STRUCTURAL AND ENVIRONMENTAL VARIABLES AFFECTING BIODIVERSITY CONSERVATION IN AGROFORESTRY SYSTEMS IN THE NORTHERN ECUADORIAN AMAZON

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ABSTRACT

The Northern Ecuadorian Amazon (NEA) is recognized as biodiversity hotspot that contains unique endemic plant species. However, unsustainable agricultural practices, such as more frequent cycles of shifting agriculture (SA), threat the NEA's forests endurance with negative consequences for biodiversity levels and ecological functions. In this study, I examined the spatial and temporal dynamics of the diversity of native trees across various types of agroforestry systems (AFS) subjected to SA. That is, the degree of existing risk of endangerment of tree species, the rapid change in floristic composition of mature forests converted to AFS, and the recovery pace of forest communities following abandonment. Transforming mature forest communities (MFC) to different AFS leads to a decrease in alpha diversity up to 75%. AFSs preserve 56% of the beta diversity compared to MFC; at least 8% of the species are threatened and the demographic status of 92% species is unknown. MFCs seem to regain their original structure after AFS abandonment. In the second part, I investigated whether AFS reverses the effect of intensified SA in cocoa (*Theobroma cacao*) agrosystems. I addressed the extent to which multispecific cocoa AFSs buffer the impact of reduced fallows in SA on loss of species. Tree diversity showed a gradual decrease from low to intermediate to high intensification SA in cocoa AFS, with values of 46, 29, and 12 species richness. The absence of fallows in SA affects tree presence, leading to changes in floristic composition in 30% fewer species compared to the beta diversity in cocoa AFSs experiencing long resting phases. Nonetheless, the similar beta diversity between low and intermediate intensification levels of SA suggests a concomitant delay in forest degradation rates. Finally, I examined the extent to which beta diversity in AFS reverses the effect of shorter SA fallow periods in the soil properties of cocoa (*T. cacao*) agrosystems. Agroforestry systems, combined with SA, shields the negative outcome of intense land-use on the soil's nutrients. The arboreal cover maintains the soil fertility needed for crop performance and food sustainability. The dominance of certain tree species (*Vochysia leguiana*, *Inga edulis, Cordia alliodora*) is essential to support adequate dynamic levels of nutrient cycling with more intense fallow periods, whereas some other species (*Virola flexuosa*, *Chrysophyllum amazonicum, Ocotea bofo*) have an apparent effect on soil acidity. I conclude that AFS have the potential for enhancing sustainable forest management and preservation of endangered tree species.

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CHAPTER 1: INTRODUCTION

1.1 Biodiversity, ecosystem services, and deforestation in tropical forests

The biosphere encompasses all ecological systems hosting the totality of the Earth's biological diversity, including described and undescribed species. Regrettably, with increasing human population and land conversion over the past half a century, the flora, fauna, and functional integrity of the biosphere's ecosystems have seen abrupt and irreversible modifications, ultimately causing loss or shifts in species' demographic and distributional patterns (Pacifici et al. 2017). These unprecedented changes have profound effects in forest landscapes by changing the structure of associated horizontal and vertical forest layers, key components for assessing successional stages and regeneration, and/or degradation rates of plant communities. Further, most anthropogenic changes have compromised ecosystem services. That is, the complex natural cycles sustaining the working force of the biosphere with ensuing benefits from ecosystems to human society. In view of the fast-changing landscapes, understanding the key forces that shape the dynamics and spatial structure of ecosystems, and the response to changes, is fundamental to achieving a more productive use, management, and safeguard of biodiversity.

To put the course of world's forest conversion in context, desertification or the process of fragmentation and forest loss, has been amplified by unsustainable logging and clear-cutting practices. According to the Food and Agriculture Organization (FAO 2020), the Earth's wooded land has been reduced by 178 million ha (an area equivalent to the size of Libya) since 1990. This timberland loss has led to drastic habitat transformation and ecosystem instability for hundreds of animal and plant species in a relative short term. Yet, tree extraction is a continuous and untenable predominant practice in tropical and subtropical areas of the planet (FAO 2020). The different devastation levels of these natural resources have triggered ecological challenges, essentially biodiversity conservation and global warming (Porro et al. 2012, Homeier et al. 2013, Tapia-Armijos et al. 2015). Regardless of size and number, each species is a fundamental unit of biodiversity and plays an important role, often unique, e.g., keystone species, in the ecosystem, and in conjunction with biotic and abiotic factors, creates a more dynamic and productive biological network (Harrington et al. 2010, Mace et al. 2012). Simply put, high values of species diversity in forests increase acquisition and utilization of resources that improve the efficiency of ecosystems and its services (Liang et al. 2015). For instance, a large scale and long term-meta analysis of more than 700,000 permanent forest plots worldwide demonstrated a strong positive relationship between tree volume growth and species richness (Liang et al. 2016). Conversely, human-induced changes to average climate events, e.g., increasing the frequency of "El Niño" climatic episodes, pose considerable threats to forest communities. These modifications have led to recurrent and often erratic patterns of severe droughts and heat waves (Allen et al. 2018), rise in wildfire intensity (de Groot et al. 2013, Doerr and Santín 2016), and shifts in rainfall patterns that ultimately modify hydrological cycles, water quality and availability (Schewe et al. 2014, Döll et al. 2018, Lee et al. 2018, Saeed et al. 2018).

There is strong evidence that functional diversity (the importance and range of species traits), rather than species numbers *per se*, is strongly correlated with ecosystem functioning. Species loss and over-simplification of communities affects the net productivity of environmental networks and ecosystem services worldwide (Liang et al. 2015). Over the past few decades, studies have improved our understanding of biological diversity and the consequences associated with its loss (Naeem et al. 2012, Cardinale et al. 2012). The basic regulating mechanism of the relationship between diversity-ecosystem services is resource partitioning due to niche complementary (Naeem et al. 1994, Tilman 1997, Hector 2011). This theory states that the ecosystem acts in response to plant richness. Specifically, it balances the use of natural resources when plant taxa fluctuate in ways they extract nutrients, light, and water, sources due to differences in root depths, phenology, nutrient preferences, and others (Hooper and Vitousek 1998). Thus, the coexisting ability of many plant species is explained based on the spatial and temporal competitive interaction for resource partitioning in an ecological niche (Tilman 1982). The longstanding interface between primary producers, i.e., plants, and underground organisms induced by greater plant diversity allows access to a greater proportion of resources. This leads to an increase in the net uptake of resources by plants associated with lower nutrient losses and increase in biomass production in the ecosystem (Barnes et al. 2020). Hence, high levels of diversity in autotrophic organisms is critical to maintain functional composition and ecosystem functions. On the other hand, several debates indicate that the causal effect biodiversity-ecosystem services can be confounded with "sampling effect", i.e., the treatments with highest diversity have a greater probability of being controlled by the most productive organisms within the entire species pool (Wardle 1999). However, it has been claimed that the sampling effect is a rather valid mechanism by which biodiversity affects are manifested (Tilman 1997), but it can be ignored (van der Heidjden et al. 1998, Liang et al. 2015).

Numerous studies have shown that the depletion of natural resources and loss of plant taxa impact several ecological mechanisms in forests, such as resilience capacity and nutrient cycling, which are requirements for ecosystem services. These natural services represent the tangible and intangible ecological benefits to human well-being (MEA 2005, Polania et al. 2011). The welfares of these natural aids are direct, such as food and energy resources (Gasparatos et al. 2011) and indirect, e.g., soil fertility, pollination, carbon sequestration, and weather mitigation (Power 2010, Wratten et al. 2012). Because the resilient structural design of forest status relies on species diversity, it is understandable that higher diversity is a driver for ecological stability in plant communities. Species-rich communities enhance ecosystem stability, also known as portfolio effect (Schindler et al. 2010, 2015), in time and space by retaining ecological variables, e.g., biomass cycles, taxonomic composition, height and layer complexity (Loreau 2000, Hugues et al. 2002, Thompson et al. 2009, Yan et al. 2011). Another important ecosystem function dependent of high levels of biodiversity is nutrient cycling. Optimum functional groups of plant species require, and yet sustain macro- and micronutrient dynamics including the retention and availability of soil chemical components through interactions among biotic and abiotic drivers, such as plant-soil network mechanisms (Hiremath and Ewel 2001, Ehrenfeld et al. 2005, Hooper et al. 2005, Kulmatiski et al. 2008, Mangan et al. 2010). These biological processes are particularly relevant for farmers in tropical areas because ideal soil properties influence plant performance, i.e., crop productivity. Similarly, from the climate standpoint, suitable levels of biological diversity regulate environmental change. As such, forests can mitigate severe weather effects with successive cycles of evaporation, cooling, sequestration, and storage of large amounts of carbon (Bonan 2008). However, the capacity of forests to adjust major climate change depends on the amount and assortment of plant species (Zhang et al. 2012, Liang et al. 2015, 2016, Ammer 2019). Therefore, biodiversity is vital in forest ecosystems because of the explicit benefits to regulate and maintain efficient levels of energy flow and a wide variety of ecosystem services.

Tropical forests (TF) represent the largest reserves of biodiversity among forest ecosystems in the world. With approximately 50% the global forest land area (FAO 2020), these plant communities support different landscapes composed of numerous endemic plant and animal species (Duivenvoorden et al. 2002). The Amazon Basin (AB) of South America, is the largest tropical rainforest biome on Earth. It includes over 250 tree species ≥ 10 cm dbh (diameter at the breast height) in one hectare compared to ~20-30 tree species in temperate forest regions (Gentry 1992, Condit et al. 1996, ter Steeg et al. 2019). This hyper-species diversity places the AB in a privileged position of high ecological productivity. It stores approximately 95 t ha^{-1} of above- and below-ground biomass compared to the world average of 62 t ha^{-1} (FAO 2015). However, the environmental benefits of this and other tropical regions of the world could experience significant collapse as a result of intensifying deforestation rates. Causal agents of these problems are mainly anthropogenic. In the past 60 years, the conversion of forests to agricultural land has been considered the main reason for the loss of forest areas and numerous tropical species of flora and fauna. The main cultivation systems practiced in the tropics are shifting agriculture, silvopastoral systems, and monocultures, but the conversion of forests to farmland is often at the expense of regional and global environmental and biodiversity costs. Thus, the investigation of farming systems in relation to biodiversity and sustainability is of high priority in tropical forests. It is in these world areas where fostering the development of proactive solutions and alternatives to reduce the overuse of natural resources at all geographic and social levels is critically needed. In view of the global intensification of tropical deforestation in connection with farming activities, the present research focuses on shifting agriculture.

1.2 Shifting agriculture, food security, and tropical forests

Crop domestication, including shifting agriculture (SA) also known as shifting cultivation or swiddening, have been practiced around the world thousands of years ago (Simmonds 1979, Simmons and Leakey 2004, Dale and de Blois 2006, Ramakutty et al. 2018). Shifting agriculture may include the use of fire as a slash-and-burn, an old practice by human settlers (Kato et al. 1999, Cairns 2015, Erni 2015, Kurien et al. 2019). This farming system has long been replaced by modern agricultural methods in most geographic regions of the planet but remains quite active around rural communities of the tropical belt (Olofsson and Hickler 2008, van Vliet et al. 2012). Shifting agriculture is composed of a three-phase cycle that encompasses the use of natural forests as the main component. These are: clearing of trees (sometimes followed by burning), use of cleared land (for agriculture and/or pasture systems), and fallow period (land abandonment) that favors successional ecological stages, such as the establishment of secondary forests, eventually evolving into a mature/primary forest community structure (Kapp and Manning 2014). To date, the practicing patterns of SA are not clear, in part because of the spatial and temporal changes of the land being cultivated as well as the lack of a consistent definition of SA. This rather rudimentary farming exercise is important across the world and early estimates have revealed that 90 tropical and subtropical countries use SA in an area of approximately 400 Mha (FAO 1982, Lanly 1985). Current estimates about the cultivated land area for SA is between 260 and 280 Mha worldwide (Silva et al. 2011, Heinimann et al. 2017). Given the numerous and often negative criticisms about SA have been made mainly because of the disparate use of fire as clearing method. More recently, the intensification of this farming system with more frequent crop cycles has also been objected because of the adverse effect on biological diversity and ecosystem dynamics, in particular the removal of native plant species and harm to soil fertility.

One of the disadvantages of SA is associated with fallow periods being longer than cropping time resulting in an imbalance between years of cultivation and fallow length in the slash-and-burn method thereby requiring large areas of forest land to be sustainable (Delang and Li 2013). The expansion of SA using fire as the clearing method also contributes to net carbon emissions; however, data for slash-and-burn carbon release is lacking. This routine has led to the belief that SA is an inefficient farming method, promoting the destruction of ecosystems (Ayanu et al. 2011, Henley 2011, Ellen 2012). Another issue is that any reduction of fallow length is a consistent threat to land degradation. This implies more frequent cycles of cultivation, which in turn, cause changes is species demography, distribution and even loss, with eventual impacts to the regenerative capacity of the ecosystem (Uhl 1987, Kennard 2002, Dale and de Blois 2006, Fukushima et al. 2007, Tran et al. 2010, Tran et al. 2011). For example, Fukushima et al. (2008) found that plant taxa from old forests in Thailand was only 49% comparable to a plot of land under 26-year fallow period that had been previously subjected to intense swidden cultivation. However, species diversity of the same old forest was 67% analogous to a 26-year-long fallowed plot with a former low occurrence of SA cycles. This information suggests that short fallow time lessens the post-disturbance recovery rate of forest areas with evident costs associated with expected ecological successional stages (Ross 1954, Uhl 1987, Chazdon et al. 2007, Fukushima et al. 2007, 2008, Lebrija-Trejos et al. 2008, Tran et al. 2010, Jakovac et al. 2015, 2016).

The effects of short resting periods also impact food security. Fallow periods are important for restoration of natural nutrient cycles and fertilizers (Nye and Greenland 1960, Kapp and Manning 2014, Brookfield 2015), but it is unclear whether shorter resting intervals allow the required cycles for rebuilding soil and nutrient conditions for future crops. According to Delang and Li (2013), approximately 2.4 billion hectares of tropical and subtropical forests are used for food production, and that almost half a billion people in the developing world depend on forest reserves for their livelihood (World Bank 2019). In the late '90s, for example, shortening fallows from 10 to 4 years caused ca. 30% reduction in crop yield (Kato et al. 1999). Similar evidence has been provided by Mertz (2002), Dalle and de Blois (2006), Wood et al. (2016). Under the world's current scenario with anthropogenic deforestation reaching exceptional levels, the decrease in fallow length with more intensified agricultural practices will potentially have more severe environmental impacts on species diversity, ecosystem recovery, and challenges to food security worldwide.

Farming systems used around the world are in the need of innovative transformation to support environmental sustainability, safeguard vital ecosystem services, and ameliorate food insecurity (Hoffmann 2013). Forest structure, particularly in the tropics, represents the main option to alleviate climate change and access to food and nutrition needs. Nevertheless, agriculture and other related land uses represent ca. 23% of world's anthropogenic greenhouse gasses (GHG) emission (IPCC 2019), with ca. 75% attributed to developing countries replacing forests with crops (Hoffmann 2013). Shifting agriculture, on the other hand, is intended for local economic development and food security relies on forest recovery after long fallow periods (Arévalo 2009). This conundrum has been the focus of discussion for several years and while several potential solutions have been proposed, the most viable is the trade-off between food security and forest loss to maintain equilibrium in levels of alpha and beta diversity in and around farmland in tropical and subtropical regions. Within this scenario, more deliberate land management with a selection of shade trees combined with diverse crops emerge as a promising alternative. This practice, known as Agroforestry Systems (AFS), has been widely endorsed, e.g., Guiracocha et al. (2001), Ashley et al. (2006), Dalquish et al. (2007), Bhadwat et al. (2008), DeClerck et al. (2010), Schroth (2004), Cerda et al. (2014), Vaast and Somarriba (2014) because it preserves tropical biodiversity, reduces anthropological pressure on the primary forest, and enhances ecosystem services and connectivity with conservation areas. Thus, this natural method of amalgamating native trees and crops in rural farms emerges as a new activity with a promising sustainable approach to promote biological diversity and welfare of land users in vulnerable areas of the developing world. However, the benefits of using AFS under SA have scarcely been investigated. With this in mind, this study explores the environmental value of traditional farming methods in areas of the Ecuadorian Amazon as explained in the following section.

1.3 The Ecuadorian Amazon forest: an ideal location for investigation of biodiversity

Forest clearance and the simultaneous intensification of agriculture represent early anthropological exercises broadly known to explain landscape disruption and biodiversity changes worldwide. In order to comprehend this idea, first it is necessary to put in context the socio-economic reality that has drastically and negatively affected land use and biological diversity in tropical countries of Latin America and second, to appreciate why this geographic region is an ideal site for investigation. Foremost, the deforestation rate in this area is among the highest around the world. In the last decade the annual rate of net forest loss was 2.6 million ha (FAO 2020). That is, 41% of the world's current annual proportion of clear cutting. In addition, the socio-economic situation, especially in Andean countries in South America, is alarming. According to the Economic Commission for Latin America and The Caribbean (ECLAC 2019), the current number of people in Latin America countries living in multidimensional poverty is 182 million, of which 62 million are in extreme need. This number will likely increase to 30 million in the next decade because of people's vulnerability to maintain permanent income (PNUD 2016). It is also worth noting that these data are concentrated in rural areas, which are regions revealing the lack of multiple basic needs, such as health care access, drinkable, clean water, electricity, and food security. The intricate situation between poverty and inadequate use of natural resources is reflected in low-cost agricultural systems with inferior productivity and high carbon emissions. Additionally, tropical Latin America has the highest proportion of forest in protected areas. According to FAO (2020), this region holds approximately 40% of safeguarded forest, ca. 76.4 million ha mostly located in South America.

Thousands of endemic organisms inhabiting these sanctuaries are vulnerable or at risk of extinction. Within this context, and in response to a global policy framework in accordance with the Paris agreement (UNFCCC 2015), it is essential to undertake initiatives aiming to reduce poverty and preserve natural resources in this area. At present, numerous studies in the tropics of Central and South America, e.g., Johns (1999), Guiracocha et al. (2001), Reitsma et al. (2001), Schroth et al. 2004, Harvey et al. (2006), aimed to reduce land degradation and global warming exist. Within this approach, I focus my research interest on small-holder farming systems located in vulnerable and isolated geographic areas with unreliable economies. These home-made agricultural gardens that are also part of the shifting agriculture approach, have been culturally important in the western area of the Amazon Basin (AB), specifically in the Northern Ecuadorian Amazon, for many decades, but little is known about the socio-economic productivity, environmental cost, and trade-offs of this practice in Ecuador.

The country of Ecuador has 250,000 km^2 of territory representing barely 1.5% the total surface area of South America. However, this nation possesses a privileged geographical location that enables a high diversity of native species of flora and fauna (Sierra et al. 2002). Almost half of the territory corresponds to the AB, which is situated below 1,300 meters above sea level (masl) in the eastern foothills of the Andes (Grijalva et al. 2016). These distinctive features make the Ecuadorian Amazon (EA) one of the most biodiversity-rich regions of the AB and one of the major hotspots of biological diversity in the world (Finer et al. 2008, Bass et al. 2010). Comparatively, the number of tree species in the Yasuní National Park in Ecuador is 655 ha^{-1} (Valencia et al. 2004) versus 154 ha^{-1} in La Planada Natural Reserve in Colombia (Vallejo et al. 2004) and 96 ha^{-1} in the Huai Kha Khaeng W. Sanctuary in Thailand (Bunyavejchewin et al. 2004). In addition, < 1% of the territory contains up to 34% of organismal diversity compared to the entire AB (Table 1.1) and likely sustains up to 6.7% of the endemic plants of the world (Myers et al. 2000). Clearly, this is an important area of the biosphere and habitat for numerous endemic or narrowly distributed species of plants and animals in addition to the ecosystem services they provide.

Table 1.1: Species richness in the Northern Ecuadorian Amazon (NEA). The Yasuní National Park as a comparative example in relation to the entire Amazon Basin. Source: Bass et al. (2010)

Organisms	**NEA approx. # of species**	**% of the Amazon Basin**
Area of the NEA	9,820 Km^2	0.15%
Amphibians	150	28%
Reptiles	121	33%
Birds	596	34%
Mammals	169 - 204	27 - 33%
Fish	382 - 499	12 - 16%
Vascular plants	2,704 - 4,000	7 - 10%

The Ecuadorian Amazon (EA) is primarily dominated by forest, i.e., more than six million ha out of the 13 million ha that make up the region (Veas and Moncayo 2014). This territory has an extent of 130,000 km^2 and is comprised of six provinces, namely Sucumbíos, Orellana, Napo to the north, Pastaza, Morona Santiago, and Zamora Chinchipe to the south (Acurio and Rafael 2009). The northern Amazonian provinces have seen dramatic increase in population: from 73,701 inhabitants in the early 80s to 416,565 as per the 2010 census, an increase of 565% in 30 years (INEC 2010). This growth coincides with the “oil boom” that started in 1970 triggering the colonization of this territory by non-indigenous people. Oil-related activities brought to the region one of the major episodes of deforestation (Nepstad et al. 2006, FAO 2015), to the extent that the higher rates of land conversion have been documented in these areas (Mena 2008). Clearly, new unsustainable methods for human settlements have put extra pressure on natural resources threatening numerous species and the ecosystem functionality and integrity.

The Northern Ecuadorian Amazon also includes important areas of primary forest and agricultural systems (Fig. 1.1A). Primary and mature forests are located mainly in biological reserves, such as the Sumaco Biosphere Reserve, Cayambe - Coca, Antisana, Llanganates, and other remaining wooded areas (Fig. 1.1B). These forests constitute ca. 47% of the land use in the EA (Table 1.2) but represent 60% of the protected land (MAE 2016). In contrast, the agricultural fields are situated in transitional and buffer zones of the NEA around the protected reserves (Fig. 1.1C). Permanent crops, such as cocoa and coffee are the most representative (>95%) in the NEA while grasslands are more widely distributed (60%) in the southern provinces (Table 1.2). The combination of different agroecosystems, such as forest and crops, makes the NEA a typical example of the AB a model site to investigate changes in landscape architecture and biological diversity. In these areas, several practical studies can be developed to fill knowledge gaps about the ecology, biogeography, and distribution of species, including the intrinsic relationships of plants and plant communities with indigenous and non-indigenous groups using these resources to fulfill economic needs and food security.

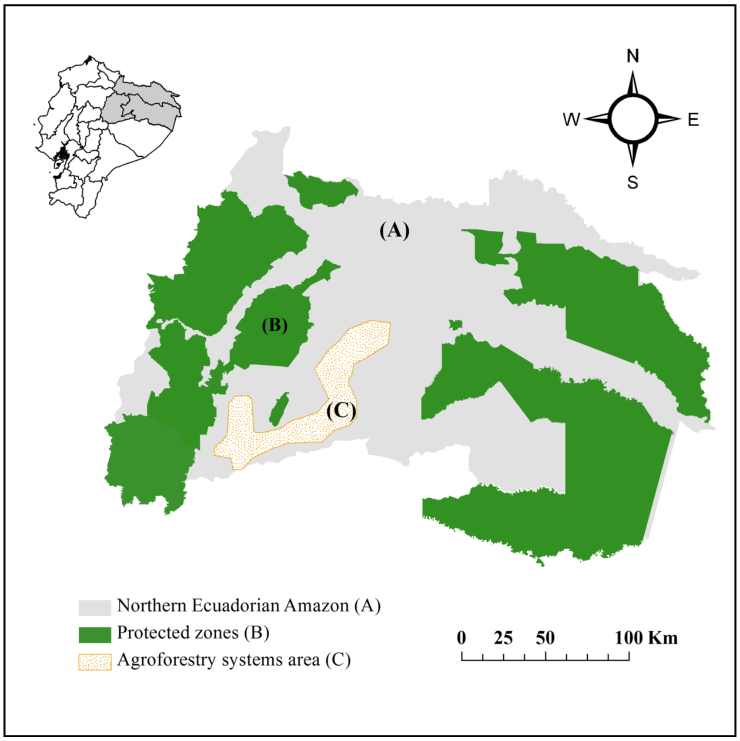

Figure 1.1: Map of the Northern Ecuadorian Amazon (NEA). (A) The three provinces included in the NEA, which encompasses both biological reserves and agricultural areas. (B) Areas designated as forest reserves located to the west and the east of the NEA, and (C) Transitional and buffer zone used for agriculture.

Table 1.2: Land use categories and total area (in ha) of the Ecuadorian Amazon (EA) region. Percentage of land in the NEA for each category compared to the Southern Ecuadorian Amazon (Source: INEC 2010)

Land use category	Total area (ha)	Northern EA (%)	Southern EA (%)
Cocoa	58,965	95.4	4.6
Coffee	22,164	95.3	4.7
Plantain	25,380	59.5	40.5
Corn	21,534	90.8	9.2
Cassava	9,386	30.0	70.0
Grasslands	361,730	39.9	60.1
Forest	2,911,341	46.7	53.3
Fallow	7,370	84.8	15.2
Moors	55,938	57.1	42.9
Other (passion fruit, pitahaya, etc.)	154,048	57.1	42.9
Total	**3,627,856**	**46**	**54**

In the Ecuadorian Amazon, the traditional AFS practiced by indigenous (Kichwa) groups in the NEA is the chakra system. It combines various features of conservation and production (Table 1.3). According to Arévalo (2009), this method involves shifting agriculture to satisfy food and income necessities in small land plots developed in forest gaps; the plots are then abandoned after 2-3 years to allow forest and soil nutrients recovery (Fig. 1.2a). In addition, according to Porro et al. (2012), one of the particularities of this AFS is the diversity in levels of multi-specific shade gradation offered by native trees left behind by farmers (Table 1.3). In all, the chakra system has the capability to preserve native floristic diversity, but the importance of those aspects is unknown, particularly aspects related to the preservation of endemic and threatened species and integrity and dynamics of ecosystem services.

Table 1.3: Components and characteristics of the chakra system (Adapted from Arévalo 2009)

Components	**Characteristics**
Crops cultivated	Cacao, cassava, corn, rice, and other
Tree management	Different levels of multispecific shadow
Technology	None. Use of small manual farming tools
Workforce	Individual and family members
Fertilization	None
Pesticides	None or minimal
Weed control	Manual
Features of producers	Small native Kichwa family production (marginal)
Objective of production	Personal food and income resource
Production management	Communities

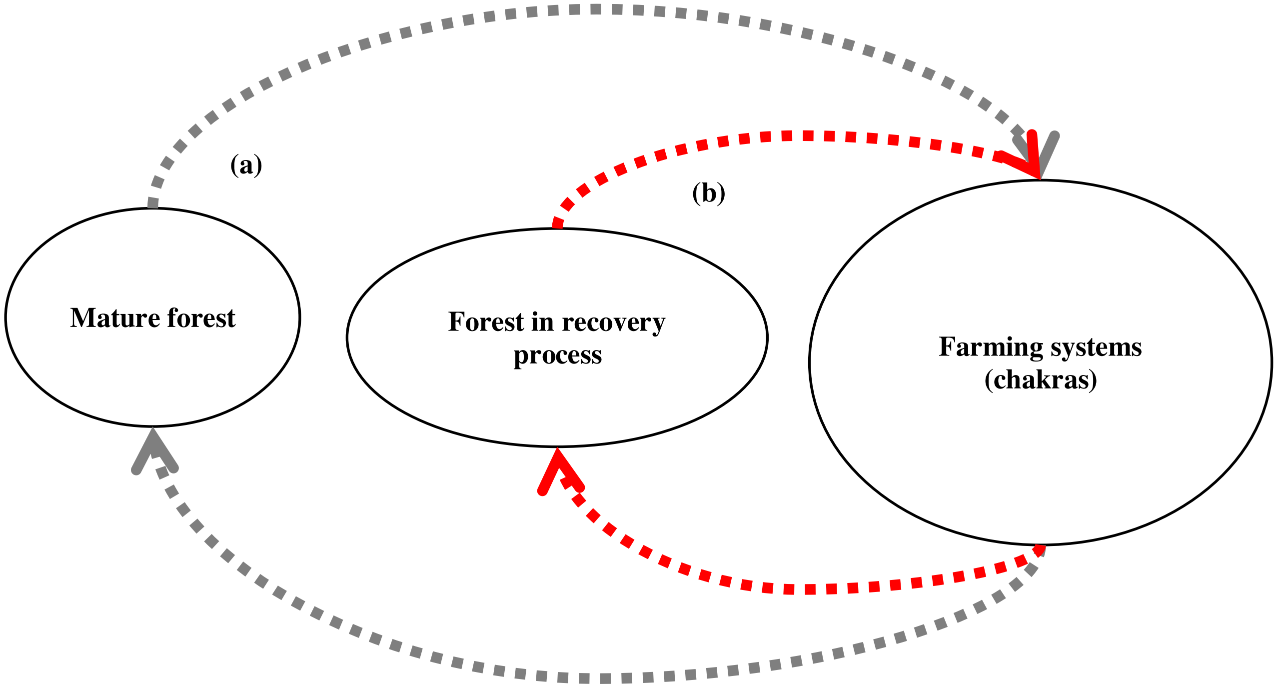

Figure 1.2: Conceptual diagram depicting the succession of shifting agriculture in the Northern Ecuadorian Amazon. (a) Cycle with long fallow periods; (b) Cycle with reduced fallow intervals.

The chakra system is considered a transitional state of disturbance, but this system can be regarded as an effective sustainable forest management approach and an alternative to preserve species and mitigate climate change. Nevertheless, changes in land use particularly AFS located close to roads, have facilitated the communication and product flow with large market and trade centers. The resulting urban exposure tends to alter the traditional cycles of shifting agriculture into a more intensified farming practice with less fallow time (Fig. 1.2b). This issue raises the following essential questions:

1) Are agroforestry farming practices best suited to maintain the structure and integrity of forest ecosystems under short fallow periods?

2) Does the reduction of fallow periods lead to more fragmented forest ecosystems?

