in the Amazon Basin or beyond. Today, many indigenous groups are disappearing or merge into larger societies—to the detriment of cultural diversity (UNEP and ACTO, 2009). Models of manioc production in which production depends on a limited number of genotypes with clear commercial advantages reduces the possibilities for social mechanisms to act in favor of promoting and sustaining manioc diversity.

The manioc diversity shown in this study represents a small sample as we only studied five of 420 ethnic groups (UNEP and ACTO, 2009). Nevertheless, this diversity is not fully represented by CIAT's world collection. *In situ* conservation of manioc diversity is possible but this can only be attained when the production systems of indigenous communities are themselves also conserved. It is therefore necessary that institutions interested in manioc conservation develop strategies to recognize and learn from these communities how they created their highly diverse manioc portfolios and help them conserve them as an important legacy for present and future generations.

Acknowledgements

We thank Tatiana Ovalle and Claudia Perea of the Manioc Genetics Laboratory of CIAT for their help in processing the manioc samples. We thank Charles Clement for his technical suggestions. We highly appreciate the help and hospitality we received by Fissi Andoke, Aurelio Suárez, José and Elías Moreno and Adriano Paky. We would especially like to show our gratitude to all the indigenous women of the communities of study for their active participation, help and willingness to share information about manioc with the research team.

Appendices

Table A 4.1. Morphological descriptors of manioc used to discriminate landraces in the field.

No.	CIAT ORACLE DATABASE (1995)	EMBRAPA (Fukoda and Guevara 1998)	Indigenous descriptors	Used	Observations
			PLANT GROWTH		
1	Form of the plant	Type of plant		No	Indigenous people recognize differences in the form of the plants but do not have specific class groups for it
2	Height of plant	Height of plant	Height of plant (tall, medium, small)	No	Plants in different stages
3	Height until the first branching	Height until the first branching		No	Indigenous people do not use metric instruments to measure it
4	Levels of branching			No	Difficult to estimate it in plants in different stages
5	Angle of branching			No	Indigenous people do not understand the metric differences between angles
6		Plant branching	Way of branching	Yes	
7		Phyllotaxis		No	Plants in different stages
8		Color of terminal branches in mature plants		No	Indigenous people consider this the same as the color of the apical leaf
			LEAF		
9	Width of leaf lobule			No	Indigenous people do not use metric instruments to measure it
10	Length central leaf lobule	Length central leaf lobule		No	Indigenous people do not use metric instruments to measure it
11		Length-width ratio of central leaf lobule		No	Indigenous people do not use metric instruments to measure it
12	Number of lobules in the leaf	Number of lobules in the leaf		No	There were plants with different numbers of lobules in leaves
13	Shape of the leaf lobule	Shape of the leaf lobule	Shape of the leaf lobule (oblong, round)	Yes	
14	Color of mature leaf	Color of mature leaf	Color of mature leaf	Yes	

15	Color of apical leaf	Color of apical leaf	Color of apical leaf	Yes	
16	Color leaf vein	Color leaf vein		No	Indigenous people consider this color is the same as that of the petiole
17	Pubescence	Pubescence		No	Not found
18		Prominences of foliar scares		No	Indigenous people do not consider it a characteristic of the plant
19		Sinusoid of leaf lobule		No	Indigenous people consider it as part of the shape of the leaf lobule
			PETIOLE		
20	Color of petiole	Color of petiole	Color of petiole	Yes	
21		Length of petiole		No	Indigenous people do not use metric instruments to measure it
22		Petiole position		No	Differences were not found
			STALK		
23	External color of stalk	External color of stalk	Outside color of stalk	Yes	
24	Color of stalk collenchyma	Color of stalk collenchyma		No	For some landraces indigenous people use it, for others they do not
25	Color of epidermis stalk	Color of epidermis stalk		No	
26	Way in which the stalk grows	Way in which the stalk grows		No	No clear differences in the way stalks grow found
27	Presence of purple stain in the stem			No	
28		Length of stipules		No	Indigenous people recognize this part in manioc plants but not as a descriptor to discriminate them
29		Margin of stipules		No	Indigenous people recognize this part in manioc plants but not as a descriptor to discriminate them
			ROOT		
30	External color of the root	Outside color of the root	Outside color of the root	Yes	
31	Color of root cortex		Color of root cortex	Yes	
32	Color of root pulp		Color of root pulp	Yes	
33		Presence of root stem	Presence of root stem	No	Indigenous people recognize it but do not consider a parameter to discriminate manioc landraces

34		Shape of root	Shape of root	Yes	
35		Root constrains		No	Indigenous people consider it as part of the shape of the root
36		Texture of root epidermis		No	Indigenous people from San Martín de Amacayacu recognize that in some cases maniocs transformed into a landrace called "caiman" and the epidermis of the root became scaly. Apparently it is related to a virus infection.
FLOWERING					
37		Flowering		No	Plants in different stages, some without flowers
			USES		
38	Use		Use	Yes	

Table A 4.2. SNPs used to estimate manioc genetic diversity, indicating the location of each SNP in the manioc genome, the most frequent allele, frequency of the most frequent allele, observed heterozygosity (Ho) as calculated by the PowerMaker software. Additional information of SNPs is available from the Cassava Genome Database (http://cassava.igs.umaryland.edu/cgi-bin/index.cgi).

SNP	Location in the manioc scaffold	Position in the scaffold	Reference nucleotide base	Alternative nucleotide base	Most frequent allele	Frequency of most frequent allele	Ho
SNPY-002	scaffold00341	522287	T	A	T	0.60	0.49
SNPY-003	scaffold00486	4139	T	C	T	0.51	0.45
SNPY-004	scaffold00506	357810	T	C	T	0.71	0.37
SNPY-008	scaffold00926	170134	G	A	G	0.79	0.36
SNPY-009	scaffold00977	131601	T	C	T	0.57	0.43
SNPY-011	scaffold01127	53623	G	A	G	0.54	0.50
SNPY-012	scaffold01131	100283	G	A	A	0.72	0.36
SNPY-014	scaffold01551	772988	A	C	C	0.80	0.35
SNPY-015	scaffold01624	211719	T	C	T	0.56	0.42
SNPY-016	scaffold01701	51387	C	T	T	0.69	0.53
SNPY-017	scaffold01782	87521	A	G	G	0.57	0.59
SNPY-018	scaffold01934	135374	C	T	C	0.55	0.51
SNPY-019	scaffold01945	1718	C	T	C	0.73	0.46
SNPY-021	scaffold02165	486046	T	G	T	0.85	0.29
SNPY-022	scaffold02242	58303	T	A	A	0.79	0.30
SNPY-024	scaffold02431	470148	C	T	T	0.41	0.46
SNPY-025	scaffold02477	29865	T	C	T	0.78	0.32
SNPY-026	scaffold02586	990	G	C	G	0.55	0.48
SNPY-027	scaffold02688	74739	A	T	T	0.52	0.42
SNPY-028	scaffold02886	10162	A	C	A	0.74	0.42
SNPY-030	scaffold02973	15845	T	A	A	0.63	0.47
SNPY-034	scaffold03049	652738	G	A	A	0.71	0.38
SNPY-035	scaffold03115	64538	G	C	C	0.90	0.19
SNPY-038	scaffold03175	199915	C	G	C	0.81	0.31
SNPY-042	scaffold03237	108434	T	C	T	0.62	0.52
SNPY-046	scaffold03363	322574	G	A	A	0.70	0.50
SNPY-047	scaffold03395	289363	C	T	T	0.71	0.38
SNPY-048	scaffold03404	16874	C	A	C	0.84	0.28
SNPY-051	scaffold03581	609409	G	C	G	0.69	0.43
SNPY-052	scaffold03602	328252	C	G	C	0.95	0.09
SNPY-053	scaffold03614	507488	A	G	A	0.83	0.29
SNPY-056	scaffold03741	509165	G	C	G	0.65	0.50
SNPY-063	scaffold03980	3811	G	A	G	0.77	0.37
SNPY-064	scaffold04043	961177	G	A	G	0.89	0.23

SNPY-066	scaffold04165	3471	C	T	C	0.62	0.48
SNPY-067	scaffold04209	58499	T	C	T	0.97	0.07
SNPY-072	scaffold04489	59448	T	C	C	0.70	0.36
SNPY-076	scaffold04803	23641	C	T	T	0.84	0.26
SNPY-077	scaffold04851	86189	T	C	C	0.72	0.36
SNPY-078	scaffold04895	248557	G	A	ND	ND	ND
SNPY-079	scaffold04953	260403	G	T	T	0.55	0.55
SNPY-080	scaffold05019	190612	C	T	C	0.80	0.38
SNPY-085	scaffold05709	65499	G	A	G	0.78	0.36
SNPY-086	scaffold05859	331862	C	T	T	0.50	0.39
SNPY-087	scaffold05865	82333	C	A	C	0.54	0.32
SNPY-090	scaffold06043	10403	T	C	T	0.98	0.03
SNPY-094	scaffold06548	79796	A	G	A	0.67	0.60
SNPY-095	scaffold06550	80150	A	G	A	0.54	0.44
SNPY-096	scaffold06582	530272	A	G	G	0.75	0.36
SNPY-098	scaffold06609	527660	T	C	T	0.69	0.43
SNPY-099	scaffold06700	120785	C	T	C	0.53	0.69
SNPY-100	scaffold06701	67024	T	G	G	0.68	0.48
SNPY-101	scaffold06707	231104	A	G	A	0.67	0.55
SNPY-102	scaffold06708	256386	G	C	C	0.76	0.33
SNPY-105	scaffold06914	436528	A	C	C	0.68	0.53
SNPY-108	scaffold07005	76128	G	A	G	0.77	0.31
SNPY-109	scaffold07035	786578	T	C	T	0.72	0.54
SNPY-111	scaffold07238	413538	T	C	C	0.69	0.43
SNPY-113	scaffold07478	906418	T	A	T	0.72	0.47
SNPY-116	scaffold07591	53616	A	C	A	0.82	0.24
SNPY-118	scaffold07778	195117	C	A	C	0.68	0.41
SNPY-120	scaffold07859	56295	G	A	A	0.90	0.19
SNPY-121	scaffold07991	525619	T	A	T	0.82	0.35
SNPY-125	scaffold08265	16150	T	C	T	0.90	0.18
SNPY-126	scaffold08359	711856	T	C	T	0.64	0.43
SNPY-127	scaffold08485	197096	G	A	G	0.80	0.33
SNPY-128	scaffold08500	174717	C	G	C	0.59	0.53
SNPY-129	scaffold08542	231091	G	A	G	0.52	0.40
SNPY-130	scaffold08655	139164	A	G	G	0.63	0.34
SNPY-131	scaffold08673	56121	G	C	C	0.66	0.47
SNPY-132	scaffold08799	195547	C	G	G	0.78	0.41
SNPY-134	scaffold08873	367474	A	G	G	0.80	0.34
SNPY-136	scaffold09260	286852	C	A	C	0.69	0.38
SNPY-137	scaffold09426	12925	T	C	C	0.75	0.37
SNPY-140	scaffold09520	7011	C	T	C	0.77	0.40
SNPY-141	scaffold09702	295652	A	T	A	0.75	0.44
SNPY-142	scaffold09876	604006	G	A	A	0.66	0.48
SNPY-145	scaffold10114	195492	G	A	G	0.63	0.48

SNPY-146	scaffold10173	304868	G	T	G	0.57	0.35
SNPY-148	scaffold10493	519834	T	C	T	0.61	0.35
SNPY-149	scaffold10504	2504	G	A	A	0.61	0.41
SNPY-152	scaffold10878	637609	T	C	T	0.52	0.59
SNPY-154	scaffold11110	114971	A	C	C	0.65	0.43
SNPY-159	scaffold11635	293538	G	A	A	0.83	0.29
SNPY-160	scaffold11661	207635	G	T	G	0.85	0.23
SNPY-161	scaffold11689	77485	A	T	A	0.56	0.57
SNPY-164	scaffold11998	903514	A	C	A	0.54	0.59
SNPY-165	scaffold12118	12855	T	A	A	0.79	0.34
SNPY-168	scaffold12248	10334	G	A	G	0.59	0.47
SNPY-170	scaffold12455	225034	C	T	C	0.70	0.40
SNPY-173	scaffold12657	33735	G	A	G	0.83	0.27
SNPY-175	scaffold12794	702004	A	T	A	0.87	0.25
SNPY-176	scaffold12828	6789	A	G	A	0.82	0.28

ND: Not determined for this SNP, as the assay did not give concluding results for some of the tested genotypes.

Chapter 5

Arbuscular mycorrhization of manioc in natural and anthropogenic soils of the Colombian Amazon region

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Abstract

Manioc (*Manihot esculenta* Crantz) is an arbuscular mycorrhiza dependent tropical crop. In the Amazon region, manioc mycorrhization has been studied mainly in acid, low-fertile soils, hardly in more fertile soils. In order to better understand manioc arbuscular mycorrhization in different Amazonian soils, research was conducted on mycorrhization of different manioc landraces cultivated in plots located on anthropogenic Amazonian Dark Earths (ADE), non-ADE uplands, and floodplains of the Colombian Amazon. The percentage of arbuscular mycorrhizal colonization of manioc roots was estimated after clearing and staining. Arbuscular mycorrhizal fungi species and communities in soils and in manioc roots were assessed using spore-based (only soil) and molecular (virtual taxa for soil and roots) approaches. Estimates of arbuscular mycorrhizal fungal diversity based on fungal DNA obtained from root samples were higher than those based on spores or DNA from soil samples. Arbuscular mycorrhizal fungal diversity was comparable across soil types. Arbuscular mycorrhization of manioc roots was independent of soil arbuscular mycorrhizal diversity, soil physico-chemical composition or the toxicity of manioc roots. Arbuscular mycorrhizal root colonization of maniocs grown on non-ADE or ADE uplands was higher than on annually flooded (low) floodplains. Particularities in the way manioc was cultivated on low floodplains and/or the prolonged annual flood affected manioc arbuscular mycorrhization. Although *Rhizophagus manihotis* was abundant in manioc roots across all observed soils and landraces, this is surprising as this species has not been reported on any forest species in the Amazon so far. Despite this abundance of *Rhizophagus manihotis* there was no evidence for co-adaptation between arbuscular mycorrhizal fungi and manioc landraces.

Key words: Arbuscular mycorrhiza, *Manihot esculenta*, indigenous agriculture, Amazonas, Colombia, ADE, virtual taxa.

5.1. Introduction

Arbuscular mycorrhization is the most common plant-fungus association between obligate endo-symbiont Glomeromycota fungi and roots of higher plants (Fitter and Moyersoen, 1996); it plays an important role in the supply of phosphorus and other immobile nutrients to host plants (Helgason and Fitter, 2009) but also has other benefits, such as protection against pathogens (Cardoso and Kuyper, 2006). That is why different studies focused on finding the best conditions for arbuscular mycorrhization of important crops. It has been hypothesized that plant ecotypes adapt to their local soil and native arbuscular mycorrhizal (AM) fungal communities producing more mutualistic AM associations (Johnson *et al.*, 2010; Herrera-Peraza *et al.*, 2011). Then, AM fungal communities are affected by soil conditions and plant species and communities, resulting in different levels of root colonization of host plants and in different levels of benefit of the AM association for these plants.

Among different edaphic variables, pH and phosphorus availability are major determinants of arbuscular mycorrhization (Entry *et al.*, 2002). Generally, AM fungi (AMF) are susceptible to acidity and plant roots are usually more colonized by AMF at near-neutral pH. However, some AMF genera such as *Acaulospora* sp. and *Gigaspora* sp., and some AMF species such as *Rhizophagus manihotis* are well adapted to low pH (Clark, 1997). Also in soils with alkaline pH specific AM fungal communities tolerant to high pH are able to colonize plant roots (Oliveira *et al.*, 2006). AM colonization of roots is more likely in soils with low phosphorus availability (less than 15 ppm). In soils with high phosphorus availability (more than 30 ppm), AM fungal communities are generally found to be reduced (Gosling *et al.*, 2013) and the AM association is inhibited or less efficient (Howeler *et al.*, 1982; Howeler and Sieverding, 1983; Habte and Manjunath, 1987). However, this pattern is not consistent for all plant species. Apparently, root colonization of maize by AMF is only affected by very high phosphorus availability (more than 140 ppm) (Gosling *et al.*, 2013).

AM fungal communities are also affected by plant species composition. In general, a more diverse vegetation is associated with more diverse AM fungal communities (Schnitzer *et al.*, 2011; Hiiesalu *et al.*, 2014). Roots of plant species from more diverse tropical forests have higher AMF richness than roots of plant species from less diverse vegetations (Öpik *et al.*, 2006); generalist plants, including crop plants, tend to associate with generalist AMF communities (Davison *et al.*, 2011).

The variable responses of AMF to pH levels and phosphorus availability across soils and plant species indicate that AMF adapt to soil conditions, and that some co-adaptation between AMF and plants grown in particular edaphic conditions can be expected. Understanding how environmental conditions favor the arbuscular mycorrhization of particular crops could provide hints for a more sustainable agriculture that secures the staple food of populations living in the tropics.

Particularly in the Amazon region, manioc (*Manihot esculenta* Crantz) is the most important staple crop for most native people (Chapter 4 of this thesis, Peña-Venegas *et al.*, 2014b). Manioc is highly dependent on and responsive to AM association, which could be due to the fact that its root system is inefficient in foraging nutrients in the soil once manioc roots are transformed to large bulky structures for starch storage (Akinbo *et al.*, 2012; Larson *et al.*, 2014). Manioc might compensate this limitation with arbuscular mycorrhization as it is always found to be associated with AMF (Howeler and Sieverding, 1983; Dodd *et al.*, 1990; Habte and Byappanahalli, 1994).

The AM association of manioc has been studied mostly in tropical soils with high acidity and low phosphorus availability (Howeler *et al.*, 1982; Howeler and Sieverding, 1983; Ceballos *et al.*, 2013). Under these soil conditions AMF species such as *Rhizophagus manihotis, Acaulospora colombiana* (Howeler and Sieverding, 1983), *Rhizophagus irregularis* (Ceballos *et al.*, 2013) and *Paraglomus occultum* (Dodd *et al.*, 1990) are important AM symbionts of manioc, establishing efficient AM associations and mobilizing phosphorus efficiently to the plant through the hyphal network. Acid, low-fertile upland soils are common in manioc cultivation in the Amazon region (Eden and Andrade, 1987; Wilson and Dufour, 2002a), but other, more fertile soils are also used. Manioc is cultivated in Amazonian Dark Earths (ADE) (Fraser and Clement, 2008; Fraser *et al.*, 2012; Chapter 2) and floodplain soils (Acosta and Mazorra, 2004; Adams *et al.*, 2005; Fraser *et al.*, 2012; chapter 2) but there is no information about manioc arbuscular mycorrhization on those soils. On the one hand, ADE are patches of anthropogenic soil usually less acid and with (much) higher phosphorus availability than non-anthropogenic soils (Glaser *et al.*, 2001). The particular conditions of ADE increase soil microbial activity (Glaser and Birk, 2012; Lehmann *et al.*, 2011), but the high phosphorus availability of ADE could also inhibit AM associations. On the other hand, floodplain soils are alluvial soils periodically enriched with nutrient-rich sediments that are transported and deposited by rivers. Floodplains are less acid and with moderate phosphorus availability compared with non-anthropogenic upland soils (Piedade *et al.*, 2001), but aerobic AM fungi might be affected by the periodical floods that floodplains experience. This is supported by the often lower root colonization in plants growing in floodplains than in non-flooded environments (Entry *et al.*, 2002).

