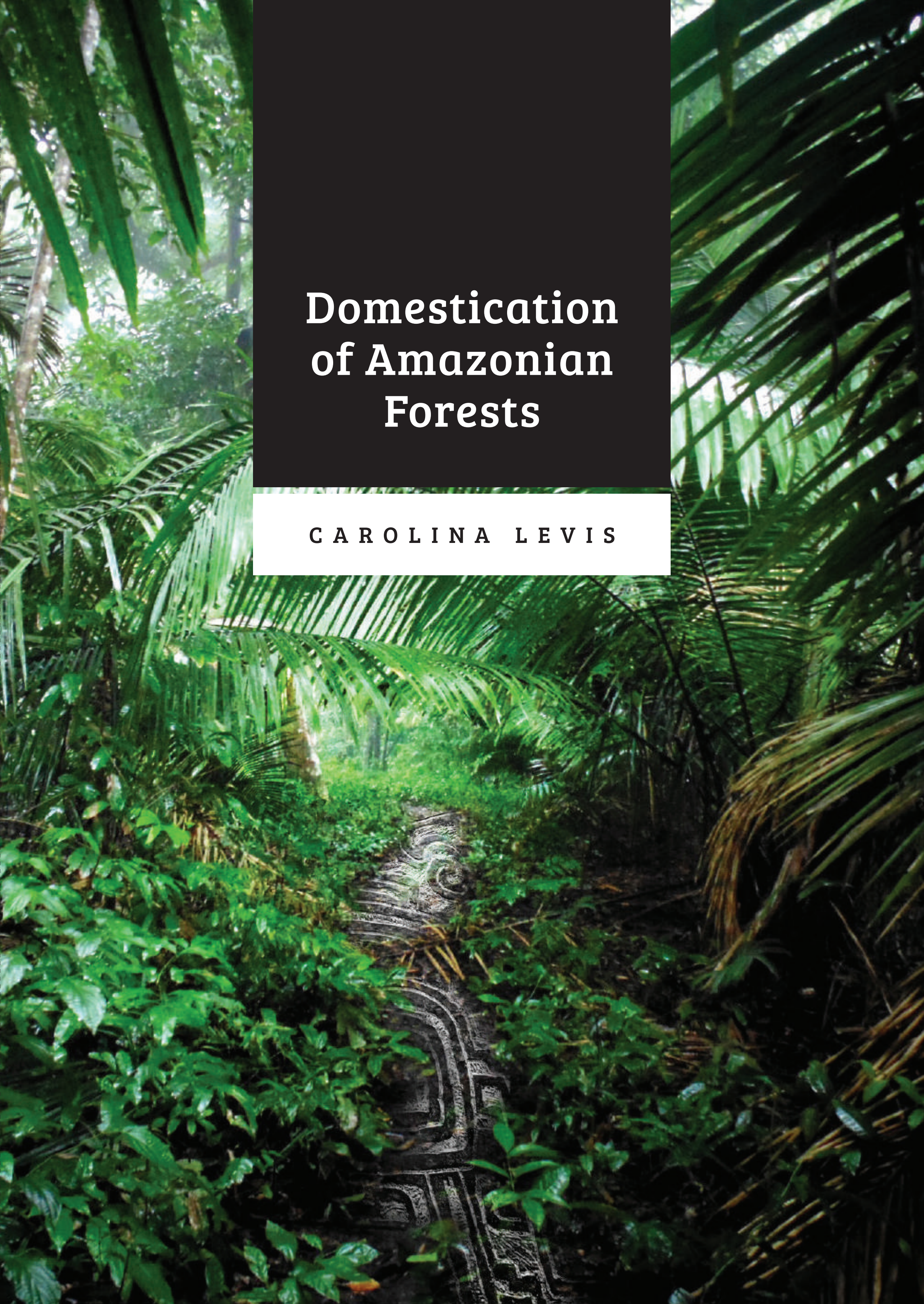

Domestication of Amazonian Forests

CAROLINA LEVIS

Propositions

1. The Amazon forest is a natural-cultural heritage of global importance.
   (this thesis)

2. Forests hold legacies of their interactions with humans.
   (this thesis)

3. To prosper in collaborative studies scientists need to practice tolerance and trust.

4. The main privilege of a scientific career is the freedom to pursue curiosity.

5. Human societies are increasing their capacity to modify the environment, but not how to deal with the consequences.

6. Effective community governance, not technology, is essential to solve socio-environmental problems.

Propositions belonging to the thesis, entitled

Domestication of Amazonian Forests

Carolina Levis
Wageningen, 14 June 2018

Domestication of Amazonian Forests

Carolina Levis

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Domestication of Amazonian Forests

Carolina Levis

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CHAPTER 1

General introduction

VISIONS OF NATURE

There was a time when humans were not yet part of the scene. Starting at least 60,000 years ago, modern humans expanded out of Africa and occupied most parts of the world (Mellars, 2006). Since then human societies have interpreted their surroundings in multiple ways, producing different visions and concepts of the natural and social worlds. A few centuries ago, Western culture defined Nature as "*The phenomena of the physical world collectively, including plants, animals, the landscape, and other features and products of the earth, as opposed to humans or human creations*"[1], suggesting that all physical and biological elements on Earth exist apart from humanity. Immersed in this dichotomy between nature and society, ecologists have historically quantified, measured and analysed nature and its parts - plants, animals and ecosystems - without considering human influences (Clark, 1996). Today, this concept is still being used among scientists who wish to keep some places on Earth separated from humans (e.g., the Half-Earth project led by Edward Wilson, created to devote half of the surface of the Earth to nature[2]).

In contrast to this dichotomous view of the world, many indigenous societies do not conceive the natural world without humans (Descola, 2013; Egleé, 2013). In Amerindian languages the word "Nature" is often non-existent: "*They do not have words equivalent or even approximating to the Western scientific idea of nature, nor do they have words to label our corresponding sociocultural sphere.*" For them, there is "*one sphere of life, a non-divisible one and all entities are in it.*" (Egleé, 2013, p. 6) Anthropologists have argued that the idea of "Nature" as a pristine refuge of wildlife is an imaginary place created by Westerners during a particular moment in their history (Dwyer, 1996; Descola, 2013). In fact, it is very complicated to find a place on this Planet where "Nature" remains pristine in its original form, i.e., in the same condition as it was before humans.

A NEW EPOCH EMERGES

Human domination of "Nature"

Humans have significantly modified their living environments while expanding their presence to most of the planet since the late Pleistocene (Smith and Zeder, 2013; Boivin et al., 2016). In the last few centuries, atmospheric and biotic alterations

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[1] Definition of nature according to the English Oxford Living Dictionary (https://en.oxforddictionaries.com/definition/nature)
[2] Half-Earth Project: half the earth for the rest of life (http://www.half-earthproject.org/)

caused by human activities have left signs in stratigraphic records that may persist for millions of years into the future (Waters et al., 2016; Lewis and Maslin, 2015). This unprecedented human footprint on Earth suggests that we are living in a new geological epoch, called the Anthropocene (Crutzen, 2006; Steffen et al., 2007; Ellis, 2011), in which most ecosystems are being shaped primarily by human agency (Ellis, 2011; Ellis, 2015).

Under this new paradigm, scientists are shifting the focus from protecting nature from people to understanding how we can minimize the negative aspects of human-nature interactions and, when possible, accentuate the benefits of positive interactions (Sanderson et al., 2002; Kareiva et al., 2007; Rockström et al., 2009). Some interactions can result in degraded ecosystems for both humans and other species; others only improve the systems for humans but not for other species; and some may result in improved ecosystems for both humans and for other species (Kareiva et al., 2007). For instance, past and modern farmers have constructed raised fields in flooded areas, expanding the living environment of ants, termites, earthworms, and woody plants (McKey et al., 2010a; Mckey et al., 2014). On the other hand, farmers have increased food production by using fertilizers that leach to nearby water bodies, often polluting river basins and coastal zones (Galloway et al., 2003). Only by facing this novel reality of the world, can scientists help humanity to understand how we create or reclaim more balanced relations with the natural world (Sanderson et al., 2002; Kareiva et al., 2007).

Historical Ecology : towards reclaiming balanced human-nature interactions

In an attempt to understand the "*temporal and spatial dimensions in the relationships of human societies to local environments and the cumulative global effects of these relationships*" (Balée, 2006, p. 77), social scientists started a research program called Historical Ecology that integrates several disciplines (anthropology, archaeology, history, geography, botany and ecology) and their methods in an attempt to create a unified framework (Balée, 1998; Balée, 2006). This program is based on four postulates (Balée, 2006): 1) almost all ecosystems on Earth have been modified by human activities; 2) human agency can lead to negative and positive effects on other species and ecosystems; 3) societies are shaped by socioeconomic, political and cultural factors that influence the degree of human impacts on landscapes; and 4) the interrelationships between humans and environments require holistic thinking, and must be analysed in their totality.

According to historical ecologists, landscapes retain the physical and human signals of both natural and cultural processes and represent a powerful integrative concept that can be used as a unit of analysis (Balée, 1998; 2006; Crumley, 2007; Armstrong et al., 2017). Since humans are considered the main agents of landscape transformation (Balée, 2006), landscapes can be seen as "*an enduring record of and testimony to the lives and works of past generations*" (Ingold, 1993, p. 152). For instance, by investigating human-made earthworks (e.g., mounds and causeways) found in the Neotropics, historical ecologists have revealed legacies of past generations in modern landscapes (Erickson and Balée, 2006). The vegetation above these structures also holds human signatures, identified by the abundance of fruit trees and other useful species (Balée, 1989; Balée, 2013; Campbell et al., 2006; Ford and Emery, 2008; Ross, 2011). Thus, earthworks and plant communities can provide insights into the various ways that landscapes were transformed over time (Erickson and Balée, 2006).

Human Niche Construction Theory

While social scientists were creating the research program of Historical Ecology, evolutionary biologists were also developing a new theory to explain how organisms - including humans - have interacted with the Earth system. Both historical ecologists and evolutionary biologists agree that humans have altered the biosphere and Niche Construction Theory can help elucidate how this happened. This theory re-examines standard evolutionary concepts by incorporating the ecological and evolutionary effects of niche construction activities (Odling-Smee et al., 2013). Odling-Smee et al. (1996) coined the term "niche construction" to define the process by which organisms modify the biotic and abiotic components of their living environment, creating new conditions to live in. Niche constructors can also be defined as ecosystem engineers that strongly transform ecosystem functioning and its organisms through time (Odling-Smee et al., 2013). By altering their environment, organisms promote changes in the natural selection pressures of the system that can influence their own niche, their descendants' niches and/or the niches of other species (Odling-Smee et al., 1996; Laland et al., 1999).

Although niche construction is applied to all species, this concept has expanded to incorporate cultural factors. Cultural factors, such as the transmission of knowledge, innovations and technologies through human generations, have allowed humans to expand their living environment (niche) more effectively (Laland et al., 2007; Laland et al., 2001). A remarkable example of this cultural and evolutionary process involves the domestication of cattle by ancient farmers to produce milk approximately 10,500 years Before the Present (BP) in the Middle East during the cultural transition from hunting to farming (Leonardi et al., 2012). Only 2,000 years later, migrants from the Middle East brought their cattle and their agriculturalist lifestyle to Europe. When a genetic mutation gave people the ability to continue to produce lactase during adolescence and adulthood and drink fresh milk in large quantities, the population of farmers and cattle grew exponentially (Salque et al., 2013). As a result, humans and cattle expanded their geographic distribution on Earth (Curry, 2013).

Domesticated landscapes and plants

Cumulative niche construction activities allowed human expansion (Ellis, 2011) and resulted in landscapes domesticated to varying degrees (Boivin et al., 2016; Kareiva et al., 2007). By domesticating landscapes, humans modified the environment where they lived, improved their welfare and created systems more suitable for humans and domesticated species (Clement, 1999). Domesticated landscapes are the main evidence of long-term human intervention in the natural world (Kareiva et al., 2007). They can be conceptualized as a continuum of management intensity around settlements from subtle interventions that involve minor transformations and less energy invested to modify the original ecosystem (e.g., managed forests) to highly transformed and cultivated landscapes that require significant investments for clearing and burning the land (Clement, 1999; Clement, 2014). For example, people cut and burn the vegetation to tame their lands and increase their security: "*It is not by chance that every village is born within a farm - a place previously socialized and tamed*" (de Oliveira, 2016, p. 118) [my translation].

While creating domesticated landscapes, people have also managed, cultivated and domesticated useful plant populations from the original landscapes or other areas. In this thesis, I define plant domestication as a long-term process in which humans increase the cultivation of useful plants and modify the direction of natural selection. In the beginning of the process, individuals of useful plants are managed *in situ* (Wiersum, 1997a; Rindos, 1984). Only later do humans select the best individuals with more desirable morphological traits (e.g., sweet or oily fruits) for cultivation outside their original population (Darwin, 1859; Rindos, 1984; Clement, 1999). Over time, humans expand the distribution and abundance of target populations in a mosaic of domesticated landscapes that favour numerous useful plants, each domesticated at different intensities and with different outcomes (Wiersum, 1997b). Thus, domesticated plants can be seen as a product of cumulative cultural niche construction activities (Boivin et al., 2016; Ellis, 2011; Smith, 2011).

DOMESTICATION OF AMAZONIA

The ancient history of Amazonia

Contrasting with most regions across the world, Meggers (1954) proposed that cultures of tropical South American forests were limited by environmental conditions, such as poor soils and climatic oscillations that constrained agricultural development during the Holocene. This assumption has been challenged by recent archaeological findings in tropical regions worldwide, including Amazonia. For at least 45,000 years, humans have co-evolved with tropical forests (Roberts et al., 2017) and from 13,000 to 9,000 BP humans expanded across South American forests (Goldberg et al., 2016). With thousands of years of human occupation, the world's largest tropical rainforests - the Amazon basin, Congo basin, and the Indo-Malay region of Southeast Asia - have experienced substantial cultural activities (Willis et al., 2004; Roberts et al., 2017).

Unlike the Congo and Indo-Malay regions, Amazonia has often been considered the last relict of "Nature" (Denevan, 1992). However, archaeologists have found a wide diversity of archaeological sites across this region, including pre-Columbian habitation sites (with and without anthropogenic soils), earthworks (mounds, causeways, raised fields, terraces, geoglyphs), megaliths, and rock art (paintings and petroglyphs) (Heckenberger and Neves, 2009; Clement et al., 2015a – see Figure 1.1). Approximately 13,000 BP humans arrived in Amazonia and occupied the most suitable environmental conditions for living (open areas with seasonal climates and caves) (Roosevelt, 2013). At least 8,000 BP, many plant species started to be domesticated in the periphery of the basin (Clement et al., 2010) and around 6,500 BP the earliest evidence of anthropogenic soils was found in the upper Madeira River basin (Mongeló, 2015). Around 2,500 BP, sedentary pre-Columbian societies expanded (Neves et al., 2004), especially along the major rivers and in seasonal areas (Denevan, 1996; Bush and Silman, 2007), where numerous earthworks and abundant anthropogenic soils have been found (Heckenberger and Neves, 2009). Bluffs at the confluence of major Amazonian rivers were probably strategic places for living and therefore they were chosen as locations for major villages (Denevan, 1996). Amazonian Dark Earth (ADE) sites – anthropogenic soils that are good markers of pre-Columbian sedentary societies – became more common from 2,500 to 500 BP. During this period, societies with intensive land-use strategies of food production and resource management occupied large portions of the basin (Clement et al., 2015a). By intensifying their domestication processes, pre-Columbian peoples have expanded their geographical distribution across Amazonia and created large settlements (1,000 persons or more) regardless of natural environmental limitations

(Clement et al., 2015a; Arroyo-Kalin, 2017).

Complex cultures, territorial polities, urbanism and large-scale landscape transformations were found in the upper Xingu River basin, covering an area of more than 50,000 km2 (Heckenberger et al., 2003; Heckenberger et al., 2008). Pre-Columbian earthworks, such as raised fields, mounds, causeways, and forest islands were mostly found in wetlands of the Llanos de Mojos region (Erickson, 2000; Denevan, 2001; Lombardo et al., 2013) and of French Guiana (Denevan, 2001; Rostain, 2008; McKey et al., 2010). Highly decorated burial urns were found in large ceremonial mounds on Marajó Island, suggesting high levels of hierarchy and complexity in this ancient society in the Amazon River estuary (Roosevelt, 1991).

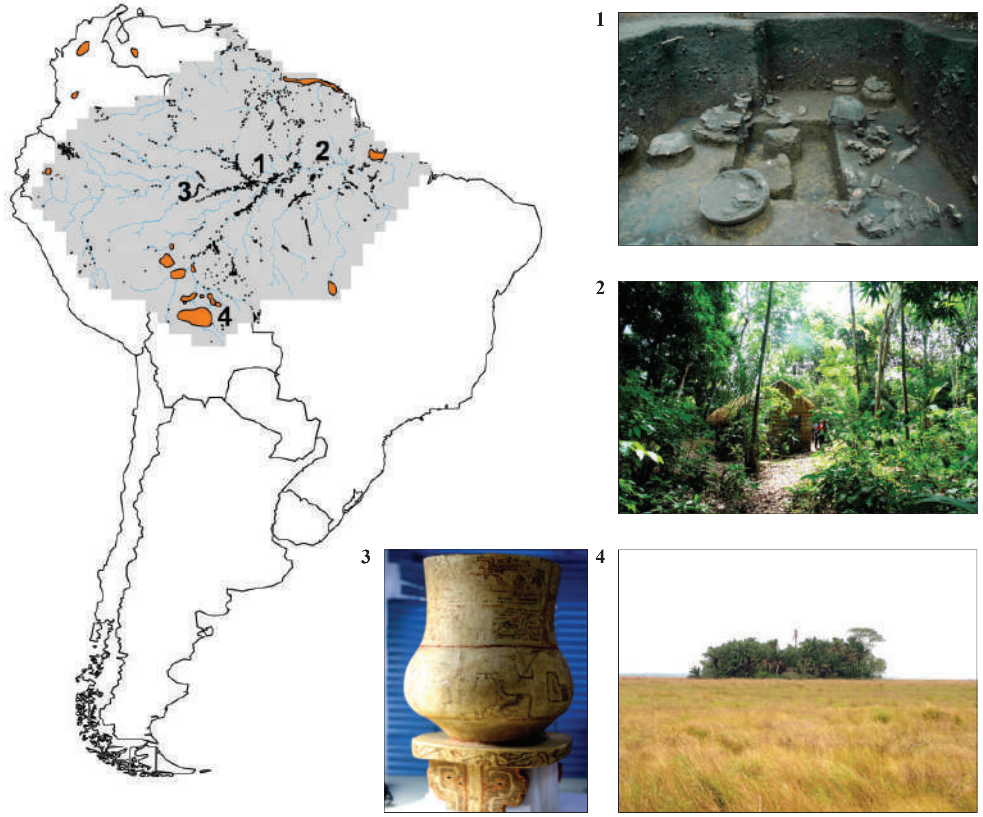

Figure 1.1. Map of archaeological sites found across Amazonia and some photos of pre-Columbian legacies. Black circles and orange polygons show the location of archaeological sites and eco-archaeological regions in Amazonia, encompassing numerous earthworks. 1) Hatahara Site with Manacapuru phase urns and anthropogenic dark soils, 2) Forest with domesticated species on anthropogenic dark soils at the FLONA Tapajós, 3) urn of the Amazon Polychrome Tradition, Tefé phase found at Tefé Lake - dated to about 700 BP, and 4) The oldest forest island - dated to 10,500 BP. Credit for archaeological sites: AmazonArch. Photo credits: Val Moraes – Central Amazon Project, Carolina Levis, Amanda Lelis, and Umberto Lombardo.