In view of the current environmental decline and loss of forest land and species, studies are needed to investigate these issues and determine minimum thresholds of forest cover in land use. Similarly, the quantification of suitable levels of biodiversity in combination with the reduction of anthropological impact on biological ecosystems to sustain the earth's carrying capacity is required to address the challenges of attaining better strategies for forest management. Because of recent significant loss of woodland areas caused by the expansion for agriculture in the Ecuadorian Amazon forests, I investigated the structure and ecological dynamics of AFS under different levels of management. Also, I examined interactions of AFS with forest diversity and ecosystem services. In my research project I have combined field data based on ecological, edaphic, and ethnobotanical information into a holistic approach to determine the different levels of interaction, complexity and sustainability of agroforestry systems in the Amazon region of Ecuador. The long-term goals, specific objectives and different research approaches are described next.

1.4 Research goals and dissertation structure

This thesis is organized into three paper-based chapters (Chapters 2 to 4). Each chapter corresponds to a published or submitted article (chapter 4) focusing on one or more objectives in a peer-reviewed scientific journal. The study is primarily focused on cocoa AFS and the assessment of biodiversity levels to establish strategic guidelines for conservation of biological diversity and sustainable use of forest resources. The long-term goal of this research is:

- To broaden the scientific knowledge about tropical mosaic landscapes in the EA and the ecological patterns within and between forest and AFS where natural habitats have been largely fragmented.

The current chapter treats the problem of unsustainable forest use in the tropics, specifically NEA, and its social, environmental, and climatic consequences. This unit includes an exhaustive review of literature pertinent to the different ecological aspects approached in my research, such as biodiversity, shifting agriculture, and agroforestry. My literature survey encompassing the databases Google Scholar and Web of Science, yielded approximately 117 relevant resources published between 1954 and 2020 that are included as references at the end of this chapter. I am optimistic that the extensive inquiries have been explicit and assisted to target the main socio-ecological issues that, although broadly known, are still poorly understood; hence, little effort has been put from scientific or proactive perspectives.

In Chapter 2 I focused on the chakra system as model of land use in the Amazon region of Ecuador to characterize and determine the impact of anthropogenic activities on the inherent horizontal and vertical structure of plant communities. Although AFS have been discussed as an alternative to monocultures, the spatial and temporal dynamics processes of these agrosystems have yet to be identified and quantified. In addition, the degree of existing risk to endangerment of numerous tree species, the substantial and rapid change in floristic composition of mature forests converted to AFS, and the relatively slow recovery pace of forest communities following abandonment, remain unknown factors. In order to examine these aspects, I estimated alpha and beta biodiversity across the study area. My survey embraced multiple novel analytical methods, including univariate and multivariate approaches, to investigate mature forest communities as well as individual chakra plots. I hypothesized that if mature forest conversion results in a multi-specific AFS, then the number of tree families and species will decrease according to the crop type established on the forest floor. I also expected that if the different AFSs maintained similar floristic composition, then the remaining species will enable an equivalent plant community recovery to that of the original forest structure after abandonment.

Chapter 3 of this thesis analyzed whether differences in land use patterns associated with farming systems under shifting agriculture (SA), i.e., more frequent cycles of cultivation, affect tree diversity and overall floristic composition in cocoa AFS. I hypothesized that if SA is established under AFS in land with different fallow periods, then there would be a buffer effect on the loss of tree species richness, particularly, endangered endemic species. I examined whether semi-sedentary agriculture under AFS scheme has adverse effects on tree diversity and floristic composition. Also, whether endangered endemic tree species are capable to withstand more intensified systems with shorter recovery time.

In Chapter 4 I focused on analyzing the patterns of covariance between the chemical-physical properties of the soil in relation to tree diversity and floristic composition in cocoa AFS with short fallow periods. Fallow stages allow forest recovery after crop land abandonment under SA, these resting periods are needed to restore soil nutrients and productivity capacity. In time, it might be expected that the intensification in SA can constrain natural ecological cycles and the appropriate rebuilding of soil nutrients. However, the relationship between species composition, nutrient recovery as well as the buffering effect of tree cover diversity on soil fertility in AFS under SA is yet to be determined. I hypothesized that if multi-specific cocoa AFS are established under SA, then soil fertility will maintain suitable levels of biological cycling dynamics and nutrient properties under more intensified fallow cycles. I provide quantitative evidence about the relevance of AFS beta diversity in maintaining this important ecosystem service under shifting cultivation practices. I examined to which extent beta diversity in cocoa AFS reverses the effect of shortening SA's fallow periods in soil properties with cocoa agrosystems.

This thesis ends in chapter 5, which provides a series of conclusions drawn from the findings according to the main questions and goals initially established and achieved in this research. I highlight both positive and negative aspects regarding the combination of agroecosystems with shifting agriculture as well as some inferences about how the integration of two traditional agricultural approaches in the tropics may reconcile socio-ecological problems in the western Amazon. In this section, I also express my satisfying working experience with Indigenous communities, whose ancestral traditional knowledge made significant contributions to this thesis. Finally, while this study has bridged some knowledge about sustainable use of forest land, it has opened the door for new ideas and scientific inquires that require future work. The details of these ideas are provided at the end of this chapter.

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CHAPTER 2: BIODIVERSITY, DYNAMICS, AND IMPACT OF CHAKRAS ON THE ECUADORIAN AMAZON

The format of this chapter has been modified from:

Vera R., Cota-Sánchez J.H., and Grijalva J.E. 2019. Biodiversity, dynamics, and impact of chakras on the Ecuadorian Amazon. Journal of Plant Ecology **12**: 34-44.

I conceived, designed, and conducted this study with the guidance of Dr. J. Hugo Cota-Sánchez and Dr. Jorge E. Grijalva. I collected the field data in 2015 and 2016, performed data analysis, and drafted the manuscript. This paper is the foundation to investigate the impacts of new agricultural approaches in tropical areas on the conservation of endangered endemic plant species. Jorge E. Grijalva established the first contacts with Indigenous communities in the Northern Ecuadorian Amazon and collaborated in developing the field methods and sampling locations. J. Hugo Cota-Sánchez provided advice on data collection, research questions, and taxonomical descriptions; and all authors provided input in the article.

2.1 Introduction

The dynamic patterns, structural composition, and functional integrity of natural ecosystems are continuously threatened by deforestation. A growing body of evidence shows that changes in biodiversity are primarily attributed to a vast number of anthropogenic activities that have negatively impacted tropical and subtropical areas (Young and Clarke 2000, Tapia-Armijos et al. 2015). Although deforestation rates have decreased substantially from 8.5 million ha year^{-1} in the 1990s to 6.6 million ha year^{-1} in the last five years (FAO 2015), the main human activities linked to species extinction, habitat loss, and climate change still persist, especially in the tropics (Porro et al. 2012, Homeier et al. 2013, Tapia-Armijos et al. 2015).

Tropical forests (TF) still host the largest reserves of biodiversity in the world. These diversity-rich areas have important ecological roles, such as supporting a high number of endemic species of plants and animals (Duivenvoorden et al. 2002), maintaining more than 50% of life forms on Earth (Givnish 1999, Mischra et al. 2013, Gatti et al. 2015), contributing to decreasing carbon dioxide (CO_2) from the atmosphere (Houghton et al. 2000, DeFries et al. 2002), storing large amounts of world's carbon (Baccini et al. 2017), protecting soils from wind and water erosion (FAO 2015), among others. These functions are essential for a healthy and integral ecosystem; however, human activities have altered the existing balance by converting the forest to other types of landscapes with lower structural complexity and biomass (Cochrane and Barber 2009, Malhi et al. 2009, Nobre and Borma 2009).

Transforming forest ecosystems to agricultural land and grasslands has been identified as the leading force causing forest loss with a concomitant contribution to shift global climate and escalation in greenhouse gas emissions (Bhagwat et al. 2008, Gatti et al. 2015, Pan and Bilsborrow 2005). In fact, structural changes in TF could be the main contributors to these deviations because these natural areas maintain approximately 120 t ha^{-1} of carbon, which is 45 t ha^{-1} more than the world average (FAO 2015). The Amazon Basin (AB), with an extension of more than 6.5 million km^2 (Mittmeier et al. 2003), undoubtedly stores large quantities of carbon that are eventually released into the atmosphere as a result of clearing of forests for agricultural use.

Within the AB, the Ecuadorian Amazon forest (EAF) is considered a salient biodiversity hotspot on Earth (Myers et al. 2000, Bass et al. 2010, Perez et al. 2015), but in the last decades it has also been seriously affected by rapid changes in land use, an activity that has caused the highest deforestation rates in South America (Mena 2008, Tapia-Armijos et al. 2015). These human-mediated disturbances alter the structural composition and integrity of climax forest communities, as well as the capacity to provide ecosystem services. Because in the long run conversion of forest land may equate to desertification, recently, researchers have endeavored to document the effects of these rather fast-occurring and alarming changes of natural landscapes to propose creative solutions to preserve protected areas (Becker and Guimire 2003, Valencia et al. 2004, Bass et al. 2010). Unfortunately, the efforts to slow biodiversity loss are still unsatisfactory, especially with the pressure exerted by population growth and the increasing exploitation of natural resources.

While the protection of wild areas is a priority in conservation endeavors, the deliberate management in using native trees together with diverse agricultural crops is emerging as a potential alternative to safeguard biodiversity. This practice is known as agroforestry systems (AFSs) (Ashley et al. 2006), and its benefits to human society and environment have been widely discussed, e.g., Bhadwat et al. (2008), DeClerck et al. (2010). AFS provides several advantages, such as preserving biodiversity, reducing anthropological pressure on primary forest communities, and enhancing ecosystem services and connectivity with conservation or protected areas (Schroth et al. 2004, Ashley et al. 2006). Hence, the amalgamation of native trees and crops in indigenous farms might promote diversification and benefits to land users while preserving some components of the original ecosystem.

In the EAF, the AFSs are traditionally called chakras, a common and environmentally friendly farming tradition practiced by autochthonous groups. This AFS does not involve fertilizers, pesticides, and heavy machinery, and the advantage of this practice lies on the preservation of mature native trees for several purposes. Typically, this method encompasses a shifting agriculture in small land plots developed in forest gaps to satisfy food necessities, which after a few years are purposely abandoned to allow forest recovery (Arévalo 2009). The existence of different native tree species in various strata, which can have social and cultural significance for the Aboriginal groups, reveals a multifunctional system with the capacity of conserving high levels of floristic diversity (Perrault 2005, Porro et al. 2012); however, the extent of this tree diversity has not been evaluated nor quantified. Although the assessment of anthropological activities in natural areas is challenging, the analysis of this arboreal structure is significant to determine the disturbance threshold in highly diverse tropical areas to ensure sustainable forest management. Filling knowledge gaps about forest tolerance levels is particularly important in the NEA to improve the quality of zones surrounding biological reserves, e.g., the Sumaco Biosphere Reserve (Torres et al. 2014). In this reserve, new human settlements situated in the transitional and buffer areas have put extra pressure on natural resources, resulting in the threat to numerous native species and ecosystem functions due to the practice of more intensive and often more aggressive and inefficient production systems (Arévalo 2009).

The buffer zone in the NEA, an area in which agroforestry is quite active, represents ca. 12,500 ha (Torres et al. 2014). The diverse ecological characteristics along with the shared areas of MF communities and different AFSs make this zone an excellent example of the AB and a worthy choice for investigation. To date, information regarding the characterization of chakras in the New World tropics is scanty. This study represents the first approach to characterize the AFS at the structural and biodiversity levels, in particular, the investigation of the forest alpha and beta diversity and organization levels in relation to different farming levels of management. The outcomes of this study will serve as a foundation to develop new approaches for sustainable agriculture practices in the tropical Amazon and other tropical and subtropical regions. We were particularly interested in 1) investigating whether traditional chakras preserve similar levels of forest diversity among the different types of AFS, 2) determining the consequences of converting MFs to chakras on forest biodiversity levels, and 3) evaluating whether native tree species recovery leads to the original forest structure following chakra abandonment.

2.2 Material and Methods

2.2.1 Study area

This study was carried out in the buffer zone located in the northern Amazon Region in Ecuador (Fig 2.1). The buffer zone lies in two provinces, namely Orellana and Napo, and covers approximately 10,606 km^2 of Ecuador's territory (INEC 2010). Within these two jurisdictions, a total of 18 areas, mostly located in the Napo province, have been declared as natural patrimony by the Minister of the Environment. This area covers the sub-basins of Jatun Yacu-Pano-Tena, Napo-Wambuno, and Puni-Arajuno and is part of an extensive mixed evergreen tropical forest characterized by a humid climate with a mean annual rainfall of 3,500 mm, monthly average temperature of 24 °C and altitudinal range from 300 to 600 meters above sea level (masl) (Arévalo 2009).

2.2.2 Field data

Sixty-one plots, each an average of 0.28 ha, representing a total of 17.44 ha were established in different fieldwork seasons from 2008-2016 as follows. Foremost, forest and agricultural areas for study were identified and selected from maps obtained from on-line databases available from the Ecuadorian Ministry of Agriculture (www.geoportal.agricultura.gob.ec). Then, four local indigenous communities were selected based on two main requirements. The first condition was that these communities should have areas under agricultural use (AFSs), post-disturbance or abandoned areas (SF), and undisturbed forest (MF). The second prerequisite was their relative accessibility to evaluate all the areas previously mentioned. Lastly, each plot was established following a disturbance gradient using stratified samples to capture the spatial variability of the MF, SF, and the AFS in the buffer zone.

The research plots included three of the most important AFSs (cocoa, corn, and cassava) in the NEA because the cultivated area dedicated to these three crops is substantially larger than the other crops grown in this zone. These crops are also relevant for their agricultural economy and cultural significance. Twenty-three plots were based on cocoa (*Theobroma cacao* L.), six dedicated to corn (*Zea mays* L.), and five with cassava (*Manihot esculenta* Crantz). In addition, 12 research plots of SF with ca. 15 to 20 years of abandonment and 15 of the MF were chosen (Table 2.1). The location and approximate ages of the SF were obtained through interviews with local landowners. The age of the climax forest was unknown and designated here as MF due to its relative inaccessibility and more diverse floristic composition. All AFS research plots varied in size because each lot represented the total land used by the landowner. The research plots belonging to the SF and MF were obtained by the aggregation of multiple plots. In the SF, 35 plots of 500 m^2 each near to each other were grouped. That is, always that plots were <100 m apart were aggregated. Thus, the cluster of adjacent plots prevents possible spatial pseudo replications. In the MF six plots were obtained using combining six to seven plots of 500 m^2 each and two more from five plots of 1,000 m^2 each. Overall, a total 61 plots (Table 2.1) were used in this study. The group of aggregated plots can be seen in Table A2.4.

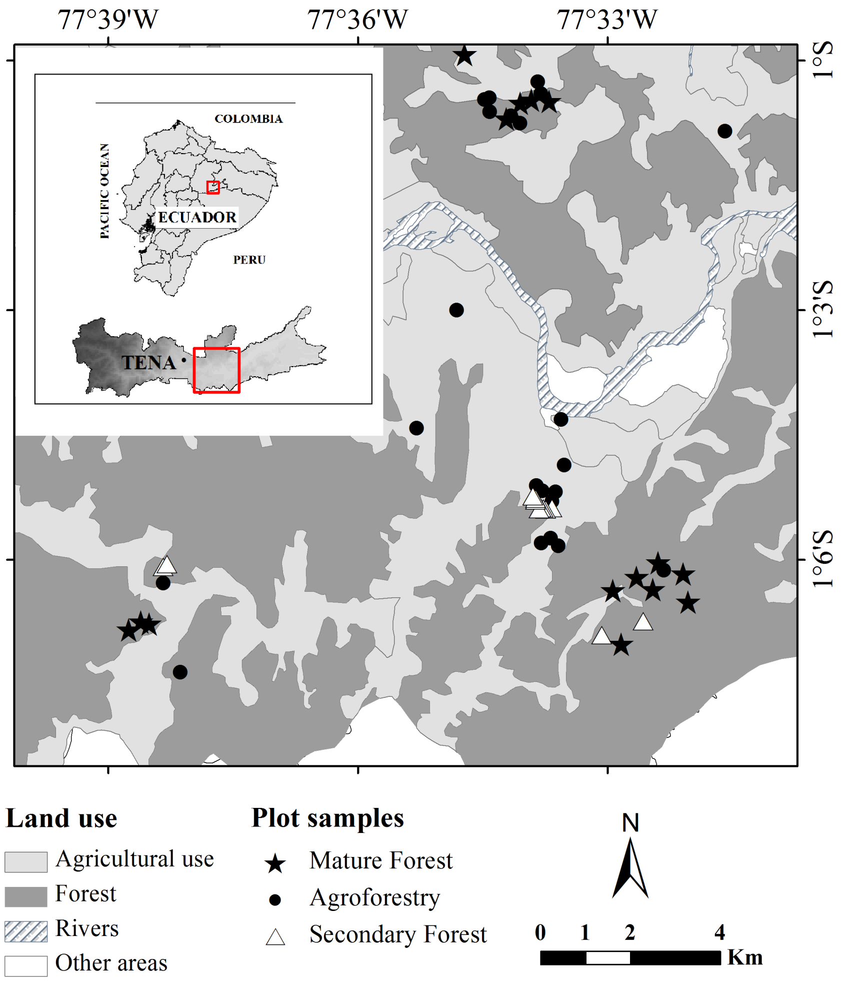

Figure 2.1: Map showing the study area in the buffer zone of the Northern Ecuadorian Amazon. Top left shows Ecuador and Tena canton maps. Red squares show the exact location of the region of study. The symbols on the map indicate the geographic location of the experimental plots. Forest plots are represented by black stars, secondary forest by white triangles, and black circles represent agroforestry plots. Different areas of land use are indicated in two different colors: light gray for agricultural land use and dark gray for forest cover

2.2.3 Species inventory

All tree species, with a diameter at breast height (dbh) ≥10 cm, were inventoried in each system being investigated (see Table 2.1) following Alder and Synnott (1992), a protocol with strategies to establish and measure permanent plots in mature tropical forests. The taxonomic identification of plants was conducted in the field at the generic and specific levels with the support of a multidisciplinary team with different areas of expertise, such as botanists (including local expert ethno-botanists), biologists, agronomists, and anthropologists. In addition, relevant literature and online resources were used to verify the identity of plants, i.e., the catalogue of Vascular plants of Ecuador (www.tropicos.org), Patzelt and Echeverría (1996), Jørgensen et al. (1995), Jørgensen and León-Yánez (1999), Ståhl et al. (2015), and the Flora of Ecuador (http://bioenv.gu.se). Tree species that were not fully identified in the field were collected and processed at the Herbario Nacional (QCNE) and duplicate voucher specimens were deposited at the National Institute of Farming Research (INIAP), both institutions in Quito, Ecuador. The floristic inventory was compiled in a data matrix constructed in MS-Excel software encompassing a list with families and scientific names. The taxonomic authorities for the taxonomic species are based on the Tropicos nomenclatural database (www.tropicos.org).

2.2.4 Data analysis

Two analytical approaches were employed with the data. First, the alpha diversity was investigated with the species richness and diversity as unique response variables in the AFS, SF, and MF. Second, the beta diversity was evaluated to determine the degree of dissimilarity among systems using a multidimensional approach involving the tree species matrix.

Alpha diversity, that is, the number of plant families and genera, were estimated in each AFS, SF, and MF included in this study. Also, species richness and the Shannon diversity index (Equation 2.1) were calculated as follows:

$$H` = -\sum_{i=1}^{S} p_i \, log_2(p_i) \qquad (Equation\ 2.1)$$

Where $H`$ represents the Shannon index and p_i is the relative abundance of each species

The Shannon index was converted using an exponential alpha to determine the effective number of species as described by Jost (2006, 2007). This more intuitive methodological approach allows the comparison of diversity levels among plant communities. The evaluation of species diversity among the five systems was based on the principle of completeness (Chao and Jost 2012), in which the samples are standardized by coverage rather than size. These different sampling efforts produce different numbers of the individuals collected. Therefore, this technique allows fair comparisons of species diversity. The estimation of these diversity indices also involved building intervals of 95% using a bootstrap method in the package iNEXT (Hsieh et al. 2016) using R statistical software (R Core Team 2017).

Beta diversity or the change in floristic composition from one system to another, was also analyzed among the five systems investigated using the Bray-Curtis distance (Equation 2.2), which is and equation suitable for datasets with asymmetric characteristics:

$$d_{BC} = \frac{\sum_i \left| x_{ij} - x_{ik} \right|}{\sum_i \left(x_{ij} + x_{ik} \right)} \qquad (Equation\ 2.2)$$

Where x_{ij} is the abundance of species i on site j, and x_{ik} is the abundance of species i on site k.

This estimation consisted of an analysis in a dissimilarity matrix to evaluate the change in species composition from MF to AFS as well as the degree of forest recovery through the dissimilarity between the MF and the SF at the landscape level. In addition, a hierarchical approach including all sampled sites was used to determine small discontinuities in patterns of species composition among all sites. This approach aimed to investigate whether species composition is alike in all AFS sites regardless of the chakra type and whether forest recovery exhibits a common trend. In order to minimize the variance within groups, we used the Ward method followed by the application of the Bray-Curtis distance to calculate the dissimilarity index. Finally, a contingency analysis (CA) followed by a multiple correspondence analysis (MCA) was conducted to determine the putative significant degree of association among tree species, AFS, and forest types according to the chi-square distribution. These inquiries were performed using R statistical software (R Core Team 2017) and Infostat (Di Rienzo et al. 2015).

2.3 Results

Among the three AFSs selected, corn and cassava represented the temporal crops, while cocoa had permanent production cycles. The largest cultivated areas of these AFSs corresponded to corn with an area of 1.03 ha on average, whereas the smallest farming spaces were those of cassava with 0.12 ha on average (Table A2.1). As expected, the three AFSs contained fewer trees (>10cm dbh) per hectare than the SF and MF (Table A2.1). Corn exhibited the lowest value of tree density (24±7) followed by cassava (104±30) and cocoa (200±36). The highest tree concentration was found in the SF (469±44) and MF (741±68) (Table A2.1).

The floristic inventory of the 17.44 ha comprising the five different systems investigated included a total of 4,060 individuals, representing 109 tree species in 96 genera and 43 plant families (Table 2.1). The most dominant plant families were Arecaceae, Myristicaceae, Fabaceae, Meliaceae, and Malvaceae, and the most representative genera included *Iriartea*, *Virola*, *Guarea*, *Ocotea*, *Cordia*, *Chrysophyllum*, and *Inga* (Table A2.2). This inventory varied in sampling coverage (SC) obtained per system. That is, 81.3±9.5% of SC in cassava, 83.9±6.7% in corn, 97.3±1% in cocoa, 98.7±0.7% in the SF, and 99.8±0.1% in the MF (Table A2.1). Accordingly, the samples were standardized at 90% for fair comparison of species diversity without doubling any reference sample size in any community to avoid biases in the calculation (see Table 2.1).

2.3.1 Alpha diversity

The effect of transforming the MF into different AFSs is reflected in the alpha diversity among all systems. The MF in the buffer zone of the study area is composed of 81±1.48 tree species, 74 genera, and 38 plant families (Table 2.1). The most common plant families were Arecaceae, Myristicaceae, Fabaceae, Moraceae, and Lauraceae, whereas the most frequent genera were *Iriartea*, *Virola*, *Ocotea*, *Guarea*, *Chrysophyllum*, *Protium*, and *Inga* (Table A2.2). The use of forest remnants in the conversion to cocoa, corn, and cassava systems represents a significant decrease in tree species, particularly in corn and cassava, with 32±2.12 and 20±1.54 species, respectively (Table 2.1), relative to the 81±1.48 species in the MF. In terms of species diversity calculated as the number of effective species in each system, the samples standardized at 90% of SC had the highest diversity value in the MF (25±0.99) whereas the cocoa, corn, and cassava showed values between 13 to 19 in species diversity (Table 2.1). This indicates that the anthropogenic influence alters the structural diversity in the MF and AFS from 52% to 75%, respectively.

All the systems under investigation showed a significant degree of association with tree species (chi-square <0.0001). Axes 1 and 2 separated chakras from forests and showed a group of tree species, such as *Cordia alliodora*, *Inga edulis*, *Cedrela odorata*, and others, associated mainly with corn and cocoa, and a few species (*Aphandra natalia*, *Vernonia baccharoides*, and *Ceiba pentandra*) linked to cassava (Fig 2.2). Another cohort of tree species, e.g., *Iriartea deltoidea*, *Vismia macrophylla*, *Pouteria lucuma*, typically associated with SF and MF, was also evident. Also, a few trees, e.g., *Chimarrhis glabriflora*, *Terminalia oblonga*, *Cedrelinga cateniformis*, and several others, seemed not to exhibit habitat or system preference and occurred infrequently in all systems (Fig 2.2).

Table 2.1: Five different systems in the Northern Ecuadorian Amazon including number of plant families, genera, and the observed species in the total sampled area. For fair comparison among the five systems the species diversity is expressed as the exponential alpha of the Shannon index ± standard error at 90% of sampling coverage. n = total numbers of plots investigated; ha = total sampled area. Same lower-case letters in table represent overlapping confidence intervals at 95%

System	**n**	**Area (ha)**	**# Plant Families**	**# Genera**	**# Species**	**Species Diversity**
Manihot esculenta (cassava)	5	0.59	18	20	20±1.54	18±5.19 b
Zea mays (corn)	6	6.19	21	30	32±2.12	13±4.47 b
Theobroma cacao (cocoa)	23	4.67	33	57	62±2.37	19±2.18 b
Secondary forest	12	1.75	31	52	54±1.79	15±1.54 b
Mature forest	15	4.24	38	74	81±1.48	25±0.99 a
Total	**61**	**17.44**	**43**	**96**	**109±9.90**	**37±1.20**

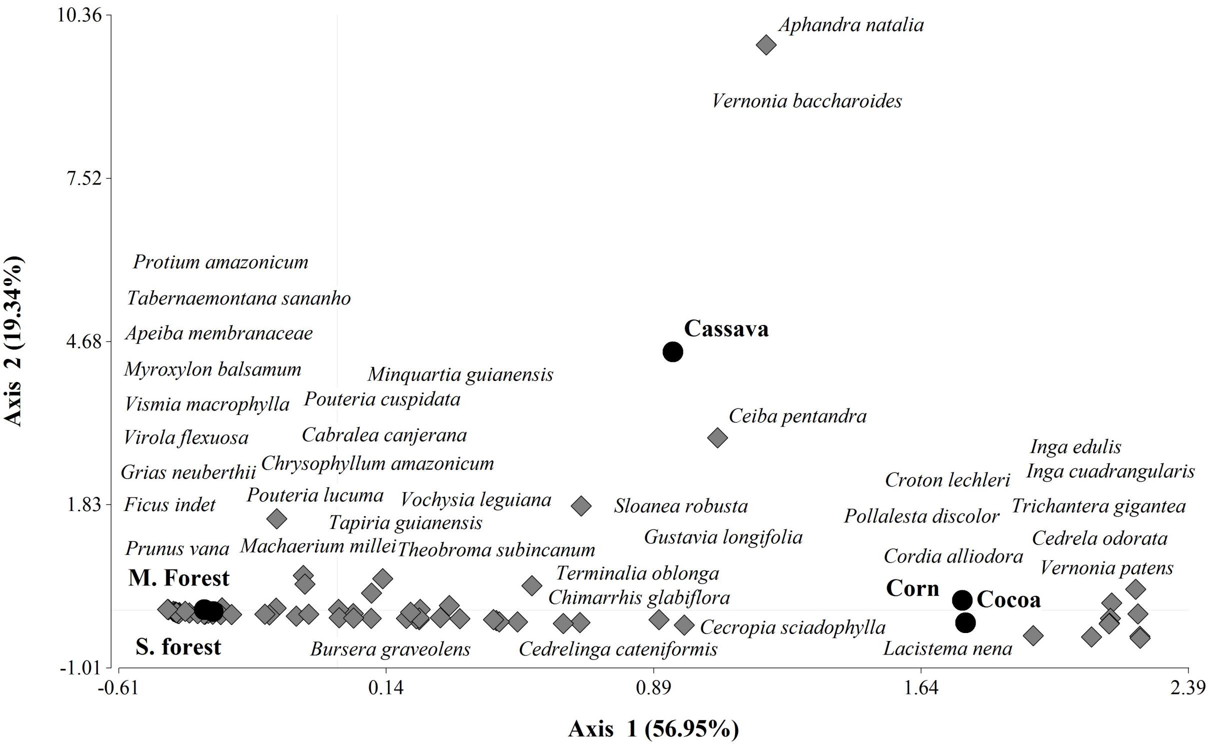

Figure 2.2: Graph depicting the degree of association between species and systems, namely cassava (*Manihot esculenta*), corn (*Zea mays*), cocoa (*Theobroma cacao*), secondary forest, and mature forest in the buffer zone of the Northern Ecuadorian Amazon based on the correspondence multivariate analysis following a contingency analysis. Black circles show the position of the five systems. Grey diamonds show the position of the tree species. For clarity of the graph, only a few species were included. Axes 1 and 2 together explain 76.29% of the total variance.

2.3.2 Beta diversity

The impact of anthropogenic activities was also evident in the magnitude of dissimilarity (beta diversity) among systems. Changing MF to corn and cassava farming systems represented a modification of 56% of the floristic structure but slightly decreased to 51% when it was converted to cocoa AFS (Table 2.2). Additionally, all sites investigated consistently formed three clusters that corresponded to AFS, MF communities, and SF (Fig 2.3). A divergence of 0.43 in tree species composition between the mature and SF represented ca. 60% of forest recovery following chakra abandonment (Fig 2.4).