Additionally and according to Davison *et al.* (2011), the transformation of forests into croplands could affect AMF community composition selecting for more generalist AMF. In the Amazon region manioc is cultivated mainly under two different types of agriculture: under swidden agriculture for one to three years in uplands and high floodplains that do not flood yearly, leaving the plot for a long fallow period of more than 10 years; and under a continuous agriculture in low floodplains where manioc is cultivated yearly, with only a brief fallow during the flooding period (Chapter 2). Manioc interacts for a longer time with native AM fungal communities in low floodplains than in uplands or high floodplains due to the differences in fallow duration. It is expected therefore that a co-adaptation as the one reported by Ceballos *et al.* (2013) is more likely to occur in low floodplains.

In addition to edaphic conditions and plant communities that could affect manioc-AM fungal associations, the interaction between manioc and AMF could depend on the level of the root toxicity of the manioc. In the Amazon region, two different manioc types with different levels of root toxicity are cultivated (Wilson and Dufour, 2002; Aristizábal *et al.*, 2007; Chapter 4): sweet maniocs (landraces with less than 100 mg/kg of cyanogenic compounds in their roots) and bitter maniocs (landraces with more than100 mg/kg of cyanogenic compounds in their roots). Cyanogenic compounds are very toxic to living organisms inactivating respiration when they are tightly bound to cytochrome-c oxidase and other metalloproteins (Raybuck, 1992). Because AMF do not have a cyanide-resistant respiration (Lambers, 1982), an inhibitory effect on the AM colonization of manioc roots with high cyanogenic contents is expected, consistent with observations that mycorrhizal colonization was lower in sorghum landraces with high levels of cyanogenic compounds in roots (Miller *et al.*, 2014).

There are many aspects of manioc arbuscular mycorrhization that have not been addressed and that are relevant to identify the best conditions in which manioc arbuscular mycorrhization occurs in the Amazon region. Research was conducted to assess how much AM fungal communities and manioc arbuscular mycorrhization differ among contrasting soils and contrasting manioc landraces of the Amazon region. We hypothesized that different Amazonian soils have different AMF communities which would be reflected in the composition of AM fungal communities in manioc roots grown in those environments. Arbuscular mycorrhization of sweet and bitter maniocs might also be different due to differences in the root toxicity of manioc types. Co-adaptation between native AMF and manioc might occur more readily in manioc landraces grown on low floodplains than in other environments.

5.2. Material and methods

5.2.1. Study area

This study was conducted at two locations in the Colombian Amazon. One was the Middle Caquetá River region in the southern part of the Caquetá state of Colombia. There, swiddens on three soil types were studied: (i) non-ADE uplands with superficial soils from sedimentary origin, originated by the erosion of Paleozoic parental materials (IGAC, 1979). These upland fields were from the indigenous communities of Guacamayo (00º31´25” South;72º22´38” West), Villazul (00º 40´00” South; 72º16´32” West), and Peña Roja (00º 44´29” South; 72º 05´09” West); (ii) ADE from Araracuara and La Sardina described by Eden (1984) and ADE with fields from the indigenous community of Aduche (00º39´21” South; 72º17´32” West) described by Peña-Venegas *et al.* (2015a, Chapter 3 of this thesis); and (iii) high floodplain soils flooded each 5 to 10 years from the Caquetá riverside with fields from the communities of Peña Roja and Villazul, and high floodplains from the Mariñame Island owned by indigenous farmers from the Peña Roja community (00°01´57.8” South; 72°06´35.1” West).

The other location was in the municipality of Leticia in the southern part of the Amazonas state of Colombia. There, swiddens on the same three soil types were studied: (i) non-ADE uplands from denudation origin, formed over old floodplains of the Amazonas River, but not affected by actual river floods (IGAC, 1979). Upland field here were from a local farm in the locality of Puerto Triunfo (4°05´29.5” South; 69°29´55.6” West); (ii) a patch of ADE located near the Tacana River (04^{0}05´29,5"South; 69^{0}29´55,6" West) and described by Morcote-Ríos and León-Sicard (2011) with fields from the Perez family, a Uitoto family part of the indigenous community Kilómetro 11; and (iii) a low floodplain soil from Fantasy Island located in the Amazonas River (4°10´09” South; 69°57´25” West) which is flooded every year with fields from Tikuna families who live in Leticia and neighboring communities.

Soil types in uplands were identified in the field as ADE when the A horizon was deeper than 25 cm, had a dark color (Munsell soil color charts codes corresponding to black to very dark brown colors) and ceramics were present and as non-ADE when the A horizon was lighter, more shallow and without ceramics. Floodplains were identified by their position relative to the river level. Indigenous farmers indicated which floodplains were high and which were low.

5.2.2. Agricultural fields sampled

Swiddens on uplands were established after logging and burning areas of mature forests or secondary forests of more than 40 years old (Appendix Table A5.1). There, manioc was planted with other crops but manioc was the dominant crop species, covering more than 70% of the swidden area. In each swidden, more than 12 different manioc landraces, including sweet and bitter types, were cultivated. Manioc harvesting started 10 months after planting and continued for just over two years. During the prolonged harvesting period farmers selectively harvest daily the few manioc plants they need. For our sampling we depended on farmers choices. Swiddens in high floodplains were established on plots with secondary forest of 5 to 10 years old (Appendix Table A5.1) also these were logged and burned prior to planting. Manioc was the dominant species. Manioc harvesting started after five months and continued for two months. Samples of manioc roots were collected in fields between 5 and 6 months old. In low floodplains manioc is cultivated annually in a production system denominated “flood-recession agriculture” (Shorr, 2000) where the fallow period corresponds to the time the floodplain is flooded. Fields on low floodplains are not burned before planting. In this agriculture system, manioc was cultivated exclusively. All manioc was harvested 5 months after planting prior to the flooding and samples of manioc roots were collected at that time. No fertilizers or other external inputs were used in any of the agriculture systems used to crop manioc.

A total of 26 fields were sampled (Appendix Table A5.1): 13 located on non-ADE upland soils, 8 on ADE upland soils, and 5 on floodplain soils.

5.2.3. Root and soil collection

Root and soil samples were taken between September 2011 and September 2012 in the 26 fields reported in Table A5.1 (Appendix). Manioc roots were collected from plants farmers were harvesting. We did not have direct control on the manioc landraces harvested as manioc selection for harvesting depended on farmers’ needs. However, in most of the cases at least three plants per manioc landrace per field were collected. Per manioc plant between 5 and 25 fine roots were collected directly from manioc bulky roots or the stem roots. The local name of each manioc landrace and whether it was sweet or bitter according to the farmer was recorded. Sweet landraces were those indigenous farmers did not consider toxic and that did not need a post-harvesting process before consumption. Bitter landraces were those indigenous farmers considered toxic and that needed a post-harvesting process to decrease their toxicity before consumption.

Fine-root samples were stored in paper bags within a plastic bag with silica gel as dehydrating agent until arrival at the laboratory (after one week). Some of the manioc landraces were collected in more than one community. At the end, a total of 174 root samples of 47 different manioc landraces including 39 sweet and 135 bitter maniocs were collected (Table 5.1). During manioc root collection, simultaneously a sample of the soil adhering to roots and from the hole where the cassava was growing was collected. Per field these soil samples were mixed to obtain a composite soil sample of about 500 g. At laboratory, soil samples were dried at room temperature (25°C and 50% humidity).After soils were dry, they were temporarily stored at 4°C for one month.

After, a subset of the 174 root samples and corresponding soil samples collected was selected to determine AM fungal community composition based on spore morphotyping (soil samples) and molecular analyses (soil and root samples).

The subset was based on whether a landrace had been sampled in all three soil types and consisted of 12 soil samples and 37 root samples organized in a factorial (incomplete) design of 3 soil types × 5 manioc landraces (Table 5.2).

Table 5.1. Manioc root samples evaluated in this study.

Soil	Location	No. samples	No. manioc landraces	No. of samples per manioc type	
				Sweet	Bitter
Non-ADE	Amazonas	8	6	5	3
	Caquetá	65	25	4	61
ADE	Amazonas	8	6	4	4
	Caquetá	53	21	7	46
Floodplain	Amazonas	18	4	11	7
	Caquetá	22	12	8	14

Table 5.2. Description of the subset of samples used to assess arbuscular mycorrhizal community composition of soils and manioc landraces. Numbers correspond to the number of samples analyzed per manioc landrace in each soil.

		Manioc landrace				
Soil	Sample	Sweet	Bitter			
		Cáscara morada	*Guava*	*Borugo*	*Yucuna*	*Amarilla*
Non-ADE	1	1				
	2		5		2	
	3			2		
	4					2
ADE	1	2				
	2		3			
	3			2		
	4			1		
	5				5	
	6					1
Floodplain	1	2	3		3	1
	2	1		1		

From each 500 g soil sample three sub-samples of 50 g were taken and stored at 4°C to assess AM fungal communities by a spore-based approach; a sub-sample of 100 g was taken and stored at -70°C to assess AM fungal communities by molecular analyses. The remaining 250 g was conserved at room temperature until processing to assess soil physico-chemical composition. Each one of the 37 root samples of the subset was divided into two. One half was stored at 4°C for later use to assess AM colonization, and the other half was stored at -70°C for later use to assess AM fungal communities by molecular analyses.

5.2.4. Laboratory analyses

Laboratory analyses were carried out between January 2013 and October 2014. Manioc root staining and AM spore isolation and description of morphotypes from the soil samples were done at the Laboratory of Microbiology of the Instituto Amazónico de Investigaciones Científicas Sinchi in Leticia, Colombia. Molecular analyses to estimate AM fungal community composition of soil samples and of manioc root samples were done at the Institute of Botany and Ecology of the University of Tartu, Estonia. Soil physico-chemical analyses were done at the National Soil Laboratory of the Instituto Geográfico Agustín Codazzi-IGAC in Bogotá, Colombia.

5.2.5. Estimating AM root colonization

Root samples were processed by clearing, and thereafter staining roots with trypan blue (Phillips and Hayman, 1970). The percentage of AM root colonization was estimated by the gridline intersect method (Giovannetti and Mosse, 1980), to obtain the total percentage of AM root colonization in 100 root intersections observed. The procedure was repeated thrice per sample.

5.2.6. AM fungal communities of different Amazonian soil types

5.2.6.1. Molecular investigations of soil and root samples

The PowerMax® Soil DNA Isolation Kit (MoBio laboratories, Inc.) was used for soil DNA isolation, following the instructions of the provider but with a modification in the quantity of soil processed. Five grams of each soil sample was processed instead of 10g as suggested in the protocol.

For root DNA isolation, 70 mg of fine manioc roots were placed in tubes with 1.1 mm and 2.3 mm tungsten carbide beads in a mixer mill run at 30 revolutions per sec to crush the roots. The samples were shaken three times for 2 min, moving each time the position of the tubes to secure a complete crushing of all roots. The PowerSoil® DNA Isolation kit (MoBio laboratories, Inc.) was used for root DNA isolation, following the instructions of the provider and with a slight modification during the elution of the samples. During elution, the sample was divided into two 50-µl sub-samples. The first 50µl were eluded with the solution for elution and centrifuged at room temperature for 30 sec at 10.000 *g*. The remaining 50 µl were added to the same tube with the solution of elution and centrifuged in the same way before discarding the spin filter.

After DNA isolation of soil and root samples, the samples were processed together for PCR amplification, including a sample of non-mycorrhizal *Plantago* roots as negative control. PCR was done using Qiagen'sHotStarTaq Master Mix and using the SSU rRNA NS31 and rRNA AML2 primers for AM detection (Öpik *et al.*, 2009). The final PCR reaction volume was 12.5 µl composed of 6.25 µl of HotStarTaq Master Mix (2x); 0.5 µl of the forward SSU rRNANS31 primer (5-10 pmol/µl); 0.5 µl of the reverse SSU rRNAAML2 primer (5-10 pmol/µl); 1.0 µl template DNA; and 4.25 µl of PCR water. The PCR was run under the following conditions: 95°C × 15 min followed by 35 cycles of 94°C × 30 sec, 58°C × 30 sec, and 72°C × 1 min, and finalizing 72°C × 10 min, 10°C hold and end. PCR products were checked by electrophoresis in a 1.5% agarose gel in 1×TBE plus 1 µl of ethylene bromide per 100ml. Five µl of each PCR product was mixed with 1µl of 6× Loading Dye and placed in the electrophoresis wells.

PCR products were purified from the gel using the QiagenQIA quick Gel Extraction kit (Quagen GmbH, Germany). A second PCR was done using a 1:10 dilution of the products first obtained. In this PCR adaptors were added to the primers used before. The first primer was composed off an A adaptor+6bp barcode in addition to NS31 and the second was composed off a B adaptor+8bp barcode in addition to AML2. The conditions for the second PCR were: 95°C × 15 min, followed by five cycles of 42°C × 30 sec, 72°C × 90 sec, and 92°C × 45 sec, and 20 cycles of 65°C × 30 sec, 72°C × 90 sec, and 92°C × 45 sec, and finalizing with 65°C × 30 sec, 72°C × 10 min hold and end. The PCR products were purified as before and quantified using NanDrop 1000 (Thermo Scientific, Wilmington, USA). Three µg of the DNA obtained was used for sequencing on a Genome sequencer FLX system.

5.2.6.2. Assessing AM fungal communities by morphotyping of spores

The same subset of 12 swidden soil samples was also used to assess AM fungal community composition of the different soil types by a spore-based approach, recovering AMF spores directly from the swidden soils. Three replicates of 10 g of each soil were wet-sieved and centrifuged in a sucrose gradient as explained by Gerdemann and Nicolson (1964). AMF spores were quantified per sample and separated in morphotypes. About 10 spores of each morphotype were placed on microscope slides with lactoglycerine and on microscope slides with lactoglycerine and Melzer's reagent (1:1) for genus and species identification. Spore characteristics of each morphotype were recorded in drawings and pictures for identification. AMF determination was done comparing AMF spore morphotypes with vouchers described on the INVAM webpage (2012); in the Peña-Venegas *et al.* (2006) catalogue; and in the Schenck and Perez (1988) catalogue. As AMF inventories were done based on field-collected spores, not all spores recovered were fresh. Therefore, the information for spore-based inventories is provided in presence-absence terms and not as quantitative values.

5.2.7. Soil physico-chemical analysis

Analyses included soil texture (granulometry), pH (1:1 in water), percentage of organic carbon (Walkley – Black), cation exchange capacity expressed in ppm (with normal and neutral ammonium acetate), Ca, Mg, K, Na expressed in ppm (by DTPA extraction), percentage of total bases (base saturation with normal and neutral ammonium acetate), and available phosphorus expressed as mg kg^{-1} of dry soil (Bray II), executed according to the standardized methodologies of the laboratory (IGAC, 2006).

5.2.8. Statistical analysis

The 454 sequences fasta file obtained from root and soil sample sequencing was cleaned in Java using bioinformatics pipeline (Öpik *et al.*, 2006). First, primers and Tag of 100% of identity was checked. Then, individual sequences (amplicons) of 170 nucleotides in length or longer were included in the analysis. When they were longer than 520bp, sequences were cut at that base number and the remaining bases were eliminated. The presence of chimeric sequences was checked using UCHIME. The percentage of possible chimeras was less than 1% and these were removed.

A closed reference OTU (Ordinary Taxonomic Units) picking strategy was used to compare the sequences obtained against those in the MaarjAM database to find hits and no-hits of sequences with virtual taxa (VT; as are called OTU in MaarjAM database). It was considered a hit when a sequence matched for 97% or more and the alignment was more than 95% for the shorter sequences through a BLAST analysis. After comparisons, a pivot table was constructed with the obtained hits. For further analyses, virtual taxa that only appeared once (singletons) in the complete matrix were considered artefacts and removed. For statistical analysis, the information obtained in the thus cleaned pivot table was used.

As two different types of samples (soil and root) and three different types of soils were used to assess the AMF community richness, two redundancy analyses (RDA) were done to evaluate, on the one hand, the influence of the type of sample used in the observed composition of the AMF community, and on the other hand, if there were differences in the AM fungal community composition of soil types. For that, the sequence values of each one of the virtual taxa were transformed into their log (x+1). RDA was done using the vegan option in the R package.

Kruskal-Wallis one way ANOVA tests were done to evaluate the differences between the number of virtual taxa recovered from soil and root samples, the number of virtual taxa in each type of soil, the abundance of AMF genera in soil types, and the abundance of AMF spores in the different soil types.

Additional Kruskal-Wallis tests were done to evaluate differences in the root AM fungal communities of manioc growing in different soil types, differences in the number of virtual taxa colonizing manioc roots, differences in the root AM colonization and the number of virtual taxa of the two types of maniocs (sweet and bitter), and among manioc landraces. Kruskal-Wallis tests were done using the Analytical Software Statistix 9.0 (Statistix, 1998) with $p \leq 0.05$ as criterion to consider differences significant. When significant differences were found, a Tukey multiple pair wise comparison test was used to check the source of those differences.

5.2.9. Permissions

The research was undertaken in the frame of the Agreement of June 2004, signed by the Sinchi Institute and the AZICATCH, CRIMA and ACITAM indigenous organizations to work together on swidden agriculture. Soil and manioc root sample collection was done in the frame of the legislation for research institutes associated to Colombia's Ministry of Environment in which the Sinchi institute does not need permission for research activities (Decreto 302 de 2003, MINAMBIENTE) and could make collections when the material collected is for research purposes only, without a commercial interest (Decreto 1376 of 2013). Soil and roots used for molecular analysis were transported with the phyto-sanitary certificate of the ICA No. 013-07211 and exported from Colombia under the permission No. 00369 of the Autoridad Ambiental de Licencias Ambientales - ANLA of Colombia, and allowed into Estonia under the Letter of Authority No. 29 of Estonia for the introduction and/or movement of organisms, plants or plant products for scientific purposes.