Intrigued by these recent findings, Neves (2012, p. 279) has proposed a new theory to understand how Amazonian societies evolved: "*Maybe it's time to turn the picture upside down and work with the premise that abundance, not scarcity, is the starting point for a reflection on an ancient history of the Amazon*" [my translation]. In fact, when Europeans arrived in Amazonia five hundred years ago, they described large villages with abundant food resources and surrounded by orchards. During the first European expedition along the Amazon River, Frei Gaspar de Carvajal (1542) reported how much food was stored in one village at that time: "*so much that it would support a crowd of a thousand men during a year*" (de Mattos, 2011, p. 106) [my translation]. This scenario changed completely in the subsequent centuries of conquest and colonization, as Native Amazonian populations collapsed due to infectious diseases, wars, slavery and political efforts that encouraged local people to live in the Jesuit Missions (Denevan, 1992). Denevan (1992; 2014) estimated that approximately 95 % of the perhaps 10 million Native Amazonians died during these three centuries (1550 to 1850). This rapid collapse caused the abandonment of cultivated areas that then experienced extensive reforestation (Nevle and Bird, 2008). During the nineteenth century, European naturalists reported the forest as pristine, inhabited by small scattered groups of primitive people in harmony with nature. In reality, this naive image reflects the unawareness of the demographic collapse of Amerindian societies (O'Fallon and Fehren-Schmitz, 2011). Although there have been major advances in Amazonian archaeology in the last decades, remote forest landscapes remain poorly studied (McMichael et al., 2017a), challenging scientists to evaluate the effects of past and modern societies on the ecology of this immense region.

The ecology of Amazonian forests

Ecologists are describing numerous environmental conditions, biotic interactions and natural evolutionary processes that influence the distribution and abundance of plant species across Amazonia. For instance, the distribution of large-seeded species in tropical rainforests is mainly driven by mammals that transport seeds over long distances (Jordano, 2017) and is negatively affected by the depletion of large non-human vertebrates in heavily-hunted Amazonian areas (Peres et al., 2016). Shifts in species composition at large scales are mainly explained by climate, geology and soils (ter Steege et al., 2006; Quesada et al., 2012; Toledo et al., 2012), while at the local scale, topographic and hydrologic variation associated with the water-table depth promote significant changes in species composition (Schietti et al., 2014). Interactions with other organisms (Lortie et al., 2004), such as herbivores and pathogens, have also played important roles at local scales (Terborgh, 2012). All these ecological filters are acting together, shaping plant composition in Amazonian forests, but most ecologists overlook the possibility of human agency in the forests they study.

In total, ter Steege et al. (2013) identified 4,962 trees and palm species in the ATDN forest plots and estimated that about 16,000 arboreal species may occur in Amazonian forests. Although forests have been shown to be very diverse in terms of species numbers, only 227 "hyperdominant" species collectively account for half of all the individuals found in the 1,170 forest plots of the Amazon Tree Diversity Network (ATDN) (ter Steege et al., 2013) and just 182 species store 50 % of the forest biomass (Fauset et al., 2015). Some hypotheses have been proposed to elucidate these patterns. Surprisingly, chance alone is enough to explain the hyperdominance of few species in natural systems (Scheffer et al., 2017). Another possible reason is the competitive advantages of some species with particular traits that dominate large areas of Amazonian forests (Pitman et al., 2001; Pitman et al., 2013). These traits may be associated with species' adaptations to thrive in multiple environmental conditions and to disperse over long distances. At local scales, extreme environmental conditions (e.g., poorly-drained soils) and dispersal limitation may promote aggregated forest patches dominated by a few species (Hart, 1990; Valencia et al., 2004).

Figure 1.2. Examples of useful hyperdominant species of the Amazonian forests. First, boy collecting açaí berries of *Euterpe precatoria*, an Amazonian hyperdominant domesticated species in a communal forest of the Madeira River basin. Second, Amazon-nut trees, also called Brazil nut (*Bertholletia excelsa*), growing on anthropogenic dark soils in the Madeira River basin. Third, cacao-do-mato (*Theobroma speciosum*) fruiting on anthropogenic brown soils in the Tapajós River basin. Photo credits: Carolina Levis

Humans have also played a role in expanding the abundance and distribution of plant species. Numerous useful palms and trees (e.g., *Elaeis oleifera and Bertholletia excelsa*) were shown to be associated with archaeological sites (Balée, 1989; Erickson and Balée, 2006; Junqueira et al., 2010; Levis et al., 2012; Thomas et al., 2015) and were probably dispersed across the basin by past societies (Morcote-Rios and Bernal, 2001; Guix, 2005; Shepard and Ramirez, 2011; Thomas et al., 2015). Since many hyperdominant species are used by current indigenous people (see Figure 1.2 for examples of hyperdominant and useful species), pre-Columbian management and cultivation might partly explain why these species are extremely dominant.

CONNECTING THE HISTORICAL AND ECOLOGICAL VIEWS OF AMAZONIA

Vast portions of the basin have not been studied to date, which makes the predictions of where and how much humans transformed forests speculative. While some scholars argue that most of the Amazon basin was domesticated to some degree by past societies (Heckenberger et al., 2003; Heckenberger et al., 2008; Erickson, 2008; Clement and Junqueira, 2010; Clement et al., 2015a), others argue that large pre-Columbian settlements were confined to the most suitable environmental settings and therefore forest disturbances were scarce and highly localized (Bush and Silman, 2007; Barlow et al., 2012; McMichael et al., 2012a; Piperno et al., 2015; Bush et al., 2015).

Contrasting scientific evidence existed to support both views when I started this thesis. For instance, the idea that past human impact was highly localized was supported by paleoecological studies. Bush and Silman (2007) reconstructed the regional fire and vegetation history using 22 pollen records of lakes of Western and Eastern Amazonia and found low charcoal concentrations and no pollen from corn or manioc in most lakes studied. Similarly, McMichael et al. (2012a), using new data on phytoliths – silica bodies of ancient plants – and charcoal distributions in 55 soil pits, found low frequencies of charcoal and lack of phytoliths of corn and cultivated plants in most soil samples of western and interfluvial parts of the basin. These findings supported the hypothesis that wetter and remoter forests were occupied by smaller human groups that created only sporadic and highly localized impacts on the vegetation (Bush et al., 2015; McMichael et al., 2012a; McMichael et al., 2012b; Piperno et al., 2015). However, their small sample sizes and methodologies are too limited to detect subtle human activities across vast areas and to reveal the diversity of ancient domestication processes (Stahl, 2015; Clement et al., 2015a).

Other techniques discovered legacies of large societies with considerable capacity for niche construction in environments previously described as unable to support large numbers of people. For instance, anthropogenic soils (ADE), rich in nutrients, domesticated species, charcoal and ceramics (Levis et al., 2012; Stahl, 2015; Quintero-Vallejo et al., 2015), and monumental geoglyphs (Schaan et al., 2007; Pärssinen et al., 2009) were found in interfluves not only along major Amazonian rivers. By investigating the long process of plant cultivation and forest management among indigenous people, Balée (1989; 2013) estimated that cultural forests covered 11.8 % of the Amazon basin. People cultivated at least 138 native and exotic plant species with some evidence of domestication - called domesticated species in this thesis - before European conquest, including important crops such as manioc, hot peppers, sweet potato and cacao (Clement, 1999). This number helps to place Amazonia as one of the major centres of plant domestication in the world (Meyer et al., 2012).

In this thesis, I integrate social (archaeology and anthropology) and natural (ecology, biogeography and botany) scientific disciplines to understand how much of the Amazon forest has been domesticated by long-term human activities. To achieve this aim, I applied the concepts of landscape and plant domestication to the Amazonian context (Figure 1.3).

Signatures left by past peoples vary according to the energy invested, and the tools and practices they used to transform landscapes (Clement, 2014). In settlement areas, the most common signatures of past human populations are anthropogenic soils, indigenous pottery and mounds (see number 1 in Figure 1.3). In cultivated areas, charcoal records integrated with pollen and phytolith records of domesticated plants (Bush et al., 2008; McMichael et al., 2012a; Piperno et al., 2015) and ancient raised fields (McKey et al., 2010a; Iriarte et al., 2010) have been used to identify human actions (see number 2 in Figure 1.3). In managed landscapes, legacies of past human management can be found by assessing the distribution and abundance of useful tree and palm species (Campbell et al., 2006; Ross, 2011; Levis et al., 2012; Clement, 2014) (see number 3 in Figure 1.3). The intensity of historical management practices has been shown to decrease from major and tributary rivers towards interfluvial areas in Central Amazonia (Levis et al., 2012; Bush et al., 2015) - see graph in Figure 1.3). Outside this continuum of landscape domestication, either undisturbed old-growth forest may occur (Bush et al., 2015) or landscape domestication has not yet been examined. If hunters and gatherers acted throughout Amazonia, as Barlow et al. (2012) argue, most of today's "pristine forests" were domesticated to some degree, especially during the pre-Columbian population expansion in the late Holocene (Clement et al., 2015a).

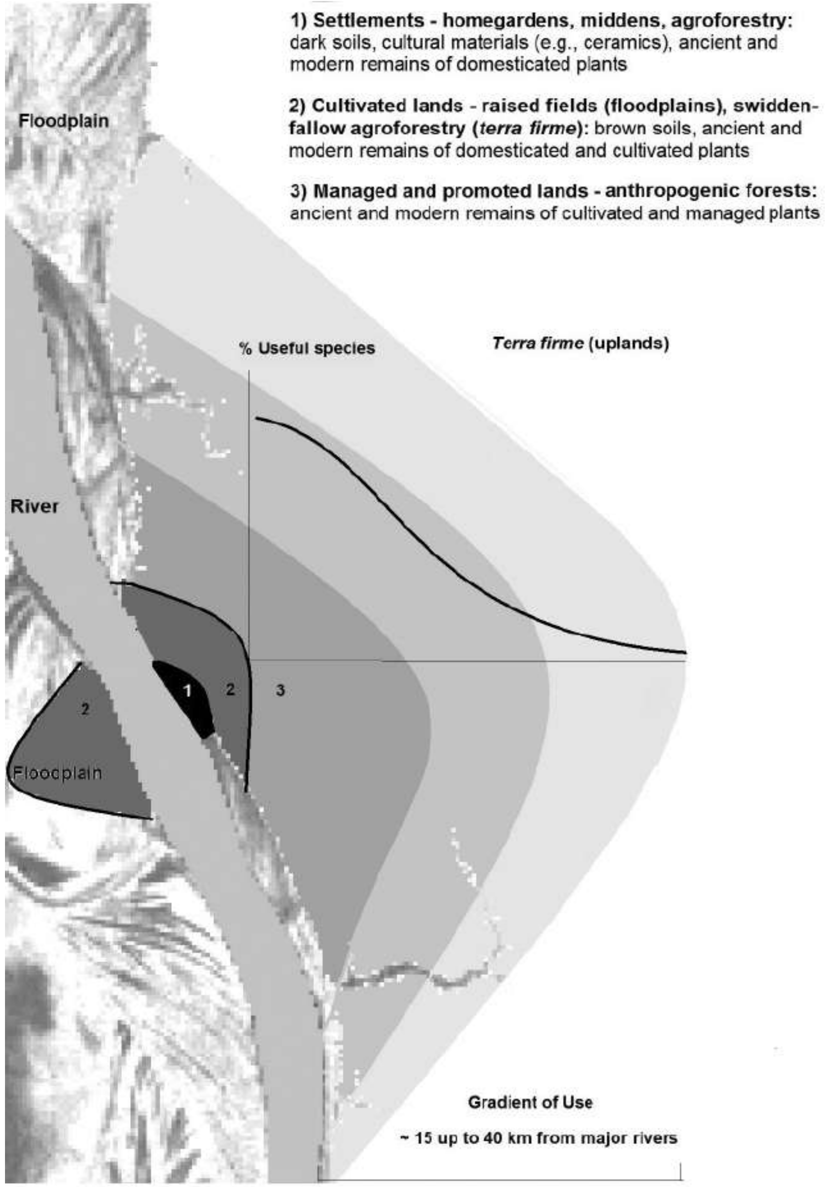

Figure 1.3. Illustration of the Landscape Domestication Model. The model shows the theoretical gradient of human influence from settlements (1), through cultivated landscapes (2), to managed and promoted landscapes (3). The black-grey colours illustrate our expectation that the proportion of useful plant species and the intensity of management practices in the landscape decreases along this gradient, predicted to be a 15-km distance curve from major rivers in Bush et al. (2015) and a 40-km distance curve in Levis et al. (2012). This figure was inspired by Clement (1999; 2014) and Heckenberger et al. (2008) and developed when I started this thesis, thus it does not incorporate the findings after 2015 that are presented and discussed in **Chapter 7** using an expanded model.

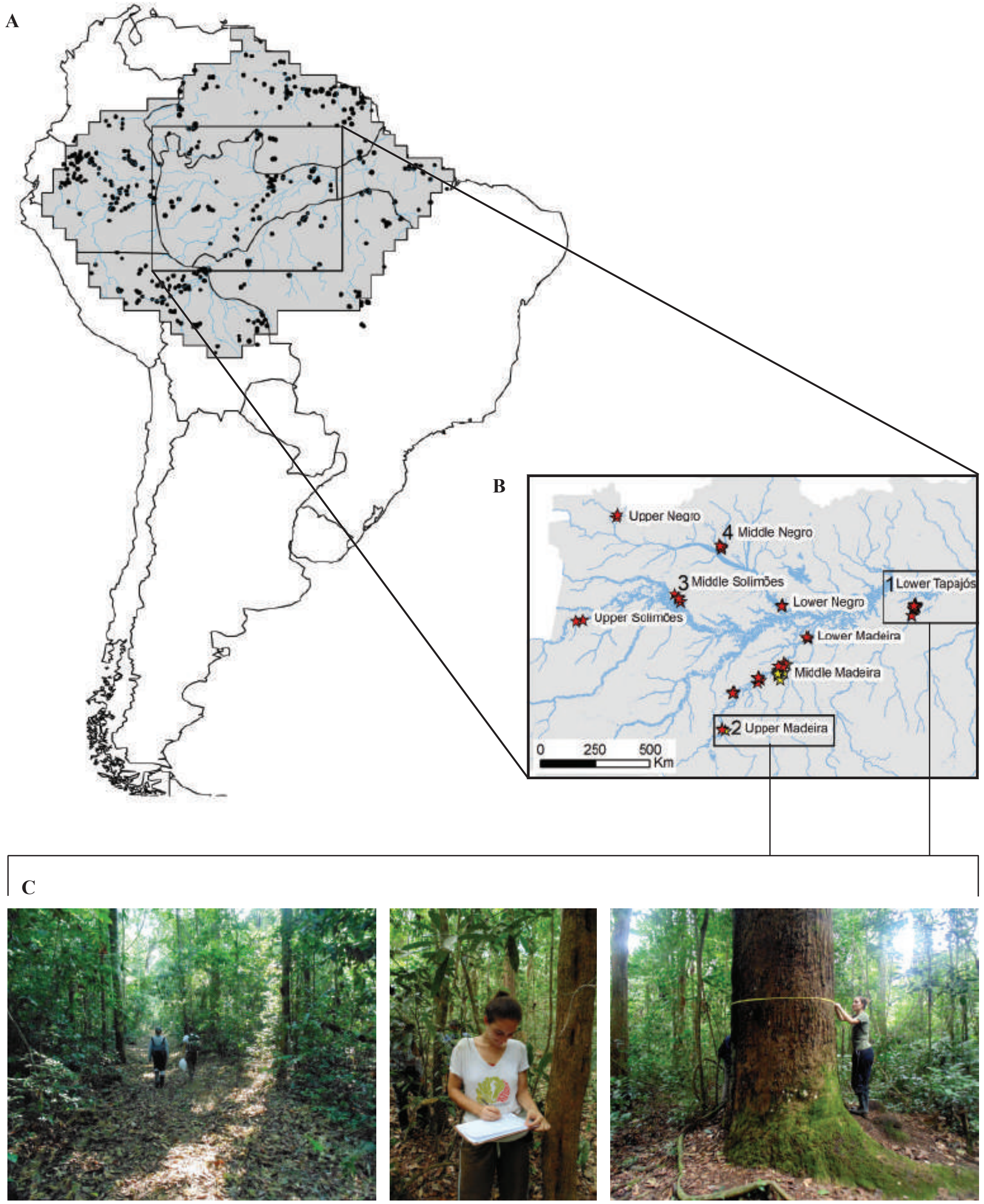

Figure 1.4. Maps showing the different spatial scales studied in this thesis. A) South America map, indicating the geological regions in which Amazonia is subdivided and the location of ATDN (Amazon Tree Diversity Network) forest plots (**Chapter 3 and 4**). Black dots are forest plots. B) Villages on the archaeological sites visited across major basins of Brazilian Amazon in which archaeological sites and forest patches of edible plants were studied (**Chapter 2 and 5**). C) Forests around villages of the lower Tapajós River and upper-middle Madeira River basins were studied in detail (**Chapter 6**). Photo credits: Rubana P. Alves (first two photos) and Bernardo M. Flores (last photo).

OVERVIEW OF THE THESIS

Objectives and hypothesis

This thesis aimed to produce a more realistic view of the effect of past and current domestication processes on modern Amazonian forests. I tested the hypothesis that Amazonian forests were domesticated to different degrees by past societies and continue to be modified by present-day management practices. The main questions of this thesis are:

1. What are the relative roles of human and environmental factors in shaping the distribution of useful and domesticated plants across Amazonian forests?
2. How do management practices and natural ecological processes interact to form forest patches dominated by useful plants?
3. How do ancient and current effects of human activities vary across forest landscapes?

To answer these questions, I investigated the patterns and processes of forest domestication in Amazonia at different spatial and temporal scales (Figure 1.4), using an interdisciplinary approach. I combined data from floristic inventories, archaeological sites, environmental measures, ethnographic assessments and literature review of useful plants. In some of parts of my thesis (**Chapter 2-4**), I used existing databases of archaeological sites[3] and floristic inventories collected and organized by other researchers[4], and basin-wide data on environmental factors that are available online (for more details about these databases see methods section in **Chapter 3**). I also carried out field surveys along gradients of human influence in different river basins of the Brazilian Amazon (**Chapter 5-6**). In the field, I interviewed local people, and together with them I carried out participatory mapping and guided tours around their villages. Additionally, I collected soil and plant vouchers of useful species to compare ancient and current land-use histories.

Thesis chapters

This thesis consists of seven chapters designed to evaluate long-term human influence in modern Amazonian forests.

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[3] The Amazonian Archaeological Sites Network (AmazonArch - https://sites.google.com/view/amazonarch) - AmazonArch is the major international network that shares data and information about archaeological sites distributed across Amazonia in a georeferenced database.

[4] Amazon Tree Diversity Network (ATDN - http://testweb.science.uu.nl/Amazon/atdn/) - ATDN is the major international network that shares data and information on arboreal composition of Amazonian forests. This network holds floristic data for all trees and palms with DBH > 10 cm from approx. 1400 1-ha plots in the Amazon basin and the Guiana Shield.

In **Chapter 1**, I present this general introduction, contextualizing the long-term effects of humans on our planet and explaining why the effects of past societies on Amazonian forests are highly controversial.

In **Chapter 2**, we compare the density of Amazonian Dark Earth (ADE) – a particular type of archaeological site that indicates sedentary human occupation – between major and tributary rivers of the Amazon basin. We also compare the extension of bluffs between these two types of rivers to evaluate if the distribution of pre-Columbian habitation sites depends on the availability of these natural conditions. Then, we discuss the implication of past occupation patterns for understanding the domestication of Amazonian landscapes.

In **Chapter 3**, we analyse the effect of past human influences and environmental factors by overlaying data from 1,091 floristic inventories of the Amazon Tree Diversity Network (ATDN) on a map of more than 3,000 archaeological sites across different Amazonian geological regions. We then tested if the distribution, abundance and richness of 85 tree and palm species domesticated by pre-Columbian people are correlated with the distribution of ancient people. Our analysis also incorporates environmental data to distinguish anthropogenic signals from environmental influences in Amazonian vegetation.

In **Chapter 4**, we reinforce our discoveries with a technical comment to illustrate how the effect of pre-Columbian peoples on Amazonian forests is still overlooked or criticized by other scientists. In this comment, we compared the influence of ancient and modern peoples in the abundance and richness of the 85 domesticated species found in Amazonian forests at basin-wide and landscape scales.

In **Chapter 5**, we develop a conceptual model about how forests have been domesticated by Amazonian people across different spatial and temporal scales using data from an extensive literature review and field surveys. In this chapter, the spatial association of domesticated forests and archaeological sites is investigated in detail using field data. In the field, we investigated the distribution and composition of forest patches of edible perennial species surrounding riverside villages located on archaeological sites in four major river basins of Brazilian Amazonia.

In **Chapter 6**, we evaluate the effect of pre-Columbian and current management practices on Amazonian forest soils, structure and composition at the landscape scale. To compare the effects of ancient and current management practices on modern forests, we carried out forest inventories at different distances from ancient and contemporary human settlements in riverine and interfluvial areas.

In **Chapter 7**, I synthetize the findings of this thesis and discuss the importance of considering long-term human activities for understanding the ecological patterns found in Amazonian forests.