Discrepancies in the levels of dissimilarity are also apparent in terms of dominant tree species. In the cassava AFS, *C. pentandra*, *Iriartea deltoidea*, *A. natalia*, *Apeiba membranaceae*, and *Cordia alliodora* represented 51% of the species. In the corn AFS, *C. alliodora*, *Cedrela odorata*, and *I. deltoidea* were the most dominant (56% abundance) trees (Table A2.2). In contrast, in the cocoa AFS, *C. alliodora*, *Pseudolmedia rigida*, *I. edulis*, and *Vochysia leguiana* were the most frequent trees (52%). In the SF and MF, the dominant species were similar. For instance, in the SF *I. deltoidea*, *Virola flexuosa*, and *Guarea kunthiana* revealed 53% of the tree diversity, and in the MF *I. deltoidea*, *V. flexuosa*, *G. kunthiana*, *Ocotea bofo*, *Chrysophyllum amazonicum*, and *Protium amazonicum* were the most common (52% frequency) trees (Table A2.2).

2.3.3 Threatened, vulnerable, and endemic plant species

Our study revealed that the buffer zone of the NEA has nine species in the sensitive categories, particularly threatened, vulnerable, and endemic taxa, as proposed by IUCN (2016). For instance, *Alseis lugonis* and *Minquartia guianensis* are among the threatened taxa, *C. odorata* and *Swietenia macrophylla* are vulnerable, and *A. lugonis* and *Stryphnodendron porcatum* are listed in the endemic category. Lastly, *C. alliodora*, *I. deltoidea*, *S. porcatum*, *Astrocaryum murumuru*, and *Inga pavoniana* are included in the group of least concern (Table A2.3). All these taxa were found both in chakras and forests and represented only 8% of the tree species inventoried in this zone. However, data regarding the remaining 92% of species are still lacking (Table A2.3), indicating that the assessment of the rarity status of native trees is virtually unexplored and needed to make more educated inferences about conservation practices of the NEA forests.

Table 2.2: Dissimilarity matrix calculated with Bray-Curtis distance to analyze the change in tree species composition (≥ 10 cm dbh) among the five agrosystems in the buffer zone of the Northern Ecuadorian Amazon.

	Cassava	Corn	Cocoa	SF	MF
Manihot esculenta (cassava)	0.00				
Zea mays (corn)	0.24	0.00			
Theobroma cacao (cocoa)	0.30	0.30	0.00		
Secondary forest	0.34	0.38	0.36	0.00	
Mature forest	0.56	0.56	0.51	0.43	0.00

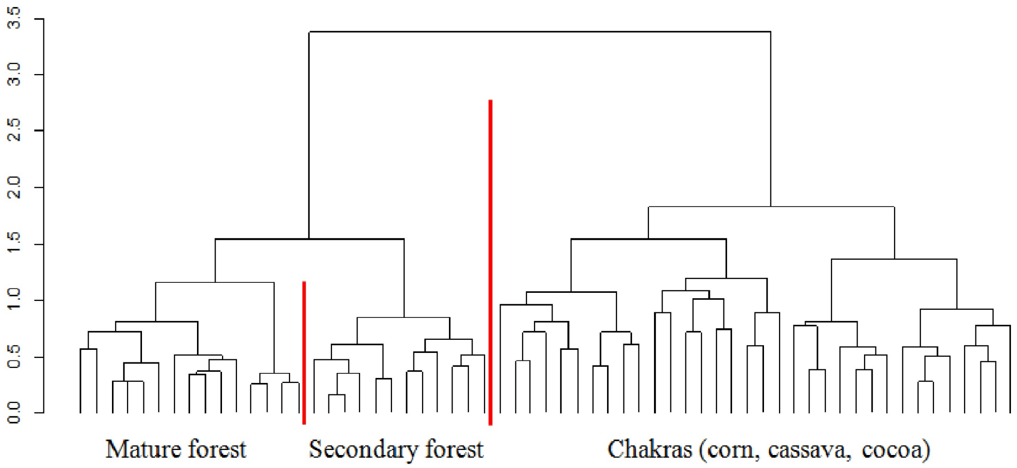

Figure 2.3: Dendrogram showing the degree of qualitative dissimilarity among all sites investigated in the five systems: cassava (*Manihot esculenta*), corn (*Zea mays*), cocoa (*Theobroma cacao*), secondary forests, and mature forests in the buffer zone of the Northern Ecuadorian Amazon. The Ward and the Bray-Curtis distance methods were used. The Y axis shows the height of the Bray-Curtis distance as it was calculated using the *vegan* package and the *hclust* function in the R statistical software. Note two different groups divided by a red line: the secondary forest and mature forest group and the AFS. The scale line indicates the degree of dissimilarity. A pair of branches close to 0 means more similarity in sites

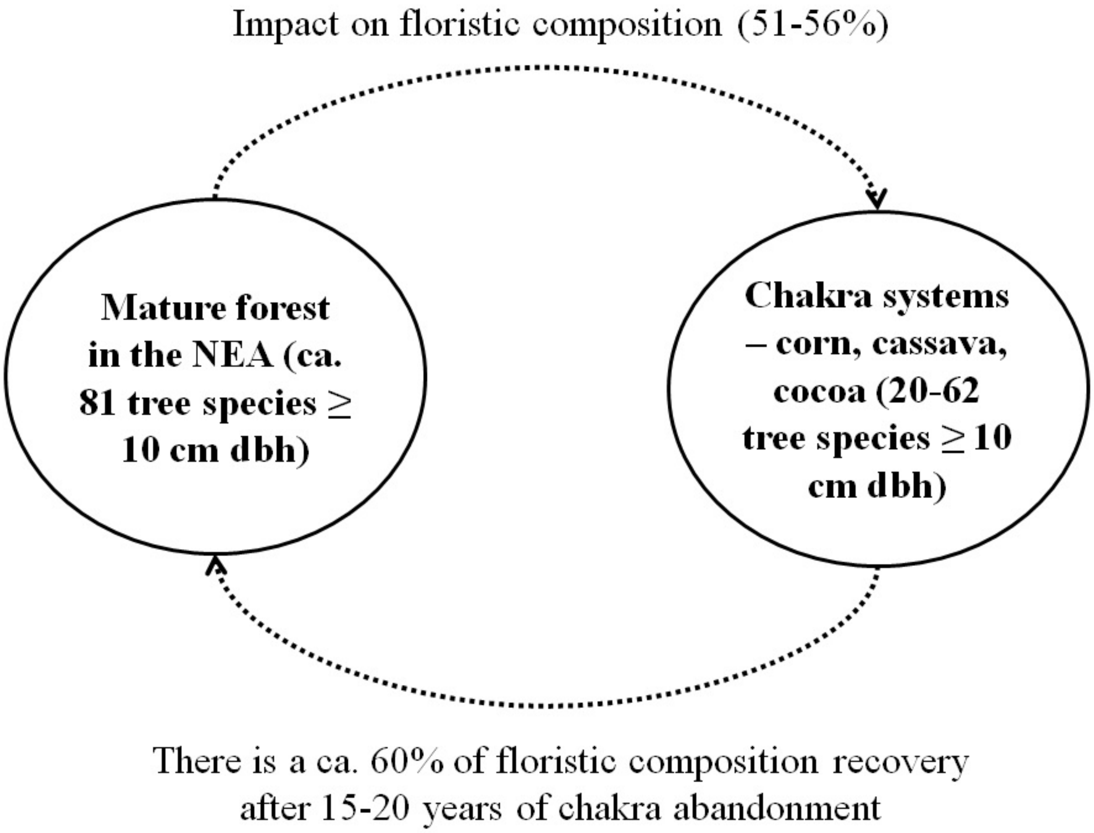

Figure 2.4: Cyclic description of the chakra system in the buffer zone of the Northern Ecuadorian Amazon. The two circles represent the tree species richness in the MF and the chakras. The lines indicate the process of transforming MF to chakras, the forest recovery after chakra abandonment, and their effects in the floristic composition, respectively. This cycle starts when the MF is transformed into different chakra systems with their impacts in alpha and beta diversity. Then, the chakra is abandoned allowing forest recovery.

2.4 Discussion

With the increase of agricultural land at the cost of removing natural vegetation to satisfy food and income needs in rural communities, the conservation of biodiversity hotspot areas is becoming a more complex challenge. Concrete actions to deal with this dichotomy in the tropics should be addressed to implement an efficient and sustainable integrated system involving protected and non-protected zones. For instance, the increasing use of the buffer zones with agroforestry practices (Bhagwat et al. 2008) should be considered as a multipurpose approach intended to reduce the vulnerability of forest reserves, but at the same time, adequate yield crop productivity and the preservation of rare and/or endangered species is desired. Our study revealed that the chakra is a practical shifting agriculture system that maintains the natural components of surrounding areas because it is beneficial in the conservation of the forest structure and food production for local communities.

Overall, the chakras involve an adaptive strategy directly associated with socio-economic conditions aimed at food security, land management, and balanced use of forest resources using environmentally friendly approaches. The first aspect of this approach is to guarantee adequate food supplies and income. For example, corn and cassava are two of the most important crop plants for global foodstuff in the tropics (Godfray et al. 2010), but cocoa beans are preferred for economic returns in this and other areas of South and Central America, Africa, and Asia (Schroth and Harvey 2007, Porro et al. 2012, Cerda et al. 2014). The second feature of this farming strategy is the cultivated area. The chakra plots in the NEA oscillated from 0.05 to ~3.0 ha (Table A2.1). Similar integrated crop systems in the East African highlands have comparable sizes from 0.4 to 3.0 ha (Abebe et al. 2005). These small areas theoretically represent a strategic organization to optimize a family's labor force capacity to secure adequate crop yields. A third characteristic of the chakras is the deliberate change of MF into AFS, which does not necessarily represent a random tree selection for logging but rather the result of a systematic process intended to provide suitable ecological and soil resources for crops to thrive. For example, cocoa farmers in Ghana prefer nutrients and incidence of light; thus, certain tree species are selected in order to harmonize the above-ground interaction with the shade trees to enhance root systems and maintain more consistent levels of soil moisture (Abebe 2005, Anglaaere et al. 2011). Although a farmer's tree selection is intended exclusively to increase crop productivity, the presence of some native trees, such as *Ilex guayusa, Urtica urens,* and *Aphandra natalia* (Table A2.3) in AFS of study area, suggests preferences for arboreous species that are associated with the preservation of the indigenous identity and cultural believes, e.g., traditional beverages, rituals, and handcrafts (Perreault 2005, Arévalo 2009). Thus, the Kichwas culture of the western Amazon is also represented in the chakras. In all, AFSs in the NEA are adaptations to more diversified, ecologically healthy, and sustainable agrosystems based on use of resources adjacent to forests.

Our inquiries also showed that the shifting agriculture in the buffer zone of the NEA denotes a permanent dynamic structure between MF and chakras that keep significant levels of alpha and beta diversity (see Fig 2.4). The first feature regarding this interesting configuration is that the alpha diversity in the MF is limited by continuous modifications of the arboreal strata. Our results disclosed ca. 81 tree species (>10 cm dbh) in 4.04 ha (Table 2.1). It is noticeable that this value is lower compared to other similar inventories of tree species >10 cm dbh. For instance, 307 tree species ha^{-1} inventoried in the *Reserva Faunística Cuyabeno* (Valencia et al. 1994), 251 tree species ha^{-1} in the Yasuní National Park (Valencia et al. 2004), and 217 tree species ha^{-1} in the Jatun Sacha forest (Palacio and Jaramillo 2001), all of these reserve forests in the NEA, a region with remarkably high biodiversity values. This information suggests that the degree of maximum post-disturbance recovery and biodiversity levels of the MF communities in the Ecuadorian Amazon buffer zone is significantly lower compared with protected forests as shown by the 81 species (Table 2.1), which is the result of the uninterrupted use of this forest for agriculture. In all, this structural richness may well represent the adequate threshold for recovery when Aboriginal people use forests plots for farming.

Following the conversion of the MF to chakra, the second dynamic characteristic is directly related to the impact of decreasing levels of alpha diversity from as low as 52% to up 75%. However, even after this transformation, the AFSs have slightly higher effective number of species of trees ≥ 10 cm dbh, i.e., 13 in corn, 18 in cassava, and 19 in cocoa (Table 2.1), than other AFSs in the tropics, specifically compared with cocoa systems in Ghana (Asase and Tetteh 2010) and Mexico (Ramírez-Meneses et al. 2014), with 15 and 13 effective number of tree species ≥ 10 cm dbh, respectively. This means that there are higher biodiversity levels in the AFSs of Ecuador, as evidenced by >20% of tree species, compared to other tropical regions. Hence, the degree of intensification exercised in MF in the conversion to AFS in the western Amazon is likely lower than the integrated systems in other tropical areas of the world. The combination of MF and chakras increases ca. 25% the total diversity, which translates in a contribution of ca. 28 species to the total floristic richness (Table 2.1). Thus, both types of land use (109±10 species richness) have a synergetic effect in the alpha diversity of the buffer zone of NEA. Although these species richness values are relatively low compared to protected forests in the same area (Valencia et al. 1994, Valencia et al. 2004) and other preserved regions of the upper Amazon (Gentry 1988), the dominant plant families in the buffer zone are the same as those reported in the *Reserva Faunística Cuyabeno* located also in the same zone. That is, seven of the 10 main plant families, i.e., Fabaceae, Lauraceae, Sapotaceae, Annonaceae, Moraceae, Burseraceae, and Myristicaceae, concur with the list presented in Valencia et al. (1994). This finding supports the idea that changes in alpha diversity in the buffer zone are mostly driven at the species level.

Specific structural dynamics were also observed between the MF and chakras in relation to changes in the floristic composition (Fig 2.4). Our results showed that beta diversity varied between 51% and 56% in tree species ≥10 cm dbh (Table 2.2). These changes are significantly lower than the cocoa AFSs in Africa. For instance, the modification of natural forests to young replanted cocoa (3-5 years old) plots represented an estimated 88% change of the floristic structure in Ghana (Anglaaere et al. 2011) and ca. 82% in Cameroon (Zapfack et al. 2002), values substantially higher than those reported in this study, i.e., 51% and 56%. Thus, unlike Africa, the anthropogenic actions in the NEA appear to have fewer negative effects on forests communities, which is illustrated by higher levels of Shannon diversity found in this study, which fluctuated between 13 and 19 effective number of species. Evidently, the management of tree diversity by farmers is intended to preserve stratified floristic components associated with ecological functions more similar to the natural climax forest, which ultimately benefit crop establishment and development.

Another major argument for the preservation of levels of plant diversity is in connection with the active cycle of shifting agriculture, which concludes with the abandonment of the chakra. The spatial and temporal practice of the AFS facilitates rapid forest recovery as suggested by our dissimilarity values (0.43) between the SF (~15-20 years old) and the MF. These indices denote a significant floristic recovery of ca. 60% after chakra abandonment (Fig 2.4), which is consistent with a small-scale shifting agriculture in which pioneer species and surrounding vegetation in ecozone areas drive a new successional process (Chazdon 2003). Specifically, these characteristics could influence the AFS in the buffer zone of the NEA allowing seeds from native species to germinate and re-emerge regardless of the chakra type, eventually leading to a singular floristic structure. Therefore, despite the existence of diverse AFS with different floristic composition, upon abandonment, these tree assemblages are less differentiated during the recovery process until the characteristic structure of the MF is reached, suggesting a remarkable forest resilience (Fig 2.2).

An additional central aspect underlying the significance of chakra farming is the opportunity for biodiversity conservation, particularly endemic, vulnerable, and threatened species as well as basic ecological and genetic fingerprints. Based on our findings, the existence of two endemic species, i.e., *A. lugonis* and *S. porcatum,* has probably been facilitated by indigenous farming practices and the resilience and stability of forests. The same can be said for endangered species because the buffer zone includes four taxa listed in this category, which along with other species form part of the dominant elements of this unique floristic assemblage. These plants are also useful resources for both local indigenous people and fauna. For example, *C. odorata*, *S. macrophylla,* and *Cedrelinga cateniformis* are valuable for timber (Porro et al. 2012); *Croton lecheri* is used for medical purposes (Jones 2003); and *P. rigida* is eaten by animals, especially spider monkeys (Suarez 2006). Nonetheless, according to the IUCN (2016), the rarity status of the vast majority (92%) of the species in this area remains to be evaluated, which is a serious knowledge gap posing constrains to propose proactive options for conservation of species. On the other hand, the intrinsic dynamics of the chakras may have repercussions on diverse ecological attributes associated with species turnover. It is known that AFSs and other wooded areas generate different ecosystem services, such preventing erosion of soils from wind and water and retaining nutrients and water table levels (FAO 2015); nevertheless, the replacement of tree species from MF to AFS can influence the carbon balance. In this scenario, the new dominant and fast-growing species in chakras, such as *C. alliodora* and *Ochroma pyramidale,* can play a critical role as a carbon sink during the initial successional stages (Chazdon 2003). Although this activity may vary depending on resource availability and intensity and duration of the disturbance (Baker et al. 2003, Chazdon et al. 2007), the chakra system can be considered as a farming alternative to mitigate climate change. In all, the preservation of threatened and vulnerable taxa and the enhancement of natural corridors to connect wild fauna and flora make this system an efficient alternative for farming practices in vulnerable and fast-changing ecosystems.

In conclusion, the attributes of chakras in relation to agroforestry systems intersect in the production of local foodstuffs, conservation of adequate levels of alpha and beta biodiversity, and culturally representative native species and ethnic traditions. These are tangible characteristics allowing a more harmonious and less labor-intensive farming system used by indigenous communities to obtain major supplies for their well-being while preserving forests, natural habitats, and plant diversity. Concisely, land use involving intercropping systems, i.e., chakras, in the Amazon Region and other tropical countries has a strong potential to mitigate food security and ameliorate climate change at the local and regional levels by preserving forest ecosystem structure, integrity, and functional dynamics of natural landscapes. Similar positive effects of this agrosystem in conjunction with fundamentals of forest resilience can benefit other tropical regions of the world.

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CHAPTER 3: COCOA AGROFORESTRY AND TREE DIVERSITY IN RELATION TO PAST LAND USE IN THE NORTHERN ECUADORIAN AMAZON

The format of this chapter has been modified from:

Vera-Vélez R., Grijalva J., and Cota-Sánchez J.H. 2019. Cocoa agroforestry and tree diversity in relation to past land use in the Northern Ecuadorian Amazon. New Forests, **50**: 891-910.

I designed and conducted the field data collection in this study during 2016 and 2017 with the guidance of Dr. J. Hugo Cota-Sánchez and Dr. Jorge E. Grijalva. I also performed the data analysis and elaborated the draft of the manuscript. This article entails to analyze the impact of agroecosystems on the conservation of alpha and beta plant diversity under more frequent cycles of cultivation in shifting agriculture, and to provide alternatives of land use in tropical zones. J. Hugo Cota-Sánchez provided advice on data collection, research questions, and taxonomical descriptions. Jorge E. Grijalva collaborated in the establishment of sampling locations and contacts with local Indigenous communities. All authors provided input in the article.

3.1 Introduction

Disturbances have long been the primary driving forces influencing tropical forests dynamics and the diverse ecosystem services they provide. The unbalance of anthropogenic activities alters floristic composition, landscape structure, quality of habitats, and ecosystem services (DeFries et al. 2002, Malhi et al. 2008, Vera et al. 2017). The increasing rate of human activities, particularly those related to the expansion of agricultural and grassland areas needed for food and livelihood, has played a central role in the desertification of wooded areas (Pan and Bilsborrow 2005, Bhagwat et al. 2008, Gatti et al. 2015). For millennia, these agricultural practices have replaced natural forests in many parts of the world and have posed a threat to the integrity of ecosystems, its services, and biodiversity.

The evident population pressure, in combination with subsequent demands for crop production, timber, and personal income have led to rapid deforestation (Lean and Warrilow 1989), degradated forest ecosystems (Stanturf 2015), and unbalance in the Earth's carrying capacity. Cairns (2015) and Warren-Thomas et al. (2015) claim that shifting agriculture (SA), also known as swidden cultivation (Chan et al. 2016) or swiddening (terms used interchangeably hereafter), has been one of the leading causes of tropical forest degradation in the last few decades. According to Brookfield (2015, p. 25), this practice is defined as "*land-rotational systems... which retain a significant period of fallow intended to restore the fertility of the land.*" The seemingly negative perception of SA is likely related to the effects in the ecological successional trajectory of forest communities and species recovery (Fernandes and Standford 1995, Lawrence 2004) and in the environment, e.g., soil erosion (Brookfield 2015). However, this relatively harsh point of view regarding the practice of SA is not universal.

For some scientists this farming practice represents a beneficial alternative that lessens adverse impacts on the environment and restructures plant communities. That is, SA is generally less destructive as it combines manual tools and local labor in small scale as opposed to extensive commercial agriculture involving monocultures and machinery in large open areas lacking tree coverage (Siebert and Belsky 2014). Shifting agriculture with fallow periods over ten-year cycles potentially qualify as sustainable forest management and enrichment of carbon stocks (Van Noordwijk et al. 2015, Chan et al. 2016). These ideas, in conjunction with SA have been thus far poorly investigated and therefore underestimated. One significant concern about SA is the collapsed system, which is a space of land that no longer has appropriate soil nutrients and vegetation structure for farming (Brookfield 2015). This condition has also been described as downward spiralling "cycle of land degradation and social deprivation" (Leakey 2012, 2013, 2018). This scenario might occur as a result of short fallow intervals (also referred in this paper as intensification of SA or intensification in land use), inevitably causing pronounced degradation of land resources (Rerkasem et al. 2009, Ziegler et al. 2009) and limiting supply of food resources (Tscharntke et al. 2012). For instance, the loss of woody species in Madagascar's secondary forests (Styger et al. 2009) and decrease of crop production jeopardizing food security in rural areas (Brussaard et al. 2010) are dilemmas linked to the intensification of SA throughout the world. As a result, the reduction of fallow periods in SA areas may have negative consequences in the preservation of species and ecosystem services, and consequently, in human livelihood.

Some approaches, such as the intentional combination of agriculture and forestry, technically defined as agroforestry systems (AFS), also known as chakra systems in some tropical regions, are relevant to biodiversity conservation because of the interaction among biotic and abiotic components (Arévalo 2009, Vera et al. 2017). This idea is consistent with Weinstock (2015) who suggested that AFS improve the productivity of SA practices. Thus, not all swidden farming systems are associated with species' decline (Sajise et al. 2015). Agroforestry systems also may play an important role in buffering undesirable environmental outcomes caused by decreasing fallow intervals in SA. It is well-known that AFS have positive effects on the continuity of essential ecosystems services (Ashley et al. 2006, Harvey et al. 2008, Porro et al. 2012, Leakey 2014) by enhancing connectivity with conservation areas (Schroth 2004, Bhadwat et al. 2008, DeClerck et al. 2010), avoiding changes in soil temperature, moisture regimes, and nutrient cycling (Young 1997). Accordingly, the AFS is an important approach in tropical forests with high biodiversity levels (Arévalo-Vizcaíno et al. 2013, Grijalva et al. 2016) especially in regions experiencing elevated deforestation rates.

To our knowledge the ecological effects of SA on arboreal structural, floristic composition, and diversity under AFS have not been effectively evaluated and there is so far limited quantitative data available in evaluating the consequences of SA on the above parameters. Some studies (Guariguata and Ostertag (2001), Lawrence (2004), Blanc et al. (2009), and Van Do et al. (2011)) have addressed aspects about plant species succession and floristic composition following SA and logging. However, the status of species diversity and structure of the plant community in agricultural parcels under AFS deriving from swidden cultivation is unknown. Investigating these issues and assessing the complexity of the vegetation cover will provide a better understanding of the threshold between levels of degradation and conservation of tropical ecosystems under SA, particularly for endemic, rare and endangered plant and animal species. In addition, it will lead to understanding of "trade-offs" vs. "trade-ons," i.e., achieving a balance between conservation of biodiversity and food security (Leakey 2018).

This chapter investigates how levels of biodiversity are intrinsically related to anthropogenic activities, specifically to the traditional farming system known as chakra systems or AFS (Grijalva et al. 2011, Vera et al. 2017) practiced by Indigenous communities in the Northern Ecuadorian Amazon (NEA). This promising, yet simple agricultural system, has the potential to reverse multiple adverse effects caused by the disruption of the natural equilibrium, quality and health of ecological habitats. Given the fact that in AFS only a portion of the natural vegetation is removed, several native tree species are preserved in the new farming plots resulting in less destructive ecological effects for the plant community (Arévalo 2009, Arévalo-Vizcaino et al. 2013). For these reasons, this agricultural approach has been regarded as an environmentally proactive and efficient sustainable forest management system (Vera et al. 2017). In this study we investigated whether AFS reverse the effect of intensification of SA in local scale cocoa (*Theobroma cacao*) agrosystems. We aimed to 1) quantitatively characterize species diversity in cocoa AFSs under SA with reduced fallow intervals; 2) predict the ecological impact on floristic composition, particularly in endangered endemic species, within the cocoa AFS with increasing levels of SA intensification; and 3) identify whether changes in floristic composition and species diversity in cocoa AFS under different SA fallow periods are restricted to certain strata or whether structural changes are widespread throughout the plant community.

3.2 Material and Methods

3.2.1 Study site

This study was conducted in the buffer zone of the Northern Ecuadorian Amazon (NEA) in Ecuador (Fig 1.1), which includes areas of primary forest, remnants of mature forests, and agricultural production systems (Fig 1.1A). The primary forests are mainly located in ecological reserves, such as the Sumaco Biosphere Reserve, Cayambe-Coca, Antisana, Llanganates, Yasuní, among others (Fig 1.1B). The farming areas (mainly AFS) and remnants of mature forests (MF) are found in the transitional and buffer zones of the NEA where SA takes place (Fig 1.1C). Among the crops, cocoa (*Theobroma cacao*) represents more than 95% of agricultural land (INEC 2010). The climatic characteristics of the agricultural zone correspond to pre-montane wet forest distributed from 300 to 600 meters above sea level (masl), with annual average temperature of 25ºC and annual average precipitation >3000 mm (Arévalo 2009, MAE 2014). The topography includes gentle hills and plains with predominant soils of the order Dystropepts and Tropofluvents and in lesser proportion, Hydrandepts (MAE 2014).

3.2.2 Field work

Thirty-nine plots of 0.1 ha each were established during two field-work seasons (2016 and 2017). These plots were created in agricultural and forests areas in the buffer zone of the NEA (Fig 1.1C) encompassing three Indigenous communities located in the sub-basin areas, namely Jatun Yacu-Pano-Tena, Napo-Wambuno, and Puni-Arajuno, province of Napo. Thirty out of the 39 established plots represented the cocoa AFS (cocoa agroecosystem in cultivation for 8-9 years), and nine remaining plots belonged to MF. The plot design followed the methodology described by Gentry (1982, 1988) modified by Boyle (1996). In this approach, ten parallel subplots of 2 x 50 m nested within each plot were laid out 10 m apart from each other. This procedure allowed us to capture the variability of arboreal coverage in each site. For analytical purposes, the whole 0.1 ha plot was considered a single unit to avoid spatial pseudo-replications. The cocoa AFS were assigned to three categories indicating the intensification levels (low (L.I.), intermediate (I.I.), and high intensification (H.I.)) of the SA in regard to the previous fallow period (see Table 3.1 for details). These levels are described as follows: (1) cocoa AFS L.I. established following the removal of the MF, which corresponds to a traditional cycle of shifting agriculture with a long fallow period (L.I. level), (2) cocoa AFS I.I. established within a secondary forest, which represents a farming level with intermediate activity and shorter fallow time, and (3) cocoa AFS H.I. implemented immediately following a previous cropping system and directly related to intense agricultural activity with no fallow time. For each Indigenous community, a group of approximately three to four cocoa AFS plots were established per category of intensification of SA. The nine additional plots represented MF areas in the same three local communities and were used for comparative reasons. Information about the previous fallow period of cocoa AFS and location of MF were obtained through interviews with local landowners and from Arévalo's (2009) diagnosis about rural agricultural practices in these human settlements.

3.2.3 Data collection

In order to quantify the intensification effect of the SA on the floristic composition in the cocoa AFSs, all trees over 2.5 cm in diameter at the breast height (dbh) were identified at the species level whenever possible (Table A3.1). All the identified trees were grouped in three diameter classes (DC), i.e., 2.5-9.99 cm, 10-19.99 cm, and >20 cm. We assumed that the first DC (2.5-9.99 cm) represents saplings that might be part of the forest's regenerative process, i.e., primary and secondary plant successional stages. The second DC (10-19.99 cm) represented a combination of trees belonging to primary succession and those intentionally left standing during the implementation of the 58grosystems. The third DC (>20 cm) was presumed to contain trees purposely left standing by farmers and make part of the AFS structure. Plant identification at the generic and specific levels was conducted in the field with the support of local expert ethnobotanists and based on previous collections described in Vera et al. (2017) in the same area. Voucher specimens were deposited in the Herbario Nacional (QCNE) and duplicates at the National Institute of Farming Research (INIAP), both institutions in Quito, Ecuador. In addition, relevant literature and online resources, i.e., the catalogue of vascular plants of Ecuador (www.tropicos.org), Patzelt and Echeverría (1996), Jørgensen et al. (1995), Jørgensen and León-Yánez (1999), Ståhl et al. (2015), and the Flora of Ecuador (http://bioenv.gu.se), were used to verify the identity of plants. The floristic inventory encompassed the compilation of a taxonomic list in a matrix including family and scientific names. Taxonomic authorities for scientific names are based on Tropicos nomenclatural database (www.tropicos.org). The RED list status for each species determined according to the red-book list of the International Union for Conservation of Nature and Natural Resources (IUCN 2017) was added to the dataset.

Table 3.1: Categories of intensification level of the SA for the cocoa AFS. N = number plots established (0.1 ha each) per category investigated in the buffer zone of the NEA. L.I. = low intensification, I.I. = intermediate intensification, and H.I. = high intensification.