5.3. Results

5.3.1. Arbuscular mycorrhizal fungal community composition of the study area

The molecular approach recovered 85,530 sequences of Glomeromycota from root samples and 4,056 sequences from soil samples. From all sequences 67,628 (75.5%) matched with sequences previously recognized as virtual taxa in the MaarjAM database. The other 21,958 sequences (24.5%) corresponded to no-hits. From these sequences, some were grouped in sequence types that could belong to 14 new virtual taxa.

A total of 92 known virtual taxa were recovered. RDA analysis showed that the virtual taxa richness was significantly affected by the type of sample used to assess it ($p< 0.01$). From the 92 virtual taxa, 49 virtual taxa were recovered from soil samples and 89 were recovered from root samples. These virtual taxa belonged to nine AMF genera: *Acaulospora*, *Ambispora*, *Archaeospora*, *Claroideoglomus*, *Gigaspora*, *Glomus* (Figure 5.1), *Paraglomus*, *Rhizophagus* and *Scutellospora* (Tables 5.3 and 5.4).

RDA analysis showed that the virtual taxa richness was significantly affected by the type of sample used to assess it ($p< 0.01$). From the 92 virtual taxa, 49 virtual taxa were

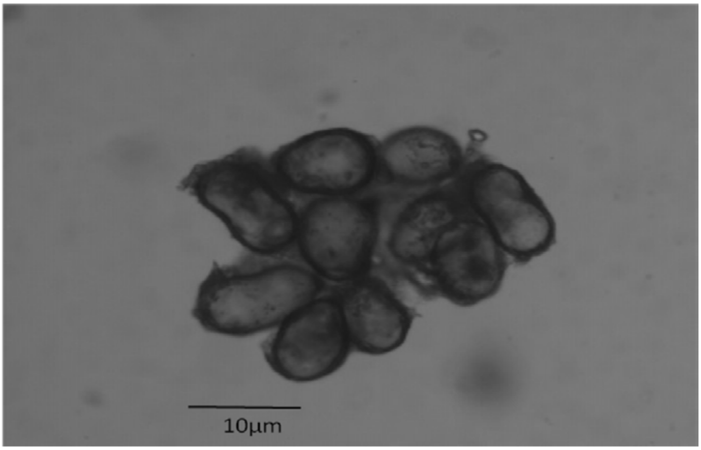

Figure 5.1. Spores of an undetermined *Glomus* which might be represented in some of the sequences obtained by molecular approaches.

recovered from soil samples and 89 were recovered from root samples. These virtual taxa belonged to nine AMF genera: *Acaulospora*, *Ambispora*, *Archaeospora*, *Claroideoglomus* *Gigaspora*, *Glomus*, *Paraglomus*, *Rhizophagus* and *Scutellospora* (Tables 5.3 and 5.4). Although all genera were present in both manioc root samples and soil samples, the frequency of appearance was different among samples. For example, *Scutellospora* was recovered only from ADE soil samples but was recovered from root samples of plants obtained in all three soil types (Tables 5.3 and 5.4). Additionally, most virtual taxa present in soil samples were also present in manioc roots except three that were only recovered from soil samples: *Ambisporaleptoticha* (VTX00103) and two *Glomus* sp. (VTX 00125 and VTX 00130).

Significant differences were observed in the virtual taxa richness of soils with both soil samples (p=0.02) and manioc root samples (p= 0.05). From soil samples, the most abundant virtual taxa in non-ADE, ADE and floodplain soils were *Glomus* VTX00126, *Glomus* VTX00082, and *Glomus* VTX00410 respectively. From roots samples, the most abundant virtual taxa in non-ADE, ADE and floodplain soils were *Glomus* VTX 00280; *Glomus* VTX00093, and *Rhizophagus manihotis* (VTX00090) respectively. Generally, exclusive virtual taxa were always found in low amplicon number while common virtual taxa shared by two or three soils were always frequent (Tables 5.3 and 5.4). For soil samples, non-ADE presented more exclusive virtual taxa (13) than the other soils while for root samples floodplain soils presented more exclusive virtual taxa (13) than the other soils (Tables 5.3 and 5.4).

For the spore-based approach, spores collected directly from swidden soils were evaluated. The number of AMF spores collected in 10 g of soil sample was between 83 and 114 spores without significant differences in the number of AMF spores isolated among different soil samples (p= 0.62).The spore-based approach yielded seven AMF genera (*Acaulospora, Ambispora, Funneliformis, Gigaspora, Glomus, Rhizophagus* and *Sclerocystis*) in 38 AM spore morphotypes, and four unidentified spore taxa (Table 5.5). The AM community composition of soils based on spores differed among soil types. Exclusive morphotypes in specific soils were more common in non-ADE and ADE than in floodplain soils. In floodplain soils only one exclusive morphotype was registered. Only three morphotypes were found in all three soil types (Table 5.5).

Table 5.3. Inventory of virtual taxa (VTX based on MaarjAM database (version March 31st of 2013)) recovered from swiddens in non-anthropogenic uplands (Non-ADE), Amazonian Dark Earths (ADE), and floodplains of the Colombian Amazon. Relative abundance as the average number of sequences recovered of each virtual taxon.

Virtual taxa	AM species	Non-ADE	ADE	Floodplain
VTX00126	*Glomus* sp.	240.5	17.7	5.5
VTX00399	*Glomus* sp.	236.5	1.8	0.0
VTX00270	*Glomus* sp.	26.3	0.0	0.0
VTX00280	*Glomus* sp.	23.8	8.7	0.0
VTX00089	*Glomus* sp.	34.0	9.0	0.0
VTX00080	*Glomus* sp.	23.0	0.2	0.0
VTX00070	*Glomus* sp.	20.5	6.7	0.5
VTX00167	*Glomus* sp.	12.0	1.7	0.0
VTX00028	*Acaulospora* sp.	10.5	0.7	0.0
VTX00004	*Archaeospora* sp.	7.3	0.2	0.0
VTX00312	*Glomus* sp.	3.3	0.0	0.0
VTX00108	*Glomus* sp.	4.8	0.0	0.0
VTX00253	*Glomus* sp.	3.3	0.0	0.0
VTX00398	*Glomus* sp.	1.0	0.0	0.0
VTX00242	*Ambispora leptoticha*	1.0	0.0	0.0
VTX00092	*Glomus* sp.	0.8	0.0	0.0
VTX00248	*Glomus* sp.	0.5	0.0	0.0
VTX00087	*Glomus* sp.	0.3	0.0	0.0
VTX00057	*Claroideoglomus* sp.	0.3	0.0	0.0
VTX00163	*Glomus* sp.	0.3	0.0	0.0
VTX00360	*Glomus* sp.	0.3	0.0	0.0
VTX00030	*Acaulospora* sp.	0.3	0.0	0.0
VTX00082	*Glomus* sp.	3.3	42.8	0.0
VTX00024	*Acaulospora* sp.	0.0	17.7	0.0
VTX00368	*Glomus* sp.	0.0	1.7	0.0
VTX00096	*Glomus* sp.	0.0	1.5	0.0
VTX00255	*Scutellospora heterogama*	0.0	0.8	0.0
VTX00222	*Glomus* sp.	0.0	0.7	0.0
VTX00124	*Glomus* sp.	0.0	0.5	0.0
VTX00212	*Glomus* sp.	0.0	0.3	0.0
VTX00166	*Glomus* sp.	0.0	0.3	0.0
VTX00069	*Glomus* sp.	0.0	0.2	0.0
VTX00283	*Ambispora fennica*	0.0	0.2	0.0
VTX00219	*Glomus* sp.	0.0	0.2	0.0
VTX00410	*Glomus* sp.	0.0	0.0	8.5
VTX00342	*Glomus* sp.	0.0	0.0	0.5
VTX00093	*Glomus* sp.	31.8	24.2	0.5
VTX00026	*Glomus* sp.	21.8	16.5	0.0
VTX00238	*Paraglomus occultum*	19.8	18.2	0.0
VTX00090	*Rhizophagus manihotis*	1.5	1.2	0.0
VTX00039	*Gigaspora decipiens*	4.0	4.8	0.0
VTX00375	*Paraglomus* sp.	0.5	0.2	0.0
VTX00403	*Glomus* sp.	0.5	0.7	0.0
VTX00130	*Glomus* sp.	0.3	0.3	0.0
VTX00076	*Glomus* sp.	1.5	0.0	1.0
VTX00113	*Glomus* sp.	0.3	0.0	0.5
VTX00199	*Glomus* sp.	0.0	0.2	0.5
VTX00143	*Glomus* sp.	0.0	0.2	0.5
VTX00125	*Glomus* sp.	0.0	0.2	0.5

5.3.2. Arbuscular mycorrhizal fungal communities in different soil types

Soils were variable in their physico-chemical composition (Appendix Table A5.2). Contrary to what was expected, ADE showed the lowest average values for the pH and the lowest content of magnesium and potassium, although ADE had higher organic carbon (between 1.1 and 2.6%) and available phosphorus (between 16.4 and 720 mg kg^{-1}) than non-ADE or floodplain soils.

Although soil types were very variable, and anthropogenic and non-anthropogenic uplands were not contrastingly different, RDA analysis showed that there were significant differences in the virtual taxa colonizing manioc roots (of the subset, Table 5.2) related with the type of soil where maniocs were growing ($p= 0.01$). An RDA triplot (Figure 5.2) shows that there was a large group of virtual taxa common between the three soils such as *Rhizophagus manihotis* which was the most abundant taxon colonizing manioc roots across soil types. It was the most abundant in floodplains with 764.5 reads on average, the second most abundant in non-ADE with 393.5 reads on average, and the third most abundant in ADE with 240.9 reads on average (Table 5.4). But the RDA triplot also shows that there were some virtual taxa specific to soil types. *Glomus* VTX00089 (as X-89 in the graph) was more frequent in ADE with an average number of reads of 58.9, than in non-ADE uplands or floodplains with 0.8 and 5.6 reads, respectively, (Table 5.4); *Glomus* VTX00312 (as X-312 in the graph) was more frequent in floodplain soils with an average number of reads of 180.6, than in non-ADE or ADE uplands with 13.5 and 34.6 reads, respectively (Table 5.4); and *Acaulospora* VTX00024 (as X-24 in the graph) was more frequent in non-ADE with an average number of reads of 353.7, than in ADE or floodplain soils with 37.8 and 28.0 reads, respectively (Table 5.4).

Differences were not only in the virtual taxa colonizing roots grown in different soils, also in the genera colonizing them. Significant differences were obtained for the genus *Achaeospora* ($p< 0.01$) observed only in roots of plants grown in ADE and *Claroideoglomus* ($p=0.05$) observed more frequently in roots of plants grown in floodplains (Table 5.6).

Although there were differences in the AMF colonizing manioc roots in the different soils, the number of virtual taxa colonizing manioc roots in each type of soil was marginally different among soil types ($p=0.08$). Manioc roots cultivated in non-ADE, ADE and floodplain soils were colonized by 14±6, 15±5, and 19±5 virtual taxa respectively.

Table 5.4. Inventory of virtual taxa recovered from root samples of manioc plants growing in swiddens in three soil types of the Colombian Amazon: non-anthropogenic uplands (Non-ADE), Amazonian Dark Earths (ADE), and floodplains. The relative abundance of each virtual taxon (VTX) is estimated according to the average number of sequences recovered for each VTX. Taxonomic determinations based on the identification of virtual taxa from the MaarjAM database (version March 31st of 2013).

Virtual taxa	AM species	Non-ADE	ADE	Floodplain
VTX00024	*Acaulospora* sp.	353.7	37.8	28.0
VTX00418	*Glomus* sp.	97.5	0.0	0.5
VTX00028	*Acaulospora* sp.	65.0	6.4	0.7
VTX00248	*Glomus* sp.	48.1	0.0	2.5
VTX00178	*Glomus* sp.	41.8	0.7	0.4
VTX00227	*Acaulospora* sp.	33.4	10.0	5.5
VTX00115	*Glomus* sp.	20.0	0.1	1.5
VTX00113	*Glomus* sp.	19.2	0.2	3.9
VTX00087	*Glomus* sp.	10.3	0.0	0.0
VTX00359	*Glomus* sp.	8.9	0.0	0.0
VTX00292	*Glomus* sp.	8.3	0.6	0.5
VTX00153	*Glomus* sp.	6.8	0.0	0.0
VTX00039	*Gigaspora decipiens*	2.6	0.9	0.0
VTX00109	*Glomus* sp.	2.6	0.0	0.0
VTX00129	*Glomus* sp.	2.1	0.1	0.0
VTX00084	*Glomus* sp.	1.5	0.5	0.0
VTX00370	*Glomus* sp.	0.9	0.0	0.0
VTX00199	*Glomus* sp.	0.1	0.0	0.0
VTX00030	*Acaulospora* sp.	0.7	0.0	0.0
VTX00091	*Glomus* sp.	0.2	0.0	0.0
VTX00093	*Glomus* sp.	174.3	290.2	74.7
VTX00420	*Glomus* sp.	0.0	142.8	51.6
VTX00070	*Glomus* sp.	10.6	68.1	2.5
VTX00089	*Glomus* sp.	0.8	58.9	5.6
VTX00004	*Archaeospora* sp.	0.0	32.2	0.0
VTX00080	*Glomus* sp.	4.8	28.4	1.1
VTX00255	*Scutellospora heterogama*	1.2	23.7	2.7
VTX00167	*Glomus* sp.	0.0	11.1	0.7
VTX00051	*Archaeospora* sp.	0.0	9.4	0.0
VTX00249	*Archaeospora* sp.	0.0	4.0	0.0
VTX00410	*Glomus* sp.	0.0	3.3	1.2
VTX00361	*Glomus* sp.	0.0	0.9	0.0
VTX00247	*Glomus* sp.	0.0	0.5	0.1
VTX00343	*Glomus* sp.	0.0	0.4	0.1
VTX00253	*Glomus* sp.	0.2	0.4	0.2
VTX00222	*Glomus* sp.	0.0	0.2	0.0
VTX00079	*Glomus* sp.	0.1	0.2	0.0
VTX00122	*Glomus* sp.	0.0	0.2	0.0
VTX00342	*Glomus* sp.	0.0	0.1	0.0
VTX00143	*Glomus* sp.	0.0	0.1	0.0
VTX00090	*Rhizophagus manihotis*	393.5	240.9	764.5
VTX00312	*Glomus* sp.	13.5	34.6	180.6
VTX00108	*Glomus* sp.	0.3	77.9	116.4
VTX00092	*Glomus* sp.	0.2	0.4	101.3
VTX00268	*Glomus* sp.	0.1	78.4	70.3
VTX00264	*Rhizophagus clarum*	14.8	22.1	69.2

VTX00269	*Glomus* sp.	9.2	7.2	54.1
VTX00124	*Glomus* sp.	0.0	2.9	48.8
VTX00403	*Glomus* sp.	10.6	1.7	25.5
VTX00076	*Glomus* sp.	2.3	4.6	16.5
VTX00212	*Glomus* sp.	0.0	0.0	11.1
VTX00057	*Claroideoglomus* sp.	0.0	0.0	10.3
VTX00069	*Glomus* sp.	0.1	0.1	10.0
VTX00383	*Glomus* sp.	0.0	0.0	8.3
VTX00163	*Glomus* sp.	2.8	0.1	6.1
VTX00193	*Claroideoglomus lamellosum*	0.0	0.0	2.1
VTX00295	*Glomus* sp.	0.0	0.7	1.4
VTX00204	*Glomus* sp.	0.0	0.0	2.1
VTX00283	*Ambispora fennica*	0.0	0.0	1.8
VTX00360	*Glomus* sp.	0.0	0.1	1.4
VTX00112	*Glomus* sp.	0.2	0.2	0.5
VTX00077	*Glomus* sp.	0.0	0.0	0.5
VTX00001	*Paraglomus* sp.	0.0	0.0	0.5
VTX00186	*Glomus* sp.	0.0	0.0	0.5
VTX00159	*Glomus* sp.	0.0	0.0	0.4
VTX00215	*Glomus* sp.	0.0	0.0	0.3
VTX00074	*Glomus* sp.	0.0	0.0	0.2
VTX00055	*Claroideoglomus* sp.	0.0	0.0	0.2
VTX00219	*Glomus* sp.	0.0	0.0	0.1
VTX00082	*Glomus* sp.	150.3	214.0	7.1
VTX00238	*Paraglomus occultum*	4.7	3.0	0.6
VTX00368	*Glomus* sp.	0.6	0.6	0.0
VTX00375	*Paraglomus* sp.	0.1	0.1	0.0
VTX00166	*Glomus* sp.	0.1	0.1	0.0
VTX00364	*Glomus* sp.	0.1	0.2	0.0
VTX00318	*Scutellospora* sp.	0.1	0.1	0.0
VTX00419	*Glomus* sp.	0.1	0.1	0.0
VTX00041	*Scutellospora castanea*	0.1	0.1	0.0
VTX00327	*Glomus* sp.	0.1	0.1	0.0
VTX00280	*Glomus* sp.	513.0	1.2	609.1
VTX00126	*Glomus* sp.	352.1	161.4	226.9
VTX00398	*Glomus* sp.	0.3	0.0	0.2
VTX00072	*Glomus* sp.	0.1	0.0	0.1
VTX00399	*Glomus* sp.	0.3	0.1	0.3
VTX00270	*Glomus* sp.	20.3	257.6	226.0
VTX00026	*Glomus* sp.	1.3	9.1	5.6
VTX00096	*Glomus* sp.	0.1	11.4	12.5
VTX00105	*Rhizophagus intraradices*	0.3	0.6	0.5
VTX00397	*Glomus* sp.	0.1	0.1	0.1

Table 5.5. Presence of AMF spores of identified morphotypes in swidden soils located in Amazonian Dark Earths (ADE) and non-ADE uplands, and high floodplains of the Colombian Amazon. Numbers indicate the number of swiddens in which the AMF morphotype was recovered.