GLOSSARY

Definition of important concepts presented in this thesis

AMAZONIA	Encompasses the Amazon basin and the Guiana Shield.
USEFUL SPECIES	A species considered useful for humans.
EDIBLE PLANT	A plant that provides a food resource to humans.
DOMESTICATED SPECIES	A species with some evidence of selection and propagation by humans during the plant domestication process (see the definition of this process in the text).
HYPERDOMINANT SPECIES	Tree and palm species that account for half of the total estimated number of individuals or biomass in Amazonian forests.
HUMAN INFLUENCE	Changes caused by past or current human societies in the natural ecological processes.
ANCIENT HUMAN HISTORY	The history of Amazonian people before the arrival of the Europeans, also called as pre-history.
ARCHAEOLOGICAL SITES	Places where material remains of past human activities are still visible in the landscape.
NATIVE AMAZONIANS	First people to live in Amazonia.
PRE-COLUMBIAN PEOPLES	People living in Americas before the arrival of Christopher Columbus in 1492.
INDIGENOUS PEOPLES	The descendants of native ethnic groups and members of an indigenous community that retains historical and cultural connections with the social organization of pre-Columbian indigenous societies.
TRADITIONAL PEOPLES	Culturally differentiated and recognizable groups that have their own forms of social organization using knowledge, innovations and practices generated and transmitted by tradition.
LOCAL MANAGEMENT PRACTICES	Practices resulted from process of making and effectuating decisions about the use and maintenance of resources within a local territory.
PRISTINE FORESTS	Forests without human influence, untouched.
OLD-GROWTH FORESTS	Mature forests without recent human influence, but not necessarily pristine.
CULTURAL FORESTS OR DOMESTICATED FORESTS	Forest transformed by local management practices.

CHAPTER 2

Widespread distribution of ancient peoples along tributary rivers of Central Amazonia

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ABSTRACT

The Amazonas River and its larger western tributaries transport huge sediment loads from the Andes with nutrient-rich waters in their fertile floodplains. Conversely, most of the northern and southern tributaries have black or clear nutrient-poor waters and less fertile floodplains. Because of this, there is a long-held but unproven tendency in the archaeological literature to consider white-water *várzeas* more suitable for past human occupation than hinterlands or areas along black or clear-water rivers. Such assumptions then migrated from Archaeology to Ecology in current debates about the extent of pre-colonial human impacts on shaping the composition and structure of Amazonian landscapes. The aims of this study are to: 1) show the presence of ADEs along tributary rives; and 2) test the hypothesis that the density of ADEs along black or clear-water tributaries is comparable to that along the major white-water rivers nearby. Finally, we discuss the implications of ADEs along tributaries to understand the past human impact on current Amazonian landscapes. In this study, ADEs were mapped along 12 km long river sections of 14 tributaries of the Madeira, Solimões and Negro Rivers. Where we investigated, we found many ADE sites along tributaries and confirmed our hypothesis. Hence, the lower resource availability of tributaries may not have been a limiting factor for pre-Columbian occupation. We found that past sedentary populations established on bluffs of the lower courses of tributaries. If there were so many people along tributaries, adjacent forests on the interfluves were also manipulated in some degree by people who settled on their margins. We also suggest some attenuation of the impact left by pre-Colombian people in forests of Central Amazonia from the mouth of tributaries toward their headwaters. Our data indicate that if research projects focus more on tributaries, a significantly larger number of ADEs and other signs of past human impact in inter-fluvial areas of Amazonia will be found. We conclude that the overall density of pre-Columbian occupation and landscape intervention in Central Amazonia is being underestimated.

The challenge to understand the influence of past human occupation on Amazonian forested landscapes has led to a considerable debate among natural and social scientists. On the one hand, some defend that humans significantly modified Amazonian forests during the Holocene (Heckenberger et al., 2007; Clement and Junqueira, 2010; Levis et al., 2012; Balée, 2013). On the other hand, others propose that such influences were only locally significant and should not be considered in discussions about conservation of Amazonian biodiversity (Bush and Silman, 2007; Barlow et al., 2012; McMichael et al., 2012a). Despite the scientific disagreement, most agree that past human impact on the landscape was heterogeneous, with high impact within and immediately adjacent to archaeological sites. The sites that are most accepted by both groups as old long-duration settlements are Amazonian Dark Earths (ADEs – Smith, 1980) or *Terras Pretas de Índio* (TPIs), sites known to be good markers of past sedentary human occupation (Neves et al., 2003).

Archaeology, therefore, has an important role in this debate, since knowledge of "where" these sites are distributed across the Amazonia, and "when" they were occupied, as well as the footprint left by their ancient inhabitants, can help us understand the changes associated with their occupation. Within the range of archaeological sites known for Central Amazonia, we focus on one particular kind of archaeological site - ADE.

The effort of mapping ADEs has been concentrated along major Amazonian rivers (WinklerPrins and Aldrich, 2010). Floodplains of white-water rivers, locally known as *várzeas*, host high biomass and biodiversity of plants and fish species (Junk et al., 2011). The abundance of fishes in whitewater rivers attracts other animals (amphibians, reptiles, birds and aquatic mammals), making white-water rivers a great location for obtaining animal protein (Beckerman, 1994). The greatest extension of *várzeas* is in the central and western parts of the Amazon basin (Junk et al., 2011). Denevan (1996) suggests that long-term settlements were placed on bluffs along major rivers where people could exploit a wide variety of resources from the whitewater floodplains and *terra-firme* forests throughout the year.

Tributaries of these rivers, on the other hand, usually have black or clear nutrient-poor waters, with floodplains unsuitable for agriculture and are considered to contain lower biomass of aquatic resources (Junk et al., 2011). The middle and upper courses of such tributaries are narrower and penetrate into remote areas that appear to provide fewer resources for sedentary human occupations. However, blackwater floodplains are geologically more stable and have been shown to yield fish crops comparable to white-water systems (Henderson and Crampton, 1997). They are also much more abundant: *várzeas* occupy perhaps 5% of Amazonia, while other wetlands, including tributaries, lakes and swamps, occupy another 25% (Junk et al., 2011 -

Figure 2.1A). Due to the complicated logistics to survey numerous tributaries for ADEs, archaeological surveys have so far given less attention to tributaries, leading to a lack of information about the distribution of ADEs along these rivers.

The aims of this study are to: 1) show the presence of ADEs along black and clear-water tributaries of major white-water rivers; 2) test the hypothesis that the density of ADEs along black or clear-water tributaries is comparable to that along the major Amazonian white-water river nearby. We then discuss some of the implications of this new analysis in terms of the impact of past human occupation for current Amazonian forests.

STUDY AREA

The study was carried out along the Madeira and Solimões River basins (Figure 2.1A), with broad extensions of *várzeas* and *paleo-vázeas*. Many *várzeas* and river islands were used as crop fields during the sixteenth century (Myers, 2004). Conversely, tributaries of the Madeira and Solimões are smaller rivers and streams (*igarapés*) with floodplain forests (*igapós*) and lakes, all with black or clear nutrient-poor waters (Junk et al., 2011).

Floodplains are subjected to a predictable annual flood-pulse that varies in amplitude and duration (Junk et al., 1989). Flood-pulses expose river banks to erosion and sedimentation processes, particularly during high water levels, eroding and burying old humic layers. These processes occur intensively along white-water rivers banks, causing the phenomenon of "fallen lands" (Sternberg, 1998) – the collapse of river banks and bluffs.

Archaeologists have surveyed the Madeira Basin for over 90 years: 129 sites were identified between the Rio Machado (tributary) and the city of Borba, along the main channel (Moraes and Neves, 2012). Most ADE sites were located on bluffs of the Madeira River and of nearby *várzea lakes*. Only three tributaries have been well studied: 9 sites were found along the Madeirinha River, 14 along the lower Aripuanã River and 7 along the lower Manicoré River (Moraes and Neves, 2012).

Archaeological studies of the Solimões Basin started later and are restricted to particular areas, especially to the interfluve between the lower Solimões and lower Negro Rivers, where more than 60 sites were found, most of them ADEs. For over 60 years, archaeologists have discussed the importance of this huge river (approximately 1,700 km) for understanding the pre-history of Amazonia. The Solimões River is considered the main route used by ancient Amazonian people to connect the Andes to the Atlantic Ocean (Meggers and Evans, 1957).

During the last decade, 73 archaeological sites have been found along one transect of approximately 600 km from Coari to Manaus (Neves, 2010). Archaeologists from a multidisciplinary project called PIATAM (Strategic Environmental Intelligence for the Petroleum Industry in Amazonia) also surveyed the Solimões and its tributaries: 86 additional sites were identified in the same area (Lima and Tamanaha, 2007; 2008). Currently, archaeologists are surveying tributaries and lakes of the Middle Solimões, such as the Tefé River and the Amanã Lake (Costa, 2008; Gomes, 2011; Belletti, 2013).

DATA ANALYSIS

Identification of ADEs along the tributaries of the Madeira and Solimões Rivers

In this study, ADEs were mapped (using participatory mapping techniques or marked in the field with a GPS) along the Puru-puru, Mariepaua, Jatuarana, and Acará Rivers, all tributaries of the Madeira. In the Solimões River Basin, ADEs were mapped along the Manaquiri, Janauacá, Manacapuru, Anamã, Coarí, Tefé Rivers and Amanã Lake. All sites in the Solimões basin were identified and marked in the field. The density of ADEs along all tributaries was quantified considering the length between the first and last ADE site found in each tributary river.

Comparison of ADE density and bluff availability between the major river and its tributaries

The density of ADEs along nine sections of 12 km for both types of river (major and tributary) was estimated. We selected sections of the Madeira and Solimões as close as possible to the mouth of the tributaries that we used in the analyses and where archaeological studies had been concentrated. Shuttle Radar Topography Mission (SRTM) and Landsat TM images were used to identify floodplains and bluffs on river banks, and the extension of bluffs on both sides was measured using ArcMap tools, which calculate linear sections. To test the difference of ADE density and bluff availability between major rivers and tributaries we used ANOVA (Crowley, 2007).

RESULTS AND DISCUSSION

In the Madeira Basin, we found 8 ADE sites along a 16 km stretch of the Purupuru River, 6 sites along 56 km of the Mariepaua River, 6 sites along 11 km of the Jatuarana River and 3 sites along 12 km of the Acará River (Figure 2.1B). In the Solimões Basin, we found 6 sites along a 5 km stretch of the Manaquiri River, 5 sites along a 16 km stretch of the Janauacá River, 6 sites along 68 km of the Manacapuru River, 9 sites along 46 km of the Anamã River, 10 sites along 115 km of the Coari River, 25 sites along 124 km of the Tefé River, and 29 sites along 126 km of Amanã Lake (Figure 2.1B).

We found dense distribution of ADEs along all tributaries we studied in the Madeira and Solimões Basins, which supports the argument that the previously considered remote interfluvial areas were in fact occupied by human sedentary populations. In some tributaries within 10 km of the Madeira floodplains, ADEs are larger than 40 ha, thus comparable to ADEs found along the major rivers. We also found ADE sites more than 120 km away from mouth of tributary rivers, e.g., along the Tefé and Coari Rivers (Figure 2.1B), indicating that sedentary human occupation also occurred in the middle courses of tributaries. Surveys have not yet reached tributary headwaters.

The density of ADEs found along the Madeira River was lower than the density of ADEs found along some of its tributaries (Figure 2.2A), but we didn't find a significant difference between types of rivers. Bluff extension along the Madeira River, however, was significantly lower than along its tributaries (Figure 2.2B, $p < 0.01$).

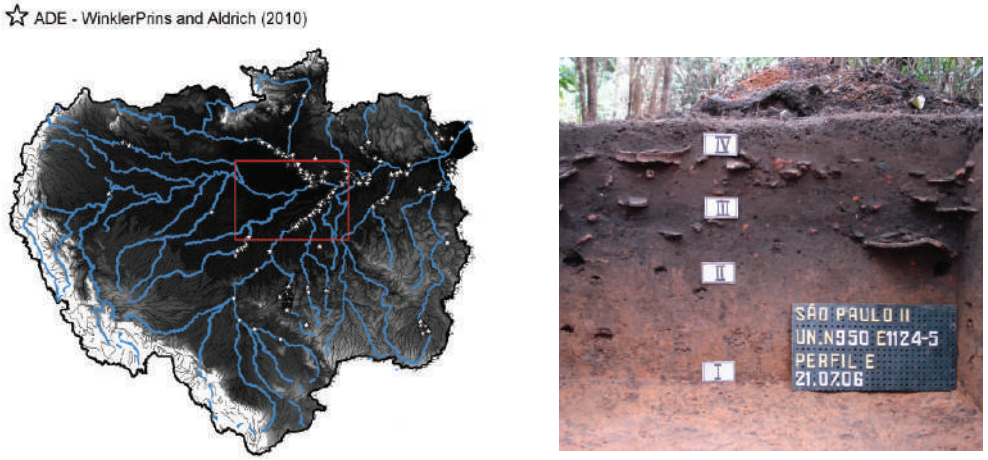
For the Solimões, the density of ADEs found along the main channel was lower than along its tributary rivers (Figure 2.2A), but again this difference was not significant. The floodplains of the lower Solimões are larger than those of the lower Madeira, resulting in a much lower extension of bluffs, when compared to its tributaries (Figure 2.2B, $p = 0.001$). In fact, many ADE sites are located on the floodplains of the Solimões River.

These results confirm our hypothesis: the density of ADE sites along the lower courses of black or clear-water tributaries is comparable to that along the two major white-water rivers associated with these tributaries.

Dynamism of várzeas: many ADEs may have been eroded and buried by white-water rivers

The Madeira River is one of the major Amazonian rivers and archaeological records indicate a long-term history of occupation with large settlements around 1000 AD

A. Amazon Basin **C.** Amazonian Dark Earth (ADE)



B. Study Area: Madeira and Solimões River Basins

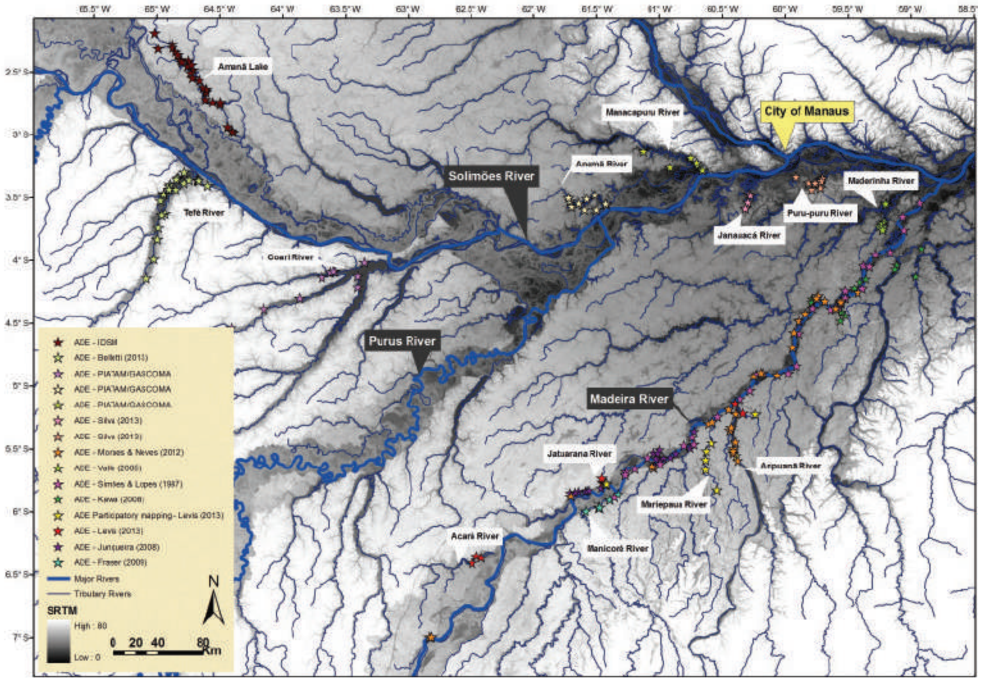


Figure 2.1. A) Major Amazonian rivers with the Amazonian Dark Earth sites identified by WinklerPrins and Aldrich (2010); B) Study area that covers part of the Madeira and Solimões River Basins, tributaries and ADEs found in the area; C) Picture of an Amazonian Dark Earth found in the study area. Shuttle Radar Topography Mission (SRTM) image obtained at http://www.relevobr.cnpm.embrapa.br/download/am/am.htm. Photo credits: Helena Lima – Central Amazon Project.

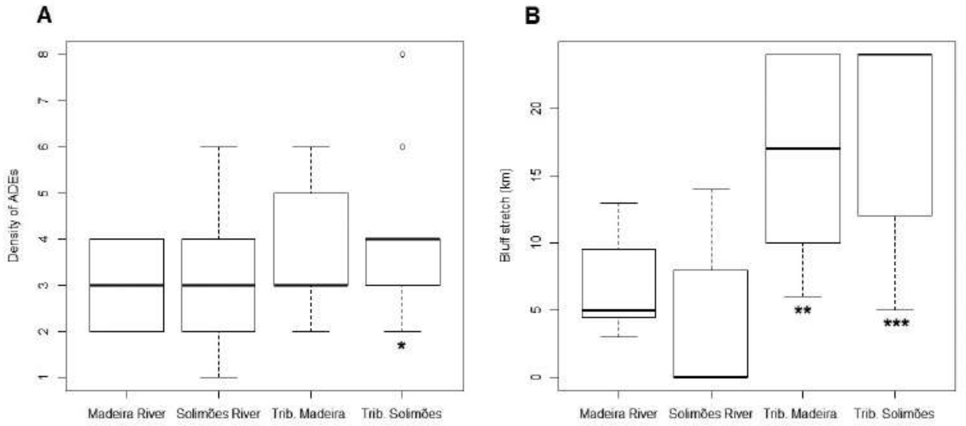


Figure 2.2. A) Boxplot showing the density of Amazonian Dark Earths (ADEs) along 12 km river sections for the Madeira, Solimões and their tributary rivers; B) Bluff extension on river banks of the Madeira and Solimões compared to their tributaries. Codes (p values: ≤ 0.001 '***'; ≤ 0.01 '**'; ≤ 0.1 '*') and number of river sections per treatment = 9.

(Moraes and Neves, 2012). Although many ADEs were found on its banks, our findings revealed an unexpected pattern: more ADEs are located on the banks of some tributaries than on the Madeira River itself. Could this pattern be explained by the great dynamism of whitewater floodplains?

The fluvial dynamics of the Madeira are intense, with strong sedimentation and erosion along the floodplains (Teixeira and Maia, 2009). The same processes occur, but even more intensively, along the floodplains of the Solimões (Sternberg, 1998). Additionally, the river's sediments can bury old soil layers during high water levels each year, covering archaeological sites (Tamanaha, 2012). Floodplain margins of today are very different than those of only two decades ago, and certainly even more different when compared to 1000 years ago, when large human populations were living there (Moraes and Neves, 2012; Tamanaha, 2012). As a result, many ADEs on the banks of white-water rivers may have been eroded or buried through time, which may in part explain why we found fewer ADEs on major rivers. This was already noted by Curt Nimuendaju, when he tried unsuccessfully in the 1920s to relocate the Miracanguera site, excavated adjacent to Itacoatiara by Barbosa Rodrigues in the 1880s and almost completely destroyed by the erosion of the Amazon River by then (Nimuendaju, 2004).

Bluff Model: complementarity of habitats and resources

We found fewer bluffs along the banks of the Madeira and Solimões Rivers than along their tributaries. Thus, another explanation for our findings could be that the limitation of bluffs along the Madeira and Solimões led sedentary societies to spread along tributaries, occupying any suitable places to live, as described by Denevan (1996). The significance of tributaries to understanding the history of occupation in Amazonia is probably much greater than previously thought.

The complementarity of habitats and resources around bluffs of major white-water rivers is thought to have been important to sustain large populations before European conquest (Denevan, 1996). The great number of ADE sites found in the confluence of the Negro and Solimões Rivers, some with a long history of occupation (Neves and Petersen, 2006), indicates that this region was a strategic place to live. This region is composed of a variety of habitats, including floodplains of both white and black water rivers, lakes, grasslands and interfluvial forested uplands. This combination of abundant resources and different habitats form a perfect scenario for the development of long-duration settlements in Central Amazonia (Neves et al., 2003).