System	Previous use	n	Degree of intensification of the land use
Cocoa AFS L.I.	Forest	10	Less intensification. Direct transformation from mature forest to AFS. Longer time for forest recovery
Cocoa AFS I.I.	Fallow	10	Intermediate intensification. Limited time for forest recovery (ca. 8 – 10 years)
Cocoa AFS H.I.	Crop	10	High level of intensification. No time for forest recovery (<1 year)
Mature forest	Mature forest	9	Representation of the mature forest communities for comparative reasons

3.2.4 Data analysis

Species richness (*S*) and effective number of plant species (*N*) were used to compare the diversity level in each category of land use according to the level of intensification of SA in the cocoa AFS (Table 3.1). The coefficient *S* denotes the total number of species, which is weighted by the number of rare taxa (Hill 1973, Loo et al. 2017). The *N* in equation 3.1 is an indicator of the plant diversity considering the number of species present in an area weighted by their frequency and has higher values when the proportion of individuals within taxa is similar (Loo et al. 2017). The value of *N* is calculated using the exponential alpha in the Shannon formula (Hill 1973, Jost 2006, 2007). Similarly, the analyses of *S* and *N* were performed for each DC to assess species diversity in the different arboreal strata in cocoa AFSs. This methodological approach allows comprehensive comparison of diversity levels among categories of land use in the cocoa AFSs and for each DC. All the estimations were performed with the package *vegan* (Oksanen et al. 2017) and R statistical software (R Core Team 2017).

$$N = \exp(-\sum_{i=1}^{S} p_i \, log_2(p_i)) \qquad \text{(Equation 3.1)}$$

Where N represents the effective number of species and p_i is the relative abundance of each species.

The evaluation of species diversity (*S* and *N*) among the categories of land use is also involved in the construction of rarefaction curves (Gotelli and Colwell 2001, Magurran 2004). This procedure explains patterns in species diversity produced by differences in sampling efforts, e.g., number of individuals assessed (Loo et al. 2017). The estimation of these diversity indices encompassed also building confidence intervals of 95% using the bootstrap method in the package iNEXT (Hsieh et al. 2016) and R statistical software (R Core Team 2017).

In order to assess the biological impact of arboreal species on the forest communities under investigation, a species importance value (IV %) was calculated according to Curtis and McIntosh (1951). This index is based in the summation of three arboreal structural aspects (see Equations 3.2-3.2.3 below). First, the relative dominance of one species based on the basal coverage area relative to other species in the vegetation stand (RD, Equation 3.2.1). Second, the relative abundance of each species (RA, Equation 3.2.2), and third, the relative frequency of one species as the occurrence in a sample plot relative to other species in the plant community (RF, Equation 3.2.3). The sum of these relative percent values divided by three denotes the species importance value, i.e., rank values for each taxon ranging from 0 to 100%. The higher the value the higher the importance of the species, only in the statistical sense. These calculations were performed using MS Excel software.

$$\mathrm{IV\%} = \frac{\mathrm{RD\%} + \mathrm{RA\%} + \mathrm{RF\%}}{3} \qquad \text{(Equation 3.2)}$$

$$\mathrm{RD\%} = \left(\frac{\mathrm{BA}}{\sum \mathrm{BA}_t}\right) \qquad \text{(Equation 3.2.1)}$$

$$\mathrm{RA\%} = \left(\frac{\mathrm{A}}{\sum \mathrm{A}_t}\right) \qquad \text{(Equation 3.2.2)}$$

$$\mathrm{RF\%} = \left(\frac{\mathrm{F}}{\sum \mathrm{F}_t}\right) \qquad \text{(Equation 3.2.3)}$$

Where IV= species importance value as a percentage; RD= relative dominance of each species; RA= relative abundance; RF= relative frequency; BA= basal area of each species calculated as π * (dbh / 2)^2, then summing the values of all individuals for the target taxa; t= sum of all values of all species per plot.

The similarity in floristic composition among the three categories of land use in cocoa AFS was analyzed as follows. First, the number of trees per species were *log*-transformed to avoid the double-zero issue (Legendre and Legendre 2012). Second, the Steinhaus coefficient (Equation 3.3 below, Legendre and Legendre (2012)) was used to calculate the similarity in species composition among the land use categories in cocoa AFS. This coefficient is equivalent to the *percentage difference distance* (Odum 1950) and is also known as Bray-Curtis distance (Legendre and Legendre 2012). It is calculated using the function *vegdist* in the *vegan* package of the R software (R Core Team 2017). The Steinhaus coefficient was considered suitable because it is designed to deal with quantitative datasets having asymmetric properties (Legendre and Legendre 2012). The third step consisted in determining whether the floristic composition, i.e., the similarity matrix obtained in step two, reveals significant differences among the categories of intensification of SA in cocoa AFS. In doing so, the analysis of similarity (ANOSIM), a multivariate equivalent of the ANOVA, was performed using the function *anosim*. Finally, a non-metric multidimensional scaling (NMDS) ordination was executed to visualize patterns of floristic composition and differences found in the ANOSIM. The NMDS was performed using the function *metaMDS*. All statistical procedures and packages used in this study were performed in R statistical software (R Core Team 2017).

$$d_{BC} = \frac{\sum_i |x_{ij} - x_{ik}|}{\sum_i (x_{ij} + x_{ik})} \qquad \text{(Equation 3.3)}$$

Where d_{BC} refers to Bray-Curtis distance, x_{ij} is the abundance of species i on site j and x_{ik} is the abundance of species i on site k.

3.3 Results

3.3.1 Floristic diversity in relation to levels of intensification of SA

The different plots investigated vary in plant density and number of species. Our data show variation in the frequency of arboreal species as well as differences in the total number of native and endangered endemic taxa. Our records show 558 trees (Table 3.2) representing 54 species belonging to 49 genera in 31 plant families (see Table A3.1 for details) in all cocoa AFS. In contrast, the MF encompassed 966 individuals representing 64 species in 60 genera and 37 plant families (Table 3.2, Table A3.1). In total, the plant inventories in the cocoa AFSs and the MF of the study area include 1524 individuals (among 83 tree species, 76 genera, and 43 families). The dominant plant families in cocoa AFS were Bombacaceae, Boraginaceae, Fabaceae, Meliaceae, and Moraceae, and the most representative genera included *Cordia*, *Cedrela*, *Pollalesta, Ochroma*, and *Vernonanthura* (Tables A3.2 and A3.3). In the MF, the most abundant families were Myristicaceae, Sapotaceae, Lauraceae, Fabaceae, and Meliaceae (Table A3.3). The dominant genera were *Virola*, *Ocotea*, *Chrysophyllum, Iriartea,* and *Guarea* (Table A3.2).

Table 3.2: Basal area, tree density, diversity indices (*S* and *N*), # of plant families, genera, native, endemic, and endangered taxa calculated in each category of intensification level of SA in the cocoa chakras (C. AFS), i.e., high (H.I.), intermediate (I.I.), and low (L.I.), among three diameter classes (DC1= 2.5-9.99 cm, DC2 = 10-19.99 cm, and DC3 = >20 cm). * The values calculated in the mature forest correspond to an area of 0.9 ha.

Indices	Cocoa AFS H.I.	Cocoa AFS I.I.	Cocoa AFS L.I.	Mature Forest*
Total basal area (m^2 ha^{-1})	3.93	4.88	7.02	36.53
Basal area DC1 (m^2 ha^{-1})	0.06	0.16	0.72	1.69
Basal area DC2 (m^2 ha^{-1})	0.25	0.67	1.99	5.29
Basal area DC3 (m^2 ha^{-1})	3.62	4.05	4.31	29.55
Total density (No. stems ha^{-1})	52	136	370	966
Density DC1 (No. stems ha^{-1})	16	40	190	432
Density DC2 (No. stems ha^{-1})	15	44	113	287
Density DC3 (No. stems ha^{-1})	21	52	67	247
Species richness ha^{-1} (*S*)	9	29	46	64
S DC1	4	13	36	43
S DC2	5	14	26	43
S DC3	7	14	19	50
Effective # of species ha^{-1} (*N*)	4	12	17	29
N DC1	2	8	19	25
N DC2	4	9	10	22
N DC3	4	7	8	26
# plant families	7	21	29	37
# genera	9	27	44	60
# native species	8	26	40	62
# endemic species	0	0	2	2
# endangered species	2	3	3	4

It is worth noting that around 66% (370 trees out of the above 558) of the inventoried arboreal individuals are present in areas with less intensified cocoa AFS with extended fallow periods (Table 3.2). There were 46 species in 44 genera (*Cordia*, *Inga*, *Cedrela*, *Pollalesta*, and *Ochroma* among the dominant - Table A3.2) and 29 plant families, with Boraginaceae, Fabaceae, Meliaceae, Asteraceae, and Bombacaceae among the most abundant (see Table A3.3). This less intensified category of land use hosts 40 native taxa, e.g., *Bursera graveolens*, *Caryodendron orinocense*, among others (Table 3.2, Table A3.1) including two endemics, i.e., *Alseis lugonis* and *Stryphnodendron porcatum* and two introduced species, i.e., *Citrus limon* and *C. sinensis*. In addition, one native taxon (*A. lugonis*) is in the threatened category and two others (*Cedrela odorata* and *Swietenia macrophylla*) are considered vulnerable (Table 3.2, Table A3.1). In turn, in the cocoa AFS with intermediate category of intensification of SA the inventoried individuals included ca. 24% of the total record, i.e., 136 out of 558 trees. Overall, 29 species belong to 27 genera, including *Cordia*, *Cedrela*, *Vochysia*, *Vernonanthura*, *Chimarrhis*, among the dominant (Table A3.2), and 21 plant families, e.g., Boraginaceae, Meliaceae, Fabaceae, Vochysicaceae, and Asteraceae as the most abundant (Table A3.3). In this intermediate category of land use, 26 taxa e.g., *Iriartea deltoidea*, *Vernonanthura patens*, *Sloanea robusta*, *Browneopsis ucayalina*, *Chrysophyllum amazonicum*, among others, are native, and three species (*Citrus aurantifolia*, *C. limon*, and *C. sinensis)* are introduced. Furthermore, one species (*Minquartia guianensis*) is in the threatened category and two (*C. odorata* and *S. macrophylla)* listed as vulnerable (Table 3.2, Table A3.1). Finally, the highly intensified cocoa AFS with no fallow periods contain only ca. 10% of the taxa catalogued. That is, 52 out of 558 trees represented only nine species in nine genera, such as *Cordia*, *Terminalia*, *Cedrela*, *Citrus*, and *Chimarrhis*, among the most frequent, belonging to seven families, i.e., Boraginaceae, Meliaceae, Combretaceae, Rutaceae, Rubiaceae, Fabaceae, and Lauraceae (Table A3.3). Eight taxa are native, e.g., *Terminalia oblonga*, *Cordia alliodora*, *Chimarrhis glabriflora*, *Inga edulis*, *Erythrina poeppigiana*, one (*C. sinensis*) introduced, and two (*C. odorata* and *S. macrophylla*) vulnerable (Table 3.2, Table A3.1).

3.3.2 Species diversity in relation to intensification of SA

Another major finding indicates that species diversity, i.e., *S* and *N*, varied across the cocoa AFS established at different fallow periods. Thus, tree diversity showed a gradual decrease from less to intermediate to highly intensified SA in cocoa AFS, with S and N values of 46 and 17, to 29 and 9 to 12 and 4, respectively (Table 3.2). MF shows distinctly higher diversities (*S* 64, *N* 29). These results indicate that the disparity in species diversity is perceptible among the different categories of intensification of SA, with the cocoa AFS under low and intermediate levels of intensification having more than twice the species diversity of the H.I. cocoa AFS (Fig 3.1). However, the shared shaded areas between cocoa AFS under L.I. and I.I. show no significant differences (p-value <0.05) in species diversity (Fig 3.1) indicating that the structural diversity is similar in these two AFS under different farming activity. Conversely, the species diversity, i.e., *S* and *N*, shows similar pattern among the three DC in all categories of fallow periods in SA except for the less intensified cocoa AFS (Table 3.2) with tree diversity values higher for the low DCs, i.e., *S* = 36 and *N* = 19 in saplings of 2.5 to 9.99 cm in dbh, compared to the *S* and *N* values of trees in DC2 (10-19.99 cm) and DC3 (>20 cm), i.e., *S* = 26, 19 and *N* = 10, 8 respectively (Table 3.2). In addition, the structural characteristics showed some differences among the categories of intensification of SA, and as expected, tree density decreases with reduction of fallow intervals, i.e., the higher the human activity in the cocoa AFS, the lower the tree diversity and density, and the same applies to the basal area (see details in Table 3.2). However, the basal area in higher DCs (>20 cm in dbh) shows similar values (between 3.62 m^2 ha^{-1} to 4.31 m^2 ha^{-1}) among the three categories of intensification in SA in cocoa AFS whereas the MF has trees with stem density and basal area of 966 trees ha^{-1} and 36.53 m^2 ha^{-1}, respectively (Table 3.2).

3.3.3 Species importance value

The importance value (IV) index varied among cocoa agrosystems with different categories of SA fallow periods. The leading ten IV taxa accounted for 100.00%, 74.15%, and 63.65% of the inventoried tree species in high (H.I.), intermediate (I.I.), and low (L.I.) categories of intensification of the SA, respectively. Meanwhile, the top ten species in MF accounted for 50.13% of the tree species found in this plant community (Table A3.2). Four out of the top ten taxa were shared among all categories of intensification in SA in cocoa AFS, i.e., *C. alliodora*, *C. odorata*, *Inga edulis*, and *I. spectabilis*; nevertheless, none of these species were among the dominant top ten characterizing the MF (Table A3.2). Conversely, seven out of the common ten families are frequent in both cocoa AFS and MF, i.e., Arecaceae, Fabaceae, Lauraceae, Meliaceae, Moraceae, Sapotaceae, and Vochysiaceae (Table A3.3).

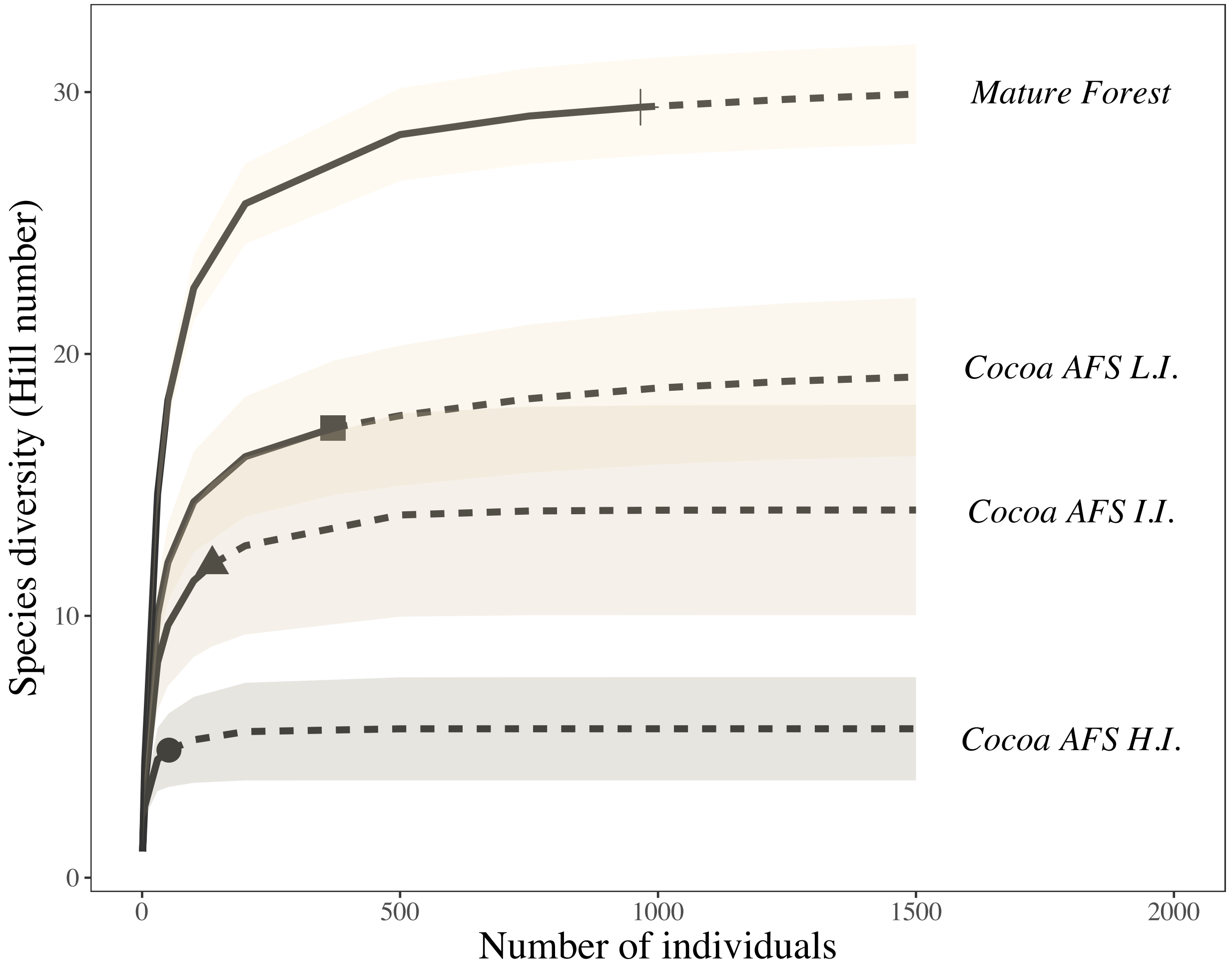

Figure 3.1: Rarefaction curve of the species diversity (*Y* axis) indicating the effective number of species (Hill number). The curves are based on the number of individuals inventoried (*X* axis). Each curve represents different land use, i.e., cocoa AFS under three categories of intensification of SA and the mature forest. Solid lines indicate the effective number of species. Dashed lines represent the extrapolated values of the diversity index using the rarefaction method. Shadow areas show the confidence interval zone (95%) for each calculated line

Intensification in the SA creates different proportions of shared taxa among cocoa AFS. Species dissimilarity is significant (0.41, p-value <0.001; Table 3.3). As expected, the major divergences were observed comparing the MF to each of the categories of SA's fallow intervals in cocoa AFS. Contrasting values with MF ranged from 0.87 (p-value <0.001) in cocoa AFS H.I. to 0.77 (p-value <0.001) in cocoa L.I. (Table 3.3). This variability can be observed in axis 1 of the NMDS analysis (Fig 3.2), which ordinates the MF sites to the right of the axis and move progressively to the cocoa AFS sites on the left according to category of intensification, revealing an evident trend in forest degradation (arrow in Fig 3.2). Also, there were significant differences in floristic composition between the MF with the categories of intensification along all DCs (Table 3.3). The highest divergence was observed in trees >20 cm in dbh (0.40, p-value <0.001) and the lowest difference in trees between 10 and 19.99 cm in dbh (0.33, p-value <0.001) (see details in Table 3.3). Less contrasting differences were found in floristic composition among the categories of intensification and the most significant dissimilarity was observed between cocoa AFS L.I. and cocoa AFS H.I. (0.30, p-value = 0.002). Lesser disparity was found in high DC, i.e. in trees >20 cm in dbh (0.19, p-value 0.046) (Table 3.3). Lastly, there is no evidence indicating differences in floristic composition among the DCs within each category of intensification of SA. The only notable discrepancy was found within MF between DC1 (2.5-9.99 cm in dbh) and DC3 (>20 cm in dbh) with dissimilarity value of 0.19 (p-value = 0.018, Table A3.4).

Table 3.3: Analysis of dissimilarity in beta diversity between categories of intensification levels of SA in cocoa chakras (C. AFS), i.e., high (H.I.), intermediate (I.I.), and low (L.I.), among three diameter classes (2.5-9.99 cm, 10-19.99 cm, >20 cm). The table shows the Steinhaus coefficient, i.e., values from 0 = least dissimilar to 1 = most dissimilar, and the p-value calculated in the ANOSIM (in parenthesis). Bold = p-values <0.05.

Categories of intensification of SA	**Total**	**2.5-9.99**	**10-19.99**	**>20**
C. AFS H.I. - C. AFS I.I.	0.06 (0.179)	0.03 (0.338)	0.06 (0.719)	0.01 (0.498)
C. AFS H.I. - C. AFS L.I.	**0.30 (0.002)**	0.08 (0.225)	0.08 (0.147)	**0.19 (0.046)**
C. AFS H.I. - Mature Forest	**0.87 (0.001)**	**0.77 (0.004)**	**0.80 (0.001)**	**0.91 (0.001)**
C. AFS I.I. - C. AFS L.I.	0.05 (0.194)	0.07 (0.219)	0.01 (0.382)	0.04 (0.801)
C. AFS I.I. - Mature Forest	**0.84 (0.001)**	**0.62 (0.001)**	**0.61 (0.001)**	**0.67 (0.001)**
C. AFS L.I. - Mature Forest	**0.77 (0.001)**	**0.55 (0.002)**	**0.58 (0.001)**	**0.80 (0.001)**

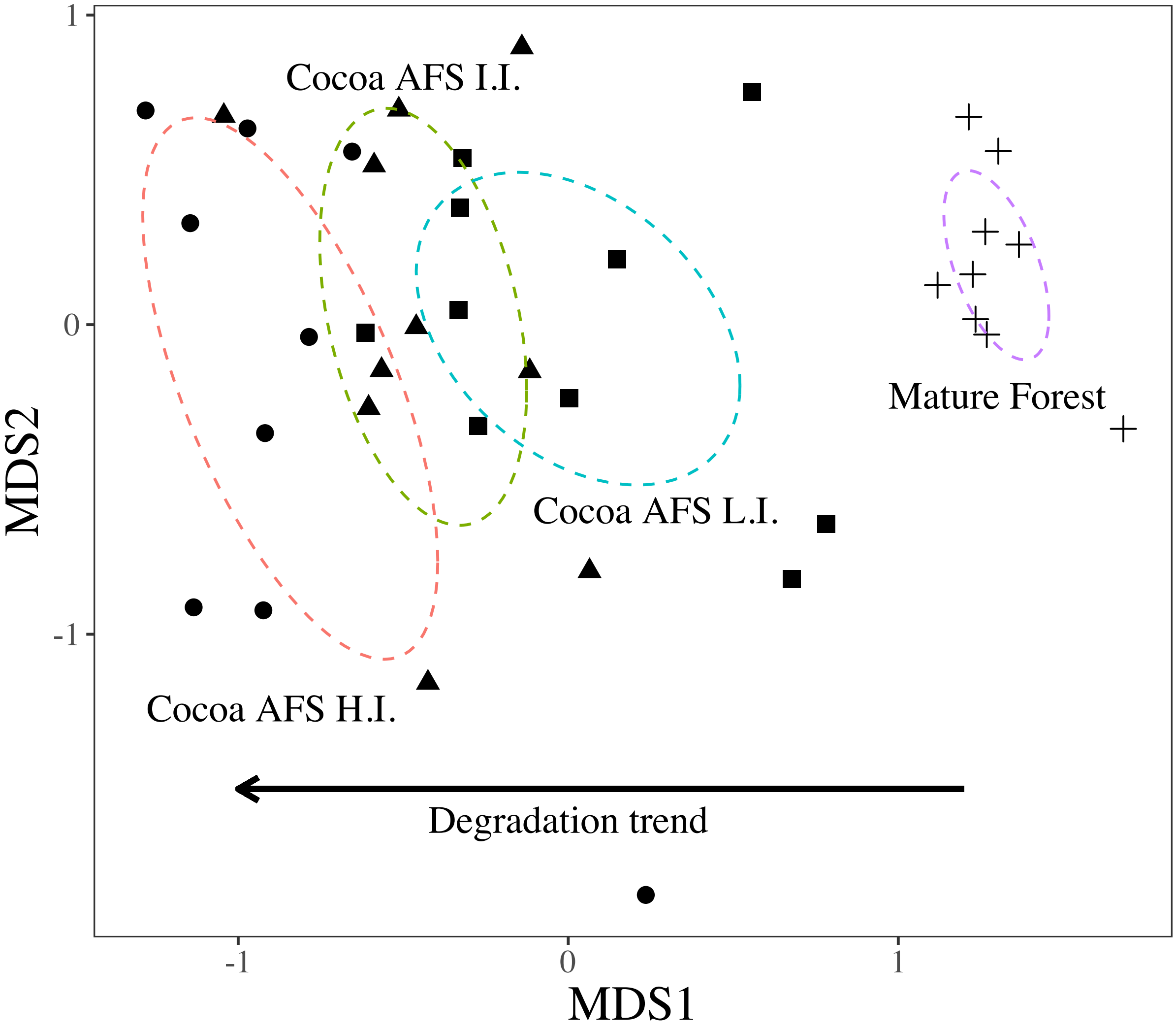

Figure 3.2: Ordination plot using Non-Metric Multidimensional Scaling (NMDS) based on Steinhaus coefficient to visualize differences in floristic composition among the investigated categories of intensification of SA under cocoa AFS, i.e., H.I. (round symbols - red ellipse), I.I. (triangle symbols - green ellipse), L.I. (square symbols - blue ellipse), and mature forest (plus symbols - pink circle). Ellipses in dashed lines represent the standard deviation (SD) from the centroid of each category of land use. The black arrow shows the forest degradation trend across different land uses. The NMDS was calculated under 2 dimensions (k = 2; MDS1 and MDS2) with a stress value of 0.14

3.4 Discussion

Extensive and continuous tropical wooded areas, such as the Amazon Basin, are important reserves of biodiversity in the world. These areas host high levels of the Earth's diversity and have significant ecological roles, including protection of soils from wind and water erosion (FAO 2015), contribute to the storage of atmospheric carbon dioxide (CO_2) (Houghton et al. 2000; Malhi and Grace 2000, DeFries et al. 2002), and stabilize global climate patterns (Tchouto et al. 2006). The capacity of these extensive zones in providing health and integrity to the ecosystem relies on their biodiversity-rich regions, including hotspot areas such as the NEA (Sierra et al. 2002, Finer et al. 2008, Bass et al. 2010). Unfortunately, such areas have experienced the highest deforestation and degradation rates thereby affecting Earth's carrying capacity. Progressive anthropogenic processes have resulted in the conversion of NEA forest area into a mosaic of mature and secondary forest fragments and agricultural (chakras) plots. Our study revealed that distinct levels of land use have drastic effects on the levels of diversity being preserved. Different degrees of intensification of the SA directly affect conservation rates in the buffer zone of the NEA. These changes lead to degradation in this vulnerable area and other regions highly dependent on fallow periods, e.g., Condor Bioreserve in Ecuador (Louma 2004), the Colombian Andes (Rodríguez et al. 2013), Bhutan's areas in the Himalayas (Siebert and Belsky 2014), and the West Kalimantan in Indonesia (Lawrence 2004). However, the use of AFSs under SA, specifically the case of the chakra systems (Vera et al. 2017), suggests that alleviating the lost structural diversity of native taxa is possible and that this recovery can have a synergistic effect to protect native endangered endemic species.

3.4.1 Effect of intensification of SA on the AFS arboreal structure

The structure and diversity of the cocoa AFS in the three categories of land use studied differed. That is, as the degree of intensification in land-use of SA increases, the plant density and basal area of the arboreal component decreases in the cocoa agrosystems. Nevertheless, AFS maintain similar structural characteristics to those of the MFs communities. Accordingly, several individuals, e.g., *Cedrela odorata*, and *Inga edulis*, are present in different strata or DCs (Table 2), a characteristic of the cocoa AFS in the NEA (Torres et al. 2014, Jadán et al. 2016, Vera et al. 2017) that makes possible a level of natural regeneration analogous to those of primary forest communities (Loo et al. 2017). The comparable basal area in the upper arboreal strata along the categories of land use suggests that the prevalence of trees >20 cm in dbh rapidly increases to reach a land coverage with asymptote regulated by intra- and inter-specific competition, as observed in other cocoa AFS (Isaac et al. 2007) and managed forests (Garcia-Gonzalo et al. 2015). This fast-growing effect on the forest canopy might affect cocoa yield by competing for soil nutrients. However, the major inter-specific competition for cocoa plants is located in the lower shaded strata in AFSs (Salazar-Díaz 2017). Therefore, cocoa bean production might not be compromised by these structural changes.

3.4.2 Effect of intensification of SA on the number of native species

The number of taxa present in the different cocoa AFS increases along the levels of intensification of SA decreases. Although the diversity is significantly lower under intense SA, the composition of the AFS allows the preservation of several native trees including endemic (*Alseis lugonis*, *Stryphnodendron porcatum*) and endangered (*Swietenia macrophylla*) species (see also Table 3.2, Table A3.1). However, taxa in the rare category were only observed in the SA experiencing the least degree of human activity (L.I.). It should be noted that the taxonomic inventory in the endangered categories follows the IUCN (2017), the only organization that thus far has evaluated the tree species in the Amazon forests. Our study shows a relatively low proportion of species in the critical or endangered categories because more than 90% of the species have not been officially assessed by the IUCN due to the lack of field exploration and quantitative analyses (Table A3.1). Hence, we suspect that the incidence of species in the most vulnerable categories should be higher. Conversely, the absolute diversity values analyzed under high and intermediate intensified SA, i.e., $N = 4$ and 9 respectively (DC2, Table 3.2), are lower than other cocoa agrosystems, e.g., Ghana (Asase and Tetteh 2010) and Mexico (Ramírez-Meneses et al. 2014) with 15 and 13 species. This output represents a major degradation of the existing forested area, and consequently ecosystem services. Nevertheless, we also observed that the influence of intermediate intensified SA is minimized, as shown by the overlapping confidence intervals of the effective number of species between cocoa AFS L.I. and I.I. (Fig 3.1). This similarity in species diversity suggests that in the AFS approach the SA's fallow periods can be reduced to at least eight years without affecting the number of tree species. This is a period of time two years shorter than Van Noordwijk et al. (2015)'s proposal to meet the criteria as a sustainable practice. Our data show a significant buffer effect of the AFS in species diversity in areas with SA strongly suggesting that cocoa agroecosystems (chakra system) is an effective, yet indirect, potential approach for *in-situ* and *circa situm* (farmer-based) conservation (Dawson et al. 2013) and likely minimizing “trade-offs” with food production (Leakey 2018), a major goal for conservationists and activists involved in the protection of the rapidly vanishing tropical forests of the world.