MORPHOTYPE	DESCRIBED BY	Non-ADE (n=4)	ADE (n=6)	High floodplains (n=2)
Acaulospora rehmii	Sieverding & Toro 1989	1	0	0
Acaulospora sp2		1	0	0
Gigaspora gigantea	Nicolson & Gerdemann 1968	1	0	0
Glomus pansihalos	Bech & Koske 1986	1	0	0
Sclerocystis rubiformis	Gerdemann & Trappe 1974	1	0	0
Glomus sp2		1	0	0
Glomus sp16		1	0	0
Ambispora leptoticha	Schenck *et al.* 1984	2	1	0
Funneliformis geosporum	Walker 1982	2	3	0
Glomus magnicaule	Hall 1977	3	1	0
Glomus microaggregatum	Koske & Gemma 1986	1	1	0
Glomus sp5		1	1	0
Glomus sp6		1	1	0
Glomus sp8		1	1	0
Glomus sp9		2	1	0
Glomus sp10		1	1	0
Glomus sp11		1	3	0
Glomus sp14		1	1	0
Glomus sp17		1	1	0
Glomus aggregatum	Schenck & Smith 1982	2	2	0
ND* sp3		3	1	0
Acaulospora foveata	Janos &Trappe 1982	3	3	2
Acaulospora sp 1		2	2	1
Glomus sp1		1	2	1
Glomus sp7		1	0	1
ND* sp4		1	0	1
Gigaspora sp1		0	2	0
Glomus reticulatum	Bhattacharjee & Mukerji 1980	0	1	0
Glomus sp3		0	3	0
Glomus sp12		0	1	0
Glomus sp13		0	1	0
Glomus sp15		0	1	0
Rhizophagus manihotis	Schenck *et al.* 1984	0	3	0
Glomus sp4		0	2	1
Acaulospora morrowiae	Schenck *et al.* 1984	0	2	1
Acaulospora tuberculata	Janos &Trappe 1982	0	1	1
ND* sp2		0	1	1
ND* sp1		0	0	1
Average number of AMF morphotype per soil type		9	9	6

* ND corresponds to unidentified samples as the morphotypic features of spores were not enough to establish the genus.

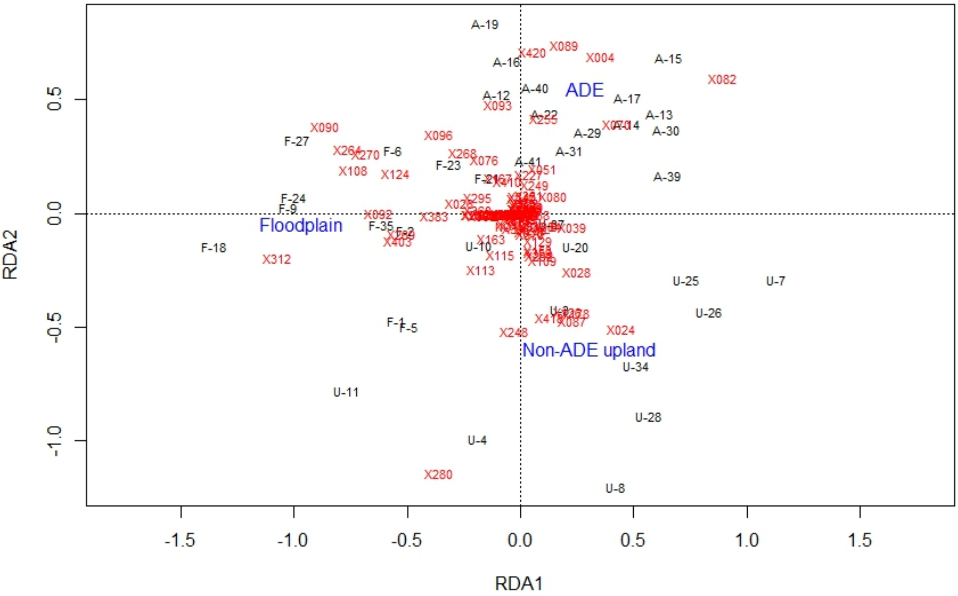

Figure 5.2. RDA triplot showing the distribution of virtual taxa (red labels) colonizing manioc roots and the sampling sites (black labels). Sequence values of virtual taxa were transformed as log (x+1) before analysis. U, A and F as prefix in site labels refer to non-ADE upland, ADE and floodplain sites respectively. Virtual taxa are indicated by the letter X followed by the number of the virtual taxon, according to the nomenclature used in the MaarjAM database (Axis 1 explained 7% of the variation of virtual taxa ($p<0.01$) and Axis 2 explained 5.1% of the variation of virtual taxa ($p= 0.01$)).

Table 5.6. Frequencies (as numbers of reads) of arbuscular mycorrhizal fungal genera in manioc roots grown in three soil types. Values correspond to means with standard deviations between brackets.

Genus	Non-ADE (n = 12)	ADE (n = 14)	Floodplain (n = 11)
Acaulospora	452.8 (593.9)	54.2 (55.6)	34.3 (55.3)
Ambispora	0	0	1.8 (6.0)
Archaeospora	0	45.6 (75.4)	0
Clareideoglomus	14.8 (34.2)	22.1 (35.7)	81.7 (89.2)
Gigaspora	2.6 (5.4)	0.9 (1.2)	0
Glomus	1536.6 (1041.2)	1472.6 (973.3)	1891.1 (1508.4)
Paraglomus	4.8 (14.9)	3.1 (10.9)	1.2 (1.9)
Rhizophagus	393.8 (752.3)	241.5 (372.6)	765.0 (897.9)
Scutellospora	1.3 (4.0)	23.9 (74.8)	2.7 (7.5)

All manioc roots collected in the three type of soils were colonized by AMF. Manioc root colonization was dominated by hyphae; vesicles or arbuscules were rarely present. The AM colonization of manioc roots was not significantly affected by differences between soils (p = 0.82). On average, fractional root AM colonization of maniocs grown on non-ADE, ADE and floodplain soils was 52±23, 58±15, and 51±23 % respectively. When the root AM colonization of the 174 manioc roots sampled was compared, there were significant differences among soils (p=0.01). The average AM colonization of manioc roots was similar between non-ADE and ADE (62±21 and 63±21 % respectively), but root AM colonization of maniocs grown on floodplain soils was lower (39±32 %).

AM colonization of manioc roots was significantly different among the different floodplains (p<0.01). Root samples collected from low floodplains of Fantasy Island had significantly lower percentages of root AM colonization than roots from high floodplains of Mariñame Island or the Caquetá riverside (Table 5.7).

Table 5.7. Percentage of arbuscular mycorrhizal colonization of manioc roots in floodplain soils. Values correspond to means with standard deviations between brackets Difference were significantly different (p<0.05) according to a Kruskal-Wallis ANOVA text. Averages followed by the same letter were not significantly different as established with a multiple pair-wise Tukey test (p=0.05).

Floodplain where the swidden was located	Number of samples evaluated	Mycorrhizal root colonization (%)
Caquetá riverside (Caquetá)	18	64.5 (22.8) a
Mariñame Island (Caquetá)	4	56.5 (11.1) a
Fantasy Island (Amazonas)	18	9.2 (5.8) b

5.3.3. Co-adaptation of arbuscular mycorrhizal communities with manioc landraces

The root AM colonization of sweet and bitter maniocs was not significantly different in the sub-set of 37 samples (p=0.78). No significant differences occurred (p=0.90) either in the number of virtual taxa colonizing sweet manioc roots (15±6) or bitter manioc roots (15±5) or in the number of virtual taxa colonizing individual manioc landraces (p=0.60). *Cáscara morada* was colonized on average by 15±6 different virtual taxa, *Guava* by 15±5, *Borugo* by 15±7, *Yucuna* by 13±5, and *Amarilla* by 19±7. However, the virtual taxa colonizing sweet and bitter maniocs most frequently differed in their abundance (as number of reads). *Glomus* VTX00280 was the most abundant AM fungus colonizing sweet maniocs, followed by

Rhizophagus manihotis and *Glomus* VTX00092. *Rhizophagus manihotis* was the most abundant AM fungus colonizing bitter maniocs, followed by *Glomus* VTX00126 and *Glomus* VTX00280.

When all 174 manioc root samples were analyzed, significant differences occurred in the AM root colonization of sweet and bitter maniocs (p =0.01) (Table 5.8). However, because the AM root colonization of manioc was significantly affected by flooding regime, a second test was done excluding root samples collected from all floodplains. In this case, the differences in the root AM colonization of manioc types were not significant (p = 0.88).

Table 5.8. Arbuscular mycorrhizal fungi colonization of root length expressed as percentage. Values are averages with the standard deviation in parenthesis. The asterisk indicates significant differences based on a one-way Kruskal-Wallis ANOVA test (p ≤ 0.05).

Manioc type	n	% root length colonized by AMF All samples	n	% root length colonized by AMF excluding floodplain samples
Sweet maniocs	39	43 (29)	20	62 (21)
Bitter maniocs	135	61 (23)	114	63 (21)
Significance		*		ns

5.4. Discussion

5.4.1. Estimation of AM fungal community composition by different approaches

Both methodologies, the spore-based approach and the molecular approach, identified the same AMF genera in soils (*Glomus* sp., *Acaulospora* sp., and *Rhizophagus* sp.) as principal, and many unidentified species (4 spore morphotypes and 21,958 sequences). Results are in concordance with previous reports where *Glomus* sp. (including *Rhizophagus* as formerly included in this genus) and *Acaulospora* sp. were identified as the main genera present in Amazonian soils (Peña-Venegas, 2010; Freitas *et al.*, 2014), and where the number of uncultured taxa from Glomerales was high (Ohsowski *et al.*, 2014).

Inventories obtained with the two methodologies showed differences. Differences in this study between the genera reported from spore-based approaches and molecular approaches may have partly be caused by imprecise classifications of AMF spores of closely related genera (*Archaeospora* with *Ambispora*; *Claroideoglomus*, *Funneliformis*, *Rhizophagus*, and *Paraglomus* with *Glomus* in its traditional sense). The identification of virtual taxa as AMF species or the correspondence of the described spores with virtual taxa is at present difficult, because of the low number of virtual taxa with an AMF species name assigned. There are few reports in which AM spores are clearly identified based on genomic barcode sequences from these spores (Stockinger *et al.*, 2010). Additionally, for some AMF genera such as *Glomus* sp., spores do not provide enough morphological parameters to easily distinguish different species, and, therefore, most spore collections are multi-species mixtures where DNA sequencing then yields results of poor comparability (Stockinger *et al.*, 2010). That is why some previous studies suggested a combination of different methodologies to provide a more comprehensive picture of AM fungal communities (Gamper *et al.*, 2008). Our work provides additional support to this approach.

Additionally, the type of sample used to assess soil AM fungal communities showed to have an effect on the inventories reported. On the one hand, a higher number of virtual taxa was recovered from roots than from soils as a consequence of a higher concentration of AMF in roots than in soils (Saks *et al.*, 2013). On the other hand, the virtual taxa recovered in the highest frequency (number of reads) from soil samples are likely to be those that also produce most propagules in the soil (spores). These differed clearly from the most abundant virtual taxa colonizing manioc roots. This result supports previous reports that AMF that sporulate abundantly in soils are often not those colonizing abundantly plant roots (Sanders, 2004).

Two AMF genera seem to have some soil specificity: *Achaeospora* and *Claroideoglomus*. *Archaeospora* is an AM genus with a broad geographic distribution, reported in natural and anthropogenic landscapes associated to wild and cultivated plants, but commonly reported in low frequencies. *Archaeospora* seems to occur in relatively high frequencies in acid soils (Bhatia *et al.*, 1996) with high percentages of sand (Stutz *et al.*, 2000; Blaszkowski *et al.*, 2002; Shi *et al.*, 2012), which could explain the presence of *Archaeospora* on some of the sandy ADE (Table 5.4) and non-ADE uplands (Table 5.3) of this study. *Claroideoglomus* is a genus that produces abundant spores in soils. It has been suggested that *Claroideoglomus* tends to dominate crop fields while *Rhizophagus* tends to dominate areas with long fallows (Jemo *et al.*, 2014). In our study *Claroideoglomus* was more abundant in high floodplains with short fallows than in ADE or non-ADE uplands with long fallows, or in the continuously cultivated low floodplain.

From the few virtual taxa with correspondence to a specific AMF species, most were

AMF species with a worldwide distribution. *Ambispora leptoticha*, first denominated as *Acaulospora appendiculata* (Schenck *et al.*, 1984) was reported for the first time for croplands of Colombia, but it has been reported around the world associated with croplands and natural forests (Kojima *et al.*, 2004). *Claroideoglomus lamellosum* was first reported in North America, but also reported in Europe (Walker and Vestberg, 1998; Blaszkowski *et al.*, 2002). *Rhizophagus clarum,* currently considered closely related to or a synonym of *Rhizophagus manihotis* (INVAM, 2014) but in this study with a different DNA sequence, is a well-known AM symbiont of many different tropical crops around the world. *Rhizophagus manihotis* was initially isolated from croplands of Colombia (Schenck *et al.*, 1984), but it has been reported in anthropogenic and disturbed tropical soils of Asia and Africa (Higo *et al.*, 2011; Voko *et al.*, 2013). *Gigaspora decipiens* has been reported in Australia and India (Hall and Abbott, 1984). *Paraglomus occultum* has been reported in North America and Europe (Walker, 1982; Stutz *et al.*, 2000). *Rhizophagus intraradices* was first reported in the south of the United States (Schenck and Smith, 1982) and associated with different crops. *Scutellospora castanea* was first reported in Europe (Walker *et al.*, 1993). *Scutellospora heterogama* was first reported in North America but has also been observed in Central and South America (Morton and Msiska, 2010). From the above, *Ambispora leptoticha* (Stürmer and Siqueira, 2008), *Gigaspora decipiens* (Stürmer and Siqueira, 2008), *Rhizophagus clarum* (Stürmer and Siqueira, 2008), *Paraglomus occultum* (Cordoba *et al.*, 2001), *Scutellospora castanea* (Schneider *et al.*, 2013) and *Scutellospora heterogama* (Novais *et al.*, 2014) have been reported in Brazil. In addition, *Paraglomus brasilianum* was described first in Brazil (Spain and Miranda, 1996). The only AM species that has not been described before in Colombia, the Amazon region or surrounding countries is *Ambispora fennica* which has been reported as a AM native species of Finland (Walker *et al.*, 2007).

5.4.2. Co-adaptation of AMF and manioc landraces in different soil types

All soils where manioc roots were collected were acid with pH values below 4.4 and with high variability in their percentage of organic carbon and phosphorus availability (Appendix Table A5.2). Those are the edaphic conditions where native AMF communities evolved.

It has been suggested that ADE might have more diverse and abundant microbial communities than non-ADE in response to the higher amounts of biochar and organic matter in ADE that provide enhanced conditions to microorganisms (Lehmann *et al.*, 2011), expecting more diverse and abundant AMF in ADE than in non-ADE. In addition, AMF are aerobic organisms sensitive to low soil oxygen concentrations (Entry *et al.*, 2002; Freitas *et al.*, 2014). AMF spore germination is inhibited at low oxygen concentrations and AM root colonization is directly correlated with soil redox potential (Entry *et al.*, 2002). Therefore, more diverse and abundant AM fungal communities could be expected in uplands than in floodplains. Contrary to what was expected, the AM fungal community composition of soils was different but all were equally diverse (based on the number of virtual taxa). Reports on the microbial composition of ADE showed that bacterial communities were different when compared with adjacent non-ADE, but not more diverse (Grossman *et al.*, 2010). Our results are in line with the findings by Grossman *et al*. in the sense that the anthropogenic changes to the soil led to differences in AM fungal communities when compared to background soils, but the abundance or diversity was neither increased nor decreased.

Regarding floodplains, periodical floods as occur on high floodplains did not considerably affect the AM fungal community composition of soils or root AM colonization. AM colonization of manioc roots was around 60% at five months after planting (Table 5.7) comparable with values previously reported for manioc in uplands (Ceballos *et al.*, 2013). This was different for low floodplains in which root AM colonization was around 10%. Low floodplains differed from the other soils in that they are annually flooded and are cultivated continuously. All manioc is harvested before the water rises, leaving the soil almost clean of vegetation and so clean of living roots to “host” AMF. The fallow period corresponds to the flooding period. Therefore, after the flood, there is little remaining vegetation that could support an AM hyphal network to quickly colonize the manioc that is planted. Colonization will have to start most likely from spores and pieces of root coming from other sites. This could explain the much lower root AM colonization values for maniocs roots grown on low floodplains from Fantasy Island (Table 5.7).

The two manioc types and the five manioc landraces tested on all soils were colonized by a similar number of virtual taxa and presented similar values of AM colonization of roots, independent of the soils in which they were grown or the type of agriculture used. This is in concordance with observations made by Burns *et al.* (2012) who also found that sweet and bitter maniocs had similar AM root colonization in poor soils of Mozambique. Two of the three most frequent virtual taxa colonizing manioc roots were shared between sweet and bitter maniocs. Therefore, evidence of co-adaptation between manioc and AMF was not observed in this study. Signs of co-adaptation between plants and native AMF have been reported for grasses in pot experiments (Johnson *et al.*, 2010) and coffee in semi-natural environments (Herrera-Peraza *et al.*, 2011). It is possible that due to the nature of manioc as an AM-dependent and highly responsive plant it is always highly colonized by AMF, irrespective of AMF species present in the soil, contrary to grasses and coffee plants that are largely mycorrhizal independent species. Additionally, the way manioc is currently planted in the Amazon region does not favor a co-adaptation process. Manioc interacts for a short time with native AMF in the swidden (usually 1 to 2, but never more than 3 years) in comparison with the long time forest species interact with native AMF due to the long fallow periods (between 15 and more than 100 years) (Chapter 2). Interestingly in our study, a single manioc root was associated on average with 16±5 AMF species which is closer to the commonly observed 18.2 AMF species in forest species than to the 5 AMF species commonly observed in crop species (Öpik *et al.*, 2006). In other words swiddens here seem to maintain a biology closer to natural systems.

It was not possible to argue that manioc, a crop species, were associated with generalist AMF species as suggested by Davison *et al.* (2011). In this study manioc was associated with a high number of AMF (16±5 in average) which included what could be considered as generalist AMF species such as *Rhizophagus manihotis*, but also with unknown *Glomus*. It seems that the relation of crops with generalist AMF species depends on temporal dynamics of the vegetation.

Rhizophagus manihotis was frequent and abundant in manioc roots. Disturbing soils broke the external mycelia of AMF, but particularly in *Rhizophagus manihotis* those pieces of mycelia may have become effective propagules to infect roots (Boddington and Dodd, 1999). Additionally, *Rhizophagus manihotis* is more abundant in cropland located in sites previously covered by forests (Jemo*et al.* 2014). Swidden agriculture could thus favor the presence of *Rhizophagus manihotis* in swidden soils, favoring manioc root colonization by *Rhizophagus manihotis* independently from the edaphic conditions. This AMF species was also mentioned in previous reports in soils where manioc grew exceptionally well (Howeler and Sieverding, 1983; Howeler, 2002) which may suggest some manioc-*Rhizophagus manihotis* specificity. The affinity of manioc-*Rhizophagus manihotis* has been reported always in acid soils with low phosphorus availability. We additionally showed that *Rhizophagus manihotis* can colonize effectively manioc roots in soils with high phosphorus availability. In this study *Rhizophagus intraradices* was also colonizing manioc roots in all three soil types but in very low frequencies (number of reads). Although *Rhizophagus intraradices* seems to be an adequate AMF to inoculate manioc (Ceballos *et al.*, 2013), the authors based their selection more on the capacity to produce enough propagules to inoculate manioc than on the affinity between manioc and this AMF species. Therefore, the observed good effect of *Rhizophagus intraradices* on manioc might be also found with other AMF strains.