We found that past human populations were also established on bluffs of the lower courses of tributary rivers. Along the Unini River, a tributary of the Negro River, ADEs dating to nearly 2000 years before present were found at Floresta and Lago das Pombas sites, 110 km from its mouth (Lima, 2012). *Igapós* and *terra-firme* forests were close by, and people living in these distant settlements certainly found other advantages. Black and clear water rivers may be nicer places to live, compared to white-water rivers, with drinking waters containing less or no sediment, fewer pests and parasites, such as mosquitos, and easier navigation because of slower currents and wind-driven waves. Possibly there were so many people living along the Madeira and Solimões at that time that bluffs were crowded, and the need to spread and occupy tributary sites was inevitable, perhaps also avoiding cultural conflicts and war.

Sampling method as a possible explanation for the pattern we found

Most of the archaeological surveys reported here were opportunistic; in other words, surveys were based on sites easily identified in the landscape (Richards, 2008). Landscapes were not equally represented and sampling was not systematic. Also, the broad extension of *várzeas* in the Solimões has challenged archaeologists to access hidden bluffs. Therefore, false absence of ADEs along major rivers may be the consequence of sampling.

The same problem may have happened in areas where ADEs were mapped using participatory mapping techniques. Participatory mapping is based on local people's knowledge of the landscape in their living-area. Consequently, this technique covers a large area, but may fail to identify those sites that are not well known by locals. Mariepaua River, for instance, is a tributary of the Madeira River that was sampled only by participatory mapping. Using systematic and judgment sampling designs, we should be able to detect more sites than the ones identified using participatory mapping and opportunistic techniques. Future archaeological surveys must focus on these vast empty spaces, improving our knowledge of the distribution of ADEs.

Cultivation in várzeas was not necessary for the existence of long-duration settlements

Abundant ADE sites along tributaries are an indication that proximity to fertile floodplains is not always vital to sustain sedentary human populations in Amazonia. Ancient Native Amazonians knew techniques for soil management, plant domestication and for long-term cultivation or management of non-domesticates, such as palms that allowed subsistence independent from *várzea* resources (Wood and McCaan, 1999; Clement, 1999; Denevan, 2001).

Our data suggests that the resource availability of black and clear water systems may not have been a limiting factor for pre-Columbian occupation. Additionally, fish yields in black-water lakes have been found to be higher than in white-water systems during the high water season (Henderson and Crampton, 1997). The abundance of fish attracts other animals making black and clear-water systems also good for obtaining animal protein.

What is the relation between ADEs and the transformation of Amazonian forests by pre-Columbian people?

Useful plants found in secondary forests on ADE sites are associated with past human selection and management (Junqueira et al., 2010). Evidence of plant manipulation was also found in forests near settlements (Levis et al., 2012), where the surrounding forests were transformed by agricultural, hunting and gathering activities. Levis et al. (2012) found higher proportions of useful species in forests closer to ADEs compared to those located in more distant areas. Junqueira and Clement (2013) showed that the human footprint in mature forest located on ADEs decreases after site abandonment. Nevertheless, even forests located almost 40 km from Solimões and Madeira still contain a floristic composition altered by past human management (Levis et al., 2012; see also Figure 2.3).

Implications for understanding the impact left by pre-Columbian people in Central Amazonia

Since the archaeological sampling effort has been concentrated along the main Amazonian rivers, such as the Madeira and the Solimões, the overall density of ADEs and the extent of pre-Columbian influence on Amazonian forests are being underestimated. We also need to investigate the bluffs of tributary rivers to better understand the history of occupation and impact left by pre-Columbian people in Amazonia, as these areas were also densely occupied before European conquest. If there are so many ADE sites along tributaries, forests on interfluves were also manipulated to some degree by people who occupied their margins.

The human impact on the vegetation decreases as one moves away from rivers (Bush and Silman, 2007; Levis et al., 2012) and with time following the abandonment of the site (Junqueira and Clement, 2013). Tributaries penetrate interfluves of major rivers, allowing the existence of sedentary populations in places often considered remote. Consequently, even forests considered primary were managed, and thus concentrated useful plants (Figure 2.3). We still don't know how far and how long after abandonment the persistence of human management is identifiable in the forest landscape, although this depends upon the species involved, their growth habit and longevity (Clement, 1999). Our data indicates, however, that many more ADEs are to be found and that past human impact in inter-fluvial areas of Central Amazonia was greater than imagined.

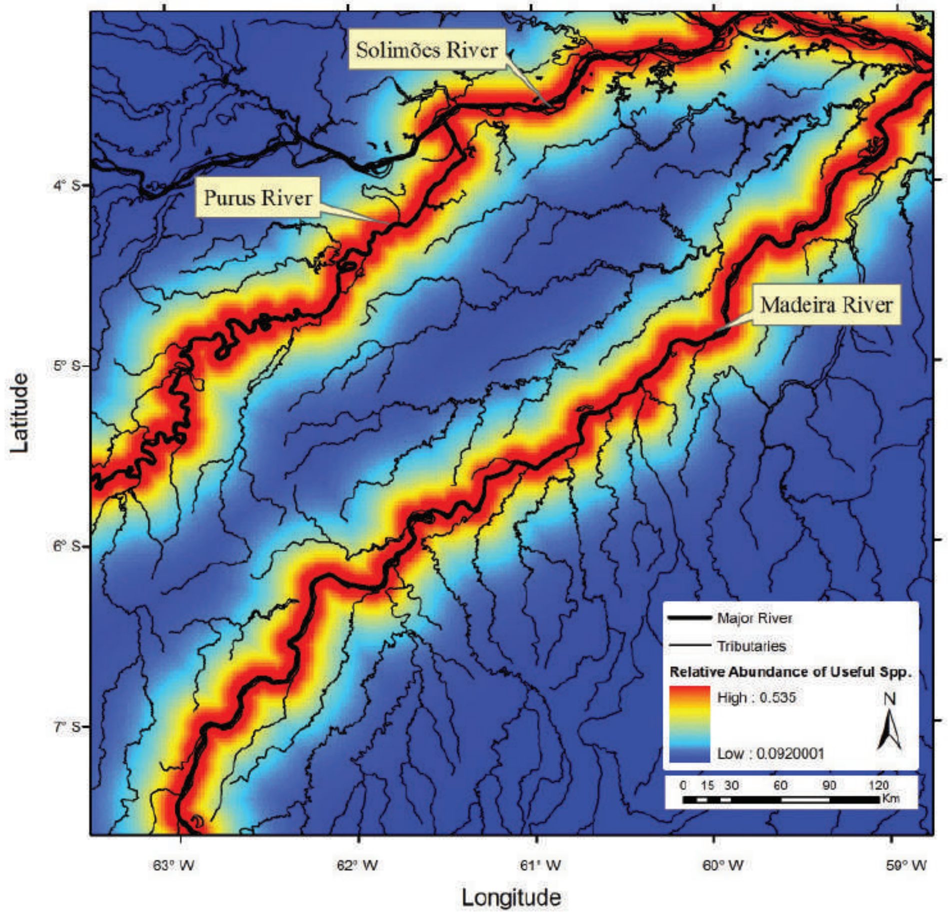


Figure 2.3. Map showing that past human impact on the vegetation decreases as one moves away from major rivers (based on regression model developed by Levis et al., 2012). In this extrapolation, the model only addresses three major Amazonian rivers, the Madeira, Purus and lower Solimões. ADEs, however, are also abundant along there tributaries. If we also investigate the past human influence on the vegetation as we move away from tributaries, dark blue areas of this map will shrink towards the center of the tributaries interfluves.

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AUTHOR CONTRIBUTIONS

C.L. and C.R.C. conceived the study; C.L., M.S.S., M.A.S., C.P.M., E.K.T., B.M.F., E.G.N. collected data; C.L. designed and carried out most of the analyses; C.L., E.K.T., B.M.F., E.G.N., C.R.C. wrote the manuscript; all authors discussed further analyses, and commented on various versions of the manuscript.

CHAPTER 3

Persistent effects of pre-Columbian plant domestication on Amazonian forest composition

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ABSTRACT

The extent to which pre-Columbian societies altered Amazonian landscapes is hotly debated. We performed a basin-wide analysis of pre-Columbian impacts on Amazonian forests by overlaying known archaeological sites in Amazonia with the distributions and abundances of 85 woody species domesticated by pre-Columbian peoples. Domesticated species are five times more likely to be hyperdominant than nondomesticated species. Across the basin the relative abundance and richness of domesticated species increase in forests on and around archaeological sites. In southwestern and eastern Amazonia distance to archaeological sites strongly influences the relative abundance and richness of domesticated species. Our analyses indicate that modern tree communities in Amazonia are structured to an important extent by a long history of plant domestication by Amazonian peoples.

Increasing evidence suggests that the modern floristic composition and structure of Amazonian forests have been influenced by past human activity (Clement et al., 2015a). Seasonal forests and river margins are thought to have been modified more intensively than wetter and less accessible forests (Bush et al., 2015; McMichael et al., 2012a). At the basin scale, the magnitude to which pre-Columbian peoples transformed forests is still unclear (Stahl, 2015; Piperno et al., 2015). Humans transformed forests in many ways, through plant cultivation (preceded by cutting and burning), seed dispersal and propagation, and in situ tending of useful resources, such as domesticated plants (Clement, 1999; Boivin et al., 2016).

Domestication of plant populations is a result of the human capacity to overcome selective pressures of the environment by creating landscapes to manage and cultivate useful species, generating fundamental changes in ecosystems at local and global scales (Boivin et al., 2016). During the domestication of tree populations, initially the ‘best’ individuals were and are managed *in situ* (Clement, 1999), and only later, if at all, selected and propagated in home gardens and other anthropogenic landscapes. These initial actions of favouring individual trees are referred to as “incidental domestication” (Rindos, 1984). The continuation of these activities tends to expand the target populations, both in area and in abundance. Current tending, cultivation and dispersal of species that occur in high frequency and abundance in anthropogenic landscapes strongly suggest that selective practices have been used in the past (Kennedy, 2012). Initially humans cultivate the ‘best’ variety, selecting individuals with more desirable morphological traits (e.g., larger fruit size) for future cultivation (Darwin, 1859). Selection may lead to dispersal of plant populations from their original wild habitats to new anthropogenic landscapes (Zohary, 2004). This dispersal may give rise to a founder event, which occurs when new populations are based on a small sample of the original population, and consequently have less genetic and morphological variability (Clement, 1999). In tree populations, genetic and morphological changes are subtle, especially when managed within forests, and changes may not continue beyond the initial category of incipiently domesticated populations (Clement, 1999). Humans have been domesticating plants since at least 10,000 BP (years Before the Present) (Purugganan and Fuller, 2009). In Amazonia, plant domestication started earlier than 8,000 BP, mainly in the periphery of the basin (Figure 3.1 and Figure A3.1), where wild populations of domesticated plants have been identified by genetic and morphological analyses (Clement et al., 2010). Five centuries after the demographic collapse of Amerindian populations (O’Fallon and Fehren-Schmitz, 2011), domesticated plants persist in Amazonian forests (Clement, 1999), frequently associated with fertile anthropogenic soils (Junqueira et al., 2010) and pre-Columbian mounds (Erickson and Balée, 2006) where human populations were once abundant (Clement et al., 2015a). Here, we used the abundance, richness and distribution of domesticated plants in forests to assess changes in Amazonian forest composition due to past human activities.

The distribution and abundance of plant species are fundamentally influenced by environmental and evolutionary processes. The synergistic effects of these processes have resulted in distinct plant assemblages across Amazonian regions (ter Steege et al., 2006; Hoorn et al., 2010; ter Steege et al., 2013). Evolutionary processes operate at all spatial scales and they are essential in determining the regional species pool. Environmental filtering (such as geology, soil, climate) and biotic interactions (such as animal seed dispersal and predation) drive differences among species assemblages across ecological gradients. For example, effective seed dispersal of large-seeded tree species decreases in heavily hunted forests because of the depletion of large vertebrates (Peres et al., 2016). Composition and dominance patterns of plant assemblages in Amazonian forests differ from one phytogeographical region to another (ter Steege et al., 2006; ter Steege et al., 2013), vary along spatial and temporal gradients of rainfall (ter Steege et al., 2006; Esquivel-Muelbert et al., 2016; Bush and McMichael, 2016), terrain water saturation (Schietti et al., 2014) and soil fertility (ter Steege et al., 2006), and may be the result of dispersal limitation (Peres et al., 2016). We evaluated whether the plant domestication process acted together with evolutionary and environmental processes to determine the ecological patterns documented in Amazonian forests.

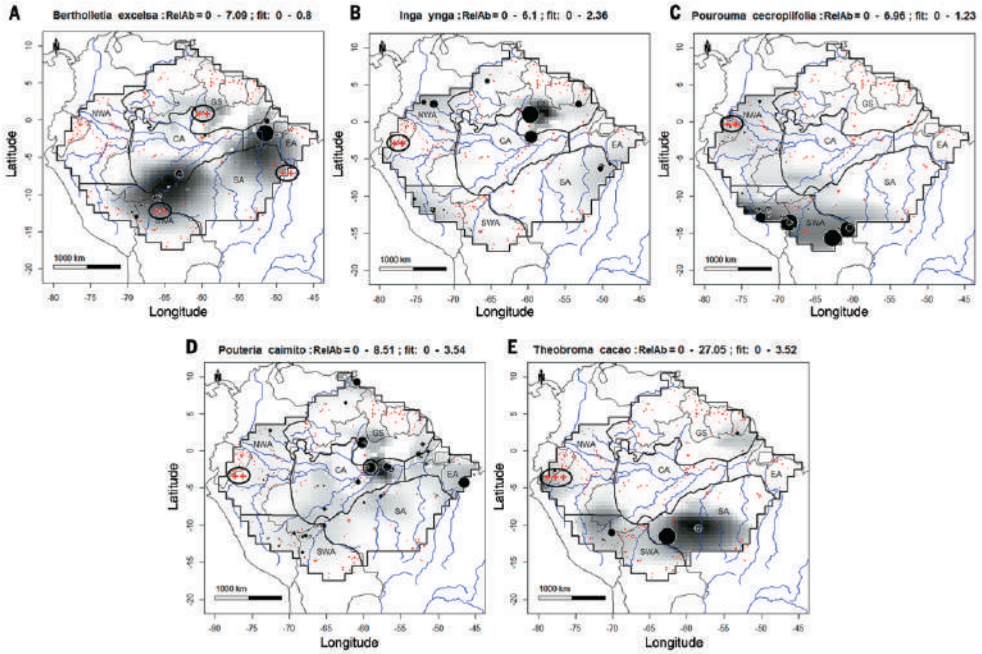

Figure 3.1. Distribution maps of five domesticated hyperdominant species in Amazonian forests and their probable origins of domestication. Distribution maps were estimated for five domesticated species that are hyperdominants: (A) *Bertholletia excelsa*; (B) *Inga ynga*; (C) *Pourouma cecropiifolia*; (D) *Pouteria caimito*; (E) *Theobroma cacao*. The origin of domestication is shown by the symbol "+++" for known origin and by the symbol "++" for hypothetical origin. Sizes of black dots indicate the relative abundance of the domesticated species in plots where the species has been recorded. Red dots indicate plots where each domesticated species has not been recorded. Shading shows the interpolated distribution of each species using loess spatial interpolation (ter Steege et al., 2013). The range of relative abundance in plots (RelAb) and the loess spatial interpolation in individual grid cells (fit) are reported in percentage above each map. Maps were created with custom R scripts. Amazonia was divided in six geological regions (NWA, north-western Amazonia; SWA, south-western Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia). Base map source (country.shp, rivers.shp): ESRI (http://www.esri.com/data/basemaps, © Esri, DeLorme Publishing Company.

Using 1,170 forest plots of the Amazon Tree Diversity Network (ATDN), ter Steege and co- authors (ter Steege et al., 2013) identified 4,962 species, estimated that about 16,000 woody species occur in Amazonia, and showed that only 227 hyperdominant species dominate Amazonian forests. We used 1,091 ATDN plots located in non-flooded lowland Amazonian forests to provide a list of domesticated species on the basis of evidence of at least incipient domestication processes in Amazonia and elsewhere in the Americas. We identified 85 woody species with populations incipiently, semi or fully domesticated by pre-Columbian peoples (hereafter domesticated species listed in Database A3.1). We found that 20 of these 85 domesticated species are hyperdominants: five times higher than the number of hyperdominant species expected by chance.

We then tested whether forests closer to archaeological sites and rivers have higher abundance and richness of domesticated species. Forest composition was evaluated in association with numerous types of archaeological sites, including pre-Columbian habitation sites (with and without anthropogenic soils), earthworks (mounds, causeways, raised fields, terraces), rock art (paintings and petroglyphs) and identified eco-archaeological regions (Clement et al., 2015a; more details in Appendix 3A and Figure A3.2). We included eco-archaeological regions in the analysis because they indicate environmental settings with large and abundant pre-Columbian earthworks (Lombardo et al., 2011). We also used margins of navigable rivers as proxies for pre-Columbian settlements, because they are good predictors of anthropogenic soils in Amazonia (McMichael et al., 2014). Our analyses also accounted for the effects of different geological regions of Amazonia and for four

Table 3.1. Mean, median, minimum and maximum values of all human and environmental variables used in the multiple regression models. Values were calculated at the Amazonia-wide level (All) and region-level (NWA, north-western Amazonia; SWA, south-western Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia).

Region (number of plots)	**Values**	**Distance to archaeological sites** (km)	**Distance to main rivers** (km)	**Cation Exchange Capacity** (cmol / kg)	**pH**	**Nº dry months**	**HAND**
All (1091)	Mean	45.65	14.25	12.07	4.49	2.01	37.02
	Median	25.94	10.52	11.00	4.50	1.00	22.81
	Minimum	0.00	0.00	6.00	3.90	1.00	0.00
	Maximum	349.42	70.58	35.00	5.70	6.00	539.11
NWA (197)	Mean	51.41	9.31	14.36	4.44	1.02	16.67
	Median	32.46	5.40	14.00	4.40	1.00	11.13
	Minimum	0.63	0.00	8.00	4.10	1.00	0.00
	Maximum	196.81	49.73	31.00	5.10	2.00	163.93
SWA (158)	Mean	80.07	14.16	12.57	4.91	2.68	30.77
	Median	59.07	9.23	11.00	4.90	3.00	17.16
	Minimum	0.00	0.07	7.00	4.00	1.00	0.00
	Maximum	219.94	62.94	25.00	5.60	6.00	375.98
SA (86)	Mean	67.35	11.72	9.19	4.54	3.86	39.59
	Median	43.77	5.78	9.00	4.55	4.00	25.55
	Minimum	2.03	0.04	6.00	4.00	2.00	1.06
	Maximum	349.42	46.93	13.00	5.30	6.00	293.89
CA (250)	Mean	20.54	14.79	10.07	4.16	1.99	45.45
	Median	11.64	13.24	10.00	4.10	1.00	47.78
	Minimum	0.62	0.00	7.00	3.90	1.00	0.04
	Maximum	220.35	48.55	18.00	5.10	6.00	119.93
GS (317)	Mean	41.86	19.73	12.78	4.59	1.83	48.57
	Median	32.65	14.39	12.00	4.60	2.00	24.38
	Minimum	0.93	0.09	6.00	4.00	1.00	0.00
	Maximum	127.36	70.58	35.00	5.70	6.00	539.11
EA (83)	Mean	34.18	6.11	11.96	4.51	1.89	24.84
	Median	20.23	2.72	11.00	4.50	1.00	23.38
	Minimum	0.00	0.00	9.00	4.10	1.00	0.62
	Maximum	254.99	52.79	18.00	5.10	6.00	78.72

local environmental conditions: soil cation exchange capacity (CEC), soil pH, rainfall seasonality, and height above the nearest drainage (HAND, a proxy for water-table depth). These variables were selected because they influence forest composition in Amazonia (ter Steege et al., 2006; Schietti et al., 2014; Esquivel-Muelbert et al., 2016; Bush and McMichael, 2016) and are available for basin-wide analysis.