Similar trends of *S* and *N* in the different DCs within each category of intensification of SA in cocoa AFS are noticeable (Table 3.2). Comparable species richness (*S*) in the different arboreal strata reveals the intrinsic natural stewardship of Indigenous farmers as keepers to preserve high plant diversity notwithstanding the intensification level of SA. This practice seems common in rural human settlements in the NEA where maintenance of native plant species is related to the safeguarding of indigenous identity, cultural beliefs, and traditions (Denevan 1971, Perreault 2005, Arévalo 2009, Dawson et al 2013). These ancestral practices in conjunction with market-oriented products, such as corn and cocoa, help to diversify allocation of income sources (Padoch et al. 1985, Dahlquist et al. 2007, Arévalo-Vizcaíno et al. 2013). Hence, this rural husbandry may notably contribute to forest landscape restoration in terms of biodiversity conservation and human culture and well-being (Cornellius and Miccolis 2018). Concisely, this farming system is an example of a remarkable agricultural model capable of preserving species diversity and local traditions while being commercially effective by meeting the multidisciplinary requirements to reverse the cycle of land degradation and social deprivation (Leakey 2013).

3.4.3 Effect of intensified SA on forest degradation

Another relevant aspect of the use of AFS under SA is the existing trend in slowing down forest degradation processes. Despite the fact that the SA produces an apparent divergence in the ratio of shared taxa between the AFS assessed and the MF, the arboreal assembly among cocoa AFS under different categories of intensification of SA showed low dissimilarity (Fig 3.2, Table 3.3) and also in importance values (IV) of species and families (Tables A3.2 and A3.33). These results are consistent with Bhagwat et al. (2008), who pointed out that high correspondence in plant community structure occurs when the AFS are located near or adjacent to forest reserves. In our study the buffer zone of the NEA is surrounded by ecological reserves and MF communities that probably favor plant regeneration, recruitment, and establishment of young saplings of native trees; however, other recruitment mechanisms may also influence plant renewal, such as natural seed-banks with viable diaspores (Ordóñez et al. 2014). Nevertheless, the characterization of establishment mechanisms for young plants in AFS under SA in the NEA is still unknown and needs investigation. In contrast, the presence and diversity of other organisms, such as the mutualistic associations of numerous bats and birds with tree assemblages (aspects beyond the scope of this study) can be adversely disrupted by the intensification in the land use (Harvey and Villalobos 2007). These changes in animal-plant relationship have significant roles in the natural history and reproductive biology of some plant species, including pollen transfer and seed dispersal (Cota-Sánchez and Croutch 2008, Rosado et al. 2018, Diniz et al. 2019).

On the other hand, the apparent equilibrium in tree composition among the three categories of intensification of SA reaches the breakpoint, i.e., the point in which the floristic complexity is likely to decrease, in cocoa AFS H.I., specifically in the configuration of trees >20 cm in dbh (Table 3.3). This implies that trees intentionally left standing by farmers are eventually removed. This could lead to forest degradation resulting from intensification of land use beginning with the loss of tree species in the upper arboreal strata, an outcome consistent with rubber plant agroecosystems practices in Indonesia (Tata et al. 2008). However, even though the loss of trees in the high strata affects several ecosystem services and habitat for local flora and fauna (Lawler et al. 2014, Haddad et al. 2015), forest recovery is possible after an extended period of SA abandonment (Chazdon 2003). To do that, the presence of mid- and lower arboreal layers of AFS is necessary to promote the return to the original (or similar) floristic structure after SA abandonment (Vera et al. 2017). Our results show that the existence of minor dissimilarities in lower DC among all cocoa AFS in different categories of intensification of SA may also play an important role in the regeneration of this dynamic of plant community. In fact, the species in lower DC favor plant succession to eventually converge with the same forest structure after abandonment, as documented for two human-modified forests in Taiwan (Loo et al. 2017). Hence, the floristic composition and diversity of the AFS under SA might represent a stable ecological system that buffers negative impacts on the forest resilience mechanism (Newton and Cantarello 2015). Nevertheless, the impact on the intra-specific genetic variation among tree individuals needs to be evaluated (O’Neill et al. 2001, Dawson et al. 2014).

The dynamic AFS-SA combination can be considered as a biodiversity resilience tool that could be extrapolated to other farming patterns of crops and trees in the world. Although this study is focused only in cocoa AFS, this agricultural approach is comparable to other farming schemes, such as agrosystems based on corn and plantain developed by the Waorani society aim for food security and cultural preservation in the Ecuadorian Amazon (Zurita 2018). Similarly, AFS can also be adapted to cattle and pasture systems to develop more sustainable practices (Gaglio et al. 2017) that buffer land-use pressure and contribute to lower habitat fragmentation in the Amazon and other tropical areas or the world (Haddad et al. 2015). The characteristics of the AFSs allow the perpetuation of a certain level of plant diversity and surrounding vegetation in more intensified agricultural schemes. In particular, the use of complex arboreal structures enhances the preservation of native and endangered species and slows down forest and land degradation. From this perspective, the shaded cocoa crop plays an essential role because of the balanced combination of trees essential for human well-being, culture and traditions and the preservation of forests, natural habitats, plant diversity, and ecosystem functions. In summary, the use of AFS under SA has strong potential to reduce forest degradation in other tropical and subtropical agricultural areas of the world and thus ameliorate their capacity as a sink for CO_2 to mitigate climate change.

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CHAPTER 4: BETA DIVERSITY AND LAND MANAGEMENT REGULATE SOIL FERTILITY IN COCOA AGROFORESTRY IN THE NORTHERN ECUADORIAN AMAZON

The format of this chapter has been modified from:

Vera-Vélez R., Cota-Sánchez J.H., and Grijalva J. 2020. Beta diversity and land management regulate soil fertility in cocoa agroforestry in the Northern Ecuadorian Amazon. Submitted to *Agricultural Systems*

I designed and conducted the field data collection in this study during 2016 and 2017 with the guidance of Dr. J. Hugo Cota-Sánchez and Dr. Jorge E. Grijalva. I also performed the laboratory work, data analysis, and elaborated the draft of the manuscript. This article provides the foundations to analyze the impact of agroecosystems on the preservation of ecosystem services in tropical areas under more frequent cycles of cultivation in shifting agriculture. J. Hugo Cota-Sánchez provided advice on data collection and research questions. Jorge E. Grijalva collaborated in sample collection and laboratory work. All authors provided input in the article.

4.1 Introduction

Tropical forests play a major role in controlling global weather patterns, key soil development and dynamic process, and nutrient retention, all which sustain healthy and productive topsoil useful as arable land (de Groot et al. 2002, Polania et al. 2011). Despite their benefits, these declining ecological processes are a consequence of the unprecedented destruction of forest landscapes (Berthrong et al. 2009, Crowther et al. 2014). Recent evidence suggests a complex relationship between the loss of ecosystem services and the devastation of plant communities (Liang et al. 2015, 2016, Ammer 2019). Specifically, the productivity of forest ecosystems depends on suitable levels of alpha (α)- and beta (β)-diversity (Crowther et al. 2014, Diallo et al. 2019). That is, in woodlands there is a minimum species richness requirement of specific organismal groups (α-diversity) and minimum species replacement (β- diversity) due to anthropogenic activities (Balsega 2010).

The perpetuity of healthy and nutritive soils is central to support plant productivity (Berthrong et al. 2009, Smith et al. 2015, Raj et al. 2019), but the ecological disruption on components of large natural environments increases the risk of exhausting soil ecosystem services, agricultural sustainability and food security, particularly in tropical rural areas (Vitousek et al. 2009, Porro et al. 2012, Trivedi et al. 2016). And while deforestation continues in the tropics, by 2050, the projected human population growth will require an increase of food production by at least 70% (Tilman et al. 2011, Ramankutty et al. 2018). Evidently, a major boost in crop yield will be needed either by expanding agricultural land, creating new 'miracle' crops with higher production, or intensifying existing production systems (Smith et al. 2016, Wood et al. 2016, Delaquis et al. 2018), all of this with immediate effects on natural landscapes and ultimately changes in the soil's chemical and physical properties.

In the Northern Ecuadorian Amazon (NEA) the primary agricultural practice is shifting agriculture (SA), which is also the major threat to soil vigor, land sustainability and biological diversity. This farming method consisting of land-use rotation with diverse fallow periods is intended to restore soil nutrients (Nye and Greenland 1960, Brookfield 2015). Intensification (shorter fallow phases and higher frequency of cultivation) of shift agriculture drives the degradation of multiple natural habitats, especially soil ecosystem and the numerous microbiological interactions within (Metzger 2003, Styger et al. 2007, Arevalo 2009, Neba 2009, Jakovac et al. 2015, 2017, Junqueira et al. 2016, Wood et al. 2016), albeit it is central to food security (Ziegler et al. 2009, Warren-Thomas et al. 2015, Jakovac et al. 2016). In the long term, the increasing tilling frequency of SA challenges rebuilding processes of soil nutrients due to erosion of topsoil. However, the adverse effects of SA can potentially be reversed or prevent practicing agroforestry systems (AFS), which buffer soil degradation and maintain higher level of species diversity, two biological components typically disrupted by SA (Metzger 2003, Vera-Vélez et al. 2019). In recent years, the AFS practice has been widely investigated as an alternative to reduce trade-offs between agriculture and conservation (Guiracocha et al. 2001, Dalquish et al. 2007, Bhagwat et al. 2008, Leakey 2012, Cerda et al. 2014, Vaast and Somarriba 2014, Vera et al. 2019). Essentially, the tree cover in AFS, such as cocoa agroecosystems, benefits topsoil nutrient cycling (Young 1989, Sánchez 1995, Magdoff and Van Es 2009, Mutua et al. 2014, Afolayan 2020), richness in macro- and microorganisms (Nardi 2009, Bardgett et al. 2014), mulch layer formation, and inputs of soil organic carbon (Muschler 2016). Thus, these welfares suggest that combining the tree component of AFS with SA may reduce soil infertility with shortened fallow periods.

The interaction between SA with trees (α- and β- diversity) and soil nutrients has been also investigated in Latin America and areas of Africa and Asia. However, most studies describe the aftermath of reduced fallows on species richness following phases of ecological successions and vegetation changes using a chronosequence method in post-abandoned SA areas, e.g., Ross (1954), Uhl (1987), Chazdon et al. (2007), Fukushima et al. (2007, 2008), Lebrija-Trejos et al. (2008), Tran et al. (2010). There is also research linking species diversity and soil nutrients only in secondary forests recovery after agricultural land abandonment (Jakovac et al. 2015, 2016). Although some studies have discussed soil nutrient availability in existing swidden areas, e.g., Dale and Blois (2006) and Wood et al. (2016), the direct relationship between soil and vegetation is still in need of further investigation. In this regard, research dealing with changes in soil fertility in plots that are cultivated after clearing and removal of selected tree species, are scanty. To our knowledge, the effect of β-diversity and the different forest layers on soil nutrients under combined AFS-SA approaches, is unknown. Therefore, this paper investigates whether species replacement in AFSs with reduced fallow cycles impacts soil properties in cocoa (*Theobroma cacao* L.) agrosystems. This research focuses on chakras, a farming tradition that typically merges crops and native trees, i.e., AFS, in plots subjected to SA, practiced by autochthonous groups in the Ecuadorian Amazon. Within this context, the objectives of this study were: 1) quantifying the ecological relationship between floristic composition and soil properties within the cocoa AFS with reduced fallow length, and 2) determining whether changes in floristic composition restricted to certain tree strata affects soil nutrient content in cocoa AFS under different resting periods.

4.2 Material and Methods

4.2.1 Description of the study area

This investigation was conducted in the north of the Amazon region of Ecuador (Fig. 1.1) in areas comprising natural reserves, such as the Sumaco Biosphere Reserve, Cayambe-Coca, Antisana, Llanganates, Yasuní National Park, and Cuyabeno. The Northern Ecuadorian Amazon (NEA) region possesses natural sanctuaries protecting numerous plant and animal taxa (Granizo et al. 2006, Rival 2010, Holland et al. 2017) and has been declared a national legacy by the Minister of the Environment (MAE 2015). It covers ca. 25,021 km^2 (INEC 2010) and encompasses a transitional (ecotone) or buffer section with remnants of mature forests and farming areas (mainly agroforestry) managed by indigenous communities (Kichwas, Shuar, Wuaoranis, and others) and colonizer societies or *colonos*. These people practice shifting agriculture (SA) in the buffer zone where the cocoa crop (*Theobroma cacao*) represents more than 95% of agricultural land (INEC 2010).

The study area is situated in the high basin of the Napo River within the sub-basins Jatun Yacu-Pano-Tena, Napo-Wambuno, and Puni-Arajuno. The climate is humid with mean annual rainfall of 3500 mm and monthly average temperature of 24°C. The elevation ranges from 300 to 600 meters above sea level (masl) (Arévalo 2009, MAE 2015) and the topography is characterized by gentle hills and plains with predominant soils of the order Inceptisols, primarily within the Dystropepts and Hydrandepts groups and the order Entisols with high incidence of Tropofluvents (MAE 2015).

4.2.2 Plot selection and field data

The data for this study were collected during 2016 and 2017 from 39 plots of 0.1 ha each in the ecotone area of the NEA (Fig. 1.1). These plots were located in land belonging to three Kichwas Indigenous communities (Campo Cocha, Sinchi Runa Puni Bocana, and Río Blanco). Thirty out of the 39 plots were cocoa AFS (cultivated for 8-9 years) and the remaining nine parcels were mature forests (MF) for comparative reasons. Plot design followed Gentry (1982, 1988) modified by Boyle (1996) and ten parallel subplots of 2 x 50 m nested within each lot were laid out 10 m apart. This design encompassed the variability of tree diversity in each site and the subplots were aggregated to provide a single estimate for the 0.1 ha section. The 30 cocoa AFS plots were assigned to three categories (10 plots each) according to previous duration of the inactive period, specifically long fallow (L.F.), intermediate fallow (I.F.), and short fallow (S.F.). The length of these resting periods is as follows: (1) cocoa AFS L.F. corresponds to ~30 uncultivated years and established following removal of understory species and selected tree clearing from the MF, (2) cocoa AFS I.F. with 8 to 10 years of unseeded period and established within a secondary forest after underbrush and selected tree removal, (3) cocoa AFS S.F. established in plots with no previous use or less than one year of fallow phase . The characteristics of the plots in the last category include: 1) previous land use for around 5 to 6 years, 2) multiple intercropping of corn, cassava, peanut, rice, banana, plantain, etc., with sporadic fallow time of ca. one to six months, and 3) presence of trees with understory crops, i.e., AFS. Information about land's natural history and use, including fallow time before planting of cocoa plants was obtained following Arévalo (2009) through interviews with local farmers and landowners.

The implementation of cocoa chakras followed one of the traditional methods used by Indigenous people in the NEA. That is, manual clearing of the forest floor vegetation followed by removal of selected trees from different strata. The process of vegetation purge takes one and three months depending on the size of the chakra and no fire is involved. Upon elimination of the selected flora the next step consists in planting cocoa saplings at a density of ca. 645 individuals ha^{-1}, i.e., at 4 x 4 m, under the canopy of the remaining trees. As cocoa plants develop, temporal (annual and biannual) crops, e.g., corn, cassava, peanut, rice, banana, are lined-up in the middle of cocoa plant rows. This phase lasts between 3 and 4 years or until cocoa trees reach 1.5 m height or more, period of time elapsed for the canopy to cover a sizable area of the ground. At this time farmers start collecting cocoa fruits annually the next 12 to 15 years and then the field is abandoned. In general, the cultivating period of cocoa chakra lasts between 16 and 20 years before fallows initiate and the original vegetation begins to re-emerge.

4.2.3 Measurement of soil properties

The chemical and physical characteristics used as indicators of forest soil quality were determined for the 39 plots cocoa AFS and MF communities. For this, one composite soil horizon consisting of a mixture of 15 to 20 soil subsamples per plot from the upper 30 cm of the soil surface was collected using a 1” diameter x 12” length soil auger. All measurements of soil properties were carried out according to standard protocols in the Soil Analysis Laboratory at the Central University of Ecuador in Quito. For each trial, the following parameters were determined: pH in aqueous solution at 1:25 ratio, soil organic matter (SOM) based on Walkley-Black’s wet combustion method (Walkley and Black 1934), total nitrogen (N^{3-}) using Kjeldahl’s procedure, available phosphorus (P^{+}) with photo-colorimeter with Olsen’s modified method (Olsen et al. 1954), cations and micronutrients (potassium (K^{+}), calcium (Ca^{++}), Magnesium (Mg^{++}), Iron (Fe^{++}), Manganese (Mn^{++}), Copper (Cu^{++}), and Zinc (Zn^{++})) using atomic absorption spectrophotometry. The cation exchange capacity (CEC) used the ammonium acetate’s method and soil textural content (sand, silt, clay) was according to Bouyoucos’ method (Bouyoucos 1926).

The soil bulk density (SBD) for analysis of organic matter and particle size(s) was also determined for each plot. This estimate consisted of five sub-samples from three sections collected in each plot from the first 30 cm of soil horizon profile using the cylinder metallic’s undisturbed sample method. The samples were collected in the middle of each section, with each section corresponding to three soil depths, i.e., 0-10 cm, 10-20 cm, and 20-30 cm. Hence, the plot was divided into five equal parts to encompass the variability of soil density, both in depth and space. Each sub-sample collected was dried out in an oven at 105°C for 24 hours and then re-dried under the same conditions and weighed thereafter. This procedure was repeated until all the samples had constant, stable weight. The final mass of each sub-sample was used to calculate soil density based on the volume of the metallic cylinder. This method yielded a total of 585 sub-samples and the SBD values were averaged at 30 cm depth per plot to avoid spatial pseudo-replication during the statistical analysis.

4.2.4 Tree taxonomic inventory

Trees with diameter at breast height (dbh 1.30 m above the ground) over 2.5 cm were catalogued at the generic and specific levels in all cocoa AFS and MF plots. Identified trees were grouped in three diameter classes (DC), i.e., 2.5-10 cm, 10-20 cm, and >20 cm, representing the floristic composition on each forest layer. Diameter was measured in arboreal tree species only, hence, cacao plants were excluded. Taxonomic identification was conducted in the field with the support of local expert ethnobotanists and previous botanical collections described by Vera et al. (2019) in the same study area. In addition, relevant literature and online resources, i.e., the catalogue of Vascular plants of Ecuador (MBG 2017), Jørgensen et al. (1995), Patzelt and Echeverría (1996), Jørgensen and León-Yánez (1999), Ståhl et al. (2015), and Flora of Ecuador (http://bioenv.gu.se), were used to verify the identity of some plants. Botanical collections were processed and deposited at the Herbario Nacional (QCNE) and duplicate voucher specimens were deposited at the National Institute of Farming Research (INIAP), Quito, Ecuador.

4.2.5 Data analysis

The relative influence of decreasing fallow length of SA and changes in species composition (*β*-diversity) based on soil chemical and physical properties of cocoa AFS in the Northern Ecuadorian Amazon (NEA) were examined. In order to quantify the tree taxonomic make-up dissimilarity between plots using Hellinger transformation was exercised. The species variation among plots and fallow length was analyzed against soil variables using redundancy analysis, a method that has been successfully used for plant community analysis in other studies, e.g., Duivenvoorden et al. (2002) and Dalle and Blois (2006). The procedure is explained below.

The soil dataset was assembled based on the chemical and physical properties calculated in the 39 cocoa AFS and MF plots. Twelve chemical variables (pH, SOM, N^{3-}, P^{+}, K^{+}, Ca^{++}, Mg^{++}, Fe^{++}, Mn^{++}, Cu^{++}, Zn^{++}, and CEC) and four physical components (sand, silt, clay, and SBD) comprised the soil data. With the intention to explain soil fertility, we reduced the dimensionality of the soil dataset, i.e., new highly correlated factors with soil components. In doing so, factor analysis (Crawley 2013), an exploratory statistical method that posits high correlated variables explained by common underlying factors, was used. In this procedure all soil measurements were standardized using the function *scale* so that all variable scales or units of measurements were excluded to create comparable coefficients of unit variance. Afterwards, the factor analysis was executed with the new standardized soil matrix using the function *factanal* and Bartlett's weighted least-squares scores (Crawley 2013). Factors were continuously added to reach an acceptable model based on the χ^2 distribution, i.e., new factors model match the original soil matrix (p-value >0.05). The functions *scale* and *factanal* were performed in R statistical software (R Core Team 2017).

Factor analysis, an exploratory statistical method that theorizes that high correlated variables are explained by common underlying factors, was used (Crawley 2013). In this procedure all soil measurements were standardized using the function *scale* so that all variable scales or units of measurements were removed to create comparable coefficients of unit variance. Afterwards, the factor analysis was executed with the new standardized soil matrix using the function *factanal* and Bartlett's weighted least-squares scores. Factors were continuously added to reach an acceptable model based on the χ^2 distribution. The functions *scale* and *factanal* were performed in R statistical software (R Core Team 2017).

The accounts for floristic composition dissimilarity among plots per DC (at each forest layer) were organized into a data matrix and added to the analytical scheme. Hellinger transformation with species community data prevented the double-zero issue in order to deal with quantitative datasets with asymmetric properties to perform additional ordination analyses with linear trends, such as redundancy analysis (Legendre and Gallagher 2001, Legendre and Legendre 2012). This transformation was executed with the ‘vegan’ package (Oksanen et al. 2007) in R Statistical Software (R Core Team 2017). In addition, the fallow length categories were included in the redundancy analysis as dichotomic variables.

The redundancy analysis (RDA) with simple (marginal) and conditional (partial) variance partitioning (Borcard et al. 1992, Økland and Eilertsen 1994) investigated the influence of decreasing fallow length and changes in species dissimilarity among plots (*β*-diversity) in relation to soil properties. In the case of the simple RDA, the reduced soil dataset (only relevant variables explaining fertility) was analyzed against the tree composition dissimilarity among plots. This simple RDA model was executed four times, i.e., with the total flora dissimilarity and with the tree dissimilarity matrices representing each diametric class (DC), in order to evaluate the explained variance of each plant community data in relation to changes in soil fertility. A partial RDA analogous to the simple RDA, with the difference of fallow length included in each model trial, was also used to examine whether the soil response to changes in species composition is conditional or depends on unseeded period. Both, the simple and partial RDA allowed separating the variance of the species and fallow length data in three fractions: one explaining total species dissimilarity among plots alone, another describing dissimilarity of individual forest layers (DC) among plots, and the last one explaining the species dissimilarity among plots (total and by each DC) sustained by fallow length. All statistical procedures were performed in R Statistical Software (R Core Team 2017).

4.3 Results

4.3.1 Variation in soil components

The investigated soils of cocoa AFS and MF plots revealed high variability in chemical and physical parameters. Foremost, in terms of the chemical content, cations, such as K^+, Ca^{++}, Mg^{++}, and Cu^{++}, showed a variation higher than 60%, whereas inconsistency in physical components, e.g., soil bulk density and texture, was relatively lower, i.e., <40% (Table 4.1). On the other hand, the factor analysis (FA) showed that six orthogonal factors explain the variability in the soil matrix in all the 39 sites, χ^2 (6, N=39) = 46.01, p-value = 0.205 (Table 4.2). These six factors account for 71.3% of the cumulative variance in soil attributes and indicate that cations such as Ca^{++} and P^+ in addition to clay, pH, silt, and SOM content, represent the top loading values (Table 4.2) among the chemical and physical components. Furthermore, factors one, two, and six in the FA are associated with the soil chemical elements, whereas factors three to five are related to the soil physical properties. Within factor one, Ca^{++} is positively correlated to Mg^{++}, K^+, and CEC, and negatively linked to Fe^{++} (Table 4.2). Factor two shows that pH is positively associated with Cu^{++} but negatively related with Mn^{++}. Factor three in turn, represented by silt, is negatively correlated with sand content while in factor four, the soil's organic matter is positively related to N^{3-} and negatively linked to SBD, but in factor five, clay is negatively associated with sand. Finally, in factor six, P^+ is positively correlated with Zn^{++} (Table 4.2).

4.3.2 Variation in arboreal structure

The different tree aspects (basal area, tree density, No. genera, No. species) investigated also displayed high variability. Our data showed a coefficient of variation higher than 60% in all arboreal calculations (Table 4.1). In general, the structural characteristics disclosed an average of basal area (G) of 13.09 m^2 ha^{-1} with maximum values of 36.53 m^2 ha^{-1} (Table 4.1). The tree trunk density also showed high variability with an average of 381 trunks ha^{-1} and a maximum density of 966 stems ha^{-1}. On the other hand, the tree taxonomic diversity showed that the maximum values, attributed to MF, are 37, 60, and 64 for number of plant families, genera, and species, respectively (Table 4.1), which is low relative to NEA's pristine forests and consistent with uninterrupted use of this forest for agriculture. The cocoa AFS SF displayed the lowest values of α-diversity with only seven plant families, nine genera, and 9 species. In general, all the cocoa AFSs included 558 individual trees encompassing 54 species belonging to 49 genera circumscribed in 31 plant families.

The taxonomic fluctuations in β-diversity from MF to cocoa AFSs varied at the family, generic and specific levels. The most abundant plant families in cocoa AFSs were Bombacaceae, Boraginaceae, Fabaceae, Meliaceae, and Moraceae, and the most representative genera included *Cordia*, *Cedrela*, *Pollalesta, Ochroma*, and *Vernonanthura* (Table A3.2, Table A3.3). In the MF, the dominant families were Myristicaceae, Sapotaceae, Lauraceae, Fabaceae, and Meliaceae, and the most frequent genera were *Virola*, *Ocotea*, *Chrysophyllum, Iriartea,* and *Guarea*. The discrepancy in species composition is also evident in cocoa AFSs with different fallow lengths. That is, there were 46 species in 44 genera (*Cordia*, *Inga*, *Cedrela*, *Pollalesta*, and *Ochroma*, among others) and 29 plant families, including Boraginaceae, Fabaceae, Meliaceae, Asteraceae, and Bombacaceae in areas with long resting cycles of cocoa AFS (Table 4.1). In turn, in cocoa AFSs with I.F. of SA the inventory comprised 29 species belonging to 27 genera, including *Cordia*, *Cedrela*, *Vochysia*, *Vernonanthura*, *Chimarrhis*, and 21 plant families, e.g., Boraginaceae, Meliaceae, Fabaceae, Vochysicaceae, and Asteraceae (Table A3.2, Table A3.3). Remarkably, the cocoa AFSs with no previous fallow length contained just ca. 10% of the taxa cataloged in this study. Only 9 species in nine genera, such as *Cordia*, *Terminalia*, *Cedrela*, *Citrus*, and *Chimarrhis*, belonging to seven plant families, i.e., Boraginaceae, Meliaceae, Combretaceae, Rutaceae, Rubiaceae, Fabaceae, and Lauraceae were the most common (Table A3.2, Table A3.3).

Table 4.1: Mean ± SE and coefficient of variation (CV) values of each soil and tree structural variable (excluding cocoa plants) collected in the 39 study plots (30 cocoa AFS and 9 MF) in the Northern Ecuadorian Amazon. The CV shows the disparity value among sites.

Soil variables	**C. AFS S.C.**	**C. AFS I.C.**	**C. AFS L.C.**	**M. Forest**	**CV (%)**
pH	5.71 ±0.24	5.28 ±0.57	5.32 ±0.31	4.84 ±0.42	9.43
Soil's organic matter -SOM- (%)	3.03 ±1.54	3.16 ±0.97	2.86 ±1.21	3.82 ±0.40	36.88
Total nitrogen -N^{3-}- (%)	0.2 ±0.10	0.2 ±0.09	0.22 ±0.09	0.17 ±0.11	50.00
Phosphorus -P^{+}- (ppm)	12.95 ±4.13	8.76 ±3.97	7.99 ±3.61	8.47 ±4.86	48.07
Potassium -K^{+}- (ppm)	0.15 ±0.11	0.1 ±0.08	0.19 ±0.12	0.06 ±0.05	84.62
Calcium -Ca^{++}- (cmol kg^{-1})	5.74 ±3.10	7.74 ±4.57	8.83 ±6.55	0.47 ±0.13	92.11
Magnesium -Mg^{++}- (cmol kg^{-1})	0.83 ±0.97	2.52 ±1.93	2.66 ±1.94	0.42 ±0.41	109.14
Iron -Fe^{++}- (ppm)	171.49 ±40.70	219. 79 ±80.17	155.86 ±78.14	343.07 ±48.22	44.24
Manganese -Mn^{++} (ppm)	6.74 ±4.11	11.07 ±4.78	11.29 ±5.37	11.71 ±2.57	47.34
Copper -Cu^{++}- (ppm)	5.73 ±1.52	3.14 ±1.59	2.14 ±1.17	1.77 ±0.77	60.91
Zinc -Zn^{++}- (ppm)	2.38 ±1.48	2.94 ±1.34	2.39 ±1.21	3.02 ±1.66	54.31
Cat. Exch. Capac. -CEC (cmol kg^{-1})	14.44 ±5.76	15.23 ±5.71	18.26 ±10.32	14.03 ±6.76	48.62
Soil bulk density -SBD- (g cm^{-3})	0.95 ±0.16	0.95 ±0.10	0.92 ±0.07	0.87 ±0.14	14.13
Sand (%)	29 ±5.84	27.6 ±14.51	34.4 ±4.41	45.22 ±12.73	36.42
Silt (%)	52 ±4.90	42.8 ±13.53	40.7 ±8.47	32.33 ±5.17	26.61
Clay (%)	19 ±2.77	29.6 ±8.99	24.9 ±8.37	23.55 ±8.36	34.76
Arboreal structure variables					
Basal area -G- (m^2 ha^{-1})	3.93	4.88	7.02	36.53	119.79
Stem density (No. stems ha^{-1})	52	136	370	966	108.28
No. plant families	7	21	29	37	53.29
No. genera	9	27	44	60	62.71
No. species	9	29	46	64	67.06

Table 4.2: Loading values obtained from the factor analysis for soil variables in the Northern Ecuadorian Amazon. Columns represent six orthogonal factors and the rows indicate the soil variables. The proportion of the variance explained by each factor and the statistical values from the analysis are shown at the end of the table. The numbers in each column represent loading values for each soil parameter that varies with each factor. Values close to 1 or -1 within each factor indicate high correlation with each other and with the factor (column) they represent. Numbers and soil variables in bold characters display the highest correlation to the factors.