Manioc is propagated clonally by stems that are free of AMF. Thus, manioc roots are colonized by AMF present in the soil in which the stems are planted. *Rhizophagus manihotis* has been commonly reported as an AMF present in agricultural fields colonizing different crops (Schenck *et al.*, 1984; Jemo *et al.*, 2014). But swiddens in which manioc is cultivated came from secondary forests with long fallows. Therefore it had to be present in roots of native trees, shrubs or herbs in the vegetation that was cleared to create the agricultural fields. As *Rhizophagus manihotis* has not been reported from Amazon forest species yet (Stürmer and Siqueira, 2008; Leal *et al.*, 2009; Freitas *et al.*, 2014), our circumstantial evidence that it must be present on forest species will need further corroboration by direct observations.

5.5. Conclusions

Our results indicated that AM fungal communities of soils in which manioc is grown, are different in the number of taxa and their abundance. We are still far from knowing the AM fungal community composition of soils, the distribution of AMF species across the globe and the environmental conditions that shape AM fungal communities.

This work is the first report of AM fungal communities in Amazonian Dark Earths (ADE). However, there is a wider variation in ADE properties (pH, available phosphorus, calcium, etc.) than covered in this study and therefore more sampling in the Amazon basin is necessary with special attention to Central Amazonia, where very rich ADE soils occur (cf. Fraser and Clement (2008) and Glaser and Birk (2012)).

Through agronomic experiments scientists have tried to find specific AMF for specific crops that increase AM root colonization, and especially plant nutrition and biomass yield under different soil conditions (Ceballos *et al.*, 2013). It seems that for manioc there is no need for that specificity in any environmental condition or for any manioc landrace cultivated.

Acknowledgements

To Gladys Cardona, Edmundo Mendoza, Misael Rodriguez, and Eugenia Guayamba of the Sinchi institute for their collaboration in the field work and in processing manioc root samples. To Marcela Nuñez for her help using the statistical software. We especially thank Dr. Maarja Öpik, Dr. Martin Zobel and Dr. John Davison for their help in the molecular analysis of soil and manioc root samples. We also would like to express our gratitude to all the indigenous women of the studied communities for their help identifying and collecting samples of the different manioc landraces for this study.

Appendices

Table A5.1. Description of indigenous fields (swiddens and flood-recession plots) used to collect soil and manioc root samples to study the arbuscular mycorrhizal association. Fields are ordered by soil type, swidden age indicates the age of plants when sampled, information on fallow refers to the age of the fallow preceding the current cultivation.

Soil type	Location of swidden	Swidden age since planting (in months)	Age of the fallow / forest before transformation into agricultural field
Non-ADE (n=13)	Peña Roja (Caquetá)	13	Secondary forest 25 years old
	Peña Roja (Caquetá)	13	Forest older than 100 years old
	Peña Roja (Caquetá)	12	Secondary forest (Unknown age)
	Guacamayo (Caquetá)	13	Forest older than 100 years old
	Guacamayo (Caquetá)	10	Secondary forest (Unknown age)
	Guacamayo (Caquetá)	12	Secondary forest (Unknown age)
	Guacamayo (Caquetá)	13	Secondary forest (Unknown age)
	Guacamayo (Caquetá)	12	Secondary forest (Unknown age)
	Guacamayo (Caquetá)	12	Forest older than 100 years old
	Guacamayo (Caquetá)	12	Forest older than 100 years old
	Villazul (Caquetá)	11	Forest older than 100 years old
	Puerto Triunfo (Amazonas)	13	Forest older than 100 years old
	San Sebastian (Amazonas)	12	Forest older than 100 years old
ADE (n= 8)	Aduche (Caquetá)	15	Secondary forest 20 years old
	Aduche (Caquetá)	11	Secondary forest 32 years old
	Aduche (Caquetá)	9	Secondary forest 15 years old
	Aduche (Caquetá)	10	Forest older than 100 years old
	Araracuara (Caquetá)	12	Secondary forest 70 years old
	La Sardina (Caquetá)	12	Secondary forest 5 years old
	Villazul (Caquetá)	11	Secondary forest 10 years old
	Tacana (Amazonas)	10	Secondary forest 5 years old
Floodplain (n=5)	Peña Roja (Caquetá)	5	High floodplain riverside forest 10 years old
	Peña Roja (Caquetá)	6	High floodplain riverside forest 5 years old
	Villazul (Caquetá)	5	High floodplain riverside vegetation 3 years old
	Mariñame Island (Caquetá)	6	High floodplain forest 5 years old
	Fantasy Island (Amazonas)	6	Flooding period of 6 months

Table A 5.2. Physico-chemical composition of swidden soils used to estimate the composition of arbuscular mycorrhizal communities by molecular approaches. Values correspond to means with standard deviations between brackets.

Soil	Sand[a]	Silt[a]	Clay[a]	pH[b]	% CO[c]	CEC[d]	Ca[e]	Mg[f]	K[g]	Na[h]	T.B.[i]	%BS[j]	P[k]
Non-ADE uplands (n=4)	49.1 (12.8)	34.9 (10.4)	15.9 (2.3)	4.4 (0.5)	2.3 (0.5)	12.8 (3.3)	0.9 (0.7)	0.7 (0.4)	0.3 (0.2)	0.1 (0.1)	2.0 (0.1)	16.7 (7.9)	19.3 (27.8)
ADE uplands (n=6)	87.7 (5.4)	7.3 (3.1)	5.1 (2.7)	4.1 (0.6)	1.6 (0.7)	8.8 (5.2)	0.7 (0.6)	0.4 (0.4)	0.1 (0.1)	0.1 (0.0)	1.3 (0.7)	14.2 (5.8)	281.9 (339.9)
Floodplains (n=2)	32.4 (10.3)	48.3 (11.7)	19.2 (1.4)	4.3 (0.3)	1.4 (0.4)	12.1 (0.6)	2.4 (2.3)	1.6 (1.5)	0.2 (0.0)	0.1 (0.0)	4.2 (3.9)	36.1 (34.0)	9.1 (12.8)

[a] Percentage Sand, Silt, or Clay (Granulometry); [b] pH-H_2O; [c] Percentage of organic carbon (Walkley – Black); [d] Cation exchange capacity ppmkg^{-1}(using normal and neutral ammonium acetate); [e] Calcium ppm kg^{-1} (DTPA-extractable); [f] Magnesium ppmkg^{-1} (DTPA-extractable); [g] Potassium ppmkg^{-1}(DTPA-extractable); [h] Sodium ppmkg^{-1} (DTPA-extractable); [i] Total of bases; [j] Percentage of base saturation; [k] Available phosphorus mg kg^{-1} (Bray II).

Chapter 6

General Discussion

This thesis contributes to the debate about the relative importance of humans in the shaping of the Amazon's diversity (which ranges from a limited one to transforming the full natural landscape into an anthropogenic environment) in two ways:

1. By throwing light on the way in which indigenous farmers in Colombia perceive an environment with Amazonian Dark Earths (ADE) in the context of wider access to other soils, and
2. By providing information about indigenous knowledge and indigenous land use that may help to better understand how indigenous people currently use and create diversity in the region.

In the introduction to this thesis an analytical framework (Figure 1.3) was proposed in which the interactions between cultural diversity, land diversity and manioc diversity could be studied to answer four research questions:

1. How did cultural preferences and conditions of natural and anthropogenic environments determine land use among indigenous people of the Colombian Amazon?
2. How did cultural and environmental conditions jointly shape manioc diversity in indigenous communities of the Colombian Amazon?
3. How different are arbuscular mycorrhizal communities of natural and anthropogenic soils of the Colombian Amazon and how much do these differences affect manioc mycorrhization?
4. Does indigenous agriculture in the Colombian Amazon reflect a co-adaptation between people and environment that has enhanced Amazonian diversity, supporting the scientific hypothesis that humans had an important role in the conservation and creation of Amazonian diversity?

In this final chapter, the answers to those questions are elaborated on the basis of the results obtained and described in Chapters 2 through 5. We discuss how the findings of this research might contribute to support or reject the positions in the debate on the extent to which people contributed to shaping diversity in the Amazon region. Finally, some recommendations for further research are provided.

6.1. How do cultural preferences and conditions of natural and anthropogenic environments determine land use among indigenous people of the Colombian Amazon?

The Amazonian landscape can be divided into two main environments: uplands and floodplains. In this particular study floodplains are restricted to *várzeas* - defined as floodplains periodically flooded by white-water rivers coming from the Andes and crossing the Amazon region. Within *várzeas*, two distinct environments were studied: low floodplains which are flooded every year, and *restingas* which are high floodplains flooded once every 5-10 years when river levels are at their highest. Within uplands, two distinct environments were studied: natural uplands and anthropogenic uplands with ADE. Indigenous people also recognized these particular environments. Indigenous people distinguish between environments suitable and not suitable for agriculture (Table 3.1), with the latter having important roles in the maintenance of other environmental services (water, air) and natural populations (plants, fish, game) vital for their livelihood (Chapter 3).

Researchers have emphasized the importance of soil composition for land use and made predictions on how different environments could provide the food pre-Columbian societies needed (Denevan, 1996; German, 2003). In general, it is assumed that ADE provide better conditions for agriculture than background soils (German, 2003; Glaser and Birk, 2012). Indigenous groups also ranked ADE first in suitability for agriculture (Chapter 3); however, a larger number of cropping plots were opened in non-anthropogenic uplands. When the soil composition of ADE and non-ADE uplands was compared, ADE showed chemical changes in their soil composition typical of an anthropogenic soil (Chapter 2) but the only variable that differed drastically between these two soils was phosphorus availability, which on average was around 60 times higher in ADE (Chapter 2, Table 2.2). Additionally P/K and Ca/Mg ratios were higher in ADE (Chapter 2). Soil composition of ADE and non-anthropogenic soils was similar, and indigenous people managed fields in ADE and non-ADE in a similar way. Both ADE and non-ADE were cultivated under similar swidden agriculture and farmers spent a comparable amount of time controlling weeds, leaving sites for a similar period of time fallow before using it again. Although higher phosphorus availability in ADE did not contribute to cultivating more crops on indigenous swiddens (Table 3.2), ADE were used more often for the establishment of agroforestry systems of perennial native and exotic species unable to grow in nutrient-poor soils. More starch-rich manioc landraces highly appreciated by Andoke and Muinane people were preferentially grown on ADE. Maintaining of grasslands for aesthetic reasons was more common on ADE (Chapter 3).

Our results contrast with reports for downstream areas along the Amazon where larger differences were reported between ADE and non-ADE soils, and where this difference affects the way in which swiddens are managed. In general, swiddens on ADE are situated in sites with shorter fallows, weed control takes more time, and specific manioc landraces with faster root bulking are cultivated (Fraser and Clement, 2008; Fraser *et al.*, 2012). However, differences between soil composition of ADE from Colombia and ADE from the Central Amazon (Brazil) do not fully explain the results obtained: in the Central Amazon ADE composition also varies considerably. This suggests that soil composition of ADE should be considered as a continuum, independent of the location sampled (Fraser *et al.*, 2011a). Along the Madeira River (one of the most studied areas for ADE), for example, between 30 and 60% of anthropogenic soils sampled in five locations had high levels of phosphorus availability but low amounts of calcium and magnesium (Fraser *et al.*, 2011a). This is comparable with our studies (Chapter 2, Table 2.2).

When a general picture of the composition of ADE reported for areas downstream of the Colombian Amazon is presented, 40% of ADE had low calcium amounts, 36% of ADE had low magnesium amounts, and 25% of ADE had low phosphorus availability (Figure 6.1). Although ADE are commonly associated with high fertility (Glaser and Birk, 2012; Costa *et al.*, 2013), the reality is that this is not always true. A high variability of ADE could be expected as the parental materials from which ADE originated are variable (Quesada *et al.*, 2010), but also the time when background soils were transformed, the amounts and quality of organic matter used, and the cultural practices of people responsible for this soil modification (Glaser and Birk, 2012).

Since indigenous communities from the Middle Caquetá region are composed of only a few families, there are plenty of areas covered by forests older than 40 years that accumulate enough above- and below-ground biomass to provide manioc and other crops cultivated in low densities sufficient nutrients to allow adequate growth and production. Therefore ADE are not needed for indigenous food security. Indigenous socio-economic conditions contrast with those of farmers from the Central Amazon where population densities are higher and manioc covers household needs but is also produced to supply local and regional markets (Fraser, 2010); this explains the differences in the preference to open

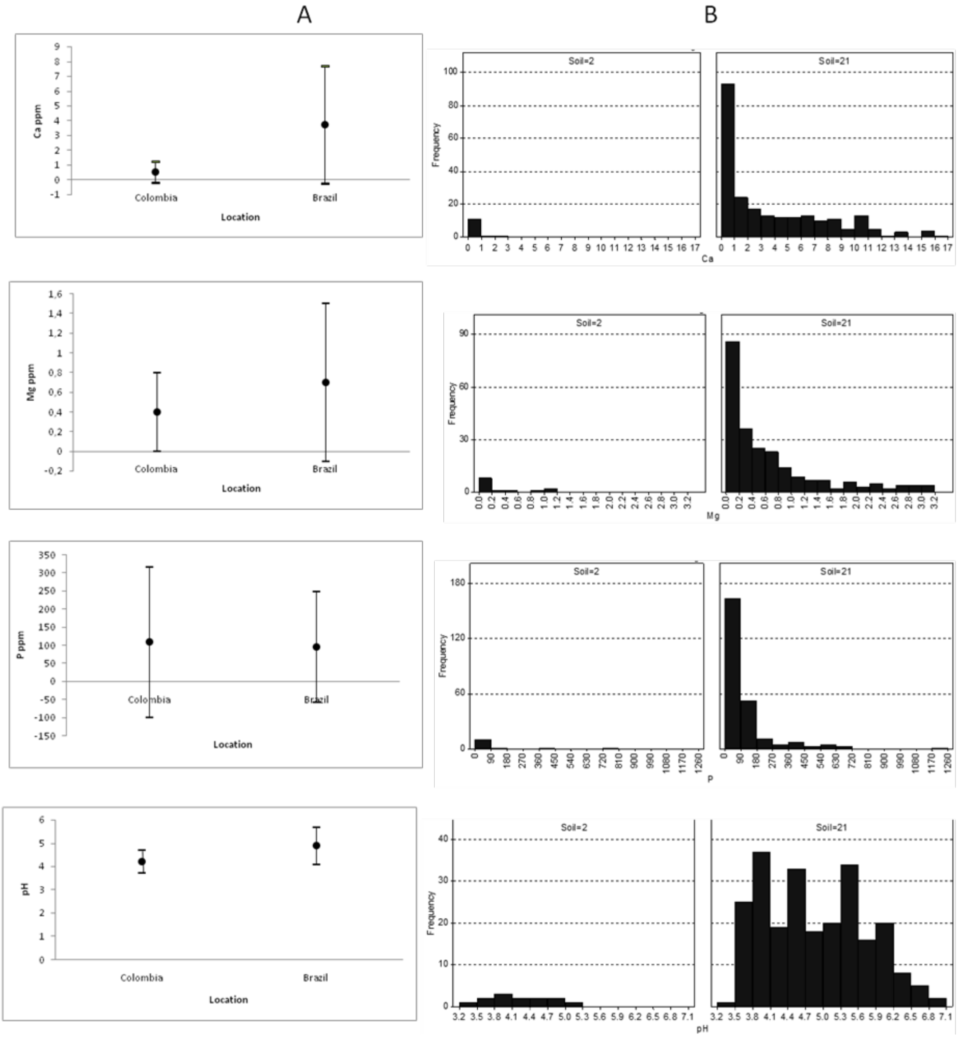

Figure 6.1. Comparison of Amazonian Dark Earths from the Upper Amazonia (Colombia) reported by Eden and Andrade 1984, Morcote-Ríos and León-Sicard 2011, and original data of this thesis; and the Central Amazonia (Brazil) reported by Madari et al. 2003, Falcão et al. 2009, and Fraser et al. 2011. A. Mean and standard deviation for DTPA-extractable calcium (Ca) (n = 13 for Colombia; n = 237 for Brazil); DTPA-extractable magnesium (Mg) (n = 13 for Colombia; n = 237 for Brazil); available phosphorus (P) by Bray II (Colombia, n = 13) and Mehlich I (Brazil, n = 248) assumed here as homologous methodologies; and pH in water (n = 13 for Colombia; n = 238 for Brazil). B. Histograms of the distribution of the data of each variable for the upper Amazonia (Soil = 2) and the Central Amazonia (Soil = 21).

swiddens on ADE between our study and previous reports.

When the use of *várzeas* among communities with and without access to ADE was compared, important differences were observed. Tikuna farmers from San Martín de Amacayacu (where ADE are not present) cultivated low floodplains continuously while farmers from the Middle Caquetá region (where ADE are present) cultivated *restingas*. The production systems on the two types of floodplains were also different: Tikuna farmers from San Martín de Amacayacu used flood-recession agriculture (Shoor, 2000) while farmers from the Middle Caquetá region used swidden agriculture. The flood-recession agriculture practiced by Tikuna farmers consisted of the yearly cultivation of floodplains with a brief fallow period during flooding. Differences in the use of *várzeas* among communities could not be associated with the presence or absence of ADE uplands. An intensive cultivation of *várzeas* by Tikuna farmers from San Martín de Amacayacu was also not associated with market pressure as has been observed in communities where subsistence agriculture is transformed to produce more in order to satisfy the local or regional market demand for food (Shorr, 2000; Fraser *et al.*, 2012). This study shows that development of a continuous agriculture is not always a response to external pressures. In the case of Tikuna farmers it is a traditional practice to produce their staple food with traditional technologies to preserve high volumes of harvested manioc roots and to process roots to prepare *farinha* (Acosta and Mazorra, 2004) (Chapter 2). Why the Tikuna from San Martín de Amacayacu cultivate floodplains permanently is not well understood, but their population growth could be an important factor. Certainly, San Martín de Amacayacu is one of the indigenous communities that has significantly increased its population over the last 40 years (Chapter 4). As their staple food is based on sweet manioc, and some landraces are adapted to bulk quickly (within the time during which the low floodplains are not flooded), the production of floodplains can provide important amounts of food in a short time - food that is preserved for the whole year in the form of *farinha*.