We found a significantly higher abundance and richness (in absolute and relative terms) of domesticated species in south-western Amazonian forests, followed by north-western, southern and eastern forests, and the lowest values in the Guiana Shield (Figure 3.2, Figure A3.3). The total number of individuals of domesticated species per hectare (abundance) ranged from 0-292 and the total number of domesticated species (richness) from 0-19. The relative abundance ranged from 0-61 % and the relative richness from 0-19 %. Forests with a diverse assemblage of domesticated species tended to have a high abundance of these species (Figure A3.4). The abundance of all domesticated species was, however, mostly due to 20 hyperdominant species. Domesticated hyperdominant species were more widespread across Amazonian forests than nondomesticated hyperdominant species. We found that 70 % of the 20 domesticated hyperdominant species studied here occur in all Amazonian regions (Database A3.1) versus only 47 % of the 207 nondomesticated hyperdominant species (ter Steege et al., 2013). Most of domesticated species that are hyperdominant have incipiently domesticated populations, rather than fully domesticated ones. This finding suggests that humans were probably managing hyperdominant species in forests instead of investing their efforts to fully domesticate populations. Humans may have fully domesticated populations of plant species that were rare in nature and easily adapted to anthropogenic landscapes.

We found that forests closer to archaeological sites had greater abundance and richness (in relative and absolute terms) of domesticated species at the Amazonia-wide level (Figure 3.3; Figure A3.5). In four of the six Amazonian regions, the relative and absolute richness of domesticated species decreased with distance from archaeological sites or rivers, and in three of these four regions the relative and absolute abundance of domesticated species also decreased with distance from archaeological sites or rivers. These results reveal that forests closer to archaeological sites or rivers within these regions harbour a richer and larger assemblage of domesticated species than forests elsewhere. The relative abundance of domesticated hyperdominant species also decreased with distance from archaeological sites (Figure 3.4). In contrast, we tested whether nondomesticated hyperdominant species in three control groups were negatively affected by the distance from archaeological sites, and we did not find a significant negative relation for any control group (Figure 3.4). Additionally, nondomesticated hyperdominant species dispersed primarily by

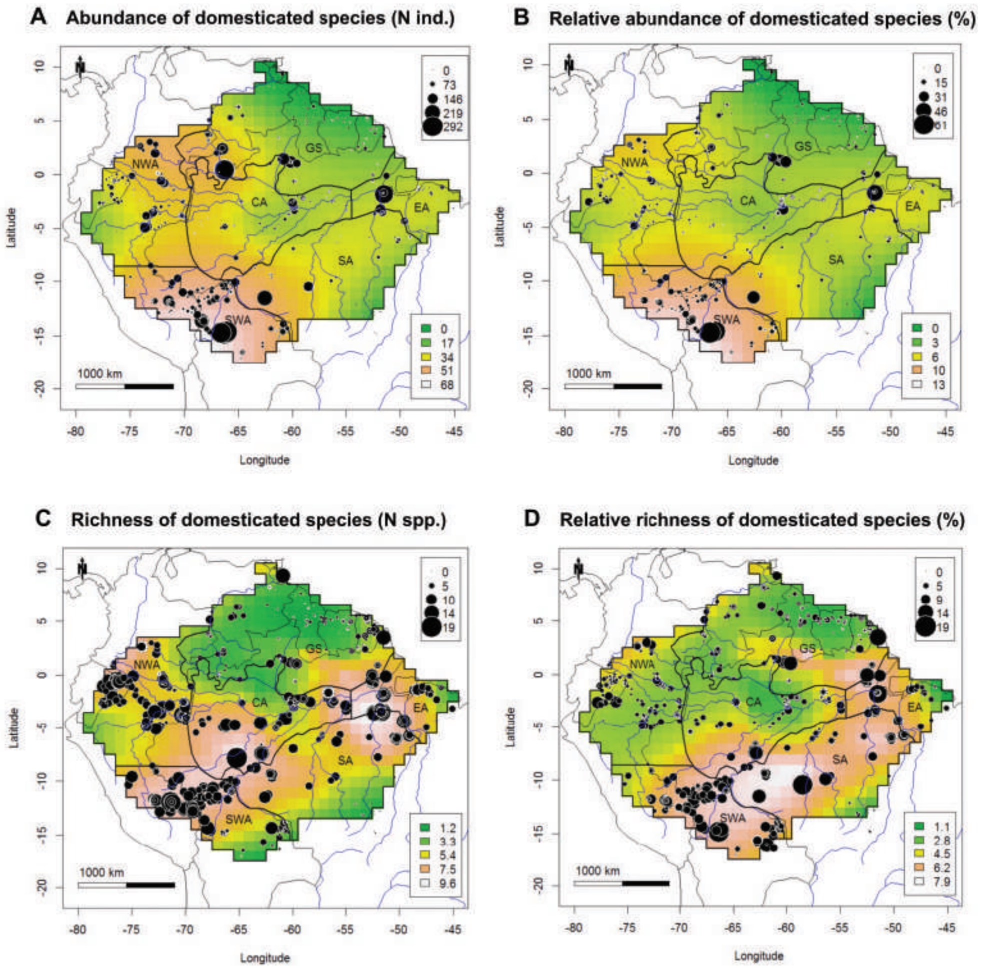

Figure 3.2. Spatial variation of 85 domesticated species across Amazonia. Maps showing (A) the spatial variation of the total number of individuals of domesticated species (abundance) per hectare (ha), (B) the relative abundance of domesticated species, (C) the total number of domesticated species (richness) per plot, (D) and the relative richness of domesticated species in lowland plots in six geological regions of Amazonia (NWA, north-western Amazonia; SWA, south-western Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia). Black circles show the observed values of (A) absolute abundance and (B) relative abundance, ranging from 0-292 individuals of domesticated species per 1 ha and 0-61 % of the total number of individuals, and the observed values of (C) absolute richness and (D) relative richness, ranging from 0-19 domesticated species per plot and 0-19 % of the total number of species. The white-green background shows the interpolation of the observed values (in percent) in each plot modelled as a function of latitude and longitude on a 1o-grid cell scale using loess spatial interpolation (ter Steege et al., 2013). Maps were created with custom R scripts. Base map source (country.shp, rivers.shp): ESRI (http://www.esri.com/data/basemaps, © Esri, DeLorme Publishing Company).

primates were more abundant farther from archaeological sites within forests in southern Amazonia and the Guiana Shield (Figure 3.4), potentially as a result from heavy hunting around villages (Peres et al., 2016). Although the absolute and relative abundance of domesticated species in forest plots decreased with distance from navigable rivers in the Guiana Shield, the opposite was observed for the distance from archaeological sites within this region. One possible explanation is insufficient information about the distribution of archaeological sites along tributary rivers, so moving away from a known archaeological site may increase the proximity to other sites that have not been mapped yet. Archaeological surveys into interfluves of major rivers in Central Amazonia documented numerous anthropogenic soils along tributary rivers, showing that these areas were also densely occupied (Levis et al., 2014 – **Chapter 2**).

The map showing the density of archaeological sites in 1°-grid cells (areas of approximately 110 km^2) indicated large areas of Amazonia without any archaeological site (Figure A3.6) and revealed that some plots with high values of the relative abundance of domesticated species are located in grid cells, most likely reflecting lack of surveys. Although simple regressions showed a pronounced decrease of human impact in forests up to 25 km from archaeological sites and 10 km from rivers (Figures A3.7-A3.11), the strongest human impact was detected in forests located on archaeological sites or within eco-archaeological regions in south-western and eastern Amazonia. Dominance of domesticated species may, therefore, help predict the occurrence of archaeological sites in Amazonian forests. Guiana Shield plots, for example, with an average of 30 % of individuals of domesticated species located close to river margins, but more than 120 km away from an archaeological site can be used to test this hypothesis and indicate that a widespread survey of archaeological sites along tributaries in interfluvial areas is critical.

Environmental conditions also controlled the abundance and richness of domesticated species (Figure 3.3; Figure A3.6), and may have influenced where and how humans shaped forests through time. We found that environmental conditions explained most (up to 30 %) of the variation in the relative abundance and richness of domesticated species in Amazonian regions (Figure 3.5), whereas the proxies for past human impacts explained up to 20 %. Approximately 70 % of the variation remains unexplained by either human or environmental factors in most of the regions. The data available for this broad-scale analysis are based on forest plots and archaeological sites unequally distributed across the study area, and on interpolations of environmental conditions. Hence, the data used may not capture the real variation of past human and environmental factors across the basin. Even so, the relative abundance and richness of domesticated species were higher in the southern periphery of the basin (Figure 3.2) and increased with rainfall seasonality at the Amazonia-wide level (Figure 3.3). Seasonal and open forests in transitional zones were important ecosystems for early humans, who started the domestication of some plants (Piperno, 2011), and the longest pre-Columbian occupation sequences have been found either in the southern periphery of the basin or near the estuary of the Amazon River (Roosevelt, 2013). In seasonal forests of south-western Amazonia, where two major crops most likely originated (manioc, *Manihot esculenta*, and peach palm, *Bactris gasipaes*) (Clement et al., 2010), plant populations that also responded well to selection and propagation were widely dispersed (Clement et al., 2010). For instance, sweet manioc was domesticated in south-western Amazonia before the initial development of small-scale farming societies in the mid-Holocene and expanded widely (Piperno, 2011; Arroyo-Kalin, 2012). It was also from the south-western periphery that two major languages expanded and where the oldest anthropogenic soils have been found, dated from around 4,800 BP (Clement, 1999; Neves et al., 2003). The Arawak language family probably originated in south-western Amazonia and expanded across Amazonia associated with the early development of farming villages (Walter and Ribeiro, 2015). The upper Madeira River is the homeland of the Tupí language family, which also spread widely (Santos et al., 2015). In south-western Amazonia, the combination of rainfall seasonality (Table 3.1), forest-savanna transition (Mayle and Power, 2008), high cultural diversity (Crevels and der Voort, 2008) and a long history of forest transformation encompassing landscape engineering by pre-Columbian societies (Lombardo et al., 2011) resulted in forests containing diverse and abundant assemblages of domesticated species.

Soil and terrain conditions also determined forest composition (Quesada et al., 2012) and influenced the abundance and richness of domesticated species in forest plots (Figure 3.3). We found in some regions higher relative abundance and richness of domesticated species on soils with lower pH. Plots with shallow water table also concentrated domesticated species. This pattern is driven by dense stands of some species (e.g., *Mauritia flexuosa*, *Euterpe oleracea*, *E. precatoria* and *Oenocarpus bataua*) on poorly-drained soils of Amazonia (Emilio et al., 2014).

Although potential confounding effects of some correlations between human and environmental factors may exist (e.g., human settlements located in seasonal forests on poorly-drained soils of south-western Amazonia), we found that human influence is exclusively responsible for about half of the explained variation of the abundance, relative abundance, richness and relative richness of domesticated species in the south-western and eastern regions (Figure 3.5; Figure A3.12). The association between domesticated species and archaeological sites raise a chicken-and-egg question: Did humans enrich forests in south-western and eastern Amazonia

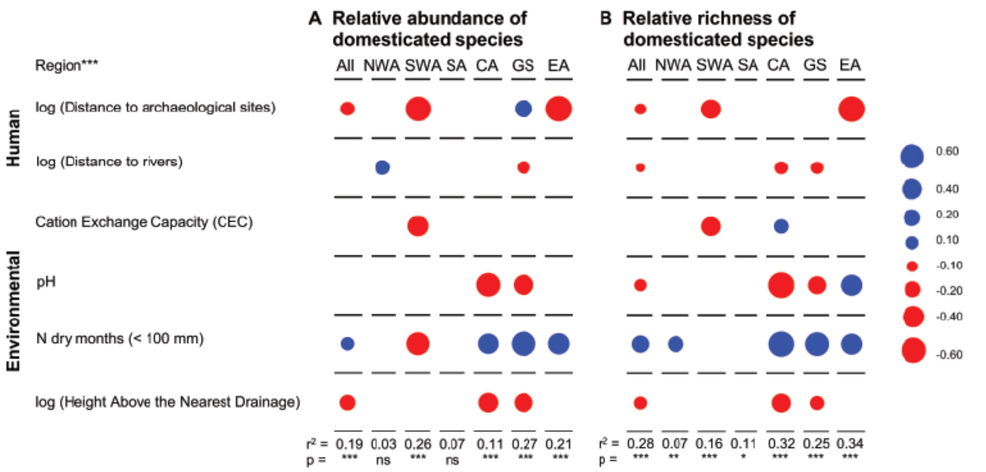

Figure 3.3. The relative abundance and richness of domesticated species as a function of human and environmental variables. Standardized regression coefficients for (A) the relative abundance and (B) the relative richness of 85 domesticated species as a function of human factors (distance to archaeological sites and eco-archaeological regions, distance to navigable rivers) and environmental conditions (soil CEC, soil pH, number of dry months and HAND). Circle size represents the relative contribution of the predictors, shown by standardized coefficients at the Amazonia-wide level (All) and region-level regression models (NWA, north-western Amazonia; SWA, south-western Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia). Red circles indicate negative effects and blue circles positive effects. Standardized coefficients are presented only for significant relations analysed in the models ($p \leq 0.05$). Adjusted coefficient of determination (r^2) and significant codes (p values: ≤ 0.001 '***'; ≤ 0.01 '**'; ≤ 0.05 '*'; > 0.05 'ns') are presented for the effect of regions at the Amazonia-wide level (All) and all regression models.

with domesticated species or did humans choose to live close to forests naturally rich in these species? Our approach cannot demonstrate causality, but the first alternative is most probable given the sum of other evidence that also support the influence of past societies in increasing domesticated species abundance and richness in forests. First, numerous archaeological sites were found in all geological regions (Figure A3.2), which shows that pre-Columbian human societies were distributed across all of Amazonia (Clement et al., 2015a) and created new landscapes for domesticated plants under different environmental conditions (Table A3.1). Dramatic changes in phytolith assemblages have been found in ancient anthropogenic soils before, during and after human occupation, indicating that humans transform forest composition once they occupy an area (McMichael et al., 2015). Second, assemblages of up

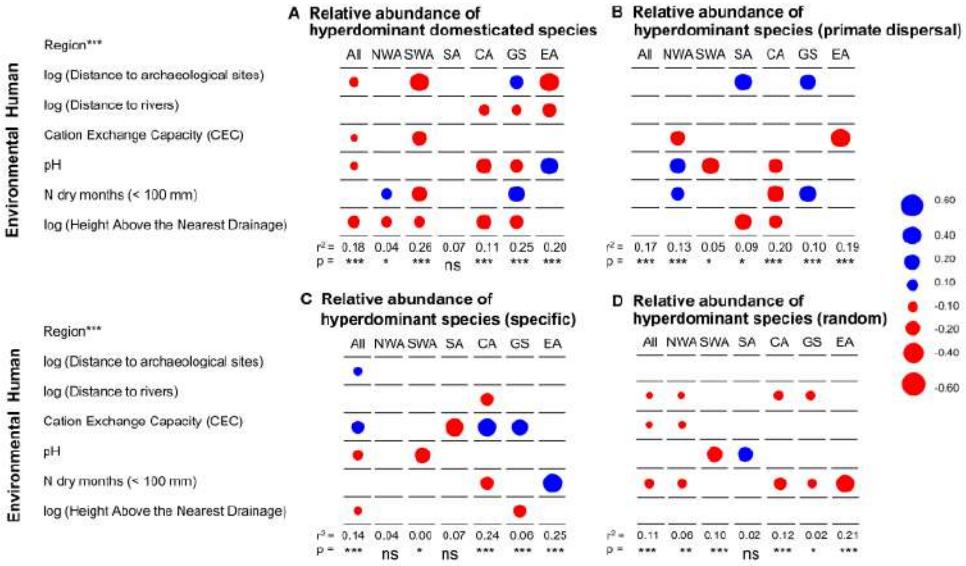

Figure 3.4. The relative abundance of hyperdominant species as a function of human and environmental variables. Standardized regression coefficients for (A) the relative abundance of 20 domesticated species that are hyperdominants, (B) the relative abundance of 20 nondomesticated species that are hyperdominants and primarily dispersed by primates, (C) the relative abundance of 20 nondomesticated species that are hyperdominants and not dispersed by primates, and (D) the relative abundance of 20 nondomesticated species that are hyperdominants selected at random, as a function of human variables (distance to archaeological sites and eco-archaeological regions, distance to navigable rivers) and environmental variables (soil CEC, soil pH, number of dry months and HAND). Circle size represents the relative contribution of the predictors, shown by standardized coefficients at the Amazonia-wide level (All) and region-level regression models (NWA, north-western Amazonia; SWA, south-western Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia). Red circles indicate negative effects and blue circles positive effects. Standardized coefficients are presented only for significant relations analysed in the models ($p \leq 0.05$). Adjusted r^2 and significant codes (p values: ≤ 0.001 '***'; ≤ 0.01 '**'; ≤ 0.05 '*'; > 0.05 'ns') are presented for the effect of regions at the Amazonia-wide level (All) and all regression models.

to 19 domesticated species with different geographical distributions and distinct ecological preferences tend to occur in forests close to archaeological sites (Figure 3.3; Figure A3.5). As an example, we found a set of domesticated species at one forest plot (*Attalea maripa*, *Astrocaryum murumuru*, *Bertholletia excelsa*, *Garcinia macrophylla*, *Hevea brasiliensis*, *Oenocarpus bacaba* and *Theobroma spp*.) that would be unlikely to occur by chance at the same location because of their distinct ecological niches. Third, species domesticated in one particular environmental setting had wide geographical distributions and tended to be more abundant in locations not associated with their known or hypothetical origins of domestication (Clement et al., 2010) (Figure 3.1; Figure A3.1). For instance, cocoa (*Theobroma cacao*) was first domesticated in wet forests on nutrient-rich soils of north-western Amazonia, and is currently more abundant in south-western and southern forests (Thomas et al., 2012)

Even though it is possible that the origin of domestication of some species is not well identified, this is unlikely for species for which extensive morphological and genetic studies have been done (more details in Appendix 3B). Domesticated species for which information about their origins of domestication exists originated in the periphery of Amazonia (Clement et al., 2010). Species can have wild populations in one part of Amazonia (where the domestication process started) and incipiently, semi or fully domesticated populations in other parts of the basin. Fully domesticated populations show substantial morphological and genetic changes and depend on human management for their long-term survival, whereas incipiently domesticated plants can survive and reproduce without humans, as is the case of most hyperdominant

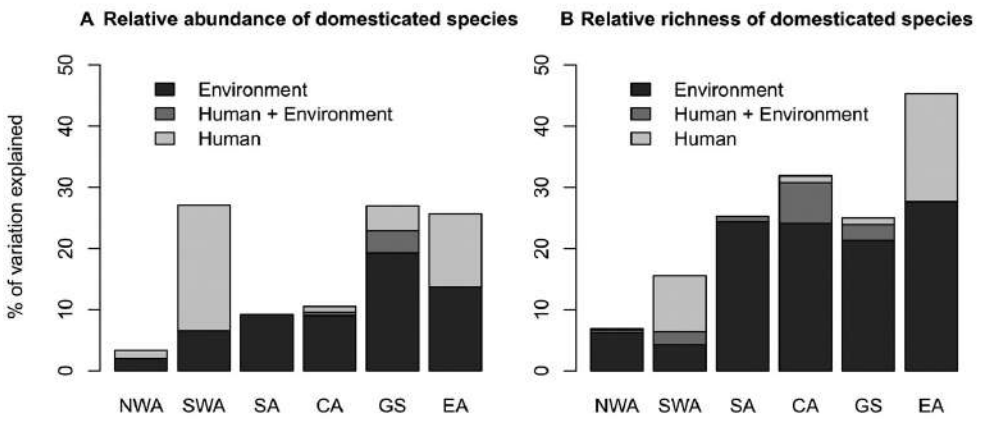

Figure 3.5. Relative contributions of human and environmental variables for explaining variation in relative abundance and richness of domesticated species in Amazonian forests. The partitioning of variation in (A) relative abundance and (B) relative richness of domesticated species uniquely explained by environmental (dark gray) or human factors (light gray), and the variation jointly explained by both (gray). Variance partitioning was conducted over the results of multiple regression analyses presented in Figure 3.3. Amazonia was divided in six geological regions (NWA, north-western Amazonia; SWA, south-western Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia).

domesticated species. Many domesticated species were dispersed from their origin of domestication to other locations where large pre-Columbian populations lived and these species eventually accumulated greater intra-specific diversity (Clement et al., 2010). Our results suggest that plant species that responded well to selection and propagation were widely cultivated and dispersed within and outside their natural range (Clement, 1999; Boivin et al., 2016) by different societies and at different moments in time. The influence of modern indigenous and nonindigenous societies in the last 300 years on the distribution of some domesticated species may be stronger than the effect of earlier societies. For instance, in the late 17th century, Portugal and Spain stimulated plantations of cocoa trees in Amazonia (Alden, 1976), which - associated with pre-Columbian cultivation - may have increased the abundance of cocoa trees in south-western Amazonian forests even more.