Soil variables	**Factor 1**	**Factor 2**	**Factor 3**	**Factor 4**	**Factor 5**	**Factor 6**
pH	0.51	**0.83**	0.05	-0.16	-0.07	-0.08
Soil organic matter (SOM)	-0.28	-0.13	0.01	**0.94**	-0.02	-0.12
Total nitrogen (N^{3-})	0.07	-0.07	0.16	0.59	0.25	0.19
Phosphorus (P^{+})	-0.22	0.48	0.25	-0.20	0.05	**0.78**
Potassium (K^{+})	0.55	0.18	-0.06	0.22	0.02	-0.13
Calcium (Ca^{++})	**0.91**	0.08	0.05	-0.16	-0.03	0.09
Magnesium (Mg^{++})	0.78	0.06	0.06	-0.14	0.06	-0.05
Iron (Fe^{++})	-0.61	-0.27	-0.22	0.27	0.18	0.12
Manganese (Mn^{++})	-0.06	-0.65	-0.09	0.13	0.21	-0.04
Copper (Cu^{++})	0.11	0.74	0.13	-0.02	-0.02	0.01
Zinc (Zn^{++})	0.12	-0.17	0.02	0.21	-0.16	0.61
Cation Exchange Capacity (CEC)	0.64	-0.01	0.16	0.12	-0.06	0.28
Soil bulk density (SBD)	-0.05	0.32	0.12	-0.39	0.17	-0.23
Sand	-0.12	-0.09	-0.89	-0.08	-0.42	-0.05
Silt	0.16	0.27	**0.90**	0.04	-0.26	0.13
Clay	-0.06	-0.24	0.05	0.09	**0.95**	-0.16
Proportion of Variance (%)	18.70	14.20	11.30	10.70	8.40	7.90
Cumulative Variance (%)	18.70	32.90	44.20	55.00	63.40	71.30
χ^2 statistic and degrees of freedom: 46.01 on 39 df; **p-value:** 0.205						

4.3.3 Redundancy analysis

The application of the RDA model indicated significant outcomes. All plant community changes drew significant results (F = 2.18, p-value <0.001; RDA, Table 4.3) and explained changes in soil parameters. Based on the adjusted R-square, the full model of the RDA showed that dissimilarity in floristic composition among plots supported 31.7% of the constrained variance, whereas 68.3% represents unconstrained variance (Table 4.3, Fig. 4.1). The first two axes of the RDA triplot described 28.4% and 14.6% of the variance, respectively, and denoted at least two clusters representing site groups of cocoa AFS S.L. and MF plots (black and white dots in Fig. 4.2). In general terms, soils with highest SOM content were associated with MF sites with diverse DC plant groups. Changes from multi-specific to mono-specific plant composition (mostly dominated by *C. alliodora* in all DC) were associated with high Ca^{++} content. These sites are predominantly located in cocoa AFSs with long and intermediate fallow lengths (Fig. 4.2). On the other hand, the reduction of resting period to less than one year was associated with less arboreal coverage and high soil P^{+} content (Fig. 4.2).

The marginal (simple) effect of the tree plant species dissimilarity matrices at each diameter class, i.e., <10 cm dbh, 10-20 cm dbh, >20 cm dbh, yielded significant association with shifts in soil properties (Table 4.3). Each matrix described different degrees of the constrained variance, i.e., 15.4%, 17.6%, and 19.2%, respectively (Fig. 4.1). The representative species associated with differences in soil composition within the understory plant community matrix were *Annona duckei*, *Chimarrhis glabriflora, Cordia alliodora*, *Guarea kunthiana*, *Ocotea floribunda*, and *Psudolmedia rigida*. The main tree species in the group between 10 to 20 cm in dbh were *Artocarpus altilis*, *C. alliodora*, *Grias neuberthii*, *Matisia bracteolosa*, and *Virola flexuosa*; and in the plant tree assembly over 20 cm in dbh *C. glabriflora*, *C. alliodora*, and *Iriartea deltoidea* (Fig. 4.2) were more predominant.

The outcome of the partial RDA also showed that all plant communities explain changes in soil parameters (F = 1.78, p-value = 0.002; RDA, Table 4.3). Based on the total explained variance of 31.70%, the fractions are represented in 20.1% from the tree assemblages' dissimilarity only, 2.8% from differences in the fallow length alone, and 8.8% of the interaction or dependence of both (Table 4.3, Fig. 4.1). The conditional effect of the resting time was also different in relation to the different tree canopy strata. For example, changes in understory species only (<10 cm dbh) supported 11.2% of the variance in soil components whereas the fallow length alone described 7.6%, and 4.1% supported by both (Table 4.3, Fig. 4.1). Similarly, the mid-story group ranges from 10 and 20 cm in dbh. Therefore, 11.2% is explained by changes in the plant mid-story cluster, 7.2% by the resting period, and 4.5% is shared by both components. However, the outcome from the tree species group over 20 cm in dbh showed slightly different values, i.e., the plant cluster alone described 12.3%, 4.8% by the fallow length only, and 6.9% of the variance is mutually explained (Table 4.3, Fig. 4.1). All these values are based on the adjusted R-square percentage and were statistically significant (F =1.90, p-values <0.01; RDA, Table 4.3).

Table 4.3: Constrained, unconstrained, and conditional variance obtained from the redundancy analysis (RDA) and partial RDA used to evaluate changes on soil variables in the Northern Ecuadorian Amazon. The table has two components: the upper panel corresponds to the RDA and the bottom panel to the partial RDA models. Rows in the RDA include all models tested (predictors or matrices) including each of the explanatory matrices and the proportion for the constrain and unconstrained variance; columns represent statistical values. The partial RDA values at the bottom show the variance partitioning and statistical outcomes F- and p-values for the constrained part of the model.

Redundancy Analysis

Predictors	Variance partitioning (Adj. R-square %)		F-value	Pr(>F)
	Constrained	Unconstrained		
All predictors	31.70	68.30	2.18	0.001
Understory (<10 cm dbh)	15.40	84.60	2.15	0.002
Mid-story (10-20 cm dbh)	17.60	82.40	2.62	0.002
Canopy (>20 cm dbh)	19.20	80.80	4.01	0.001
Fallow periods	11.70	88.30	6.02	0.002

Partial Redundancy Analysis

Predictors	Variance partitioning (Adj. R-square %)				F-value	Pr(>F)
	Shared[1]	Constrained[2]	Conditioned[3]	Unconstrained		
All plants	8.80	20.10	2.80	68.30	1.78	0.002
Understory (<10 cm dbh)	4.10	11.20	7.60	77.10	1.90	0.010
Mid-story (10-20 cm dbh)	4.50	13.20	7.20	75.20	2.29	0.002
Canopy (>20 cm dbh)	6.90	12.30	4.80	76.00	3.00	0.003

Interpretation of the significance: ‘***’ 0.001; ‘***’ 0.01; ‘**’; ‘*’ 0.05;

[1] % variance shared by the constrained (tree composition) and conditioned (fallow periods) predictors;

[2] % variance of each constrained matrix; and

[3] % variance of the conditioned variables.

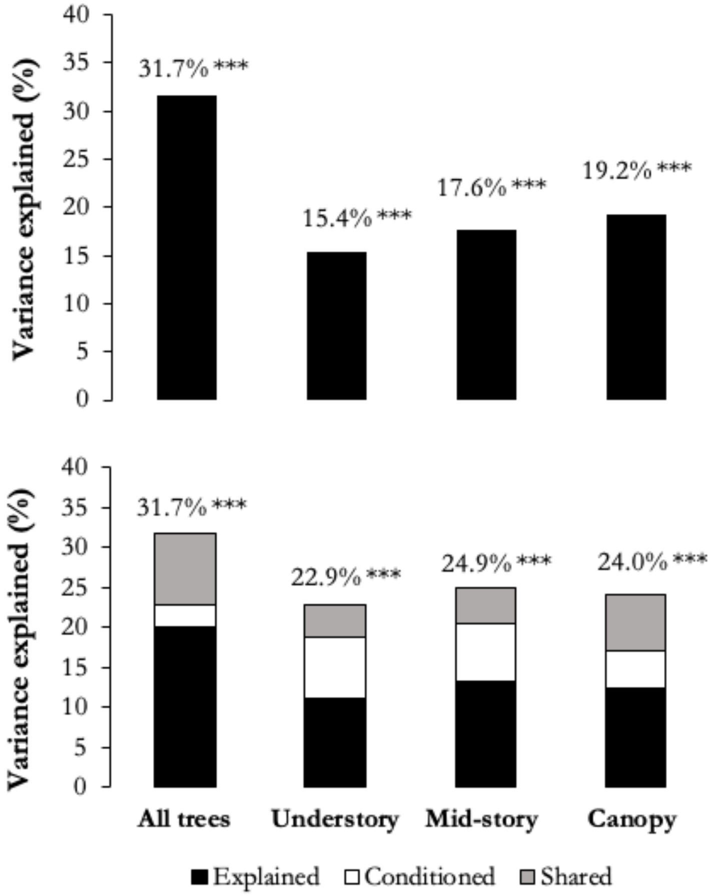

Figure 4.1: Bar plots displaying the explained variance (EV) of changes in species composition obtained from the marginal and partial redundancy analysis (RDA) used to evaluate changes on soil variables in the Northern Ecuadorian Amazon. Top panel, simple RDA showing individual EV from all tree communities, understory (DC <10 cm in dbh - diameter at the breast height), mid-story (DC 10-20 cm in dbh), and upper canopy (DC >20 cm in dbh). Bottom panel, partial RDA showing the increase in EV by adding the fallow length as conditional factor (white area) in all tree communities and for each forest layer. Grey shade represents the shared EV between plants and fallow length.

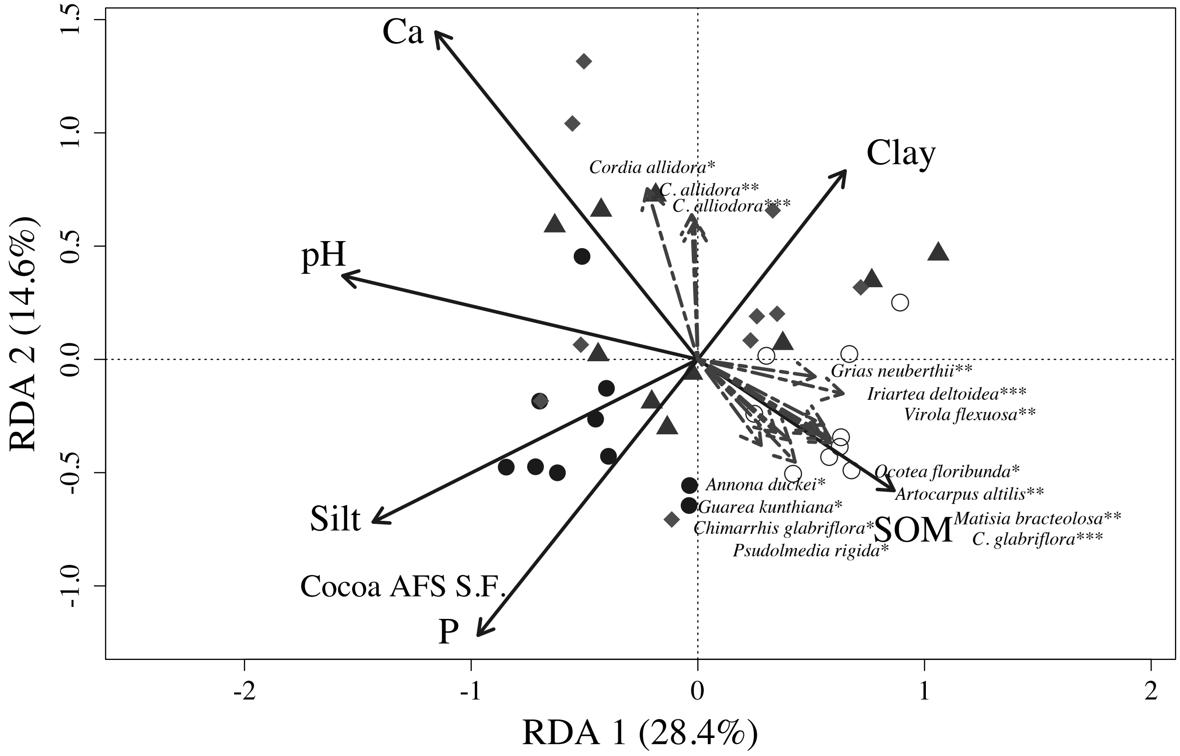

Figure 4.2: Redundancy analysis (RDA) triplot showing four components (understory <10 cm dbh (diameter at the breast height), mid-story 10-20 cm dbh, canopy >20 cm dbh, and fallow length). The response data include selected soil variables from the factor analysis. Explanatory variables are shown as dash vectors, sites as symbols, and response variables as continuous line vectors. Most abundant tree species are shown with names in italics and the symbol (*) indicates the diameter class (DC), as follows: (*) DC <10 cm in dbh, (**) DC 10-20 cm in dbh, and (***) DC >20 cm in dbh.

4.4 Discussion

The loss of soil fertility and production capacity resulting from reduced fallow lengths in shifting agriculture (SA) is among the most complex agricultural issues in the world. The simple reason behind this situation is because vegetation buffers impact from ecological landscape changes and because organic matter improves soil fecundity, which is crucial to attain high crop yields to cope with the increasing food demand (Jakovac et al 2016). Farmers all over the tropics take advantage of SA, which intersects with resilient features of soil enrichment and plant recovery to maintain an affordable system for basic food provision (Porro et al. 2012, Cairns 2015). Although β-diversity is typically driven by environmental gradients displaying high variability in ecological habitats (Legendre et al. 2005), species turnover in the Ecuadorian Amazon hardly change within an area of 100 km (Condit et al. 2002). Therefore, differences in tree composition in this region is predominantly generated by human actions, which ultimately propel shifts, sometimes irreversible, in the soil's environment and its micro- and macro-organic nutrients and inorganic components. In fact, our work revealed that the alternation of tree species (β-diversity) is interconnected with fallow length and shifts in the soil's chemical properties, particularly in the absence of resting phases. Our variance partitioning data indicate that changes in soil attributes are predominantly correlated with modifications in species composition (20.1%) and to a lesser extent to the reduction of fallow periods (2.8%) of SA in cocoa AFSs (Table 4.3). This outcome is opposed to that of Russell et al. (2004), indicating that rotation frequency in mono- and polyculture plantations of tropical trees is more influential than β-diversity. Thus, we argue that the overall role of the plant community has a holistic effect on ecological functions, but this aftermath remains hidden when soil assessments are made only in monocultures. For instance, the carbon absorption rate in forests at a global scale is highly correlated with levels of biodiversity (Liang et al. 2016) possibly due to the dynamic activities of the diverse soil microorganismal communities (Russell et al. 2018). Therefore, intra- and interspecies assembly and interactions are important foundations maintaining functional biological, e.g., edaphic, processes in tropical ecosystems.

Results from this study also partially challenge those of Powers et al. (2004), who indicated that individual plant effects on soil attributes are diluted under diverse, closed and obstructed canopies. However, it should be noted that the specific environment influencing each tree species can be based on abundance or dominance, which is a common scenario in tropical forests and several AFSs. Accordingly, changes in frequency of plant families and/or species can be the main reason behind the fluctuating effects on soil chemical and physical profiles. According to Vera-Vélez et al. (2019), 70% of MFC is dominated by nearly a dozen of plant families. For example, the Myristicaceae, Sapotaceae, and Lauraceae are among the top ten most abundant plant families in the NEA with statistical importance value (IV) of 11.69%, 10.80 %, and 9.17%, respectively. However, when these forests undergo anthropogenic transformation to AFSs, the dominance of plant cover favors the Boraginaceae with an IV higher than 24%. Thus, because different tree species have diverse effects and heterogeneity at different spatial scales, this disparity leads to diverse biochemical patterns in the landscape (Hobbie et al. 2007, Waring et al. 2015). We posit that dominant plant families are likely the main drivers shaping the chemical and physical fluctuations of soil attributes.

It is worth noting that agroforestry practices may also have a buffer effect on the soil's fertility in areas in which crop rotation or SA is practiced; however, this potential shielding impact can be lessened with increasing husbandry cycles. Typical fallow cycles of SA in the NEA can be prolonged up to or over 30 years (Arevalo 2009, Grijalva et al. 2011, Arevalo-Vizcaino et al. 2013). This lengthy resting period is favourable and allows the resurgence of several ecosystem services and processes, such as organic carbon, microorganismal communities, and macro- and micronutrient cycling in the soil (Gogoi et al. 2020), all of which benefits the recovery of the forest's successional phases to a nearly primary structural floristic composition (Vera et al. 2019). The effect of SA with fallow phases of 8-10 years is similar to more extended periods of recovery (> 30 yr.) (Fig. 4.2). However, the organization of clusters in the ordination plot (Fig. 4.2) of cocoa AFSs exposed to intense SA, i.e., absence or less than one-year fallow, suggests the existence of agricultural parcels with similar chemical and physical soil properties and low levels of tree diversity. The gradual elimination of arboreal canopy in cocoa AFSs under short fallow cycles homogenizes β-diversity to less than five effective species ha^{-1} (Vera-Vélez et al. 2019). Indeed, only three arboreal taxa (*Cordia*, *Terminalia*, and *Cedrela*) occupy 70% of the total tree community in plots under this agricultural regime. Consistent with other farming approaches, such as silvopasture (Fraterrigo et al. 2005), the parity in species composition among plots under intense SA results in homogeneous soil components. This produces vulnerable conditions that are detrimental to the soil ecosystem and limit chemical and physical interactions among nutrients, water, carbon, and nitrogen cycles, resulting in imminent infertile farming land unable to supply the much-needed crop yield and income support for locals.

The association between changes in soil variables and the species composition varies according to the arboreal strata in cocoa AFS under SA. This investigation showed that upper canopy story species, i.e., canopy >20 cm dbh, has slightly higher effects on soil properties than mid-story and understory plant species and indicated by 19.2%, 17.6%, and 15.4% of explained variance, respectively (Table 4.3). These data are restricted to fallow intervals because a significant amount of variation in each forest layer, especially in the canopy, is supported based on the reduction of fallow periods (Table 4.3, Fig 4.1). Thus, the findings imply that plant species located in the middle and understory strata influence soil development and fertility independently of the length of the fallow interval. Consistent with Perreault (2005), Arevalo (2009), and Porro et al. (2012), who noted that the removal of these plants is due to direct farming activities, but regardless of the crop type and previous land-use our data indicates that the degree of dependence from fallow intervals is relatively lower. Conversely, the effect of the upper tree layer is more dependent on intact conditions and undisturbed period (Fig. 4.1). Explicitly, farmers preserve trees over 20 cm in dbh in rotation systems of SA with up to 8 years of fallow, but with more frequent seeding cycles trees are purposely removed for farming land. Overall, the effects of the arboreal canopy on the soil productivity and fertility is particularly important because of the contribution to litterfall, root growth, erosion prevention, i.e., retention and water uptake from deep sources as well as differential shade effect (Kamei et al. 2009, Watenberg et al. 2019). Consequently, removal of arboreal species from the upper canopy of AFSs results in limited cyclic contribution to soil nutrient dynamics and other essential elements needed for restitution of ecosystem health, including soil hydrology, and chemical and physical properties (Zwartendijk et al. 2017).

In the NEA, the transformations of mature forests and changes in β-diversity for agricultural purposes impact soil nutrients and soil acidity according to the intensity of the logging. Our study shows that intentional reductions of tree cover in multitaxic forest communities, i.e., converting forests into AFSs, are correlated with the increase of Ca^{++} in the soil (Fig. 4.2), and consequently, acidity levels decrease. This suggests that high species diversity has an acidification effect of soils and is probably caused by the presence of certain tree species, e.g., *Vochysia* and *Virola* (Table 3.2). According to Russel et al. (2007), *Vochysia* is an Al^{+++}

accumulating species. In a monoculture tree plantation, this species uptake Al^{+++} from the soil and stores ca. 180 kg ha^{-1} yr^{-1} in the leaves (Russel et al. 2018). In the NEA, this species, and specifically the Vochisyaceae, is among the dominant plant families in AFSs with ~ 9% of IV% (Vera-Vélez et al. 2019). The presence of this species might induce higher levels of calcium in soils with cocoa AFSs. In turn, the genus *Virola,* which is among the top ten most common trees in MF of the NEA, is highly correlated with acid soils (Russel et al. 2018) most likely contributing to acidification. Thus, it is feasible that the change in dominance between *Virola* and *Vochysia* is one of the main factors in the modification of soil acidity in plant communities in which these two taxa are common. It should be noted that some cocoa plots showed high levels of Ca^{++} and P^{+} (Fig. 4.2), suggesting an increase of these soil chemical elements due to human intervention. However, given that Indigenous farms containing the cocoa AFS investigated here have several international organic certifications, including the United States Department of Agriculture (USDA) organic certificate (see www.kallari.com.ec), it is unlikely that people in these areas have applied man-made synthetic fertilizers or other chemical promoting plant growth or preventing weeds. On the other hand, the highly propensity to flooding of these areas and the contribution of vertebrate animals to nutrient cycling may have promoted the increase in Ca^{++}, P^{+}, and other chemical elements in the cocoa chakras (Stevenson and Guzmán-Caro 2010, Jaramillo 2019). Nevertheless, further studies are still needed.

The analysis of the relationship between soil variables and β-diversity revealed differences in the soil physical structure of cocoa agroecosystems subjected to different cycles of SA. Cocoa farming systems with long and intermediate fallow cycles show higher clay content and lower proportion of silt particles than cocoa agrosystems with short resting periods (Fig. 4.2). It is uncertain whether differences in clay and silt among cocoa plots are the result of changes in tree species composition because these features represent the soil's parental material, which is unlikely to change in a few decades. However, we believe that such gradient in clay and silt indicate the variability in soil particle sizes on land under SA (Fig. 4.2). However, the effect of reduction of tree density, changes in taxa, and natural chemical reactions in soil might induce fluctuations in the dispersion and binding of aggregates, a condition that strongly depends on soil texture (Bronick and Lal 2005). The variability in particle aggregation are likely related to modifications in the soil's abiotic factors, e.g., pH. According to Igwe et al. (2010) and Russell et al. (2018), the presence of chemical compounds, i.e., Fe^{++} and Al^{+++} , which produce and stabilize SOC (Jastrow et al. 2007), are highly correlated to low values of pH and are the main cementing agents of tropical soils. We found that the floristic composition of MFC is correlated with higher content of Fe^{++} (Table 4.3, Fig. 4.2). Therefore, breaking Fe^{++} chemical compounds possibly triggers dispersion of soil aggregates, especially the smallest and intermediate particles, such as clay and silt, respectively (Fig. 4.2). It should be noted that studies dealing with plant species influencing soil characteristics, in particular changes in structure, require long timescales (Hobbie et al. 2007, Trumbore 2000). Nonetheless, given that decomposition of the organic matter is largely regulated by temperature, i.e., warmer soils in tropical areas experience faster cycles than temperate and boreal soils (Bellamy et al. 2005, Handa et al. 2014), differences in particle accretion in the tropics can be expected in relatively short to intermediate time periods as a consequence of changes in plant composition.

In conclusion, the multitaxic attributes of AFSs in combination with SA can be deemed as a method to buffer negative, possibly irreversible effects on soil productivity and health resulting from frequent and intensive land-use. Arboreal cover facilitates the maintenance of fertility of agricultural land, which benefits crop performance and sustainability while enhancing the resilience capacity of the ecosystem to surmount changes due to natural and anthropogenic activities. Nonetheless, it is vital to highlight that the role of β-diversity is fundamental to preserve certain equilibrium of ecosystem function and services amidst the ongoing carbon emission driving higher temperatures globally. In addition, the dominance of certain tree species appears essential to maintain suitable levels of nutrients and soil particles when more intensified fallow cycles are practiced. Succinctly, the combination AFSs-SA embodies a harmonious farming system supporting food security and the safeguarding of forest communities, habitat and plant diversity enabling trophic dynamics and biological corridors for native flora and fauna. The adoption of this farming strategy in other tropical and subtropical areas of the world can, in principle, be used as an inspiring model to reduce forest degradation and increase its capacity as a sink for CO_2 to mitigate climate change, preserve ecosystem health, and ultimately, the functional dynamics of natural landscapes and people’s life.

4.5 References

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CHAPTER 5: CONCLUSIONS

5.1 Summary of rationale and main questions addressed and findings in this thesis

Plant species diversity has declined worldwide in response to deforestation and over collection (Isbell et al. 2011, Strassburg et al. 2012). Hotspot areas in the Amazon, specifically in the northern Ecuadorian Amazon (NEA), are important remnants of biodiversity at risk of disappearing due to unsustainable logging (Valencia et al. 2004, Bass et al. 2010). The diverse flora with complex structural layers plays a key role in regulating environmental functions through the inter- and intra-specific interaction of plants (Nadrowski et al. 2010, Moore et al. 2014). The dynamics of exchange of matter and energy between organisms maintain healthy forest functions, such as resiliency and nutrient cycling. Considering the complex synergistic network among all species, it is essential to bear in mind that degradation of mega diverse habitats affects the recovering capability of ecosystems from disturbances (Loreau 2000, Hugues et al. 2002, Thompson et al. 2009, Yan et al. 2011). Similarly, biological diversity regulates mechanisms and the relationships of important mutual symbiotic associations between biotic and abiotic factors. For example, soil properties, plant-animal interactions, with nitrogen fixation via rhizobia being crucial in cultivated fields (Ehrenfeld et al. 2005, Kulmatiski et al. 2008, Mangan et al. 2010). These often mutualistic relationships and the properties they confer contribute to consistent dynamic patterns essential for ecological processes and sustenance of the Earth's carrying capacity. For instance, insufficient fallow time to restore soil quality and nutrient cycling, such as those used in in traditional systems of shifting cultivation discussed in this thesis, can lead to degradation and reduction of the land carrying capacity, and upon exhaustion, it can lead the food supply scarcity and even hunger situations (Fearnside 1984).

Shifting agriculture is one of the leading farming practices in rural tropical areas because people depend on forest resources for foodstuff, income, and energy requirements (World Bank 2019). Farmers use approximately 2.4 billion hectares of the world's tropical forests for swiddening (Silva et al. 2011, Delang and Li 2013, Heinimann et al. 2017) and because of the large scale use, this agricultural practice is considered the main cause of land desertification. In Ecuador, the area of swidden cultivation is estimated at 849,355 ha (INEC 2019). Given that SA is regarded as one of the most inefficient agriculture methods promoting deterioration of ecosystems (Ayanu et al. 2011, Henley 2011, Ellen 2012), the dichotomy between preserving forest areas and biodiversity or maintaining SA and other farming systems for food security arises. Hence, the investigation of the relationship between this farming practice and implications for biodiversity conservation should be addressed soon altogether with proactive solutions to mitigate the ongoing explosive and negative anthropogenic environmental impact and overuse of natural resources.

5.2 Main findings

The outcomes of the first part of this study investigating the floristic composition in three agroforestry systems (AFSs) (cassava, corn, and cocoa), secondary forest (SF), and forest remnants in the buffer zone of the Northern Ecuadorian Amazon (NEA) indicated that:

1) Gamma diversity in NEA included 4,060 trees (dbh ≥ 10 cm) representing 109 species, 96 genera, and 43 plant families. The most dominant plant families were Arecaceae, Myristicaceae, Fabaceae, Meliaceae, and Malvaceae, and the most representative genera included *Iriartea*, *Virola*, *Guarea*, *Ocotea*, *Cordia*, *Chrysophyllum*, and *Inga*.

2) Mature forests in this zone are composed of 81 tree species circumscribed in 74 genera and 30 plant families, Furthermore, transforming MFC to different chakras leads to a decrease in alpha diversity between 52% and 75%, particularly in AFS allocated to local food security (corn and cassava).

3) AFSs preserve an estimated 56% of beta diversity of the extant native flora in MFs, in which at least 8% of the species are threatened. However, it is remarkable that the demographic status of the remaining 92% of species is still unknown, indicating that the rarity assessment of native trees is virtually unexplored and more endemic, threatened, and even undescribed species may be discovered. Additionally, all sites investigated consistently formed three groups that corresponded to AFS, MFC, and SF. These three groups indicate that the overall trend of forest regaining the original structure is facilitated by undisturbed mature native trees kept in the chakras. The results strongly support the AFSs' potential environmental success with sustainable forest management and preservation of endangered tree species.

In the second part, I investigated whether AFS reverse the effect of intensified SA in cocoa (*Theobroma cacao*) agrosystems. In general, my research revealed that short SA fallow periods in cocoa AFS have drastic and adverse effects on levels of diversity. The variety of trees showed a gradual decrease from low, to intermediate, to high intensification SA in cocoa AFS, with corresponding *S* (richness) and *N* (effective number of species) values of 46 and 17, to 29 and 9, to 12 and 4. These findings indicate that the disparity in species diversity is perceptible across the different categories of increasing SA. In turn, cocoa AFSs with low and intermediate levels of use have more than twice the species diversity than highly used cocoa agrosystems. Similarly, tree species assembly decreases across cocoa agroforestry plots with reduced fallow periods. Remarkably, the absence of fallows in SA affects tree presence/absence leading to significant changes in floristic composition in around 30% less species compared to the beta diversity in cocoa AFSs experiencing long resting phases. Nonetheless, the lack of statistical significance in beta diversity between low and intermediate intensification levels of SA suggests a buffer effect favoring the conservation of the arboreal structure (provided by native and endangered endemic species), with concomitant delay in forest degradation rates. Consequently, the conservation of native species in this agricultural model seems to meet the requirements to reverse the cycle of land degradation and social deprivation for goods. In short, shifting agriculture combined with AFS influences positively forest plant diversity, soil dynamic structure and carbon stocks as evidenced by the restoring of nutrients and rapid recovery of forest carbon stocks resulting in higher crop yields and species diversity as well as limited net carbon emissions.