The cultivation of low floodplains might also be common among other indigenous groups as *restinga* cultivation requires more labor input (opening sites, burning and controlling weeds) during the growing period than the low floodplains. However, the use of low floodplains requires a particular work organization to ensure that labor is available during harvesting - which is the most critical activity because the harvest needs to be in before the flooding season. In indigenous communities, the *minga* is an important institution of collective work in which members of the community are invited to supply the work needed for activities such as manioc harvesting in low floodplains; in compensation drinks and food are provided by the owner of the plot where the work is carried out. *Minga* is a reciprocal support institution: if people do not participate in *mingas* reciprocity is broken and the maintenance of the work structure is lost. In indigenous communities such as those of the Middle Caquetá region in which members with the capacity to participate in *mingas* prefer not to participate, indigenous farmers are pushed to cultivate *restingas* instead of low floodplains to allow harvesting with family labor only (Chapter 2). The role of the *várzea* in food production seems to have a particular importance as the *várzea* continues to be used for food production, even if its cultivation there is more difficult than on upland soils (Table 4.2). This thesis indicates that *várzeas* are not only important for the production of manioc roots, but also for a better manioc growth - which translates into more vegetative “propagules” when compared with other environments (Chapter 2).

Summarizing, our results indicate that staple food production in the indigenous communities we studied is mainly carried out on non-anthropogenic uplands. ADE are important environments for the cultivation of exotic or nutrient-demanding species which are required in low amounts and complement the staple food, manioc. The *várzeas* offer a fast production of manioc roots and an important amount of vegetative “propagules”; this triggers indigenous people to continue cropping them when the labor required for harvesting is available.

6.2. How do cultural and environmental conditions jointly shape manioc diversity in indigenous communities of the Colombian Amazon?

Agro-biodiversity in Central Amazonia is attributed to ADE; this indicates the importance of anthropogenic soils for crop selection and manioc diversification (Fraser *et al.*, 2011a). In all the environments indigenous people cultivate, manioc showed a high diversity. However, in this research the number of manioc landraces did not differ significantly among communities with or without access to ADE (Chapter 4). All studied ethnic groups cultivated sweet landraces (with low concentration of cyanogenic compounds in roots) and bitter landraces (with high concentration of cyanogenic compounds in roots), but the way they classified manioc landraces and the number of landraces of each class they cultivated depended on the cultural traditions of each ethnic group (Chapter 4). From both sweet and bitter manioc types, there were those that were ethnic identity symbols and those that were not. This particular segregation of maniocs among the different ethnic groups constituted a source of manioc diversification in the region. From indigenous narratives it seems that manioc landraces that are ethnically specific might come from volunteer seedlings while also genomes showed low recombination. Volunteer seedlings continue to be used by indigenous farmers to diversify their individual landrace portfolios but recent volunteer seedlings were not recognized as symbols of identity. The main source of new manioc landraces in the neighboring communities is the exchange of manioc seeds, as indigenous farmers call the stem pieces they use as vegetative manioc propagules.

All manioc landraces with or without ethnic specificity were cultivated under swidden agriculture and flood-recession agriculture without distinctive patterns of distribution. As manioc conserves its sexual reproduction, manioc landrace recombination can occur spontaneously in agricultural fields, allowing for the homogenization of manioc landraces' germplasm through time if no control mechanism is applied. However, our results show that more than 87% of the landraces identified by indigenous farmers were also genetically different (Chapter 4). We found no cultural practices to avoid sexual recombination, but there is evidence that cultural strategies to preserve the morphotype of the manioc landrace exist, such as for example the 'teaching' of more experienced women to help younger women clearly recognize manioc landraces, or the passing on of culinary traditions derived from the use of those landraces.

Although in our study region cultural conditions appeared to be more directly related to manioc diversity, environmental conditions also played an important role. Indigenous farmers did not consider soil-manioc landrace specificity and moved all their manioc stock from one environment to another. Independent from the environment selected, manioc roots were always well colonized by arbuscular mycorrhizal fungi and specifically by *Rhizophagus manihotis* (Chapter 5), identified as an excellent AM symbiont for manioc (Howeler and Sieverding, 1983; Howeler, 2002). This offers all manioc landraces the opportunity to secure an arbuscular mycorrhization independent from the environment selected for its cultivation and allows these landraces to produce enough roots and provide vegetative manioc "propagules" so that their permanency in new swiddens is secured. Additionally swidden agriculture on uplands promotes the growth of volunteer seedlings (Pujol *et al.*, 2002) that are, after some screening, either included or rejected as new landraces in farmers' portfolios.

Although we observed little interest to procure soil-manioc specificity among indigenous farmers, some soil-manioc specificity was mentioned by members of some ethnic groups. The Tikuna for example claimed to cultivate sweet manioc landraces whose roots bulk in three months - making them especially suitable for cultivation in low floodplains (Chapter 4). The Andoke in turn claimed that a specific group of bitter maniocs they call "to grate" accumulate more starch when cultivated on ADE. This is important because starch is the main ingredient in the Andoke's traditional cuisine (Chapter 3). Manioc specialization thus not only responds to external pressures as has been reported before (Fraser *et al.*, 2011a), but also to cultural preferences. These two examples of manioc-soil specificity did not affect manioc diversity among ethnic groups as manioc selection did not aim to reduce the portfolio of manioc landraces (as commonly occurs in modern agriculture). One indigenous principle linked to the prestige of being called a "good farmer" is to maintain as many manioc landraces as possible – which is at the same time an indication of abundance and well-being (Chapter 4).

In summary, the particular relation that indigenous people from the Colombian Amazon established with manioc, and the adaptability of this crop to grow and produce well in the different Amazonian environments, contributed to manioc diversity in the region (Chapter 4).

6.3. How different are arbuscular mycorrhizal fungal communities of natural and anthropogenic soils of the Colombian Amazon and how much do those differences affect manioc mycorrhization?

We found a number of environmental differences that could affect the arbuscular mycorrhizal fungal composition of soils and the arbuscular mycorrhization of manioc. The different soils in which manioc was cultivated have significantly different phosphorus availability (Chapter 2). The arbuscular mycorrhizal fungi are sensitive to soil phosphorus availability and high concentrations could inhibit root arbuscular mycorrhization of host plants (Gosling *et al.*, 2013). In this study two types of floodplains were studied: low floodplains which flood every year and high floodplains (known as *restingas*) which flood once every 5-10 years (Chapter 2). Differences in the flooding regime of floodplains expose arbuscular mycorrhizal fungal communities to more or less prolonged periods of anoxic soils affecting the survival of arbuscular mycorrhizal fungal communities. Additionally, because the production system used by indigenous farmers to cultivate the two floodplains is different, the plant composition of floodplains in which agricultural fields are placed is different. On the one hand, swiddens on high floodplains are covered by a secondary forest of more than 10 year old (Table 2.4) previous to its cultivation. On the other hand, flood-recession agriculture on low floodplains does not develop a plant cover during the fallow period as this coincides with the flooding period (Chapter 2). In this way, the arbuscular mycorrhizal fungal communities colonizing manioc in high floodplains would be the same as the one that colonized previous forest species. Arbuscular mycorrhizal fungal communities colonizing manioc in low floodplains can originate from AMF propagules from other sites and deposited there by the river, and from AMF that colonized manioc in a previous production cycle and survived the flood. Although we found differences in the arbuscular mycorrhizal fungal composition of soils (Chapter 5), those differences did not affect manioc root arbuscular mycorrhizal colonization (Chapter 5).

Manioc exhibits a high diversity (El-Sharkawy, 2006). In the study area, manioc diversity included 173 different morphotypes distributed across 60 manioc landraces with low root toxicity and 113 manioc landraces with high root toxicity (Table 4.1). Studies on the effect of root toxicity on the arbuscular mycorrhization of plants are rare. In sorghum landraces (*Sorghum bicolor*) with high root toxicity the arbuscular mycorrhization of roots is lower than in landraces with low root toxicity (Miller *et al.*, 2014). But in manioc, it seems that the arbuscular mycorrhization of the root is not affected by root toxicity (Burns *et al.*, 2012). The results of this thesis confirm the observations of Burns and collaborators as the number of arbuscular mycorrhizal species (as virtual taxa) colonizing roots and the root arbuscular mycorrhizal colonization were similar for the two types of manioc (Chapter 5). Since manioc requires arbuscular mycorrhization to improve the foraging of nutrients in the soil (Habte and Byappanahalli, 1994), the capacity that manioc exhibits to associate effectively with a high number of arbuscular mycorrhizal fungi in different environments explains in part why indigenous farmers can rotate their complete manioc stock from one soil to another (Chapter 2). It would also explain in some way why indigenous farmers keep the different maniocs they have in a single field (Chapter 4). The high affinity of manioc for arbuscular mycorrhizal association can be a key factor related to manioc diversification in the region as manioc stems that are exchanged are able to adapt to new environments, thus increasing the chance that they are kept by farmers.

6.4. Does indigenous agriculture in the Colombian Amazon reflect a co-adaptation between people and environment that has enhanced Amazonian diversity, supporting the scientific hypothesis that people played an important role in the conservation and creation of Amazonian diversity?

Most Amazonian uplands are acid, with toxic levels of aluminum for plants, and limited nutrient holding capacity due to the abundant kaolinite of parental materials (Ma and Eggleton, 1999) which results in a limited fertility. The organic matter which accumulates in the A horizon improves the cation exchange capacity (Glaser and Birk, 2012); it is the main source of nutrients for plants through its mineralization (Serna-Chavez *et al.*, 2013), and therefore the main source of nutrients for crops in agricultural systems. For soil scientists the A horizon is also the soil layer susceptible to degradation or improvement by human agency. Although indigenous people do not have direct knowledge of microbial and biochemical processes in the soil, they interpret the importance of the different soil horizons for agriculture in a way comparable to that of scientists (Chapter 3). They denominate the A horizon as the *workable soil* which implies this horizon is the one managed or modified by farmers, the one that is worked in to produce food. Indigenous people call the deeper soil the *dead soil* which indicates the limited importance it has for plant nutrition.

Both *várzeas* and ADE have modified A horizons. The *várzeas* are enriched periodically in a natural way with sediments deposited by rivers while ADE were transformed by activities of pre-Columbian inhabitants of the Amazon region (Glaser and Birk, 2012). For indigenous people all soils are formed naturally. They do not consider that people are responsible for ADE creation - not even the Andoke who are the traditional inhabitants of the Middle Caquetá region and have historically been in direct contact with ADE. Their historical memory goes back to a time in which the region was densely inhabited, ADE already existed and played a key role in food production. Although the Andoke consider humans are not responsible for ADE formation, they associate ADE with densely inhabited communities and the use of fire. This picture supports scientific interpretations of the conditions in which ADE were formed, yet does not provide hints of how organic matter was accumulated, nor information about the burning techniques used (which are considered key steps in ADE formation). It has been proposed that ADE are an unintentional by-products of Pre-Columbian settlements (Schmidt *et al.*, 2014). Indigenous people we interviewed indicated that ancient groups did not know how to transform natural uplands into ADE and that, therefore, different ethnic groups continuously fought over ADE possession and use. This supports the hypothesis that ADE formation was not an intentional product of indigenous activities.

Indigenous people consider manioc a native species given to them in mythical times. Presently, there is consensus among scientists that manioc is a native species from the Amazon region (Olsen and Schaal, 1999). It is suggested that sweet and bitter maniocs were domesticated at different historical moments and therefore distributed unevenly throughout the Amazon (Mühlen *et al.*, 2013). Our results show a clear genetic clustering of sweet and bitter maniocs (Chapter 4); this suggests that sweet and bitter manioc split into different manioc types a long time ago. It has been proposed that ADE played an important role in the domestication of sweet manioc (Arroyo-Kalin, 2010; Mühlen *et al.*, 2013) which was domesticated first, while bitter manioc was domesticated later on non-ADE. This hypothesis was supported by Andoke and Uitoto respondents who attributed an important role to ADE in the conservation of the first maniocs by indigenous people (Chapter 3). However, low-toxicity *Manicuera* landraces, which according to *People of the Center* (as the groups of the Middle Caquetá region call themselves, see Introduction) were the first maniocs they cultivated, are genetically closer to bitter maniocs than to sweet maniocs (Figure 4.3). Moreover, archaeological evidence of first manioc cultivation does not match with ADE creation. Archaeological evidence of manioc cultivation outside Amazonia dates back to 8,500 years BP (Piperno *et al.*, 2000; Piperno, 2011) and in Amazonia > 4,700 years BP (Mora *et al.*, 1991). The creation of most ADE dates back to between 2,000 and 500 BP (Neves *et al.*, 2004) but one of the oldest evidences of ADE in the region (found in Peña Roja in the Middle Caquetá) dates back to >4,700 years BP and coincides with the oldest report of manioc in the region (Mora *et al.*, 1991). However, the Middle Caquetá region (with the oldest occurrences of both manioc and ADE) is far from Rondônia (Brazil) where manioc was presumably first domesticated (Olsen and Schaal, 1999). Distribution of sweet and bitter manioc landraces can be attributed to crop exchange among ethnic groups connected by a dense river network (Mühlen *et al.*, 2013). However, and according to their historical narratives, bitter manioc cultivation has predominated since the origin of indigenous people in the Middle Caquetá (Chapter 4). There are thus still many unsolved issues around manioc domestication, and other possibilities might be considered. *Manihot esculenta* ssp. *flabellifolia,* the closest wild ancestor of modern manioc (*Manihot esculenta* Crantz), has a broad distribution within and surrounding the Amazon region (Duputié *et al.*, 2009) and naturally exhibits landraces with low and high root toxicity (Akinbo *et al.*, 2012). It is possible that sweet and bitter landraces of *Manihot esculenta* ssp. *flabellifolia* were selected independently for domestication among different ethnic groups - resulting in today's manioc landrace diversity of both low and high root toxicity.

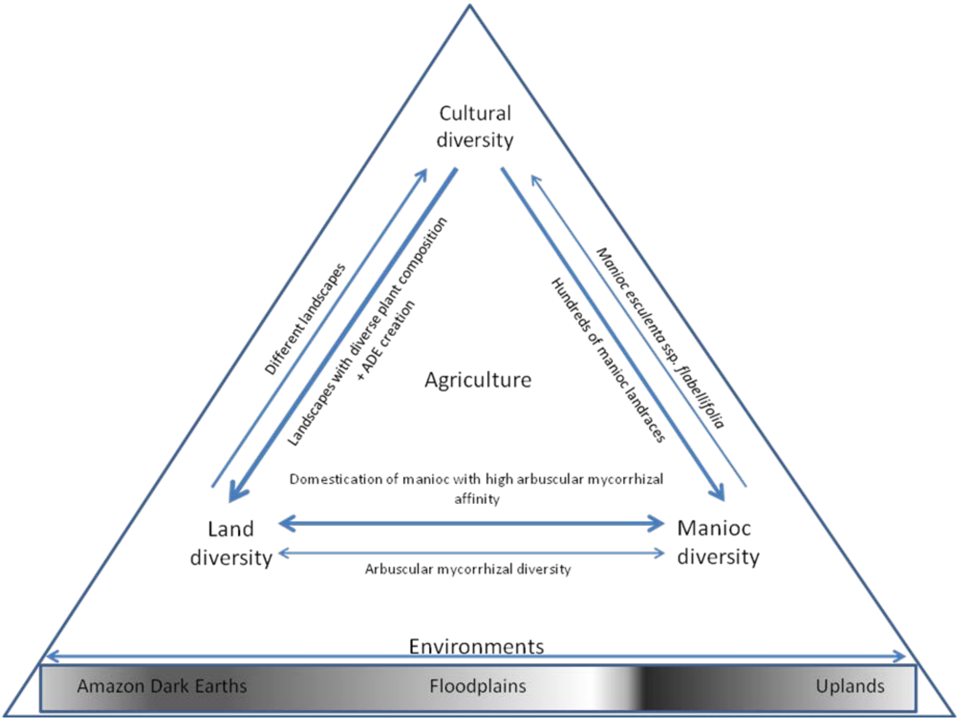

Figure 6.2. Graphic representation of the anthropogenic outputs that contributed to the increase in diversity in the Amazon region based on the framework used in this thesis. Fine arrows represent the natural baseline with which native people evolved. Thick arrows represent the anthropogenic contributions made within this natural setting. The two directions of the arrow and the black, white and grey colors of the bar in a mixed pattern indicate the observed variable soil fertility of environments.

An overview of the results of this thesis (Figure 6.2) indicates that ADE are not always more fertile than uplands or floodplain soils and that, in general, Amazonian soils are highly variable in their physicochemical composition (as indicated by the bar that varies in a grey color scale). Despite differences in soil composition, indigenous people use most of the environments for food production. In this way forest composition of uplands (with and without ADE) and (low and high) floodplains is changed. Anthropogenic interventions in the Amazon landscape have resulted in the domestication of species such as manioc (a crop with high affinity for arbuscular mycorrhizal association); this has occurred regardless of soil conditions. Cultural values associated with manioc enhance manioc diversity – evidenced by hundreds of different landraces which have contributed in shaping Amazonian diversity. Humans have therefore been an important transformation factor in the region.

It is often stated that diversity is of major importance today as diversity is the genetic base for crop improvement and the achievement of better yields, better pest and disease control, and better adaptation of crops to climate change (El-Sharkawy, 2006). Due to its high diversity and high adaptability to different edapho-climatic conditions, manioc is recognized as an important tropical crop to achieve future agricultural goals (Burns *et al.*, 2010). Our work demonstrates that manioc is highly diverse among indigenous communities of the Colombian Amazon, showing a variety of root pulp colors, root toxicity, time required for its harvesting, and culinary properties. Clearly, manioc in the Colombian Amazon is an important genetic reserve – a reserve that will continue to be protected as long as indigenous communities retain their traditions and cultural traits associated with manioc.

Efforts regarding the selection of specific crop-arbuscular mycorrhizal fungi associations have been made around the world to enhance the benefits that arbuscular mycorrhizal association can provide to agriculture (Ceballos *et al.*, 2013). One aim is to reduce the use of chemical fertilizers (and associated environmental pollution) due to a more effective arbuscular mycorrhizal association between crops and fungus. In the particular case of manioc cultivated under traditional, low-input agricultural systems this might not be an important issue. Manioc can be colonized effectively by a high number of arbuscular mycorrhizal fungi and including *Rhizophagus manihotis* (a well-recognized manioc arbuscular mycorrhizal symbiont) independent of the soil conditions or the manioc landraces selected. Modern tropical agriculture has to take advantage of this important issue and evaluate the main differences between traditional and modern agriculture that affect arbuscular mycorrhizal fungal communities (and specially the presence of *Rhizophagus manihotis*) - and how this could be improved.

6.5. Future challenges

ADE are archaeological sites and their use is regulated by national governments. Disturbing ADE is considered illegal as it compromises the cultural patrimony of the countries. In Colombia, there is limited knowledge among Amazonian researchers, soil scientists and governmental officials about what an Amazonian Dark Earth is. There is hardly any knowledge among local people that those soils are archaeological sites that have to be treated in a special way to preserve the information these soils hold. As we argued (Chapter 3) and deduced from studies in Brazil (German, 2003; Fraser, 2010; Junqueira *et al.*, 2011), ADE have been places for crop production since Pre-Columbian times and therefore disturbed many times during history. However, those disturbances are also the main reason to study these soils and understand the role they have played in the history of Amazonian societies. A discussion among scientists, governments and local communities is required to get a better grip on the importance of ADE, and how to use them both as sites for archaeological study and fields for agriculture.