Our results suggest that past human interventions had an important and lasting role in the distribution of domesticated species found in modern forests, despite the fact that the location of many archaeological sites is unknown. Almost one fourth of all domesticated species are hyperdominant, and besides their socioeconomic importance they can also help unravel the human history of Amazonian forests, largely overlooked by ecological studies. Detecting the widespread effect of ancient societies in modern forests not only strengthens efforts to conserve domesticated and useful wild-plant populations, of critical importance for modern food security (Esquinas-Alcázar, 2005), but also strongly refutes ideas of Amazonian forests being untouched by man. Domestication shapes Amazonian forests.

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AUTHOR CONTRIBUTIONS

C.L., H.t.S., F.R.C.C., F.B., M.P-C., C.R.C., and A.B.J. conceived the study and designed the analyses; C.L. and H.t.S. carried out most analyses; C.L., H.t.S., F.R.C.C., F.B., M.P-C., C.R.C., A.B.J., and N.C.A.P. wrote the manuscript; all of the other authors contributed data, discussed further analyses, and commented on various versions of the manuscript.

SUPPLEMENTARY MATERIALS FOR CHAPTER 3

Persistent effects of pre-Columbian plant domestication on Amazonian forest composition

Appendices 3

APPENDIX 3A : MATERIALS AND METHODS

Data collection: floristic data

We used 1091 forest inventory plots of the Amazon Tree Diversity Network (ATDN) database distributed across Amazonia (Figure A3.2A). Only lowland (terra firme and white-sand podzol) plots were included in the analysis; wetland plots, as defined by ter Steege et al. (2013), were excluded. The exclusion of wetlands is justified for four reasons: 1) floodplain trees have distinct and strong ecological requirements related to flood duration; 2) population turnover is probably faster in white-water floodplains and slower in blackwater floodplains than in non-flooded forests; 3) the effect of pre-Columbian domestication may be blurred as many floodplain archaeological sites have been destroyed by the annual floods; and 4) plots on floodplains are at zero distance from rivers, making it impossible to evaluate the effect of this variable.

Plots cover a wide range of soils and topographies (Table 3.1). Most plots (N = 819) measure 1 ha; others vary from 0.1 to 9 ha. In each plot, ATDN scientists inventoried all woody species with ≥ 10 cm diameter at breast height; almost all individuals were identified to the species level (95 % of plots have less than 5 % of individuals without botanical identification). Plots with more than 25 % of trees unidentified to species were excluded from the analyses of the absolute and relative richness of domesticated species. Although identification problems exist in Amazonian tree inventories, domesticated species are widely used and cultivated, and are therefore better-known to botanists and local parataxonomists.

Data collection: historical human factors

The distribution of archaeological sites was obtained from a database of 3795 archaeological sites and eco-archaeological regions in lowland South America that includes pre-Columbian habitation sites (with and without anthropogenic soils), earthworks (mounds, causeways, raised fields, terraces) and rock art (paintings and petroglyphs) updated from 3318 sites presented by a previous study (Clement et al., 2015a). Only archaeological sites that fall within the Amazon River basin were used in this study (3348 sites shown in Figure A3.2B). Archaeological sites are places where material remains of pre-Columbian human activities are still visible and eco-archaeological regions are environmental settings with large and abundant pre-Columbian earthworks (Lombardo et al., 2011). To illustrate the biased sampling of archaeological sites across Amazonia, we created a map with a background colour showing the density of archaeological sites in 1°-grid cell and forest plots in open circles indicating values of the relative abundance of domesticated species (Figure A3.6). To quantify the gradient of historical human influence, we measured the distance from each forest plot to the nearest archaeological site and to the nearest navigable river margin (Figure A3.2B), using near distance tool of ArcMap version 9.3. For plots located in 1°-grid cells with zero density of archaeological sites we measured distances from plots to the nearest eco-archaeological regions (if they exist) using near distance tool of ArcMap version 9.3. Plots located at zero distance from archaeological sites occur in south-western and eastern Amazonia (Table 3.1) and those located within eco-archaeological regions occur in south-western Amazonia and the Guiana Shield (Figure A3.6). Equal weighting was given to all the different types of archaeological sites or eco-archaeological regions because we did not have the description of all sites in the database we used for this study.

Distance from rivers was also chosen as a proxy of pre-Columbian settlements, because this is a good predictor of the probability of finding sedentary pre-Columbian occupation sites in Amazonia (McMichael et al., 2014), which reflects peoples' preferences for living along rivers. Distance from the river is not strongly correlated with the distance to archaeological sites or any of the environmental variables we tested (Figure A3.13), allowing the use of both variables in the analyses. Archaeological sites along tributaries in interfluvial forests are under-sampled compared to sites in more accessible areas (Figure A3.2), which also justifies using both distance measures (i.e., distance from archaeological sites and from rivers) in the analyses. The river network was obtained from the HydroSHEDS dataset (available at http://hydro sheds.cr.usgs.gov) (Lehner et al., 2008). 'Upcell' values are features of the HydroSHEDS dataset that represent the maximum flow accumulation at any location in the river network. We used HydroSHEDS data to define perennial and navigable rivers by selecting cells with upcell values greater than 15,000, following the study of McMichael et al. (2014). For larger rivers (more than 1 km wide) we used river polygons obtained from ANA/BRASIL (2007).

Data collection: regional and local environmental data

To account for the effect of regional environmental conditions across Amazonia we used the geological regions delimited by Fittkau (1971) and analysed by ter Steege et al. (2013), who showed that six different geological regions are dominated by different suites of tree species. To account for the effect of local environmental conditions, soil fertility (Cation Exchange Capacity), soil pH, rainfall seasonality and the Height Above the Nearest Drainage (HAND) were included in the analyses. Cation Exchange Capacity (CEC) and soil pH were obtained from SoilGrids 250 m for all plots using the mean values of 5 cm of soil depth (Hengl et al., 2013; http://www.isric.org/content/soilgrids); rainfall seasonality was calculated as the maximum cumulative number of months with < 100 mm of rainfall using the monthly data from

1998 to 2004 of the Tropical Rainfall Measuring Mission (TRMM) satellite product 3B43 V6 at a 0.25° resolution (about 28 km at the equator) (Kummerow et al., 1998); HAND was obtained from the Ambdata database (Nobre et al., 2011). Mean, median, maximum and minimum values of all variables are presented in Table 3.1.

Data collection: control groups for testes of how e nvironment and human factors affect distribution of hyperdominant non-domesticated species

To understand whether non-human primates may promote dominance of certain tree species in forests closer to archaeological sites and rivers, we analysed the effect of distance from archaeological sites and rivers on the abundance of non-domesticated species that are dispersed by primates and probably by other vertebrates. Although all vertebrates disperse forest seeds, large non-human primates have similar fruit preferences to humans and their actions in the forest can be compared with human behaviour (Bush et al., 2015). We identified 20 non-domesticated species that had estimated population sizes comparable to those of the 20 hyperdominant domesticated species, and that are primarily dispersed by non-human primates. We also selected two control groups of non-domesticated species: the first group consists of 20 hyperdominant species based on specific criteria and the second of 20 hyperdominant species selected at random. The criteria used to select the first control group were: (1) species with estimated population sizes comparable to those of the 20 hyperdominant domesticated species; (2) species that belong to the same botanical families as the 20 hyperdominant domesticated species (if possible); (3) species that are not mainly dispersed by primates. In the second control group of 20 hyperdominant species selected at random, three are dispersed mainly by primates and four were selected in the first control group. The lists of the control groups of hyperdominant species are presented in the Table A3.1.

List of domesticated species in ATDN plots

We created a list of woody species with some evidence of selection and propagation by humans in Amazonia and elsewhere in the Americas to which we refer hereafter as "domesticated species". First, we considered the list of domesticated species at European contact compiled by Clement (1999). We excluded herbs and species identified to the genus level (e.g., Hevea spp.), because herbs were not sampled in the ATDN plots and only a few species of species-rich genera were shown to be domesticated. To this first list, we added two species with evidence of past human selection that have been studied by Clement's group (*Euterpe precatoria*) (Perrut de Lima, 2014) and *Caryocar brasiliense* (Smith and Fausto, 2016), and one species considered to be the wild progenitor of a species with domesticated populations (*Bixa urucurana*) (Moreira et al., 2015).

We then conducted a bibliographical search for recent articles on domesticated plants using "domestication in Amazon*" and "domestication in Brazil*" (and all other Amazonian countries) as keywords in Web of Science and "domestication in Amazon*" in Google Scholar. Three palm species (*Attalea phalerata*, *Phytelephas macrocarpa* and *Astrocaryum chambira*) were incorporated in the list based on two recent papers (Sosnowska et al., 2015; García et al., 2015).

We also used Mansfeld's World Database of Agricultural and Horticultural Crops (Hanelt, 2001; http://mansfeld.ipk-gatersleben.de/) to add new species to the list. First, from this database we obtained a list of cultivated species in all Amazonian countries. Then, information about the natural distribution, cultivation, uses and domestication was obtained for all cultivated species that occur in the forest plots to classify the degree of domestication (DD) of each species. Cultivation is defined here as the process of growing plants, while plant domestication involves cultivation and also selection and propagation of specific populations by humans. The degree of domestication was based on the following indicators adapted from Clement (1999), Dempewolf et al. (2008) and Hammer and Khoshbakht (2015):

(A) Any degree of phenotypic differentiation between the domesticated taxon and its wild progenitor (including evidence of a smaller variance of traits subjected to selection than that of the original wild populations, as this may represent a founder effect; DD = 2).

(B) The extent of cultivation in terms of geographical area (if the geographical area of cultivation is outside its natural range of distribution within the Americas - North, Central and South America; DD = 1). The natural range of distribution of each species was obtained from Mansfeld's World Database (2001).

(C) Evidence of cultivation since 1492 (DD = 1) and before 1492 (DD = 2), both suggesting a long history of selection.

All species from the Mansfeld's World Database (10 species) with a summed degree of domestication ≥ 2 were included in the new list, resulting in a list with 85 domesticated species. Species with evidence of extensive and long-term cultivation (i.e., indicator B: the extent of cultivation and C: evidence of cultivation before 1492) are likely to have been subjected to a long history of selection and propagation even if no studies were done to investigate the degree of phenotypic variation in cultivated populations. If we look for evidence of phenotypic differentiation between cultivated and wild populations of these species, there is a very high chance of finding a signal of a reduction in phenotypic variability (for incipiently domesticated populations) or an increase in phenotypic variability (for semi-domesticated and domesticated populations) (Clement, 1999). For more information, we presented references for evidence of domestication and cultivation of each species listed in the Database A3.1. Finally, we validated all names with the Taxonomic Name Resolution Service using the Tropicos® database (Boyle et al., 2013; accessed in May, 2015). We cross-checked all scientific names of domesticated species with the list of all species present in ATDN plots.

Data analyses

All analyses were conducted in the R environment (2012). We used a spatial loess model to produce distribution maps for 11 domesticated species for which there is reasonably good information about their origins of domestication (Figure 3.1; Figure A3.1). Using the same approach as ter Steege et al. (2013), Amazonia was divided into 1° latitude and longitude grid cells, and the interactions between latitude and longitude were used as variables in the loess regression models to estimate average density of individuals in each grid cell. These densities were mapped and compared to the origin of domestication predicted by previous studies (Clement, 2010; Clement et al., 2015a) that analysed the geographic distribution of genetic and morphological diversity found in cultivated and wild populations of domesticated species (see Appendix 3B for information on the origin of domestication of each species). Higher genetic diversity often indicates the location of the origin of domestication, and the genetic variability found in the cultivated populations is often a subset of the genetic variability found in the wild population (Clement, 1999).

We used the list of domesticated species to quantify five domestication measures in each plot (Levis et al., 2012): (1) the abundance of domesticated species (the number of individuals of domesticated species per hectare); (2) the relative abundance of domesticated species (the number of individuals of domesticated species divided by the total number of individuals found in the plot); (3) the richness of domesticated species (the number of domesticated species per plot); (4) the relative richness of domesticated species (the number of domesticated species divided by the total number of species found in the plot); and (5) the relative abundance of hyperdominant domesticated species (the number of individuals of domesticated species that are hyperdominants divided by the total number of individuals found in the plot). The lists of hyperdominant non-domesticated species (control groups) were used to quantify their relative abundance in the plot as described above in (5).

We calculated the spatial variation of the absolute and the relative abundance and richness of domesticated species to understand how the proportion of domesticated species varies across Amazonia. We also used a loess regression model to interpolate the measures of domestication for the entire Amazon. The model was used to estimate the absolute and the relative abundance and richness of domesticated species for each grid cell (Figure 3.2). We used an exponential model to fit the relationship between the absolute and relative abundance of 85 domesticated species and the absolute and relative richness of 85 domesticated species in forest plots presented in the Figure A3.4.

To evaluate the relationship between the measures of domestication and the measures of abundance for control groups (response variables) and historical human and environmental conditions (explanatory variables) we used mixed-effects models and multiple linear regressions. Distance to archaeological sites and eco-archaeological regions, distance to rivers and HAND were log transformed (log10 +1) before the analysis to normalize these three variables. In the Amazonia-wide mixed-effects model, geological regions were incorporated as random factors and explanatory variables as fixed factors. Within each geological region, we analysed the effects of environmental and human factors on the response variables using separate multiple linear regression models. Mixed-effects and multiple regression models were implemented with the 'lmer' and 'lm' functions of the R 'lme4' (Pinheiro et al., 2016) and R 'sjstats' packages (Lüdecke, 2016), respectively. We included all explanatory variables in the models, because only one strong correlation (higher than 0.8) was found in south-western, but was not present in other regions nor over all Amazonia (Figure A3.13). We also used the variation inflation factor (VIF) to identify multicollinearity among explanatory variables used in the multiple regression models and we did not detect signs of strong multicollinearity in any of the models. The results of the mixed-effects and multiple regression models corrected for multiple testing (Bonferroni correction) are presented in Table A3.2. Although Bonferroni correction leads to conservative test results, the main results presented in Figure 3.3 remain significant after this correction.

After removing plots located at zero distance to archaeological sites or eco-archaeological regions from the multiple regression models presented in Figure 3.3 the relations with archaeological sites are still visible and significant within south-western and eastern regions, but are not visible for the Amazonia-wide models (Table A3.3). Simple plots of the response variables against distance from archaeological sites (and eco-archaeological regions) and rivers are presented in Figures A3.7-A3.11 and show actual units of distance. The visualization of the regression models was performed using the visreg package (Breheny and Burchett, 2013). We used a log transformation (log10 +1) of the explanatory variables to fit a nonlinear relationship between the relative abundance and richness of domesticated species and the distance to archaeological sites and rivers. Conditional plots were used for simple models within geological regions and contrast plots were used for mixed-effect models in the Amazonia-wide analyses (geological regions incorporated as random factors), because it is only possible to obtain confidence intervals for contrast plots in mixed-effect models.

We used variation partitioning (Legendre, 2008) to determine how much of the variation in the response variables can be explained by historical human factors, by environmental conditions, and by human and environmental factors together. The fractions of variation were based on the results of three multiple regression models (adjusted r^2): a model with only human factors included as predictors; a model with only local environmental predictors; and a human + environment model, including both sets of predictors. Variation partitioning was implemented using the varpart function of the R vegan package (Oksanen et al., 2016).

APPENDIX 3B : SUPPLEMENTARY TEXT

Description of the 11 domesticated species, their distribution across Amazonia and their likely origins of domestication

We analysed 11 domesticated species for which information about their origins of domestication had been described by previous studies (Clement et al., 2010), and the molecular and morphological studies used to identify their origins are described below. We divided the species in two groups: five domesticated species that are hyperdominants of the Amazonian Flora (Figure 3.1) and six that are not hyperdominants (Figure A3.1).

Five domesticated species that are hyperdominants:

1. *Bertholletia excelsa* Bonpl., Lecythidaceae

The Brazil nut or Amazon nut tree (*Bertholletia excelsa*) produces oil-rich seeds that are the most important non-timber forest product extracted from Amazonian forests. Populations with large seeds probably resulted from human selection and stands with high abundances of Brazil nut trees have been associated with past human dispersal and cultivation (Clement 1999, Shepard and Ramirez, 2011). The dispersal-mediated effect of large caviomorph rodents is considered another factor determining the existence of dense stands of Brazil nut in Amazonia (Peres and Baider, 1997). Brazil nut trees are commonly planted and/or favoured in swiddens, but the species survives into mature forests when abandoned (Paiva et al., 2011). There are three hypotheses about Brazil nut’s origin of domestication: it may have originated in south-eastern Amazonia, according to Scott Mori (Clement et al., 2010); a northern/central Amazonian origin was suggested based on an historical linguistic analysis (Shepard and Ramirez, 2011); a south-western origin is a new hypothesis (Thomas et al., 2015), supported by population genetics (Sujii et al., 2015). Brazil nut trees occur in all Amazonian regions except north-western Amazonia, and it is particularly abundant in forests of the eastern and western parts of southern Amazonia.

2. *Inga ynga* (Vell.) J.W. Moore, synonym of *Inga edulis* Mart., Fabaceae

The icecream bean tree or inga (*Inga ynga*) is widely cultivated in homegardens and swiddens for its edible fruits and is the most important useful species of the genus. Inga trees were selected by Amerindians, resulting in semi-domesticated populations with long and thick pods that die out in mature forests after abandonment (Clement et al., 2010; Clement, 1989). Clement et al. (2010) hypothesized that the species originated in western Amazonia, where it shows the most dramatic phenotypic variability. However, genetic evidence shows that cultivated inga in Peru is not associated with wild populations in the same area (Dawson et al., 2008). Inga trees occur in all Amazonian regions. New studies are needed to confirm the origin of domestication of *Inga ynga*.

3. *Pourouma cecropiifolia* Mart., Urticaceae

Amazon tree grape (*Pourouma cecropiifolia*) is a pioneer tree cultivated inside and outside its natural distribution range (Hanelt and Büttner, 2001). The presence of tree grape in forests often indicates recent human disturbance, because semi-domesticated populations cannot survive long after human abandonment (Clement, 1999). Clement (1989) suggested an origin in western Amazonia because of the phenotypic contrast between populations from western Amazonia and wild populations. Fruits with more pulp and a smooth rind have also been observed along the Vaupés River in Colombia. Tree grape occurs in all Amazonian regions, but we found the highest abundance of this species in south-western forests, where no cultivated populations are known.

4. *Pouteria caimito* (Ruiz & Pav.) Radlk., Sapotaceae

Known as abiu or caimito (*Pouteria caimito*), it is cultivated as a fruit tree in tropical America (Hanelt and Büttner, 2001). It is commonly found in indigenous agroforestry systems in the Peruvian Amazon with various fruit shapes. Its fruits can vary from 50 to 1000 g (Clement, 1989). Fully domesticated populations of this species cannot survive in mature forests (Clement, 1999). Individuals with large and spherical fruits have a restricted distribution in eastern Peru, whereas small and ovoid fruits also occur in the same location, suggesting a western origin of the domesticated populations of the species (Clement, 1989). Although P. *caimito* occurs in all Amazonian regions, we frequently found it in plots in eastern Amazonia, and its highest abundance was found in forests of the northern part of the Guiana Shield. None of these regions are hypothetical origins of domestication.

5. *Theobroma cacao* L., Malvaceae

The cocoa tree (*Theobroma cacao*) has a long history of cultivation, particularly in Mesoamerica, where seeds were used to produce a stimulant beverage called chocolātl (Hanelt and Büttner, 2001). Genetic evidence indicates that cocoa is native to western Amazonia and it was taken to Mesoamerica before European conquest. In Amazonia, the cocoa trees may have been selected for its edible pulp and it was first domesticated in the north-western region (Clement et al., 2010; Thomas et al., 2012). Although cocoa trees occur in almost all Amazonian regions, its highest frequency and abundance was found in forests of the southern part of western Amazonia. Semi-domesticated populations of cocoa are common in swiddens and the species survives in tropical evergreen forests after abandonment (Clement, 1989), which could explain their high abundance in the southern part of the Amazon basin.

Six domesticated species that are not hyperdominants:

6. *Anacardium occidentale* L., Anacardiaceae

The cashew tree (*Anacardium occidentale*) is a medium to large tree and was found in low abundances in a few plots of central and eastern Amazonia. The probable origin of domestication of cashew is in open forest ecosystems of the Northeast of Brazil, where the greatest diversity of cultivated varieties has been found (de Paiva et al., 2009). The cashew tree was domesticated for its edible (pseudo)fruits for direct consumption and for making beverages (de Paiva et al., 2009). The species is now cultivated across the tropics (Hanelt and Büttner, 2001).