The final component of this research examined to what extent beta diversity in AFS reverses the effect of shorter SA fallow periods in soil properties of cocoa (*T. cacao*) agrosystems. Quantitative analyses revealed that AFS in combination with SA shield the negative outcome of intense land-use on the soil's nutrients and productivity. Furthermore, in addition to enhancing the resilience capacity of the ecosystem, the arboreal cover maintains the soil fertility needed for crop performance and food sustainability. It is vital to highlight that the role of beta diversity is fundamental in maintaining soil nutrients. Possibly, the dominance of certain tree species (*Vochysia leguiana*, *Inga edulis, Cordia alliodora*) is essential to support adequate dynamic levels of nutrient cycling with more intense fallow periods, whereas some other species (*Virola flexuosa*, *Chrysophyllum amazonicum, Ocotea bofo*) have an apparent effect on increasing soil acidity. This outcome implies that the combination AFS-SA embodies a harmonious and environmentally beneficial farming system designed to produce essential food supplies for human well-being while preserving the plant diversity desirable to sustain natural ecological cycles and corridors nurturing the dispersal of native flora and fauna. In all, this anthropological and biological amalgamation preserves ecosystem structure, integrity, and ultimately the functional dynamics of natural landscapes with increased forest's capacity as a sink for CO_2.

5.3 Implications of agroforestry under shifting agriculture

Public concerns about deforestation in tropical regions, largely related to biodiversity loss and global climate change, have gained importance at different political and societal levels. The problems are mainly associated with forests desertification and their transformation to ecosystems with less biomass, e.g., pastures and monocultures (Porro et al. 2012). The environmental effects of these changes on natural habitats are known to cause severe heating and drying cycles impacting human livelihood (Nepstad et al. 2004, Cochrane and Barber 2009, Malhi et al. 2009, Nobre and Borna 2009), especially when farming practices involve large-scale areas with unsustainable methods, such as shifting agriculture (Silva et al. 2011, Ayanu et al. 2011, Henley 2011, Ellen 2012, Heinimann et al. 2017). The attributes of AFSs interconnect the production of local foodstuffs, conservation of adequate levels of alpha and beta biodiversity, and culturally representative native species associated with ethnic traditions. Thus, AFS ameliorate some of the negative effects in the environment and restore the degree of desertification in tropical areas of the Ecuadorian Amazon.

The model of agroecosystem in the NEA was developed by the Indigenous population. These farming traditions are productive, adaptive and ecologically based and more harmonious methods to obtain the requirements for human well-being and at the same time, preserve forests, natural habitats, and plant diversity. Concisely, the use of chakras, i.e. AFS in the Amazon Region and other tropical countries, has a strong potential to improve food security and climate change at the local and regional levels by conserving forest ecosystem structure, integrity, and functional dynamics of natural landscapes. Similar positive effects of this agrosystem in conjunction with fundamentals of forest resilience, such as soil health recovery, can benefit other tropical regions of the world depending on ecological mechanisms for crop development. The AFS-SA synergy can be considered as a resilient biodiversity tool that could be extrapolated to other farming patterns of crops and trees in the world. While this study is focused only on cocoa AFS, it can be compared to other farming schemes, such as agrosystems based on corn and plantain practiced by the Waorani society in the Ecuadorian Amazon, aimed at food security and upholding cultural traditions (Zurita-Benavides 2018). Likewise, AFS can also be adapted to cattle and pasture systems to develop more sustainable farming practices (Gaglio et al. 2017) that buffer land-use pressure and contribute to decrease habitat fragmentation in the Amazon and other tropical areas or the world (Haddad et al. 2015).

In the context of shifting agriculture, the characteristics of the AFS enable the perpetuation of beneficial levels of plant diversity and surrounding vegetation in more intensified agricultural schemes. Specifically, complex arboreal structures enhance the preservation of native and endangered species and slows down forest and land degradation. From this perspective, the multi-layered shaded cocoa crop plays an essential role because of the balanced combination of different trees essential for Indigenous life, culture and traditions in addition to the preservation of forests, natural habitats, plant diversity, and ecosystem functions. Also, the attributes of species diversity of AFS in combination with SA represent a buffering method to prevent negative effects resulting from intensive land-use.

In terms of tree species diversity, the arboreal cover is equally important as it facilitates the maintenance of soil fertility, which benefits crop performance and sustainability while enhancing the resistance capacity of the ecosystem to surmount changes resulting from natural and anthropogenic events. Clearly, the role of beta diversity is fundamental for ecosystem functions and services given that the dominance of certain tree species may be essential to maintain suitable levels of soil nutrients, chemicals and particles under more intensified fallow cycles. Overall, the combination of AFS-SA embodies a balanced farming system designed to promote food security and the safeguarding of local cultural practices, forest communities, and habitat and plant diversity, all of which enables trophic dynamics and biological corridors for flora and fauna.

Other drivers leading to the loss of biological diversity in the Ecuadorian Amazon include large-scale markets, agricultural industrialization, migration and population growth, public policy, and cultural erosion. These factors, either individually or in combination, have transformed small, traditional agroecosystems. The adoption of AFS-SA as a farming strategy in other tropical and subtropical areas of the world can, in principle, be used as a model to reduce forest degradation and enhance the forests' capacity as a sink for CO_2 to mitigate climate change, preserve ecosystem health, and ultimately, the functional dynamics of natural landscapes and people's lives. Thus, agroforestry practices are essential to meet the short- and long-term needs of environmental conservation, avoid further deforestation, and preserve environmental services. In addition, this technique can provide the economic well-being of the tropics, as components of sustainable land use systems to support local livelihoods. In a broader dynamic and sustainable natural resource management perspective, agroforestry has the potential to bridge gaps between land use policies, particularly linking environmental opportunities with current socioeconomic. These guidelines have priority as critical environmental limits are reached from drastic changes in the landscape, particularly for vulnerable social groups whose livelihood is challenged because of their sole dependence on agriculture and forestry (Swamy et al. 2018). The unambiguous implementation of environmentally friendly farming policies is needed to slow down the loss of tropical biological diversity. Positive outcomes will only be possible with the collaboration of multidisciplinary research teams, including indigenous and non-indigenous farmers, community leaders, and governments.

5.4 Future work

This thesis examined how agroforestry systems buffer the antagonistic effects of shifting agriculture in the northern Ecuadorian Amazon (NEA) in the conservation of biodiversity and ecosystem services. Despite the new findings reported in this work, several knowledge gaps in the field of agroforestry systems are open for investigation. Following, I highlight current issues for future investigation that need prompt attention.

First, changes in the net pool and flux of carbon over time. It is known that the carbon balance in agroforestry systems and undisturbed forests can remain stable in time (Van Der Sleen et al. 2015, Baccini et al. 2017). However, it is uncertain whether the carbon stock and fluctuation could change under more dynamic scenarios, as described by the amalgamation AFS-SA. Similarly, the behaviour of carbon cycles under more frequent sequences of shifting cultivation is an aspect that needs investigation as it will yield data for a more effective AFS-SA combination to maintain or improve ecosystem services.

Second, the assessment of changes in diversity in the micro- and macro-biota is also an exciting, yet challenging topic that should be priority for policymakers seeking environmental relief from disturbances in tropical areas. The diversity of soil organisms, such as fungi, nematodes, and arthropods, are often good representatives of healthy, productive environments (Aguilar-Amuchastegui and Henebry 2007, Akutsu et al. 2007, Edwards et al. 2012, Bicknell et al. 2014). The identification of changes in the diversity of such populations under more intense agriculture could lead to the implementation of biological indices useful to monitor sustainable forest management.

Third, crop performance under the combination AFS-SA in the NEA is another research aspect that requires further studies. Although my investigation involved the evaluation of the arboreal strata in cocoa agroforestry, the productivity of the cocoa plants is yet to be assessed under the AFS-SA amalgamation. It is known that the association between trees and crops is essential for crop development in tropical rural areas. For example, the increase of plant species increases fauna diversity and reduces pest insects of cocoa in Indonesia (Maas et al. 2013, Grass et al. 2016). However, the study of the pollination biology and reproductive cycle of cocoa flowers and fruits has barely been investigated. Flowers of cocoa plants require cross-pollination for fertilization and fruit production (Groeneveld et al. 2010). Typically, insects from the genus *Forcipomyia* are essential visitors involved in cocoa cross-pollination (Bridgemohan and Mohammed 2019). Nevertheless, the relation of the dynamics of the local flora under SA cycles with abundance and diversity of *Forcipomyia* species in cocoa agroforestry in the NEA is still unclear. This idea, in my opinion, represents a future pathway for investigation of cocoa pollination in relation to increasing food production in the tropics. Within the same scope, the study of local flora diversity in chakras, e.g., corn, cassava, etc., in relation to pollinators is also a relevant topic that has been poorly studied. It is known that the increase of monocultures in the NEA and other tropical areas have affected the abundance and diversity of numerous pollinator species. However, the current dynamics of these agroforestry elements under SA are unclear, which raises crucial questions such as: can the combination agroforestry-swiddening represent a system to safeguard or increase pollinator diversity? Or, can these agricultural systems represent sources of pollinators for other surrounding crop systems, e.g., monocultures? Undoubtedly, this thesis has opened the door for relevant topics for future research in plant reproductive and pollination biology.

The consequences of using natural resources from Indigenous agroecosystems and forests as part of the market economy is also a relevant study area in socio-economic botanical context. My thesis provides some insights into the importance of the chakra system as a production alternative used by Kichwa communities in the NEA. The availability of natural resources allows the preservation of people's cultural richness and the diversification of economy and subsistence-based activities on shifting cultivation. For example, hunting, fishing, and gathering forest products for food, as well as the local trade of cocoa beans, wood, and handicrafts for income (Porro et al. 2012). However, these ancestral schemes in the utilization of environmental supplies in Latin America's rural areas represent community-based approaches for conservation (Langholz 1996). Therefore, establishing a new economic model from the typical communitarian type could lead to improvements of socio-economic, environmental, and cultural problems. In addition, in response to the rise of environmental issues, a new form of tourism implemented in the late 80s, 'ecotourism,' has gained more popularity in recent years (McCormick 1989). This activity offers great potential for the economic development and conservation of fragile ecological zones (Kerr 2003). In fact, in the year 2000 it generated USD$ 154 billion in revenues (Gouvea 2004) and has become one of the main financial sources for rural Indigenous communities in Latin America (Wezel and Jauneau 2011). Nevertheless, cultural and other social related trade-offs associated to the increase of ecofarming and ecotourism have barely been investigated (Higham 2007). Recently, Santafe-Troncoso and Loring (2020) stated that the main concerns about the use of ecotourism as income tool is that commercial names understate the holistic concept of certain local traditions. For example, the "Cacao Route" is offered in the NEA to the chakras as a visitor attraction. Nevertheless, these initiatives are misinterpreted given that the whole chakra system not only involves cocoa but also other important cultural aspects, such as food harvesting and preparation of medicinal potions (Arévalo 2009). Thus, outside visitors threaten the preservation of traditional knowledge and cultural significance of these practices. Given that the agroecosystems investigated in this thesis include plants culturally representative for Indigenous communities, the massive development of ecotourism activities could affect this farming activity. The study of the bidirectional relationship and influence of ecotourism and intensification of agricultural systems on ancestral practices is a topic that must be investigated in the near future.

Finally, the forest and people long-standing relationship represent a complex sociocultural and environmental fact that deserves to be investigated. Over the past few decades, understanding indigenous people's interactions with the forest to adapt changes in the land use patterns in tropical areas has been crucial (Byron and Arnold 1999). However, as the global population grows exponentially, the trade-offs between conservation of tropical forests and the extraction of natural resources becomes more complicated (Noble and Dirzo 1997, Seymour and Busch 2016). If the unsustainable trend of clear-cutting logging and land degradation persists in the NEA and other tropical regions, the buffer capacity of AFS to maintain ecosystem services and biodiversity will be unpredictable. We know that Indigenous communities in the Amazon and other human settlements around the world tropical areas are strongly dependent on forest products but limiting access to these resources will jeopardize their welfare and survival. This leads to a fundamental social dilemma, explicitly finding ways in which Indigenous societies will adapt the management of remaining arable land and forest vestiges to local and regional demands. Similarly, scientific inquiries will eventually find ways to reconcile with the continuous deforestation necessary to maintain the lifestyle and cultural identity of Indigenous people. Addressing these complex questions requires the intervention from a multidisciplinary perspective where science, policies and politics, and local communities can come out with sustainable solutions for both parties.

In summary, I believe that the results presented in this thesis are highly relevant in at least two ways. Firstly, this research puts on the table the socioeconomic issue of agrosystems in the tropics, which is not often on the agenda of environmental studies despite the fact the possibilities that climate change, deforestation, and other ecological problems cannot be solved without the involvement of Indigenous communities. Secondly, this thesis not only quantifies ecological aspects of species conservation and ecosystem services in the northern Ecuadorian Amazon but also provides a viable alternative for land use. The use of agroforestry systems is a promising practice to assist in both biodiversity conservation and food security problems, and indirectly global warming mitigation.

The historical and cultural significance of the chakra system in the lives of indigenous communities in the NEA has been highlighted throughout this thesis. Agroforestry systems and shifting cultivation have been important elements in communal activities of these farmers for hundreds of years and the agronomic actions are strongly linked to cultural aspects. Several plant species (including trees) are maintained in chakras and forests due to the cultural, social, and religious connection with people for handicrafts, medicine, and other local traditional uses. This relationship between pants and humans inhabiting remote forests may explain in part why the Amazon region is one of the most diverse and well-preserved areas in the world. Because of their personal and cultural believes are reserved for people within their own communities, the cultural aspects represented a challenge in the field work component, particularly data collection and uses associated to each plant. Chakras are culturally representative in the cosmovision of indigenous communities. Thus, getting access to their parcels required long-term convincing work to gain permission and the trust from Indigenous leaders and individual and communitarian owners of farming plots in the forest areas. Once permission was granted, both community leaders and chakra's owners offered valuable help in identifying plant species and their uses and collecting soil samples. Their engagement in field demonstrates interest in sharing their cultural roots and relationships with forest plants. The natural resources in the NEA are important for indigenous people's livelihood and its preservation is highly correlated to the conservation of their own cultural identity.

From my own point of view, the development and completion of this study in the last 4.5 years involved a great amount of personal, professional and intellectual growth. My work includes enormous scientific and cultural enrichment that would have not been possible without the assistance of diverse personnel throughout my fieldwork years. My work experiences with local people have given me more understanding and vision of the farming systems used in rural communities. An added value of my field research is the instructive traditional knowledge existing among the Kichwa and other Indigenous societies, which was necessary to complete the floristic inventories. Similarly, local ethnobotanists and landowners were crucial to unveil the life history of the chakras, shifting cultivation, the remnants of the northern Ecuadorian Amazon forests, and the links between agricultural diversity and food security in this important geographic, biological, and cultural region of Latin America. I am for all that, very grateful and hope my work brings some benefits to their communities.

5.4 References

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APPENDIX 1: SUPPORTING INFORMATION FOR CHAPTER 2

Table A2.1: Total number of plots (n), mean value, minimum, maximum, and total sampled area (ha), tree density ha^{-1}, and sampling coverage in % in five different systems in the northern Ecuadorian Amazon. Also, below it is shown the detail of the plots established by system including size, location, and altitude.

System	**n**	**Mean**	**Min**	**Max**	**Total**	**N ha^{-1}**	**SC%**
Manihot esculenta (cassava)	5	0.12	0.05	0.22	0.59	104±30	81.3 ±9.5
Zea mays (corn)	6	1.03	0.50	2.64	6.19	24±7	83.9 ±6.7
Theobroma cacao (cocoa)	23	0.20	0.04	1.07	4.67	200±36	97.3 ±1
Secondary forest	12	0.15	0.10	0.20	1.75	469±44	98.7 ±0.7
Mature forest	15	0.28	0.20	0.35	4.24	741±68	99.8 ±0.1
Total	**61**	**0.28**	**0.05**	**2.64**	**17.44**	**361**±40	**----**

Cassava

Plot #	**Size (m^2)**	**UTM N**	**UTM E**	**Elevation (masl)**
1	656	9883484	211422	369
2	534	9883631	212987	373
3	1526	9883438	213426	366
4	2217	9883384	213919	374
5	1000	9883184	213986	367

Corn

Plot #	**Size (m^2)**	**UTM N**	**UTM E**	**Elevation (masl)**
1	5000	9881338	211700	371
2	5000	9880812	211763	398
3	8890	9875368	206403	428
4	5000	9875515	206388	419
5	26430	9876448	206342	387
6	11560	9876032	205394	403

Cocoa

Plot #	Size (m^2)	UTM N	UTM E	Elevation (masl)
1	409	9876391	205498	431
2	10000	9876420	205591	436
3	2000	9888884	214644	404
4	500	9876000	204756	489
5	2500	9881668	212342	380
6	10688	9888224	213575	413
7	3000	9888532	213567	419
8	571	9882411	212348	375
9	1000	9882156	211791	385
10	1000	9883056	213401	398
11	3000	9888127	214049	526
12	1000	9878667	214730	365
13	1000	9879941	214626	364
14	1000	9879823	214752	369
15	1000	9878063	217470	400
16	1000	9888626	214718	412
17	1000	9888489	213457	412
18	1000	9878606	215114	378
19	1000	9879590	214971	357
20	1000	9879798	215047	368
21	1000	9887965	214253	458
22	1000	9887790	218827	492
23	1000	9878771	214940	370

Secondary Forest

Plot #	Size (m^2)	UTM N	UTM E	Elevation (masl)
1	1500	9889444	213018	414
2	1500	9878075	206305	384
3	1000	9878254	206379	401
4	1500	9878309	206484	433
5	1500	9874184	208380	447
6	1500	9874081	208582	459
7	1500	9873944	208622	452
8	2000	9879388	214871	529
9	1500	9879368	214688	421
10	1500	9874090	208164	476
11	1000	9873926	208294	446
12	1500	9873867	208331	427

Mature Forest

Plot #	Size (m^2)	UTM N	UTM E	Elevation (masl)
1	3000	9875820	216468	466
2	2000	9888086	213321	423
3	2500	9878225	217344	441
4	2500	9877984	217900	430
5	2500	9877357	218007	425
6	2500	9889444	213018	472
7	2500	9888401	214907	430
8	2500	9888365	214263	468
9	2400	9888430	214507	447
10	3500	9877827	217229	512
11	3500	9877931	217224	450
12	3000	9877828	216736	478
13	3500	9876777	205255	556
14	3500	9876784	205742	441
15	3000	9876861	205927	458

Table A2.2: Absolute and relative values and percentage of dominance for the ten most dominant plant species in each agroforestry system (AFS), secondary forest, and mature forest. Plant families are arranged by order of dominance. The values were calculated according to the sampled area by each system.

Cassava AFS (0.59 ha)

Family	Species	Abs. abund.	Rel. abund.	Domin. %
Malvaceae	*Ceiba pentandra*	6	6.0	12.2
Arecaceae	*Iriartea deltoidea*	6	3.0	12.2
Arecaceae	*Aphandra natalia*	5	5.0	10.2
Tiliaceae	*Apeiba membranaceae*	4	4.0	8.2
Boraginaceae	*Cordia alliodora*	4	4.0	8.2
Meliaceae	*Cedrela odorata*	3	1.5	6.1
Sapotaceae	*Chrysophyllum amazonicum*	2	2.0	4.1
Moraceae	*Pseudolmedia rigida*	2	2.0	4.1
Elaeocarpaceae	*Sloanea robusta*	2	2.0	4.1
Combretaceae	*Terminalia oblonga*	2	2.0	4.1
	Total abundance	49		

Corn AFS (6.19 ha)

Family	Species	Abs. abund.	Rel. abund.	Domin. %
Boraginaceae	*C. alliodora*	37	9.3	30.1
Meliaceae	*C. odorata*	19	3.8	15.4
Arecaceae	*I. deltoidea*	13	4.3	10.6
Rubiaceae	*Gonzalagunia spicata*	6	6.0	4.9
Combretaceae	*T. oblonga*	6	3.0	4.9
Myristicaceae	*Virola flexuosa*	3	3.0	2.4
Bixaceae	*Bixa orellana*	2	2.0	1.6
Meliaceae	*Cabralea canjerana*	2	1.0	1.6
Urticaceae	*Cecropia sciadophylla*	2	1.0	1.6
Malvaceae	*C. pentandra*	2	2.0	1.6
	Total abundance	123		

Cocoa AFS (4.67)

Family	Species	Abs. abund.	Rel. abund.	Domin. %
Boraginaceae	*C. alliodora*	113	9.4	34.6
Moraceae	*P. rigida*	22	2.8	6.7
Fabaceae	*Inga edulis*	19	2.4	5.8
Vochysiaceae	*Vochysia leguiana*	17	5.7	5.2
Arecaceae	*I. deltoidea*	15	2.5	4.6
Meliaceae	*C. odorata*	13	1.4	4.0
Euphorbiaceae	*Croton lechleri*	12	6.0	3.7
Malvaceae	*Ochroma pyramidale*	12	2.4	3.7
Asteraceae	*Pollalesta discolor*	11	5.5	3.4
Annonaceae	*Annona duckei*	8	2.7	2.4
	Total abundance	327		

Secondary forest (1.74 ha, ca. 15-20 years after disturbance)

Family	Species	Abs. abund.	Rel. abund.	Domin. %
Arecaceae	*I. deltoidea*	213	42.6	25.5
Myristicaceae	*V. flexuosa*	156	31.2	18.7
Meliaceae	*Guarea kunthiana*	70	14.0	8.4
Fabaceae	*I. pavoniana*	43	8.6	5.1
Lauraceae	*Ocotea bofo*	35	7.0	4.2
Malvaceae	*Matisia bracteolosa*	32	8.0	3.8
Cannabaceae	*Celtis iguanaea*	21	21.0	2.5
Rubiaceae	*Chimarrhis glabriflora*	19	4.8	2.3
Burseraceae	*Protium amazonicum*	14	3.5	1.7
Sapotaceae	*C. amazonicum*	13	6.5	1.6
	Total abundance	836		

Mature forest (4.24 ha)

Family	Species	Abs. abund.	Rel. abund.	Domin. %
Arecaceae	*I. deltoidea*	479	34.2	17.6
Myristicaceae	*V. flexuosa*	393	28.1	14.4
Meliaceae	*G. kunthiana*	162	11.6	5.9
Lauraceae	*O. bofo*	160	11.4	5.9
Sapotaceae	*C. amazonicum*	113	11.3	4.1
Burseraceae	*P. amazonicum*	105	7.5	3.9
Fabaceae	*I. pavoniana*	101	11.2	3.7
Lecythidaceae	*Grias neuberthii*	76	9.5	2.8
Araliaceae	*Didymopanax morototoni*	72	8.0	2.6
Moraceae	*P. rigida*	67	8.4	2.5
	Total abundance	2725		

Table A2.3: List, location, and threat category of tree species inventoried in forest and chakras in the buffer zone of the Northern Ecuadorian Amazon

Species	**Family**	**Location**	**Category**	**Source**
Aphandra natalia (Balslev & A.J. Hend.) Barfod	Arecaceae	Chakra	Not evaluated	
Bixa orellana L.	Bixaceae	Chakra	Not evaluated	
Carica papaya L.	Caricaceae	Chakra	Deficient data	Contreras (2016)
Cedrela odorata L.	Meliaceae	Chakra	Vulnerable	ARW (1998)
Citrus aurantifolia Swingle	Rutaceae	Chakra	Not evaluated	
C. limon (L.) Osbeck	Rutaceae	Chakra	Not evaluated	
C. sinensis (L.) Osbeck	Rutaceae	Chakra	Not evaluated	
Cordia alliodora (Ruiz & Pav.) Cham.	Boraginaceae	Chakra	Least concerned	Lynsky (2014)
Croton lechleri Müll. Arg.	Euphorbiaceae	Chakra	Not evaluated	
Erythrina poeppigiana (Walp.) O.F. Cook	Fabaceae	Chakra	Not evaluated	
Eugenia stipitata McVaugh	Myrtaceae	Chakra	Not evaluated	
Gonzalagunia spicata (Lam.) M. Gómez	Rubiaceae	Chakra	Not evaluated	
Inga edulis Mart.	Fabaceae	Chakra	Not evaluated	
I. spectabilis (Vahl) Willd.	Fabaceae	Chakra	Not evaluated	
Lacistema nena J.F. Macbr.	Lacistemataceae	Chakra	Not evaluated	
Mauritia flexuosa L. f.	Arecaceae	Chakra	Not evaluated	
Ochroma pyramidale (Cav. ex Lam.) Urb.	Malvaceae	Chakra	Not evaluated	
Ocotea sericea Kunth	Lauraceae	Chakra	Not evaluated	
Otoba gracilipes (A.C. Sm.) A.H. Gentry	Myristicaceae	Chakra	Not evaluated	
Parkia multijuga Benth.	Fabaceae	Chakra	Not evaluated	
Pollalesta discolor (Kunth) Aristeg.	Asteraceae	Chakra	Not evaluated	
Psidium guajava L.	Myrtaceae	Chakra	Not evaluated	
Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin	Araliaceae	Chakra	Not evaluated	
Trichanthera gigantea (Bonpl.) Nees	Acanthaceae	Chakra	Not evaluated	
Urtica urens L.	Urticaceae	Chakra	Not evaluated	
Vernonia baccharoides Kunth	Asteraceae	Chakra	Not evaluated	
Vernonia patens Kunth	Asteraceae	Chakra	Not evaluated	
Alseis lugonis L. Andersson	Rubiaceae	Chakra&Forest	Near threatened*	Jaramillo *et al.* (2004)
Annona duckei Diels	Annonaceae	Chakra&Forest	Not evaluated	
Apeiba membranacea Spruce ex Benth.	Tiliaceae	Chakra&Forest	Not evaluated	
Artocarpus altillis (Parkinson) Fosberg	Moraceae	Chakra&Forest	Not evaluated	

Species	Family	Location	Category	Source
Cabralea canjerana (Vell.) Mart.	Meliaceae	Chakra&Forest	Not evaluated	
Calycophyllum spruceanum (Benth.) Hook. f. ex K. Schum.	Rubiaceae	Chakra&Forest	Not evaluated	
Castilla elastica Sessé	Moraceae	Chakra&Forest	Not evaluated	
Cecropia sciadophylla Mart.	Urticaceae	Chakra&Forest	Not evaluated	
Cedrelinga cateniformis (Ducke) Ducke	Fabaceae	Chakra&Forest	Not evaluated	
Ceiba pentandra (L.) Gaertn.	Malvaceae	Chakra&Forest	Not evaluated	
Chimarrhis glabriflora Ducke	Rubiaceae	Chakra&Forest	Not evaluated	
Chrysophyllum amazonicum T.D. Penn.	Sapotaceae	Chakra&Forest	Not evaluated	
Erythrina L. sp.	Fabaceae	Chakra&Forest	Not evaluated	
Eugenia L. sp.	Myrtaceae	Chakra&Forest	Not evaluated	
Grias neuberthii J.F. Macbr.	Lecythidaceae	Chakra&Forest	Not evaluated	
Gustavia longifolia Poepp. ex O. Berg	Lecythidaceae	Chakra&Forest	Not evaluated	
Ilex guayusa Loes.	Aquifoliaceae	Chakra&Forest	Not evaluated	
Iriartea deltoidea Ruiz & Pav.	Arecaceae	Chakra&Forest	Least concern	Trudgen (2013)
Machaerium millei Standl.	Fabaceae	Chakra&Forest	Not evaluated	
Minquartia guianensis Aubl.	Olacaceae	Chakra&Forest	Near threatened	ARW (1998)
Myroxylon balsamum (L.) Harms	Fabaceae	Chakra&Forest	Not evaluated	
Nectandra Rol. ex Rottb. sp.	Lauraceae	Chakra&Forest	Not evaluated	
Ocotea quixos Kosterm. ex O.C. Schmidt	Lauraceae	Chakra&Forest	Not evaluated	
Phytelephas macrocarpa Ruiz & Pav.	Arecaceae	Chakra&Forest	Not evaluated	
Pourouma tomentosa Mart. ex Miq.	Urticaceae	Chakra&Forest	Not evaluated	
Pouteria cuspidata (A. DC.) Baehni	Sapotaceae	Chakra&Forest	Not evaluated	
Pseudolmedia rigida (Klotzsch & H. Karst.) Cuatrec.	Moraceae	Chakra&Forest	Not evaluated	
Sloanea robusta Uittien	Elaeocarpaceae	Chakra&Forest	Not evaluated	
Stryphnodendron porcatum D.A. Neill & Occhioni f.	Fabaceae	Chakra&Forest	Least concern*	Neill & Pitman (2004)
Swietenia macrophylla King	Meliaceae	Chakra&Forest	Vulnerable	WCMC (1998)
Tapiria guianense Aubl.	Anacardiaceae	Chakra&Forest	Not evaluated	
Terminalia oblonga (Ruiz & Pav.) Steud.	Combretaceae	Chakra&Forest	Not evaluated	
Theobroma subincanum Mart.	Malvaceae	Chakra&Forest	Not evaluated	
Virola flexuosa A.C. Sm.	Myristicaceae	Chakra&Forest	Not evaluated	
Vochysia leguiana J.F. Macbr.	Vochysiaceae	Chakra&Forest	Not evaluated	
Astrocaryum murumuru Mart.	Arecaceae	Forest	Least concern	Montúfar & Pitman (2003)

Species	**Family**	**Location**	**Category**	**Source**
Attalea maripa (Aubl.) Mart.	Arecaceae	Forest	Not evaluated	
Brosimum utile (Kunth) Pittier	Moraceae	Forest	Not evaluated	
Browneopsis ucayalina Huber	Fabaceae	Forest	Not evaluated	
Bursera graveolens (Kunth) Triana & Planch.	Burseraceae	Forest	Not evaluated	
Calliandra angustifolia Spruce ex Benth.	Fabaceae	Forest	Not evaluated	
Caryodendron orinocense H. Karst.	Euphorbiaceae	Forest	Not evaluated	
Celtis iguanaea (Jacq.) Sarg.	Cannabaceae	Forest	Not evaluated	
C. schippii Standl.	Cannabaceae	Forest	Not evaluated	
Cestrum racemosum Ruiz & Pav.	Solanaceae	Forest	Not evaluated	
Clarisia racemosa Ruiz & Pav.	Moraceae	Forest	Not evaluated	
Didymopanax morototoni (Aubl.) Decne. & Planch.	Araliaceae	Forest	Not evaluated	
Eugenia subterminalis DC.	Myrtaceae	Forest	Not evaluated	
Ficus L. sp.	Moraceae	Forest	Not evaluated	
Garcinia macrophylla Mart.	Clusiaceae	Forest	Not evaluated	
Guarea kunthiana A. Juss.	Meliaceae	Forest	Not evaluated	
Guatteria Ruiz & Pav. sp.	Annonaceae	Forest	Not evaluated	
Humiriastrum diguense (Cuatrec.) Cuatrec.	Humiriaceae	Forest	Not evaluated	
Hyeronima alchorneoides Allemão	Phyllanthaceae	Forest	Not evaluated	
H. oblonga (Tul.) Müll. Arg.	Phyllanthaceae	Forest	Not evaluated	
Inga Mill. sp.	Fabaceae	Forest	Not evaluated	
I. pavoniana Benth.	Fabaceae	Forest	Least concern	Groom (2012)
Lacmellea lactescens (Kuhlm.) Markgr.	Apocynaceae	Forest	Not evaluated	
Leonia glycycarpa Ruiz & Pav.	Violaceae	Forest	Not evaluated	
Lonchocarpus spiciflorus Mart. ex Benth.	Fabaceae	Forest	Not evaluated	
Matisia bracteolosa Ducke	Malvaceae	Forest	Not evaluated	
Maytenus ebenifolia Reissek	Celastraceae	Forest	Not evaluated	
M. laevis Reissek	Celastraceae	Forest	Not evaluated	
Mucuna elliptica (Ruiz & Pav.) DC.	Fabaceae	Forest	Not evaluated	
Myrciaria dubia (Kunth) McVaugh	Myrtaceae	Forest	Not evaluated	
Ocotea bofo Kunth	Lauraceae	Forest	Not evaluated	
O. floribunda (Sw.) Mez	Lauraceae	Forest	Not evaluated	
Oenocarpus bataua Mart.	Arecaceae	Forest	Not evaluated	
Ormosia grandiflora (Tul.) Rudd	Fabaceae	Forest	Not evaluated	
Ouratea williamsii J.F. Macbr.	Ochnaceae	Forest	Not evaluated	

Species	**Family**	**Location**	**Category**	**Source**
Pourouma bicolor Mart.	Urticaceae	Forest	Not evaluated	
Pouteria Aubl. sp.	Sapotaceae	Forest	Not evaluated	
P. lucuma (Ruiz & Pav.) Kuntze	Sapotaceae	Forest	Not evaluated	
Protium amazonicum (Cuatrec.) Daly	Burseraceae	Forest	Not evaluated	
Prunus vana J.F. Macbr.	Rosaceae	Forest	Not evaluated	
Rauwolfia Gled. sp.	Apocynaceae	Forest	Not evaluated	
Sapium eglandulosum Ule	Euphorbiaceae	Forest	Not evaluated	
Solanum L. sp.	Solanaceae	Forest	Not evaluated	
Tabernaemontana sananho Ruiz & Pav.	Apocynaceae	Forest	Not evaluated	
Tessmannianthus heterostemon Markgr.	Melastomataceae	Forest	Not evaluated	
Trichilia P. Browne sp.	Meliaceae	Forest	Not evaluated	
Vismia macrophylla Kunth	Hypericaceae	Forest	Not evaluated	

* Endemic species located at the buffer zone of the Northern Ecuadorian Amazon

Table A2.4: Group of plots established in the secondary forest and mature forest that were aggregated. This table shows the number of the plot, size, geographic location, altitude, and distance to the closest plot in the floristic inventory performed in secondary and mature forests in the northern Ecuadorian Amazon. This procedure was performed because of the closeness of the plots may cause pseudo replication problem. To solve that, plots that were closer than 100 meters were combined in a single plot both in the secondary forest and the mature forest. The groups of aggregated plots were included to those in the table 2.1.