Throughout the Chapters of this thesis we have claimed that women play a key role in the maintenance and diversification of manioc, and in the management of crop plots. Women also play an important role in the maintenance and diversification of other cultivated crops, yet some species that are cultivated for ritual purposes are managed by men exclusively. Among the ethnic groups of the *People of the Center* the cultivation, harvesting and processing of coca (*Erythroxylum coca*) are male responsibilities. Due to my gender, this research could not address male practices around coca cultivation and the management of coca diversity as the knowledge thereof is exclusively shared among men. Despite the limited access to men’s practices, I had the opportunity to observe some interesting issues during my work in the swiddens. Coca is cultivated from stalks (like manioc) in swiddens on both ADE and non-ADE uplands. Men harvest the coca leaves every day (just as women who harvest manioc daily) to elaborate the *mambe* (coca powder) which is used during sessions in which local knowledge is orally transmitted in the *mambeadero* (the center place of the *maloka* or collective dwelling house). Men and especially traditional leaders indicated that, in mythical times, coca was given to them as their food. Among these ethnic groups, therefore, swiddens are not completely a competence of women. The male practices regarding coca cultivation and the management of coca diversity are not well understood and could provide an interesting case to study the male management of swidden agriculture and crop diversity –

something that has not been addressed before in the Amazon region.

There are many examples of how people have been interacting with the environment in the Amazon region, changing the landscape (Heckenberger *et al.*, 2003) and enhancing diversity (Clement, 1999). In this thesis we only explored the relationships that five indigenous groups established with their landscape to cultivate manioc as their staple food. But even in manioc production, a well-known Amazonian crop, there are many aspects that are not fully understood. One of these (and which has been addressed before) is the origin of sweet and bitter maniocs and their distribution throughout the Amazon region. Most studies that have explored manioc diversity by molecular approaches have used manioc landraces from Brazil (Alves-Pereira *et al.*, 2011; Mühlen *et al.*, 2013), and other studies have been based on the diversity of world´s manioc collections (Elias *et al.*, 2004). Yet, and as we have demonstrated in this thesis, these collections are not a good representation of manioc diversity in the Amazon region (Chapter 4). It will be important to establish cooperation strategies among researchers to carry out molecular studies of manioc that include manioc landraces from places not researched before, and with an aim to understand the origin of sweet and bitter manioc landraces. *Farinha* for example is a very well-known preparation, commonly associated with the detoxification and preparation of bitter maniocs. The origin of *farinha* however is not clear. The Tikuna in this study indicated that they knew the process of *farinha* preparation before they knew bitter maniocs. On the other hand, indigenous people from the Middle Caquetá region (who have traditionally managed bitter maniocs), indicated that they learned how to prepare *farinha* while working as slaves during the rubber boom era of barely a century ago. The study of the origin *farinha* might help to understand the use of bitter and sweet maniocs in the region.

One of the topics that require more attention is the arbuscular mycorrhizal fungal community composition of Amazonian soils. First of all, studies on arbuscular mycorrhizal fungal communities of other ADE are required. This thesis provides the first report of the arbuscular mycorrhizal fungal community composition of ADE, but the ADE studied in this research are not consistently more fertile than backgrounds soils. Some slight differences were found in the arbuscular mycorrhizal fungal community composition between ADE and non-ADE, but these differences could not be attributed to differences in their physicochemical composition. It is still unknown if the transformation of natural soils into anthropogenic soils has some effect on the native arbuscular mycorrhizal fungal composition. *Rhizophagus manihotis* was one of the most frequent arbuscular mycorrhizal species colonizing manioc roots. This arbuscular mycorrhizal species has been commonly identified as a frequent arbuscular mycorrhizal symbiont of different crops. However, the arbuscular mycorrhizal fungi colonizing manioc roots came from swiddens located on plots where very old secondary forests or mature forest had grown previously. *Rhizophagus manihotis* therefore had to be colonizing native forest species. There are few reports that use molecular approaches to assess which arbuscular mycorrhizal species colonize roots of plant species from Amazonian environments (Öpik *et al.*, 2013). More studies in this direction could confirm this hypothesis. In addition to this we suggest including the study of arbuscular mycorrhizal fungi associated with *Manihot esculenta ssp. flabellifolia* landraces with different root toxicity in order to assess whether or not the high affinity that modern manioc shows for *Rhizophagus manihotis* is a characteristic inherited from its wild ancestors. It is also important to do more work on swiddens to compare the arbuscular mycorrhization of manioc with that of other crops in the swiddens and assess whether these crops are colonized by the same number and the same species of arbuscular mycorrhizal fungi that colonize manioc, or if manioc arbuscular mycorrhization is a particular case.

This thesis provides evidence that humans have made important contributions to shape current Amazonian diversity. This is partially reflected in indigenous agriculture. Despite the existence of a good number of publications about the Amazon region on topics such as swidden agriculture, manioc and soils, this thesis demonstrates that these topics have not been sufficiently studied. For scientists, the Amazon region continues to be a box full of interesting surprises.

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Summary

The Amazon forest has been considered a highly diverse, well-preserved forest. However, it has been occupied by humans since the late Pleistocene, around 11,000-10,000 BP. Despite its long human occupation, human impact on the Amazonian ecosystem was considered limited. The discovery of Amazonian Dark Earths (ADE) as one clear anthropogenic modification of the Amazonian ecosystem opened the debate about how pristine the Amazon forest is and how much humans affected Amazonian diversity in pre-Colombian times. ADE not only constitute a new environment not present in the Amazon region before human presence but also an environment with enhanced conditions for food production. This thesis aims to contribute to the understanding of the role of ADE in indigenous food production, as compared with other soils, and to provide information about how indigenous people use and create diversity in Amazonia.

Most upland soils of the Amazon region are very acid, highly weathered, and with a limited nutrient holding capacity. Therefore, these upland soils are considered unsuitable for permanent or intensive agriculture. Soils in floodplains are annually enriched with Andean sediments carried and deposited by rivers that cross the Amazon region. These are known as *várzeas* and are better suited for agriculture. *Várzeas* have less acid pH, better cation exchange capacity and more calcium and magnesium than the very acid, highly weathered uplands. However, *várzeas* experience periodical floods which limit the period for cultivation and the choice of suitable crop species to those that can produce in a short time. Contrary to very acid, highly weathered uplands and *várzeas*, ADE are usually less acid, with better cation exchange capacity, good base saturation, and relatively high quantities of organic matter, nitrogen, calcium, and available phosphorus; and most of them no susceptible to experiencing floods. Therefore, ADE provide the opportunity for a more intensive agriculture, and the possibility to cultivate nutrient-demanding crop species with long production cycles unable to thrive in non-ADE upland soils or on the regularly flooded *várzeas*.

Previous studies certainly indicate that in areas where ADE are present, farmers cultivate them frequently through an intensified swidden agriculture in which swidden size is smaller and cropping cycles and fallow periods are shorter than in non-ADE uplands. But, due to the higher fertility, ADE require more labor and time to control weeds. In areas where ADE are not present, *várzeas* are also frequently and intensively cultivated through a swidden agriculture similar to the one practiced on ADE but where the cropping cycle is limited by the

flood. The results of this thesis indicate that contrary to what has been reported before, ADE from the Middle Caquetá region of Colombia are not contrastingly more fertile than the very acid, highly weathered upland soils, except for better phosphorus availability in ADE (Chapter 2). Although ADE constitute a good environment for agriculture, indigenous farmers from the Middle Caquetá region do not use ADE more frequently or more intensively than non-ADE uplands. Additionally, the swidden agriculture practiced on ADE and that on non-ADE are similar and characterized by similar plot size, with production cycles between two and three years, fallow periods of about 40 years, and with similar amount of time invested in controlling weeds.

Várzeas were also cultivated by indigenous farmers, independently whether they have access to ADE or not. However, there were differences in the type of floodplains selected and the way in which they were cultivated among farmers. In San Martín de Amacayacu, where ADE are not present, low floodplains flooded every year and farmers practiced a continuous system of production, called flood-recession agriculture. Farmers from the Middle Caquetá region, where ADE are present and used, practiced swidden agriculture on high floodplains (denominated *restingas*) flooded once every five to 10 years. Differences in the selection of floodplains and the production systems used were not related to differences in soil conditions or market pressures to grow certain crops. Differences were associated with cultural traditions related to the processing and conservation of high volumes of manioc roots; and the availability of people to organize collaborative work (locally called *mingas*) for harvesting floodplains. Farmers from the Tikuna community of San Martín de Amacayacu have the capacity to organize *mingas* and harvest manioc roots in a short period of time (1-ha plot in two days on average). They also have the knowledge of a technology to bury fresh manioc roots to conserve them, and the technique to prepare *farinha* (a fermented and roasted manioc granulate) as a way to conserve high volumes of manioc in a preparation ready to eat. Farmers from the Middle Caquetá region have limited opportunities to organize *mingas* as some profitable activities in the region compete for available labor. Therefore, all agricultural activities are carried out with family work and farmers select high floodplains which provide a longer time for harvesting than low floodplains in order to fit the capacity of individual families to harvest.

Although the use of ADE for swiddens was only important in one of the four communities of the Middle Caquetá region studied (Chapter 3), ADE were important sites for settling the communities and for the maintenance of agroforestry systems with native and exotic species not able to grow in soils with low phosphorus availability. Additionally, ADE were sometimes used to maintain grasslands for aesthetic purposes. Therefore, ADE are not an important environment for the production of the staple food of these communities as the low number of families living in the communities and the low land pressure in the area secure the availability of old forested areas with enough nutrients accumulated above and below ground to supply the requirements of swiddens where their staple food is mainly produced.

Manioc (*Manihot esculenta* Crantz) is the staple crop of the indigenous groups studied in this thesis. Manioc is cultivated on all soil types and is always the main crop cultivated in indigenous fields, occupying more than 70% of the plot area. The manioc diversity in this study was high and 173 different manioc landraces were distinguished based on morphological parameters. From them, 87% were also considered genetically different based on molecular techniques. The five ethnic groups studied cultivated sweet manioc landraces (those with less than 100 mg/kg of cyanogenic compounds in their roots which indigenous farmers did not consider toxic and did not need a post-harvesting process before consumption) and bitter landraces (those with more than 100 mg/kg of cyanogenic compounds in their roots which indigenous farmers considered toxic and needed a post-harvesting process to decrease their toxicity before consumption). The number of manioc landraces in communitarian inventories and the number of sweet and bitter landraces in those inventories differed among indigenous groups (Chapter 4). Differences of manioc inventories among indigenous groups were not predominantly related with differences among soil types used to cultivate manioc as the complete stock of manioc used by farmers were cultivated on all soil types. In fact, complete manioc stocks appeared to be moved back and forth from uplands to floodplains (low floodplains and *restingas*), and from ADE to non-ADE without specificity among manioc landraces and soils. This management of manioc stocks differed from previous reports in which specific manioc landraces were found to be cultivated on specific soils.

Why manioc is moved from one soil to another in an unspecific way might be the consequence of different factors. One was the similarity in soil composition between ADE and non-ADE which offer similar environments for manioc production. Other is the similar arbuscular mycorrhizal fungi diversity of soils, independently their physicochemical composition, offering manioc with environments rich in arbuscular mycorrhizal symbionts. Additionally, the type of indigenous agriculture practiced does not favor manioc-arbuscular mycorrhizal fungus co-adaptation as in swidden agriculture fallows are very long compared with the growing time of manioc, and in floodplains, the flood limit the time for manioc cultivation (Chapter 5). In summary, variation in soil characteristics does not account to a great extent for manioc diversity; cultural values attached to manioc (i.e., manioc landraces as symbols of ethnic identity, conservation of highly diverse manioc stocks; culinary traditions) are more important to account for the manioc variation observed in the study area.

People have been an important transforming actor in Amazonia. People have been cultivating most of the environments of the Amazon region and in this way have affected forest composition and dynamics. Additionally, pre-Colombian people created Amazonian Dark Earths, an environment not naturally present in the Amazon region before human occupation. Indigenous people associate ADE with ancient settlements densely inhabited where first maniocs were cultivated and where ADE had an important role in food production. Although today the role of ADE in indigenous food production is not considered relevant, indigenous narratives indicated that this new environment was a key factor in ancient times. In addition to ADE creation, people also domesticated native species. One of them is manioc, considered today the sixth most important crop in tropical and sub-tropical areas of Africa, Asia and America, and a potential crop to achieve adaptation of agriculture to climate change in tropical areas. As indicated before, manioc diversity is particularly high in the Amazon region, and contributes to the region's plant diversity. Humans have made important contributions to shape current Amazonian diversity. We are still trying to understand the importance of those contributions. This thesis contributes to exemplify how indigenous agriculture reflects those people-environment interactions that resulted in the particular use of a diversified landscape and the selection and management of manioc as a staple food.

Samenvatting

Het Amazonewoud wordt gezien als een zeer divers, goed geconserveerd oerwoud. Het is echter al sinds het Laat-Pleistoceen, 11.000-10.000 jaar geleden, bewoond. Ondanks deze langdurige bewoning meende men lange tijd dat de mens het Amazone ecosysteem slechts beperkt heeft beïnvloed. De ontdekking van antropogene *Amazonian Dark Earths* (ADE), als bewijs van menselijk ingrijpen in het Amazonegebied, opende de discussie over de mate waarin ook het Amazonewoud ongerept is gebleven en in hoeverre de mens de diversiteit in de Amazone al voor Columbus beïnvloedde. ADE zijn bodems die niet aanwezig waren voordat de mens in het gebied verscheen; ze bieden goede omstandigheden voor voedselproductie. Dit proefschrift stelt zich tot doel om a) bij te dragen aan ons begrip van de rol die ADE – vergeleken met andere bodems – in de voedselproductie van lokale bevolkingsgroepen spelen en b) informatie te vergaren over de wijze waarop lokale bevolkingsgroepen diversiteit creëren en gebruiken.

De meeste hoger gelegen gronden in het Amazonegebied bestaan uit sterk verweerde en zure bodems met een beperkt nutriënten-vasthoudend vermogen. Deze bodems worden daarom ook als ongeschikt beschouwd voor permanente, intensieve teelt. Bodems in de lager gelegen vloedvlaktes worden jaarlijks verrijkt met sedimenten die de rivier aanvoert uit de Andes. Deze vloedvlakten staan lokaal bekend als *várzeas* en zijn beter geschikt voor landbouw. *Várzeas* hebben een minder lage pH, een groter kationen-uitwisselend vermogen en meer calcium en magnesium dan de zuurdere, sterk verweerde hoger gelegen gronden. Daarentegen staan de *várzeas* periodiek onder water, waardoor het groeiseizoen bekort wordt. Daarmee is de gewassenkeuze beperkt tot soorten met een korte groeicyclus. In tegenstelling tot zeer zure, sterk verweerde hoger gelegen gronden en *várzeas* zijn de ADE meestal minder zuur, hebben ze een beter kationen-uitwisselend vermogen en betere basenverzadiging, beschikken ze over relatief grotere hoeveelheden organische stof en hebben ze een hoger gehalte aan stikstof, calcium en beschikbaar fosfaat; het merendeel van deze gronden is ook hoger gelegen en wordt niet overstroomd. Op ADE kan de landbouw daarom intensiever zijn en kunnen gewassen worden verbouwd die hogere eisen stellen aan de bodemvruchtbaarheid, een langere groeicyclus hebben, en slecht floreren op niet-antropogene hoge gronden of op de regelmatig overstromende *várzeas*.

Eerdere studies hebben aangegeven dat wanneer ADE voorkomen de boeren deze vaak benutten door een intensievere zwerflandbouw toe te passen, waarbij de omvang van de veldjes kleiner is en ze sneller op dezelfde veldjes terugkeren dan op de niet-antropogene hoger gelegen gronden. Door de hogere bodemvruchtbaarheid echter vergen ADE meer arbeid en tijd voor onkruidbeheer. In sommige gebieden worden *várzeas* ook veel en intensief benut voor zwerflandbouw die vergelijkbaar is met die op ADE, al moet dan rekening worden gehouden met regelmatige overstroming.

De resultaten in dit proefschrift geven aan dat, in tegenstelling tot eerdere rapportages, ADE in de Midden Caquetá regio van Colombia niet beduidend rijker zijn dan de omliggende zure, sterk verweerde hoge gronden - behalve dat de fosfaatbeschikbaarheid in de ADE wat beter is (Hoofdstuk 2). Hoewel ADE goede mogelijkheden bieden voor landbouw gebruiken lokale boeren uit de Midden Caquetá regio deze ADE niet vaker of op intensievere wijze dan omliggende niet-antropogene hoge gronden. De zwerflandbouw die wordt toegepast op ADE en niet-antropogene bodems is dezelfde en wordt gekenmerkt door veldjes van gelijke grootte, een teeltperiode van tussen de twee en drie jaar, ongeveer 40 jaar braak en een vergelijkbare tijdsinvestering in onkruidbeheer.

De lokale boeren bebouwden ook *várzeas* - of ze nu wel of geen toegang hadden tot ADE. Er waren echter wel verschillen tussen boeren in het type vloedvlakte dat werd verkozen voor bebouwing en de wijze van verbouw. In San Martín de Amacayacu, waar geen ADE voorkomen, bewerkten boeren jaarlijks dezelfde veldjes in laag gelegen vloedvlaktes die jaarlijks onderlopen in een systeem dat ‘teelt na terugtrekkend water’ wordt genoemd. Boeren uit de Midden Caquetá regio, die toegang hebben tot ADE, bebouwden hogere delen van de vloedvlaktes (lokaal *restingas* genoemd) die eens in de 5-10 jaar overstromen volgens hun zwerflandbouwsysteem. Deze verschillen in de keuze van het type vloedvlakte en daarbij passend teeltsysteem hingen niet samen met de bodemomstandigheden of vraag naar specifieke gewassen of producten vanuit de markt. Deze verschillen hingen samen met culturele tradities betreffende de opslag en verwerking van grote hoeveelheden cassave wortels en de beschikbaarheid van mensen om collectief werk (lokaal bekend als *mingas*) te organiseren voor de oogst van velden in de vloedvlakte. Boeren in de Tikuna gemeenschap van San Martín de Amacayacu zijn in staat om zulke *mingas* te organiseren en daarmee in korte tijd (gemiddeld 2 dagen voor een veld van 1 ha) de cassave wortels te bergen. Zij beschikken ook over de kennis en techniek om grote hoeveelheden verse cassave wortels goed te houden tijdens hun tijdelijke opslag en tot *fariña* (een korrelig product van gefermenteerde en geroosterde cassave zetmeel) te verwerken, een vorm waarin grote hoeveelheden cassave opgeslagen kan worden voor latere consumptie. Boeren uit de Midden

Caquetá regio zijn beperkt in hun mogelijkheden tot het organiseren van *mingas* doordat er in die regio competitie is om arbeid met betaalde activiteiten in de illegale mijnbouw. Alle landbouwactiviteiten worden daarom slechts met arbeid uit de eigen familie uitgevoerd en boeren verkiezen daarom teelt op de hoger gelegen gedeeltes van de vloedvlakte waar de oogst over langere tijd kan worden gespreid boven teelt in de lagere delen die meer arbeid vraagt per dag dan binnen het huishouden beschikbaar is.