7. *Bixa orellana* L. var. *urucurana* (Willd.) Kuntze ex Pilg.,
synonym of *Bixa urucurana* Willd., Bixaceae

The annatto tree (*Bixa orellana*) produces a red colorant used since pre-Columbian times. It is cultivated throughout tropical America, and was introduced early into nearly all tropical regions of the Old World during the first century after European contact (Hanelt and Büttner, 2001). The origin of domestication is still not clear, although *Bixa urucurana* was recently identified as the wild progenitor of B. *orellana* (Moreira et al., 2015). B. *urucurana* occurs mainly along rivers in forest-savanna-transitions and domesticated landscapes, never cultivated. The probable origin of domesticated annatto is in south-western Amazonia (Clement et al., 2010). Intriguingly, we found a high abundance of B. *urucurana* in the upper Solimões River and especially in Ecuadorian forests.

8. *Genipa americana* L., Rubiaceae

The genipap tree (*Genipa americana*) is commonly cultivated in home-gardens and swiddens of tropical America for its edible fruits and colorant properties. The species is widespread in tropical America, and it occurs in different environments in Amazonia (Hanelt and Büttner, 2001). Spontaneous and cultivated genipap trees occur especially in floodplains of white water rivers in Amazonia, but we found a high abundance of the species in south-western forests. The high abundance of genipap in south-western Amazonia is curious, probably associated with riverine vegetation or anthropogenic forests within the Llanos de Mojos (Erickson and Balée, 2006). The genipap distribution along the Guiana coast fits with its probable origin of domestication (Clement et al., 2010).

9. *Matisia cordata* Bonpl., Malvaceae

South American sapota (previously recognized as *Quararibea cordata*) is an emergent tree with edible fruits, cultivated in the eastern Andean foothills and lowlands in Peru, Ecuador and Colombia, and along the middle and upper Solimões River in Brazil (Hanelt and Büttner, 2001; Clement, 1989). The cultivated trees always have larger fruits (300-1000 g) with more pulp and less fiber than those of wild populations (150-400 g) (Clement, 1989). Trees cultivated in swiddens on fertile anthropogenic soils can have even larger fruits (> 1000 g). Western Amazonia was hypothesized as the probable origin of semi-domesticated populations of South American sapota (Clement, 1989), based on morphological analysis of fruit sizes. Sapota trees were found in highest abundances in the southern part of western forests, where wild populations also exist.

10. *Platonia insignis* Mart., Clusiaceae

Known in Brazil as bacurí (*Platonia insignis*), it is cultivated for its edible fruits, predominantly in the estuary of the Amazonas River and eastern Amazonia into Maranhão and Piauí (Hanelt and Büttner, 2001). The species occurs naturally in degraded and sandy areas, and occasionally it occurs in old-growth forests. In some indigenous agroforestry systems bacurí is very abundant (Balée, 1993), and it can also be favored in fallows through intensive management. The species commonly occurs in eastern Amazonia, whereas it rarely occurs in western Amazonia. Although we did not find any tree in the ATDN forest plots of eastern Amazonia, native populations of bacurí occur mainly in eastern Pará and Maranhão States of Brazil. It was found in forests of the Guiana Shield, Central and Southern Amazonia, with highest abundance on the Guiana coast.

11. *Theobroma grandiflorum* (Willd. ex Spreng.) K. Schumm., Malvaceae

The cupuaçu tree (*Theobroma grandiflorum*) is native in the Brazilian Amazon and is now widely cultivated in Colombia, Venezuela, Ecuador and Costa Rica (Hanelt and Büttner, 2001). Cupuaçu fruits are appreciated for their rich flavourful pulp. Cultivated plants tend to produce larger fruits than those collected from forests, certainly due to selection by humans. South-eastern Amazonia was hypothesized as the origin of domestication of the species, because cultivated and native populations are frequent in this region (Clement et al., 2010). However, genetic analysis was unable to relate wild populations from eastern Amazonia with cultivated cupuaçu, so the origin is still unknown (Alves et al., 2007). Cupuaçu occurs in forests of almost all Amazonian regions, but it rarely occurs in western Amazonia, although it is one of the most important species cultivated in agroforestry systems in northern Bolivia (Vos et al., 2015). The high abundance in southern forests is unexpected; no one has ever suggested this region as an origin of cupuaçu.

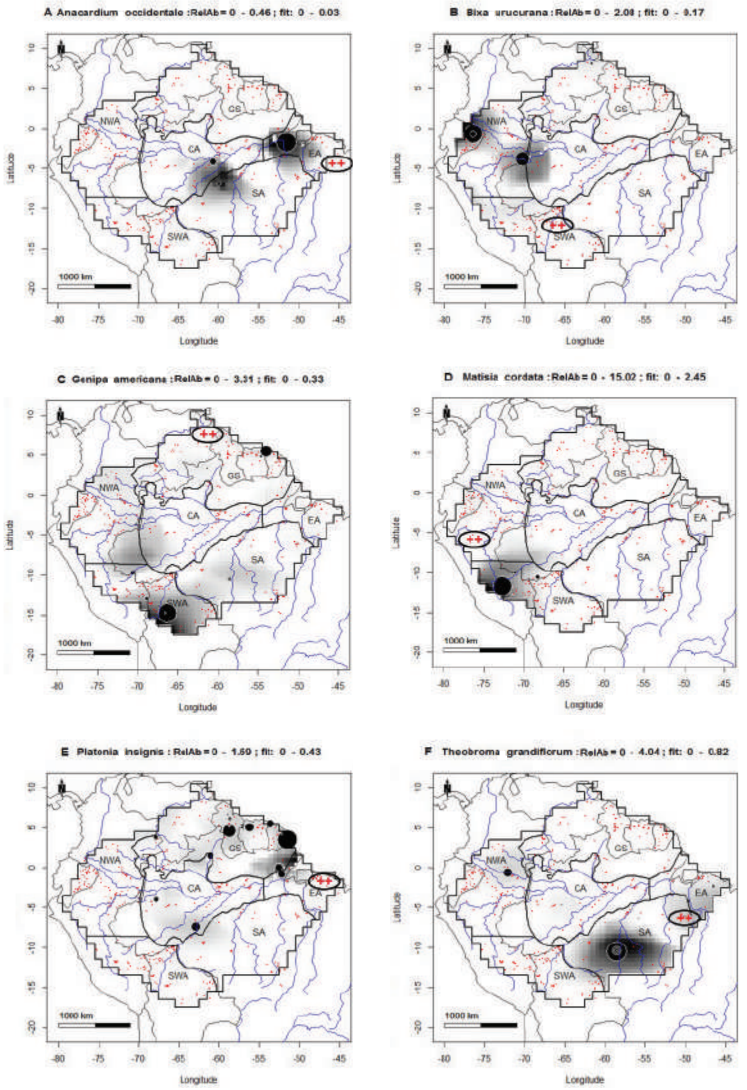
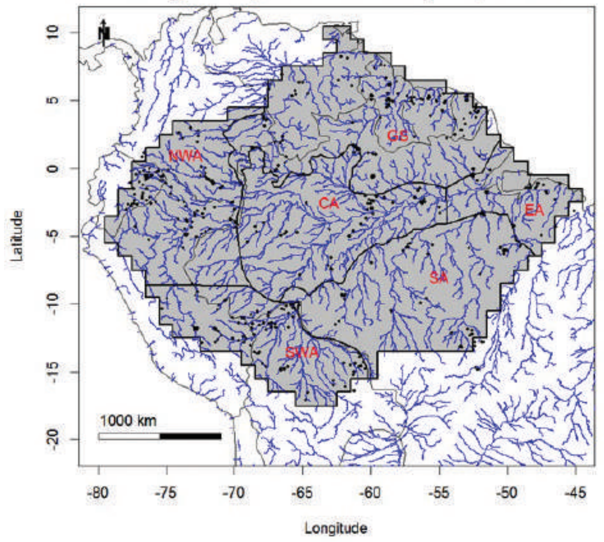


Figure A3.1. Distribution maps of domesticated species that are not hyperdominants in Amazonian forests and their probable origins of domestication. Distribution maps were estimated by the spatial loess model for six domesticated species that are not hyperdominants: *Anacardium occidentale* (A); *Bixa urucurana* (B); *Genipa americana* (C); *Matisia cordata* (D); *Platonia insignis* (E); *Theobroma grandiflorum* (F). The suspected origin of domestication is indicated in the maps by the symbol (++). The size of black dots indicates the abundance of the species in the plots where the species has been recorded. Red dots are plots where each domesticated species has not been recorded. Shading in maps shows the loess spatial average. The range of the relative abundance in plots (RelAb) and the loess spatial average in individual grid cells (fit) is reported in percentage on the top of each specific map. Amazonia is divided in six geological regions (NWA, north-western Amazonia; SWA, south-western Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia). Maps created with custom R scripts. Base map source (country. shp, rivers.shp): ESRI (http://www.esri.com/data/basemaps, © Esri, DeLorme Publishing Company).

A Geological regions and ATDN plots, n = 1091



B Rivers and Archaeological sites, n = 3348

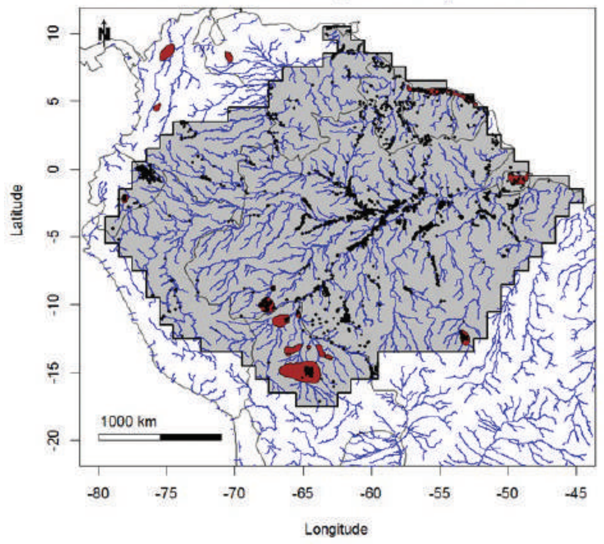


Figure A3.2. Maps of ATDN forest plots, geological regions, and archaeological sites overlaying the river network. Black circles show the location of forest plots (A) and black circles and red polygons show the location of archaeological sites and eco-archaeological regions in Amazonia, respectively (B). Red polygons are eco-archaeological regions encompassing numerous earthworks. Amazonia is divided in six geological regions (NWA, north-western Amazonia; SWA, south-western Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia). River network was obtained from the HydroSHEDS dataset with upcell values greater than 15,000. Maps created with custom R scripts. Base map source (country.shp): ESRI (http://www.esri.com/data/basemaps, © Esri, DeLorme Publishing Company).

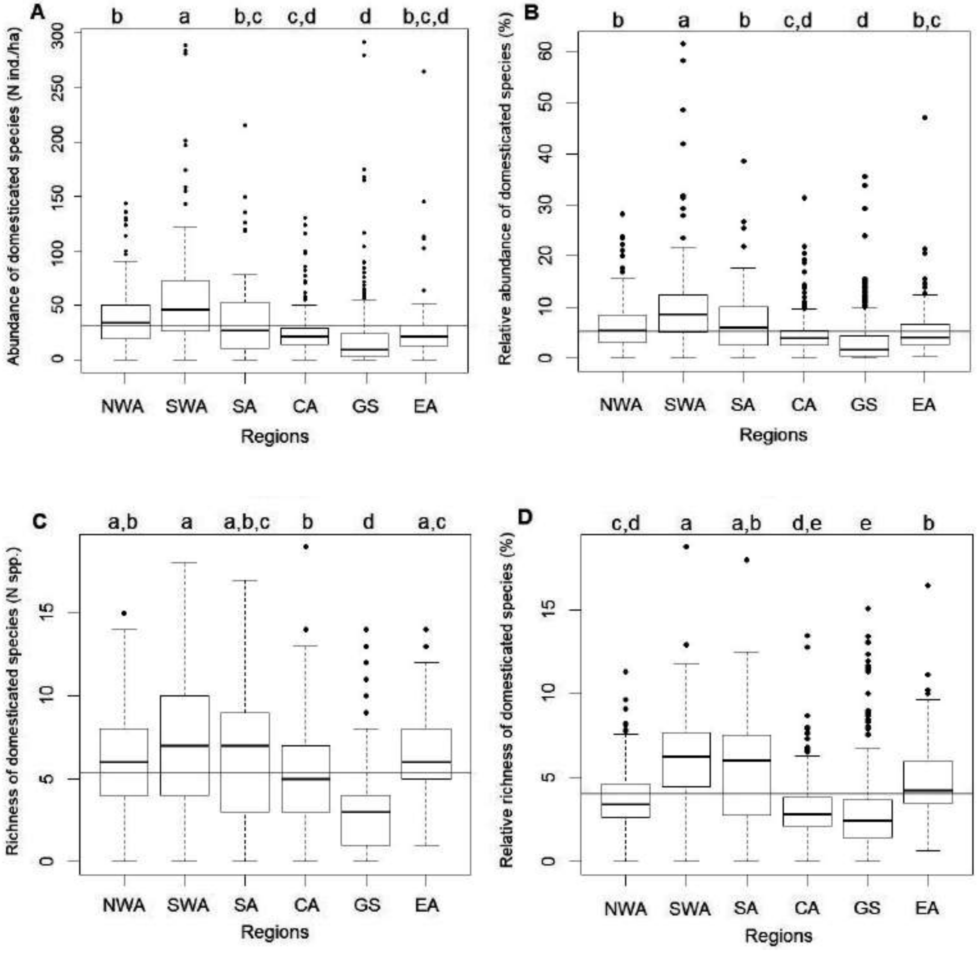


Figure A3.3. Abundance and richness of domesticated species in different geological regions. Box plots showing the abundance (A), the relative abundance (B), the richness (C) and the relative richness of domesticated species (D) in the six geological regions of Amazonia (NWA, north-western Amazonia; SWA, south-western Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia; see Figure A3.2 for the map of the regions). Different letters indicate significant differences (Tukey post hoc test, $p \leq 0.05$) and the line indicates the mean value across the whole Amazon.

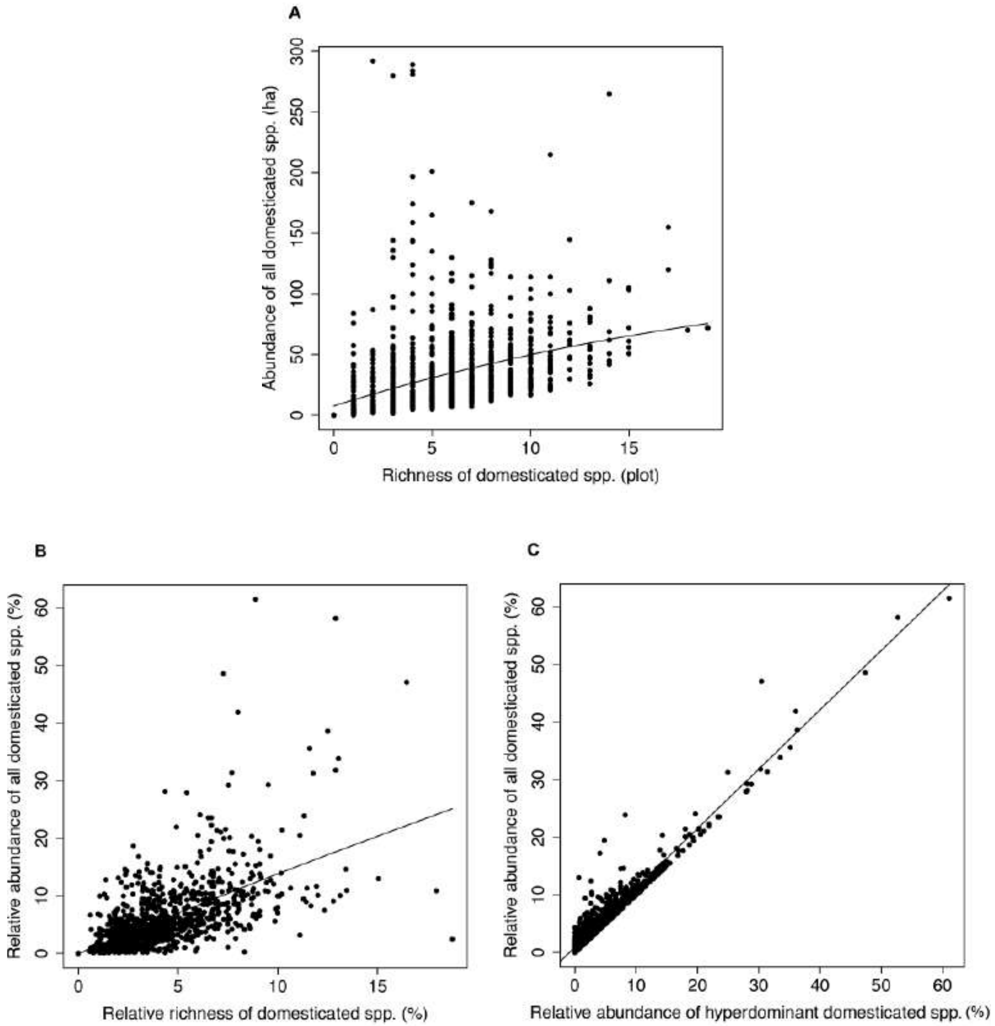


Figure A3.4. Abundance of domesticated species and their relationship to the richness and hyperdominance of domesticated species. Relationship between the abundance of 85 domesticated species per hectare (ha) and the richness of domesticated species in forest plots ($r^2 = 0.15$, A); relationship between the relative abundance of 85 domesticated species in forest plots and relative richness of domesticated species ($r^2 = 0.39$, B); and relationship between the relative abundance of 85 domesticated species and the relative abundance of 20 hyperdominant domesticated species in forest plots ($r^2 = 0.94$, C). Non-linear models created with custom R scripts.

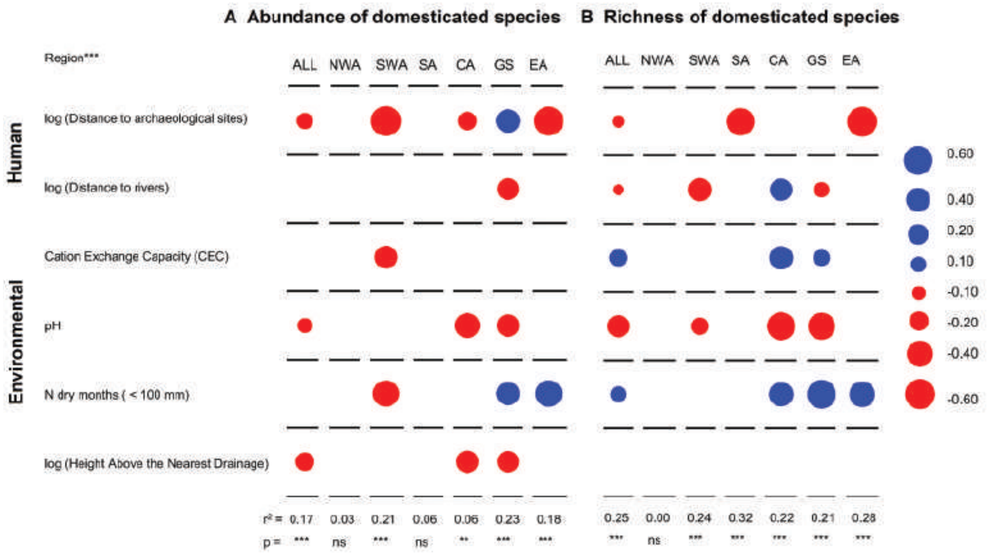


Figure A3.5. The abundance and richness of domesticated species as a function of human and environmental variables. Standardized regression coefficients for the abundance (A) and the richness of 85 domesticated species (B) as a function of human factors (distance to archaeological sites, distance to navigable rivers) and environmental conditions (soil Cation Exchange Capacity, soil pH, number of dry months and Height Above the Nearest Drainage). Circle size represents the relative contribution of the predictors, shown by standardized coefficients at the Amazonia-wide level (All) and region-level regression models (NWA, north-western Amazonia; SWA, south-western Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia). Red circles indicate negative effects and blue circles positive effects. Standardized coefficients are presented only for significant relations analysed in the models ($p \leq 0.05$). Adjusted r^2 and significance codes (p values: ≤ 0.001 '***'; ≤ 0.01 '**'; ≤ 0.05 '*'; > 0.05 'ns') are presented for the effect of human factors and environmental conditions at the Amazonia-wide level (All; using mixed-effect models and region as random factors), and at the region level (using multiple regression models).