Secondary Forest

Plot #	Size (m^2)	UTM N	UTM E	Elevation (masl)	Distance to the nearest Plot (m)
1	500	9889444	213018	414	30
2	500	9889404	213068	434	64
3	500	9889471	213032	420	30
4	500	9878075	206305	384	101
5	500	9878141	206384	371	81
6	500	9878176	206310	363	81
7	500	9878254	206379	401	104
8	500	9878309	206484	433	102
9	500	9878266	206577	419	102
10	500	9874199	208285	380	96
11	500	9874184	208380	447	71
12	500	9874158	208447	484	67
13	500	9874122	208504	471	67
14	500	9874081	208582	459	88
15	500	9873999	208538	446	33
16	500	9873975	208561	464	33
17	500	9873944	208622	452	68
18	500	9873872	208711	439	50
19	500	9873883	208760	455	50
20	500	9879388	214871	529	57
21	500	9879359	214834	451	57
22	500	9879381	214781	431	49
23	500	9879386	214732	422	47
24	500	9879368	214688	421	47
25	500	9879560	214611	408	39
26	500	9879599	214606	396	39
27	500	9879653	214543	385	82
28	500	9874090	208164	476	16
29	500	9874044	208215	434	17
30	500	9873999	208234	466	31
31	500	9873926	208294	446	69
32	500	9873825	208347	438	44
33	500	9873867	208331	427	44
34	500	9874027	208220	419	17
35	500	9874102	208152	432	16

Mature Forest

Plot #	Size (m^2)	UTM N	UTM E	Elevation (masl)	Distance to the nearest plot (m)
1	500	9877827	217229	512	7
2	500	9877728	217288	412	112
3	500	9877565	217246	411	53
4	500	9877521	217215	408	53
5	500	9877468	217170	406	69
6	500	9877522	217101	436	87
7	500	9877831	217224	450	7
8	500	9878065	217091	450	58
9	500	9878095	217041	496	58
10	500	9878289	217044	501	194
11	500	9877794	216804	433	76
12	500	9877828	216736	478	67
13	500	9877876	216688	495	65
14	500	9877863	216624	499	65
15	500	9877764	216501	504	61
16	500	9877704	216513	516	61
17	500	9877615	216341	545	84
18	500	9877557	216280	545	53
19	500	9877587	216117	544	118
20	500	9877546	216228	539	53
21	500	9876777	205555	556	32
22	500	9876715	205465	442	77
23	500	9876782	205503	432	77
24	500	9876796	205581	435	79
25	500	9876677	205613	435	58
26	500	9876630	205648	441	58
27	500	9876725	205689	441	79
28	500	9876784	205742	441	1.4
29	500	9876785	205743	444	1.4
30	500	9876931	205840	553	82
31	500	9877127	205745	462	130
32	500	9877122	205875	460	80
33	500	9876849	205811	450	64
34	500	9876859	205880	428	47
35	500	9876802	205855	440	62
36	500	9876861	205927	458	47
37	500	9877120	205955	439	80
38	500	9876747	206076	457	116
39	500	9876878	206037	451	59
40	500	9876862	206094	437	59

APPENDIX 2: SUPPORTING INFORMATION FOR CHAPTER 3

Table A3.1: List of plant families, tree species, distribution, and threatened category of each specie per categories of intensification of SA in cocoa, i.e., high (H.I.), intermediate (I.I.), and low (L.I.), and mature forest for comparative reasons. Scientific names in bold characters represent shared taxa among different categories of land use.

Family	Species	Distribution	IUCN category
Cocoa AFS H.I.			
Boraginaceae	***Cordia alliodora*** **(Ruiz & Pav.) Oken**	Native	Least concern
Combretaceae	***Terminalia oblonga*** **(Ruiz & Pav.) Steud.**	Native	Not evaluated
Fabaceae	***Inga edulis*** **Mart.**	Native	Not evaluated
Fabaceae	*Erythrina poeppigiana* (Walp.) O.F. Cook	Native	Not threatened
Lauraceae	***Nectandra*** **Rol. ex Rottb. sp.**	Native	Not evaluated
Meliaceae	***Cedrela odorata*** **L.**	Native	Vulnerable
Meliaceae	***Swietenia macrophylla*** **King**	Native	Vulnerable
Rubiaceae	***Chimarrhis glabriflora*** **Ducke**	Native	Not evaluated
Rutaceae	***Citrus sinensis*** **(L.) Osbeck**	Introduced	Not evaluated
Cocoa AFS I.I.			
Arecaceae	***Iriartea deltoidea*** **Ruiz & Pav.**	Native	Least concern
Asteraceae	***Vernonanthura patens*** **(Kunth) H. Rob.**	Native	Not evaluated
Bombacaceae	***Ochroma pyramidale*** **(Cav. ex Lam.) Urb.**	Native	Not evaluated
Boraginaceae	***Cordia alliodora*** **(Ruiz & Pav.) Oken**	Native	Least concern
Combretaceae	***Terminalia oblonga*** **(Ruiz & Pav.) Steud.**	Native	Not evaluated
Elaeocarpaceae	***Sloanea robusta*** **Uittien**	Native	Not evaluated
Euphorbiaceae	***Croton lechleri*** **Müll. Arg.**	Native	Not evaluated
Fabaceae	***Browneopsis ucayalina*** **Huber**	Native	Not threatened
Fabaceae	***Inga edulis*** **Mart.**	Native	Not evaluated
Fabaceae	***I. spectabilis*** **(Vahl) Willd.**	Native	Not evaluated
Fabaceae	***Mucuna elliptica*** **(Ruiz & Pav.) DC.**	Native	Not evaluated
Lauraceae	***Nectandra*** **Rol. ex Rottb. sp.**	Native	Not evaluated
Lauraceae	***Ocotea quixos*** **(Lam.) Kosterm.**	Native	Not evaluated
Lecythidaceae	***Grias neuberthii*** **J.F. Macbr.**	Native	Not evaluated
Malvaceae	***Theobroma subincanum*** **Mart.**	Native	Not evaluated
Meliaceae	***Cedrela odorata*** **L.**	Native	Vulnerable
Meliaceae	***Swietenia macrophylla*** **King**	Native	Vulnerable
Moraceae	***Clarisia biflora*** **Ruiz & Pav.**	Native	Not evaluated
Moraceae	***Pseudolmedia rigida*** **(Klotzsch & H. Karst.) Cuatrec.**	Native	Not evaluated
Myristicaceae	***Virola flexuosa*** **A.C. Sm.**	Native	Not evaluated
Myrtaceae	***Psidium guajava*** **L.**	Native	Not evaluated
Olacaceae	***Minquartia guianensis*** **Aubl.**	Native	Near threatened
Rubiaceae	***Chimarrhis glabriflora*** **Ducke**	Native	Not evaluated
Rutaceae	*Citrus aurantifolia* Swingle	Introduced	Not evaluated
Rutaceae	***C. limon*** **(L.) Osbeck**	Introduced	Not evaluated
Rutaceae	***C. sinensis*** **(L.) Osbeck**	Introduced	Not evaluated
Sapotaceae	***Chrysophyllum amazonicum*** **T.D. Penn.**	Native	Not evaluated
Urticaceae	***Urera baccifera*** **(L.) Gaudich. ex Wedd.**	Native	Not evaluated
Vochysiaceae	***Vochysia leguiana*** **J.F. Macbr.**	Native	Not evaluated

Cocoa AFS L.I.			
Anacardiaceae	***Tapiria guianense* Aubl.**	Native	Not evaluated
Annonaceae	***Annona duckei* Diels**	Native	Not evaluated
Araliaceae	***Didymopanax morototoni* (Aubl.) Decne. & Planch.**	Native	Not evaluated
Arecaceae	***Iriartea deltoidea* Ruiz & Pav.**	Native	Least concern
Asteraceae	*Pollalesta discolor* (Kunth) Aristeg.	Native	Not evaluated
Asteraceae	***Vernonanthura patens* (Kunth) H. Rob.**	Native	Not evaluated
Bombacaceae	***Ochroma pyramidale* (Cav. ex Lam.) Urb.**	Native	Not evaluated
Boraginaceae	***Cordia alliodora* (Ruiz & Pav.) Cham.**	Native	Least concern
Burseraceae	*Bursera graveolens* (Kunth) Triana & Planch.	Native	Not evaluated
Caricaceae	*Carica papaya* L.	Native	Data deficient
Clusiaceae	***Garcinia macrophylla* Mart.**	Native	Not evaluated
Elaeocarpaceae	***Sloanea robusta* Uittien**	Native	Not evaluated
Euphorbiaceae	*Caryodendron orinocense* H. Karst.	Native	Not evaluated
Euphorbiaceae	***Croton lechleri* Müll. Arg.**	Native	Not evaluated
Euphorbiaceae	***Hevea guianensis* Aubl.**	Native	Not evaluated
Fabaceae	*Cedrelinga cateniformis* (Ducke) Ducke	Native	Not threatened
Fabaceae	***Erythrina* L. sp.**	Native	Not threatened
Fabaceae	***Inga edulis* Mart.**	Native	Not evaluated
Fabaceae	***I. spectabilis* (Vahl) Willd.**	Native	Not evaluated
Fabaceae	***Machaerium millei* Standl.**	Native	Not evaluated
Fabaceae	***Stryphnodendron porcatum* D.A. Neill & Occhioni f.**	Endemic	Least concern
Gesneriaceae	***Columnea ericae* Mansf.**	Native	Not evaluated
Lacistemataceae	*Lacistema nena* J.F. Macbr.	Native	Not evaluated
Lauraceae	***Nectandra* Rol. ex Rottb. sp.**	Native	Not evaluated
Lauraceae	***Ocotea bofo* Kunth**	Native	Not evaluated
Lecythidaceae	***Grias neuberthii* J.F. Macbr.**	Native	Not evaluated
Lecythidaceae	***Gustavia longifolia* Poepp. ex O. Berg**	Native	Not evaluated
Malvaceae	***Theobroma subincanum* Mart.**	Native	Not evaluated
Meliaceae	***Cabralea canjerana* (Vell.) Mart.**	Native	Not evaluated
Meliaceae	***Cedrela odorata* L.**	Native	Vulnerable
Meliaceae	***Swietenia macrophylla* King**	Native	Vulnerable
Moraceae	***Clarisia biflora* Ruiz & Pav.**	Native	Not evaluated
Moraceae	***Ficus* L. sp.**	Native	Not evaluated
Moraceae	***Pseudolmedia rigida* (Klotzsch & H. Karst.) Cuatrec.**	Native	Not evaluated
Myristicaceae	***Virola flexuosa* A.C. Sm.**	Native	Not evaluated
Myrtaceae	***Psidium guajava* L.**	Native	Not evaluated
Rosaceae	***Prunus vana* J.F. Macbr.**	Native	Not evaluated
Rubiaceae	***Alseis lugonis* L. Andersson**	Endemic	Near threatened
Rubiaceae	***Chimarrhis glabriflora* Ducke**	Native	Not evaluated
Rutaceae	***Citrus limon* (L.) Osbeck**	Introduced	Not evaluated
Rutaceae	***C. sinensis* (L.) Osbeck**	Introduced	Not evaluated
Sapotaceae	***Chrysophyllum amazonicum* T.D. Penn.**	Native	Not evaluated
Sapotaceae	***Pouteria lucuma* (Ruiz & Pav.) Kuntze**	Native	Not evaluated
Tiliaceae	***Apeiba membranaceae* Spruce ex Benth.**	Native	Not evaluated
Urticaceae	***Urera baccifera* (L.) Gaudich. ex Wedd.**	Native	Not evaluated
Vochysiaceae	***Vochysia leguiana* J.F. Macbr.**	Native	Not evaluated

Mature Forest

Anacardiaceae	***Tapiria guianensis* Aubl.**	Native	Not evaluated
Annonaceae	***Annona duckei* Diels**	Native	Not evaluated
Annonaceae	*Guatteria* Ruiz & Pav. sp.	Native	Not evaluated
Apocynaceae	*Tabernaemontana sananho* Ruiz & Pav.	Native	Not evaluated
Aquifoliaceae	*Ilex guayusa* Loes.	Native	Not evaluated
Araliaceae	***Didymopanax morototoni* (Aubl.) Decne. & Planch.**	Native	Not evaluated
Arecaceae	***Iriartea deltoidea* Ruiz & Pav.**	Native	Least concern
Arecaceae	*Oenocarpus batatua* Mart.	Native	Not evaluated
Arecaceae	*Phytelephas macrocarpa* Ruiz & Pav.	Native	Not evaluated
Burseraceae	*Protium amazonicum* (Cuatrec.) Daly	Native	Not evaluated
Cannabaceae	*Celtis schippii* Standl.	Native	Not evaluated
Cecropiaceae	*Pourouma tomentosa* Mart. ex Miq.	Native	Not evaluated
Celastraceae	*Maytenus laevis* Reissek	Native	Not evaluated
Clusiaceae	***Garcinia macrophylla* Mart.**	Native	Not evaluated
Combretaceae	***Terminalia oblonga* (Ruiz & Pav.) Steud.**	Native	Not evaluated
Elaeocarpaceae	***Sloanea robusta* Uittien**	Native	Not evaluated
Euphorbiaceae	***Hevea guianensis* Aubl.**	Native	Not evaluated
Euphorbiaceae	***Hyeronima alchorneoides* Allemão**	Native	Not evaluated
Euphorbiaceae	***H. oblonga* (Tul.) Müll. Arg.**	Native	Not evaluated
Fabaceae	***Browneopsis ucayalina* Huber**	Native	Near threatened
Fabaceae	*Calliandra angustifolia* Spruce ex Benth.	Native	Not evaluated
Fabaceae	***Erythrina* L. sp.**	Native	Not threatened
Fabaceae	*Inga pavoniana* Benth.	Native	Least concern
Fabaceae	***Machaerium millei* Standl.**	Native	Not evaluated
Fabaceae	***Mucuna elliptica* (Ruiz & Pav.) DC.**	Native	Not evaluated
Fabaceae	*Ormosia grandiflora* (Tul.) Rudd	Native	Not evaluated
Fabaceae	***Stryphnodendron porcatum* D.A. Neill & Occhioni f.**	Endemic	Least concern
Gesneriaceae	***Columnea ericae* Mansf.**	Native	Not evaluated
Humiriaceae	*Humiriastrum diguense* (Cuatrec.) Cuatrec.	Native	Not evaluated
Lauraceae	***Ocotea bofo* Kunth**	Native	Not evaluated
Lauraceae	*O. floribunda* (Sw.) Mez	Native	Not evaluated
Lauraceae	***O. quixos* (Lam.) Kosterm.**	Native	Not evaluated
Lecythidaceae	***Grias neuberthii* J.F. Macbr.**	Native	Not evaluated
Lecythidaceae	***Gustavia longifolia* Poepp. ex O. Berg**	Native	Not evaluated
Malvaceae	***Matisia bracteolosa* Ducke**	Native	Not evaluated
Malvaceae	***Theobroma subincanum* Mart.**	Native	Not evaluated
Melastomataceae	*Tessmannianthus heterostemon* Markgr.	Native	Not evaluated
Meliaceae	***Cabralea canjerana* (Vell.) Mart.**	Native	Not evaluated
Meliaceae	***Cedrela odorata* L.**	Native	Vulnerable
Meliaceae	*Guarea kunthiana* A. Juss.	Native	Not evaluated
Meliaceae	***Swietenia macrophylla* King**	Native	Vulnerable
Menispermaceae	*Abuta grandiflora* (Mart.) Sandwith	Native	Not evaluated
Moraceae	***Clarisia biflora* Ruiz & Pav.**	Native	Not evaluated
Moraceae	***Clarisia racemosa* Ruiz & Pav.**	Native	Not evaluated
Moraceae	***Ficus* L. sp.**	Native	Not evaluated
Moraceae	***Pseudolmedia rigida* (Klotzsch & H. Karst.) Cuatrec.**	Native	Not evaluated
Myristicaceae	***Virola flexuosa* A.C. Sm.**	Native	Not evaluated
Myrtaceae	*Eugenia subterminalis* DC.	Native	Not evaluated

Myrtaceae	*Myrciaria floribunda* O. Berg. sp.	Native	Not evaluated
Olacaceae	***Minquartia guianensis* Aubl.**	Native	Near threatened
Piperaceae	*Piper peltatum* L.	Native	Not evaluated
Rosaceae	***Prunus vana* J.F. Macbr.**	Native	Not evaluated
Rubiaceae	***Alseis lugonis* L. Andersson**	Endemic	Near threatened
Rubiaceae	***Chimarrhis glabriflora* Ducke**	Native	Not evaluated
Sapotaceae	***Chrysophyllum amazonicum* T.D. Penn.**	Native	Not evaluated
Sapotaceae	***Pouteria lucuma* (Ruiz & Pav.) Kuntze**	Native	Not evaluated
Sapotaceae	*Pouteria* Aubl. sp.	Native	Not evaluated
Solanaceae	*Solanum* L. sp.	Native	Not evaluated
Theophrastaceae	*Clavija weberbaueri* Mez	Native	Not evaluated
Tiliaceae	***Apeiba membranaceae* Spruce ex Benth.**	Native	Not evaluated
Urticaceae	*Cecropia sciadophylla* Mart.	Native	Not evaluated
Violaceae	*Leonia crassa* L.B. Sm. & Á. Fernández	Native	Not evaluated
Vochysiaceae	***Vochysia leguiana* J.F. Macbr.**	Native	Not evaluated

Table A3.2: Top ten dominant species ranked according to the importance value (IV %) in each of the categories of intensification of SA in cocoa, i.e., high (H.I.), intermediate (I.I.), and low (L.I.), and mature forest for comparative reasons. The table also shows the basal area and density of each of the top ten taxa.

Species name	Basal area (m^2 ha^{-1})	Density (trees ha^{-1})	Frequency (%)	IV (%)
Cocoa AFS H.I.				
Cordia alliodora	0.88	25.00	23.07	31.14
Terminalia oblonga	1.18	6.00	19.23	20.24
Cedrela odorata	0.95	9.00	19.23	20.19
Citrus sinensis	0.10	6.00	15.38	9.81
Chimarrhis glabriflora	0.50	1.00	3.85	6.17
Nectandra sp.	0.06	2.00	7.69	4.34
Erythrina poeppigiana	0.24	1.00	3.85	3.94
Swietenia macrophylla	0.03	1.00	3.85	2.18
Inga edulis	0.01	1.00	3.85	1.97
Subtotal	3.93	52.00	100.00	100.00
Other species	-	-	-	-
Total cocoa H.I.	3.93	52.00	100.00	100.00
Cocoa AFS I.I.				
Cordia alliodora	1.70	48.00	15.09	28.42
Cedrela odorata	0.31	15.00	11.32	9.56
Vochysia leguiana	0.90	9.00	1.89	8.97
Vernonanthura patens	0.10	17.00	3.77	6.13
Chimarrhis glabriflora	0.32	4.00	5.66	5.04
Inga spectabilis	0.25	4.00	3.77	3.92
Swietenia macrophylla	0.03	4.00	5.66	3.10
Mucuna elliptica	0.32	1.00	1.89	3.09
Pseudolmedia rigida	0.06	3.00	5.66	3.05
Minquartia guianensis	0.16	2.00	3.77	2.86
Subtotal	4.17	107.00	58.49	74.15
Other species	0.72	29.00	41.51	25.85
Total cocoa I.I.	4.89	136.00	100.00	100.00
Cocoa AFS L.I.				
Cordia alliodora	2.66	115.00	7.84	25.62
Inga edulis	0.66	16.00	5.88	6.53
Cedrela odorata	0.47	16.00	4.90	5.29
Pollalesta discolor	0.24	38.00	1.96	5.21
Ochroma pyramidale	0.35	21.00	3.92	4.85
Stryphnodendron porcatum	0.21	21.00	4.90	4.52
Chrysophyllum amazonicum	0.15	11.00	4.90	3.33
Pseudolmedia rigida	0.21	11.00	2.94	2.95
Cedrelinga cateniformis	0.10	7.00	4.90	2.75
Inga spectabilis	0.16	6.00	3.92	2.60

Subtotal	5.20	262.00	46.08	63.65
Other species	1.82	108.00	53.92	36.35
Total cocoa I.I.	7.02	370.00	100.00	100.00

Mature Forest

Virola flexuosa	5.84	131.00	3.90	11.15
Ocotea bofo	2.74	90.00	3.89	6.90
Chrysophyllum amazonicum	3.33	35.00	3.03	5.26
Iriartea deltoidea	1.68	63.00	3.89	5.00
Guarea kunthiana	1.68	55.00	3.89	4.71
Pouteria lucuma	1.05	80.00	2.16	4.44
Inga pavoniana	1.21	35.00	3.46	3.46
Vochysia leguiana	2.14	20.00	2.16	3.36
Protium amazonicum	0.79	37.00	3.03	3.01
Clarisia biflora	0.75	29.00	3.46	2.84
Subtotal	21.18	575.00	32.90	50.13
Other species	15.35	391.00	67.10	48.87
Total cocoa I.I.	36.53	966.00	100.00	100.00

Table A3.3: Top ten dominant plant families ranked according the importance value (IV %) in each of the categories of intensification of SA in cocoa, i.e., high (H.I.), intermediate (I.I.), and low (L.I.), and mature forest for comparative reasons. This table also shows the basal area and density of each of the top ten family.

Family name	Basal area (m^2 ha^{-1})	Density (trees ha^{-1})	Frequency (%)	IV (%)
Cocoa AFS H.I.				
Boraginaceae	22.27	25.00	24.00	31.45
Meliaceae	24.81	10.00	20.00	21.34
Combretaceae	29.97	6.00	20.00	20.50
Rutaceae	2.50	6.00	16.00	10.01
Rubiaceae	12.75	1.00	4.00	6.22
Fabaceae	6.20	2.00	8.00	6.01
Lauraceae	1.49	2.00	8.00	4.44
Subtotal	3.93	52.00	100.00	100.00
Other families	-	-	-	-
Total cocoa H.I.	3.93	52.00	100.00	100.00
Cocoa AFS I.I.				
Boraginaceae	1.70	48.00	17.39	29.19
Meliaceae	0.34	19.00	15.22	12.08
Fabaceae	0.63	9.00	8.70	9.40
Vochysiaceae	0.90	9.00	2.17	9.03
Asteraceae	0.10	17.00	4.35	6.32
Rubiaceae	0.32	4.00	6.52	5.33
Moraceae	0.07	4.00	6.52	3.61
Rutaceae	0.06	6.00	4.35	3.34
Olacaceae	0.16	2.00	4.35	3.05
Lecythidaceae	0.11	2.00	4.35	2.71
Subtotal	4.41	120.00	73.91	84.10
Other families	0.48	16.00	26.09	15.10
Total cocoa I.I.	4.89	136.00	100.00	100.00
Cocoa AFS L.I.				
Boraginaceae	2.66	115.00	9.41	24.14
Fabaceae	1.14	52.00	11.76	14.02
Meliaceae	0.67	23.00	7.06	7.61
Asteraceae	0.25	44.00	3.53	6.34
Bombacaceae	0.35	20.00	4.71	5.01
Sapotaceae	0.18	14.00	7.06	4.49
Moraceae	0.22	16.00	5.88	4.47
Rubiaceae	0.12	12.00	4.71	3.21
Euphorbiaceae	0.25	9.00	3.53	3.18
Arecaceae	0.20	7.00	3.53	2.74
Subtotal	6.05	312.00	61.18	77.21
Other families	0.97	58.00	38.82	22.79

Total cocoa I.I.	7.02	370.00	100.00	100.00
Mature Forest				
Myristicaceae	5.84	131.00	5.52	11.69
Sapotaceae	4.87	131.00	5.52	10.80
Lauraceae	3.67	117.00	5.52	9.17
Fabaceae	4.69	67.00	4.91	8.23
Meliaceae	2.54	65.00	5.52	6.41
Moraceae	2.16	64.00	5.52	6.02
Arecaceae	1.84	70.00	5.52	5.93
Vochysiaceae	2.14	20.00	3.07	3.66
Burseraceae	0.79	37.00	4.29	3.43
Malvaceae	0.99	21.00	3.68	2.86
Subtotal	29.47	723.00	49.08	68.20
Other families	7.06	243.00	50.92	31.8
Total cocoa I.I.	36.53	966.00	100.00	100.00

Table A3.4: Analysis of dissimilarity of the floristic composition between the diameter classes (DC1: 2.5-9.99 cm, DC2: 10-19.99 cm, DC3: >20 cm) within each category of intensification of the SA in cocoa AFS, i.e., high (H.I.), intermediate (I.I.), and low (L.I.). The table shows the Steinhaus coefficient, i.e., values from 0 = less dissimilar to 1 = more dissimilar, and the p-value calculated in the ANOSIM (in parenthesis). Numbers in bold represent a p-value <0.05.

Cocoa AFS H.I.			
Diametric classes	2.5-9.99	10-19.99	>20
2.5-9.99	-		
10-19.99	0.08 (0.694)	-	
>20	0.18 (0.124)	0.13 (0.915)	-
Cocoa AFS I.I.			
Diametric classes	2.5-9.99	10-19.99	>20
2.5-9.99	-		
10-19.99	0.01 (0.355)	-	
>20	0.14 (0.082)	0.07 (0.106)	-
Cocoa AFS L.I.			
Diametric classes	2.5-9.99	10-19.99	>20
2.5-9.99	-		
10-19.99	0.08 (0.905)	-	
>20	0.05 (0.806)	0.02 (0.599)	-
Mature Forest			
Diametric classes	2.5-9.99	10-19.99	>20
2.5-9.99	-		
10-19.99	0.11 (0.078)	-	
>20	**0.19 (0.018)**	0.01 (0.546)	-