Hoewel het gebruik van ADE voor landbouw slechts in één van de vier bestudeerde gemeenschappen in de Midden Caquetá regio van belang was (Hoofdstuk 3), waren ADE van belang als vestigingsplek van gemeenschappen en voor bos-landbouw systemen met zowel lokale soorten als exoten die het slecht doen op bodems die arm zijn aan beschikbaar fosfaat. Voorts werden ADE soms gebruikt om grasvelden voor esthetische doelen aan te leggen. Kortom, ADE waren niet direct van belang voor de productie van het basisvoedsel van de gemeenschappen aangezien de beperkte aantallen mensen en de lage bevolkingsdruk in het gebied leidden tot ruime beschikbaarheid van oudere bosvegetaties waarin zowel boven- als ondergronds voldoende voedingstoffen waren opgehoopt om de benodigde nutriënten te leveren voor de zwerflandbouwveldjes waarin het basisvoedsel wordt verbouwd.

Cassave (*Manihot esculenta* Crantz) is het basis voedselgewas voor de in dit proefschrift bestudeerde lokale gemeenschappen. Cassave wordt op alle bodemtypes verbouwd en is met meer dan 70% van de plantplaatsen hoofdgewas in alle velden. De diversiteit aan cassave was groot met op basis van morfologische kenmerken 173 onderscheiden landrassen. Van deze rassen werd 87% ook op basis van moleculaire technieken als genetisch uniek aangemerkt. De bestudeerde vijf etnische groepen verbouwden zowel zoete cassave (met minder dan 100 mg/kg cyanide in de wortels en waarvoor geen specifieke bewerking nodig is voor consumptie) als bittere cassave (met meer dan 100 mg/kg cyanide in de wortels die de lokale bevolking als toxisch beschouwt en die een toxiciteit-beperkende verwerkingsstap nodig hebben voor consumptie). Er was een verschil tussen etnische groepen in het aantal cassave landrassen waarover men beschikte; ook was er een verschil in de verhouding tussen zoete en bittere rassen (Hoofdstuk 4). Deze verschillen in rassenassortiment tussen etnische groepen hingen niet zozeer samen met bodemtypes die bebouwd werden aangezien boeren alle rassen op alle bodemtypes verbouwden. Gehele assortimenten bleken heen en weer te gaan tussen hoger gelegen gronden en vloedvlaktes (zowel de lager gelegen vloedvlaktes als de *restingas*), en tussen antropogene en niet-antropogene gronden; er werden geen specifieke combinaties van gronden en rassen waargenomen. Dit laatste in tegenstelling tot eerder onderzoek waarin specifieke combinaties gevonden werden van cassavelandrassen en bodems.

Verschillende factoren kunnen deze ongerichte verplaatsing van cassaverassen tussen bodems veroorzaken. Enerzijds waren er geen grote verschillen in bodemkarakteristieken tussen ADE en niet-antropogene bodems: beide leverden vergelijkbare omstandigheden voor cassave productie. Anderzijds bleek ook de diversiteit aan arbusculaire mycorrhiza schimmels vergelijkbaar tussen bodems en was deze onafhankelijk van de fysische en chemische bodemeigenschappen, waardoor bodems vergelijkbare condities leverden met een rijke populatie aan arbusculaire mycorrhiza symbionten. Gezien de lange duur van braak vergeleken met de tijd dat er cassave ten velde staat, levert de lokale zwerflandbouw verder ook geen basis voor co-adaptatie van cassave en arbusculaire mycorrhiza schimmels (Hoofdstuk 5). Samenvattend draagt de variatie in bodemeigenschappen niet sterk bij aan diversiteit in cassave; de culturele waardes die toegekend worden aan cassave (d.w.z. cassavelandrassen als symbolen van etnische identiteit, het in stand houden van een breed assortiment aan landrassen, culinaire tradities) zijn veel belangrijkere verklaringen voor de waargenomen diversiteit in het studiegebied.

De mens is een belangrijke, scheppende actor in het Amazonegebied. De mens heeft landbouw bedreven op de meeste gronden in de regio en heeft daarmee de bosvegetatie en bosdynamiek beïnvloed. De mens heeft ruim voor Columbus ADE doen ontstaan - een bodem die zonder de mens niet had bestaan in de Amazoneregio. De lokale bevolking associeerde ADE met historische en dichte bewoning waar ook de eerste cassave werd verbouwd en waar ADE van groot belang waren voor de voedselproductie. Hoewel de rol van ADE in de huidige voedselvoorziening beperkt wordt geacht, geven de volksverhalen aan dat deze bodems in vroegere tijden een sleutelrol speelden. Niet alleen was de mens de motor achter de vorming van ADE: hij domesticeerde ook lokale plantensoorten. Cassave, dat inmiddels het zesde gewas is in de tropen en sub-tropen, is daar één van; cassave kan zelfs in belangrijke mate bijdragen tot aanpassing van de landbouw bij klimaatveranderingen in de tropen. Zoals aangegeven is de cassavediversiteit uitgesproken groot in het Amazonegebied en deze draagt sterk bij aan de plantaardige diversiteit daarin. De mens heeft in sterke mate bijgedragen aan het creëren van de diversiteit in het Amazonegebied. We zijn bezig ons een beeld te vormen van die bijdrage. Dit proefschrift draagt hieraan bij met zijn analyse van de wijze waarop de mens-omgeving interacties resulteerden in een specifiek gebruik van een gediversifieerd landschap en in keuzes rond het beheer van cassave als basisvoedsel.

Acknowledgements

This thesis is not complete without expressing my sincere gratitude to the various people who contributed in one way or another to it.

I want to start thanking the archaeologist Gaspar Morcote-Ríos from the Universidad Nacional de Colombia who showed me the Amazonian Dark Earths for the first time and shared with me the information to apply for a PhD position at Wageningen University. This dream that comes to an end with this thesis started with Gaspar and I want to express my deepest gratitude to him. Two other persons encouraged me to submit my curriculum vitae to the Terra Preta Program: Carlos Rodríguez, Director of Tropenbos Colombia, and Tomás León Sicard, Professor of the Universidad Nacional de Colombia, both also among the first researchers in reporting the presence of Amazonian Dark Earths in Colombia and lovers of the Amazon region.

I want to thank the two organizations that funded my research as without their support this PhD project would not have been possible. I want to thank the Interdisciplinary Research and Education Fund (INREF) and its Terra Preta Program of Wageningen University (The Netherlands) and the Instituto Amazónico de Investigaciones Científicas Sinchi (Colombia) for their financial support of this PhD.

I want to express my sincere thanks to specific persons at Wageningen University. To Thom Kuyper, Marielos Peña Claros and the team of the Terra Preta Program for giving me the opportunity to participate in the program through a sandwich PhD construction. To Paul C. Struik, the best promoter I could have had. To my supervisors Tjeerd Jan Stomph and Gerard Verschoor who always provided important contributions and interesting discussions about my research, and who helped me to grow up as a researcher. To Sjanie van Wetten and Nicole Wolffensperger, secretaries of the Crop Systems Analysis Group for their warmness with help on the final organization of this thesis.

In Colombia, first of all I would like to thank my home institute the Instituto Amazónico de Investigaciones Científicas Sinchi and especially its director Dr. Luz Marina Mantilla Cárdenas, its sub-director Dr. Rosario Piñeres Vergara, and the director of the human resources office Diego Lizcano, who offered me all the support I required to study abroad. To my colleagues Gladys I. Cardona, Marcela Núñez and Edmundo R. Mendoza for their support in Colombia and their help in shipping soil and root samples. To Luis Eduardo Acosta, coordinator of the Sinchi Institute in Leticia for his support, friendship and for sharing his

publications about indigenous swiddens. To Augusto Mazorra, who passed away before he finished helping me in designing the maps for this thesis. To Lilia Pérez for her friendship and help booking field trips. To Misael Rodríguez for his friendship, support and help with field and screen house work, and Delio Mendoza for his help during the field work in Araracuara. To Jairo Madrid, Cornelio Vanegas, Julio César Lucas, Orlando Paky for their help with the logistics and field work. To Eugenia Guayamba for her help in the laboratory processing root and soil samples.

Two persons outside Wageningen University and the Sinchi institute were key in this thesis. Luis Augusto Becerra López-Lavalle, Director of the Manioc Genetics Laboratory of CIAT (Palmira-Colombia) who saved time by helping me with the molecular processing and analysis of manioc samples; and Maarja Öpik from the Institute of Botany and Ecology of the University of Tartu (Tartu, Estonia) who welcomed me in her laboratory and taught me the molecular techniques and bioinformatics to analyze arbuscular mycorrhizal information from root and soil samples.

I want to thank important people in each one of the indigenous communities I worked with because without their help and good will I could never have understood their culture and their interactions with soils and manioc, or participate closely in their daily lives. From the community of San Martín de Amacayacu I want to thank Ignacio Peñero, Candelaria and their families, as well as Grimanesa Ruíz, Nirsa Ruíz, Eulalia Ángel, Yilmer Ramos, Susana Ramos, and Leontina Paima. From the community of Aduche I want to thank Fissi Andoke, Isabel Macuna and their families, as well as Margot Muñóz, Raquel Andoke, Irene Andoke, Hernando Andoke, Gloria Andoke, Mario Andoke, and Roberto Andoke. From the community of Villazul I want to thank Adriano Paky, Ana Rita Andoke and their families, as well as Alicia Kumimarima, Idaly Barbosa, and Carmen Andoke. From the community of Peña Roja I want to thank Elías Moreno, Virgelina and their families; José Moreno, Viviana and their families, as well as Hernán Moreno, Rubiela Miraña, Blanca Miraña, Israel Rodríguez and Elsa Hernández, Oliverio Rodríguez and Adelina Gómez, and Deyanira Da Silva. From the community of Guacamayo I want to thank Aurelio Suárez, Alcira Soeroke and their families, as well as Marleny Ramírez, Emilia Fariviaño, Juanita Castro, Rita Castro, Serafina Guerrero, María Encarnación Soeroke, and Zoork Shirley García. From Araracuara I want to thank Crispín Rodríguez and Rosalba Jacobombaire.

It is not possible to finish a PhD and a thesis without the support of the people who love you as they are the prime motivation in one's life. First, I want to express my most lovely

gratitude to my parents Marco Fidel and Clara Eugenia and my sister Claudia with whom I always shared the most important moments of my life and who made me the person I am. To my aunts Nohramerica, María Ivonne del Pilar and my uncles Leonardo and Carlos and their families who were my inspiration. To my beloved husband Oscar who always supported my decisions, and who with his love supported our family while I was in the Netherlands and gave me the courage to finish this thesis. To Dolly, María Elena, Juan Carlos and Álvaro, my family in law, who took my place in some moments of this PhD to help Oscar and the children at home. To my beloved children Waira Luna and Juan Sue who were without me for six months but later shared with me and my husband the experience of living in the Netherlands. All of them supported me emotionally to finish my thesis and the words here are not enough to express my love and gratitude.

During my thesis I lived in two worlds: Leticia, in the Southern portion of the Colombian Amazon and Wageningen in the Netherlands. From Leticia, I need to thank the people of the Cerca Viva reserve, the place where I live, for their friendship and support to me and my family when it was necessary. I want to thank Luis Eduardo Acosta, Jessenia Yawira Acosta, Jose Luis Díaz, María del Pilar Maldonado, Elisa Díaz, Antara Díaz, Valeria Meickle, Liliana Guarnizo, Manuela Mariramba Díaz, Marta Prado, Inti Asai Pinilla, and Aimar Matías Alegría Pinilla. I want to thank my other friends with whom I share a beautiful friendship and the enthusiasm to live in the Amazon forest: Carlos Zárate, María del Pilar Trujillo, Mariana Zárate, Miguel Zárate, Goran Mihaijlovic, Luka Mihaijlovic, Juan Álvaro Echeverri, and Martha Pabón. From Wageningen, I want to thank "the *cardumen*" for their academic and personal support: André Braga Junqueira, Catarina Jacovac, Estela Quintero, Edvaldo Sigrilo, Tatiana Rittl, Paulo Paiva, and Carlos Alho. I thank Wageningen students at the third floor of the Radix building for sharing with me coffees, lunches, meetings and non-scientific conversations. I thank my beautiful landlord and now close friend Marijke Wiljam who was like a second mother for me and my family. I thank all the members of the "Colombianos en Wageningen" organization and the recently created WASCA association to share with me the pride of being Colombian.

Thanks to all of you, thanks for ever.

List of publications

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Submitted papers

C.P. Peña-Venegas, T. J. Stomph; G. Verschoor, J. A. Echeverri, P. C. Struik. Classification and use of natural and anthropogenic soils by indigenous communities on the Upper Amazon region of Colombia. Human Ecology (Accepted).

C. P. Peña-Venegas, G. Verschoor, T. J. Stomph, P. C. Struik. Challenging current ADE knowledge: Indigenous agriculture in different soils of the Colombian Amazon. Culture, Agriculture, Food and Envrionment (Submitted).

Conference papers

C. P. Peña-Venegas, E. R. Mendoza, B. Betancourt, M.T. Garzón, C. H. Rodríguez, G. I. Cardona. 2013. C fixing capacity of Amazonian soils and its relationship with their state of degradation. 17th Conference of the International Organization of soil , July 8-12/ 2013. ISBN 978-958-57973-0-7.

C.P. Peña-Venegas, L.E. Acosta, G. Verschoor, C.E. Logreira-Buitrago, E. Agudelo. Mining threats to ancient anthropogenic soils and other resources associated to indigenous food security in the middle Caquetá River, Colombia. 17th Conference of the International Organization of soil , July 8-12/ 2013. ISBN 978-958-57973-0-7.

PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (6 ECTS)

- Terra Preta, Amazonian soils, actual uses of Amazonian soils

Writing of project proposal (4.5 ECTS)

- Farmer’s perception and actual use of the fertility of Terra Preta in Colombia

Post-graduate courses (4.4 ECTS)

- Introduction to R for statistical analysis; PE&RC (2014)
- World soils and their assessment; ISRIC (2014)
- Science for impact: focus on enabling conditions; PE&RC (2014)
- Consumer-resource interactions; PERC/ Ecology & Evolution/Sense (2014)

Laboratory training and working visits (3 ECTS)

- SNP’s for manioc diversity studies; CIAT-Palmira, Colombia (2013)
- AMF Molecular diversity; University of Tartu-Estonia (2014)

Invited review of (unpublished) journal manuscript (2 ECTS)

- Revista Colombia de Biotechnologica: Mycorrhizas and soils (2011)
- Revista de Biología Tropical: Arbuscular mycorrhization (2013)
- UDO Agrícola: tropical soils (2013)
- Revista Acta Agronómica: soil sciences (2014)

Deficiency, refresh, brush-up courses (3 ECTS)

- Methods, techniques and data analysis in field research (2011)

Competence strengthening / skills courses (2.4 ECTS)

- PhD Competence assessment; Wageningen Graduate Schools (2011)
- Writing and presenting a scientific paper; Wageningen Graduate Schools (2014)
- Information literacy including EndNote introduction; Wageningen UR library (2014)

PE&RC Annual meetings, seminars and the PE&RC weekend (1.5 ECTS)

- PE&RC Weekend (2011)
- PE&RC Weekend last year (2014)

Discussion groups / local seminars / other scientific meetings (4.6 ECTS)

- Plant-Soil interactions (2011)
- Terra Preta meetings (2011, 2014)
- Annual research meetings at Sinchi Institute (2011-2013)

International symposia, workshops and conferences (7.5 ECTS)

- Second international workshop Terra Preta Programme; Manaus, Brazil (2012)
- 17th Meeting of the International Soil Conservation; Medellín, Colombia (2013)
- Third international workshop Terra Preta Programme; Leticia, Colombia (2013)

Lecturing / supervision of practical’s / tutorials (1.2 ECTS)

- Microbiological of Amazonian soils (2012-2013)

Supervision of a MSc student

- Andrea Díaz Ismael: arbuscular mycorrhization in natural and anthropogenic soils

Curriculum Vitae

Clara Patricia Peña Venegas was born in Bogotá, Colombia, on 19 July, 1968. After she completed her higher school at the New York School, in 1986 she joined the Faculty of Microbiology of the Universidad de los Andes in Bogotá to study microbiology. She graduated as microbiologist in 1990 and worked for one year as a junior researcher in the Center for researches in microbiology-CIMIC of the Universidad de los Andes. Since that time she knew she would like to work as a researcher studying the microbiology of soils. In 1993 she traveled for the first time to the Amazon region of Colombia for vacations. The hot, humid and green environment and the warm people there impacted her so much that she decided to move to live to Leticia in the Amazonas state of Colombia. In 1995, she started her carrier as a junior researcher in the Instituto Amazónico de Investigaciones Científicas Sinchi to study the biological composition of Amazonian soils. In 1996, she won a scholarship from the Fulbright Commission to study her Master degree in the Environmental Sciences and Forestry College of the State University of New York in Syracuse, NY, USA. In 1999 she obtained her Master of Science degree with a thesis on arbuscular mycorrhizal fungi with the thesis “Changes of the native mycorrhizal population in a Colombian Oxisol and its impact on land productivity”. She continued working as a researcher with the Sinchi institute in the Amazon region. After coordinate different research projects which involved the knowledge of soils, she felt the need to explore a broad view of soils which include people perceptions of it. In 2010 she applied for a PhD position in the Terra Preta Program of the Wageningen University with the aim to understand indigenous perceptions of Amazonian Dark Earths. In 2011 she started her PhD degree studying the indigenous perception and use of Amazonian soils, and its relation with manioc diversity and the arbuscular mycorrhizal symbiosis in manioc. She completed her PhD in 2015 with the thesis “People, soils and manioc interactions in the upper Amazon region”. Today she continues being part of the staff of researchers of the Sinchi Institute in Colombia and working in the Amazon region.

Funding

The research presented in this thesis was financially supported by the Interdisciplinary Research and Education Fund (INREF) of Wageningen University through the Terra Preta program, The Netherlands; and by the Instituto Amazónico de Investigaciones Cientificas Sinchi of Colombia.