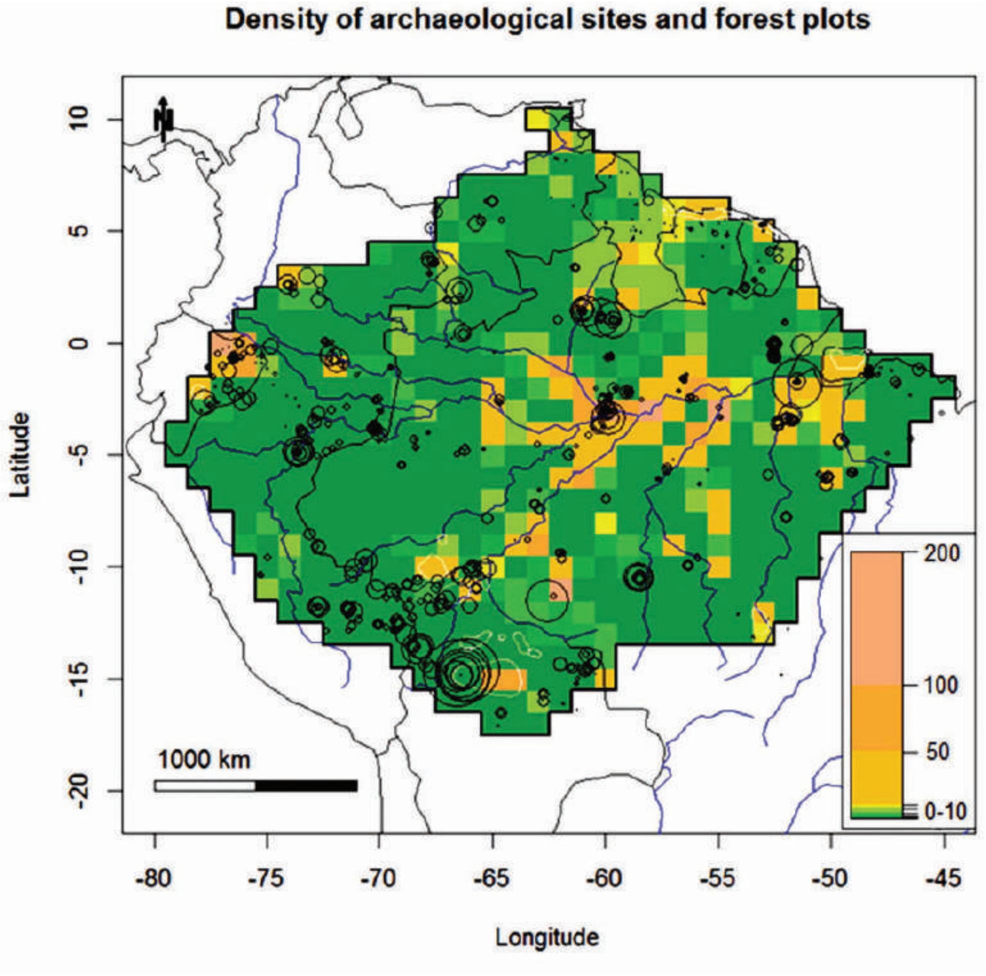


Figure A3.6. A heat map of archaeological sites in Amazonia and the variation of the relative abundance of domesticated species in forest plots. The pink-green background shows the density of archaeological sites in a 1o-grid cell scale, ranging from 0-200 sites per cell. White polygons show the location of eco-archaeological regions encompassing numerous earthworks. Circle sizes represent the variation of the relative abundance of domesticated species in forest plots shown in Figure A3.4B. Maps created with custom R scripts. Base map source (country.shp, rivers.shp): ESRI (http://www.esri.com/data/basemaps, © Esri, DeLorme Publishing Company).

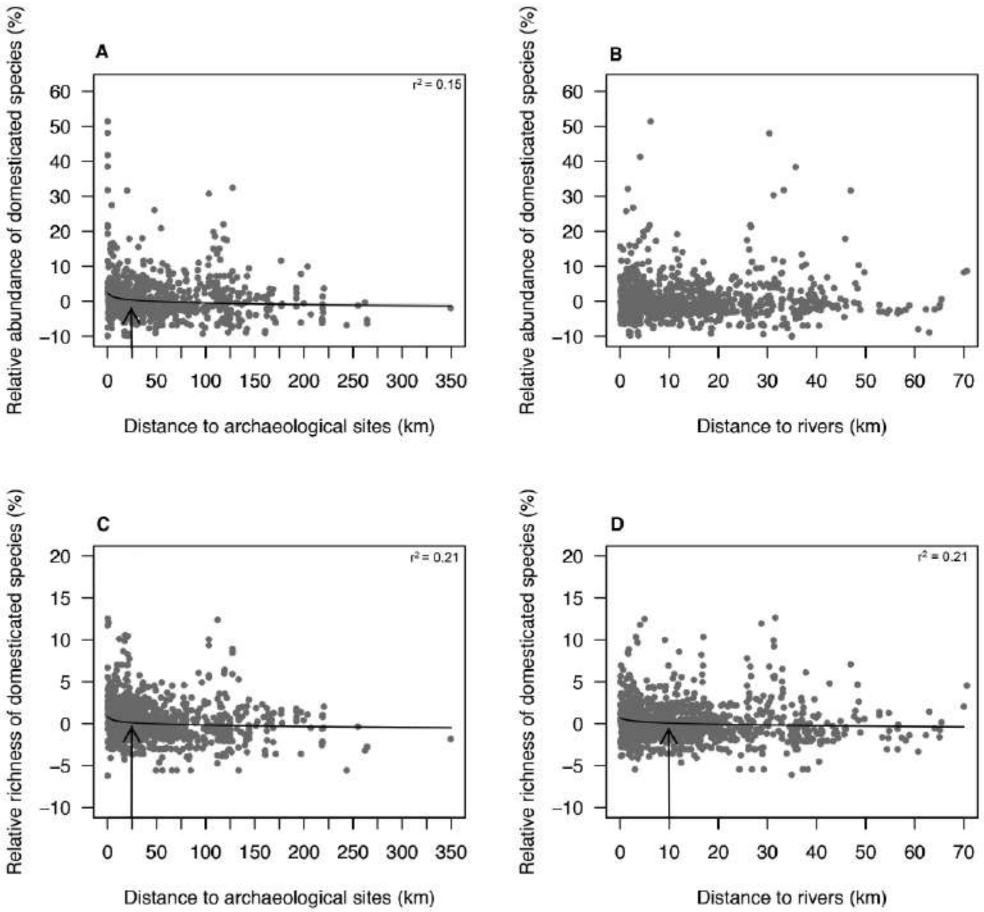


Figure A3.7. Relationships between the relative abundance and richness of domesticated species and the distance to archaeological sites (and eco-archaeological regions) and rivers in Amazonia. Note that some of these relationships may not match with the results obtained by the mixed-effect models (Figure 3.3), as these take into account the effects of environment. Black lines presented only for the significant relationships ($p \leq 0.05$). Arrows are presented to show the distance for which a pronounced decrease occurs. Mixed models fit by t-tests use Satterthwaite approximations: lmer (domestication ~ log10 (distance + 1) + (1 | Region)). Contrast plots were created with visreg function in R.

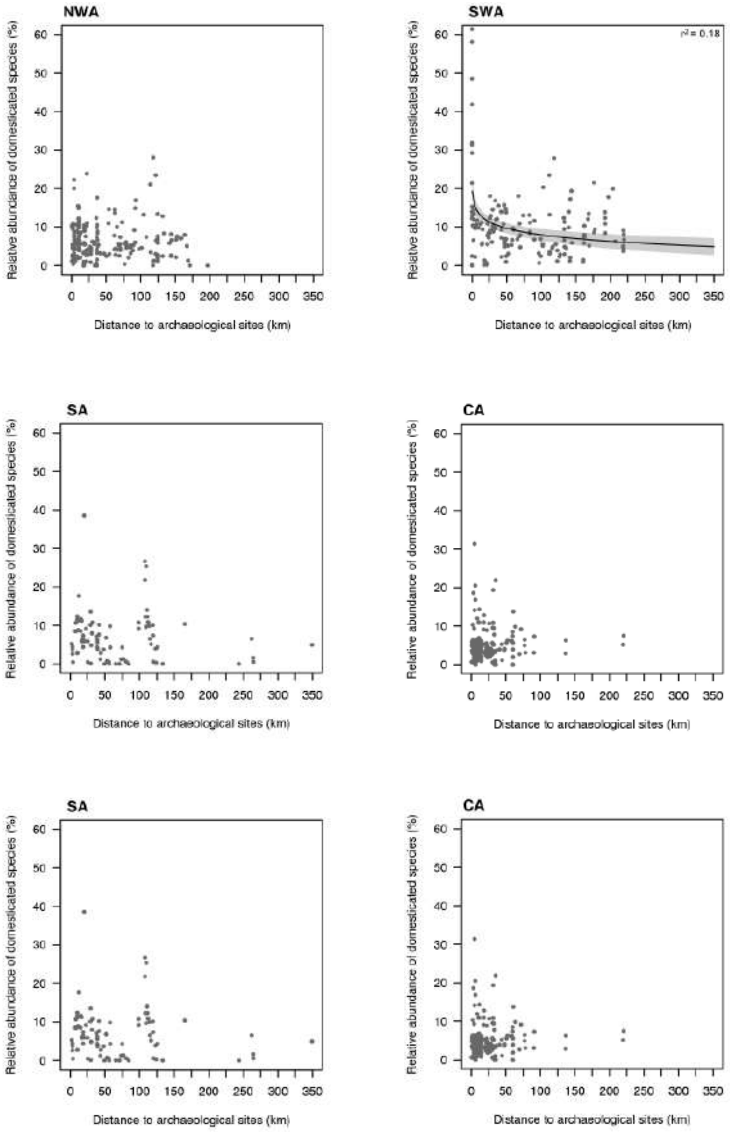


Figure A3.8. Relationships between the relative abundance of domesticated species and the distance to archaeological sites or eco-archaeological regions within Amazonian regions. Amazonia was divided in six geological regions (NWA, north-western Amazonia; SWA, south-western Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia). Note that some of these relationships may not match with the results obtained by the multiple regression models (Figure 3.3), as these take into account the effects of environment. Black lines presented only for the significant relationships ($p \leq 0.05$). Simple models were used for each geological region: lm (domestication ~ log10 (distance + 1)). Conditional plots were created with visreg function in R.

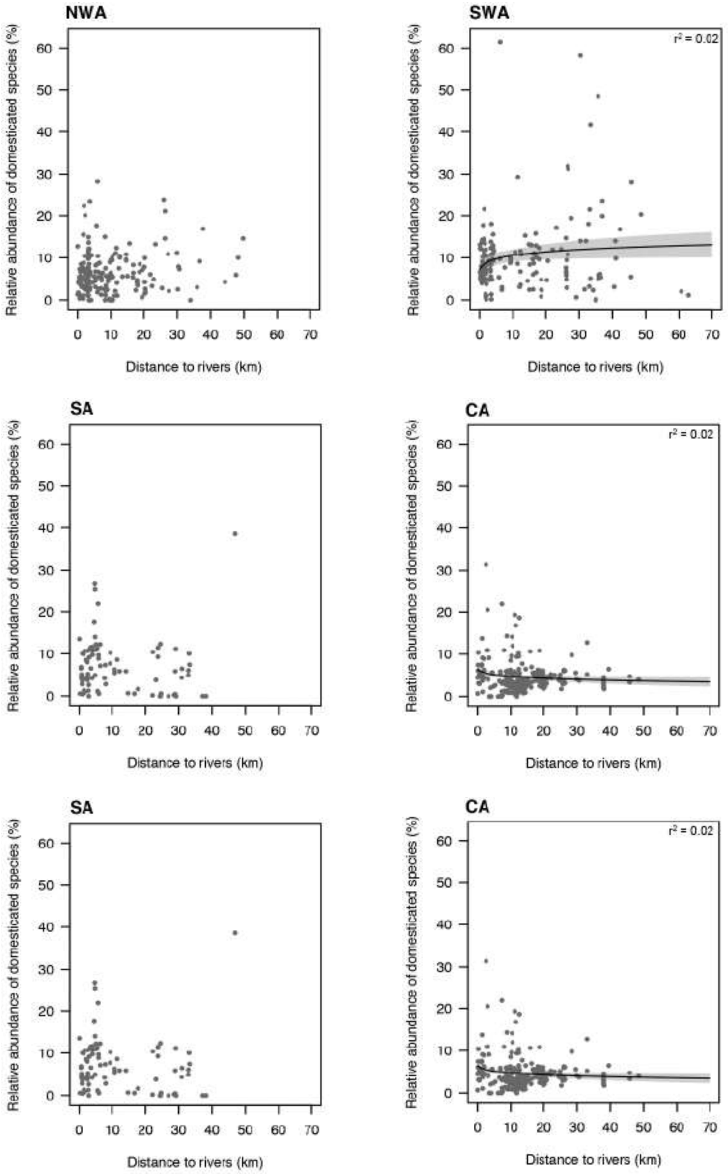


Figure A3.9. Relationships between the relative abundance of domesticated species and the distance to rivers within Amazonian regions. Amazonia was divided in six geological regions (NWA, north-western Amazonia; SWA, south-western Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia). Note that some of these relationships may not match with the results obtained by the multiple regression models (Figure 3.3), as these take into account the effects of environment. Black lines presented only for the significant relationships ($p \leq 0.05$). Simple models were used for each geological region: lm (domestication ~ log10 (distance + 1)). Conditional plots were created with visreg function in R.

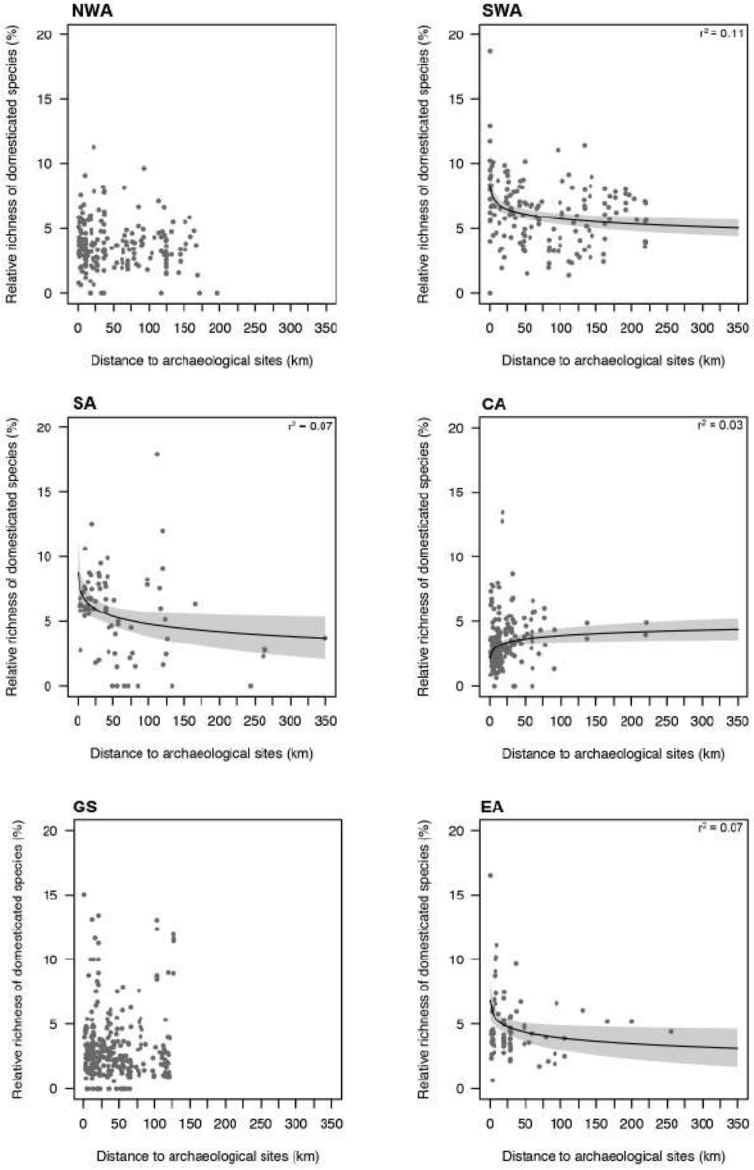


Figure A3.10. Relationships between the relative richness of domesticated species and the distance to archaeological sites and eco-archaeological regions within Amazonian regions. Amazonia was divided in six geological regions (NWA, north-western Amazonia; SWA, south-western Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia). Note that some of these relationships may not match with the results obtained by the multiple regression models (Figure 3.3), as these take into account the effects of environment. Black lines presented only for the significant relationships ($p \leq 0.05$). Simple models were used for each geological region: lm (domestication ~ log10 (distance + 1)). Conditional plots were created with visreg function in R.

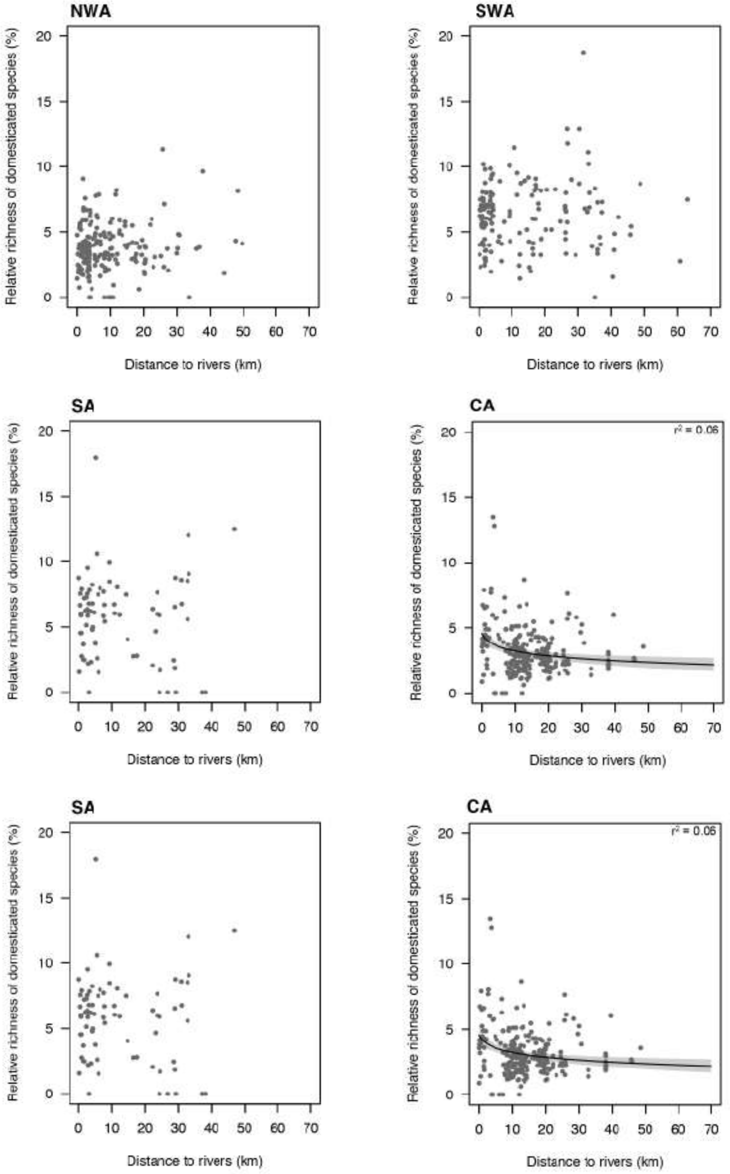


Figure A3.11. Relationships between the relative richness of domesticated species and the distance to rivers within Amazonian regions. Amazonia was divided in six geological regions (NWA, north-western Amazonia; SWA, south-western Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia). Note that some of these relationships may not match with the results obtained by the multiple regression models (Figure 3.3), as these take into account the effects of environment. Black lines presented only for the significant relationships ($p \leq 0.05$). Simple models were used for each geological region: lm (domestication ~ log10 (distance + 1)). Conditional plots were created with visreg function in R.

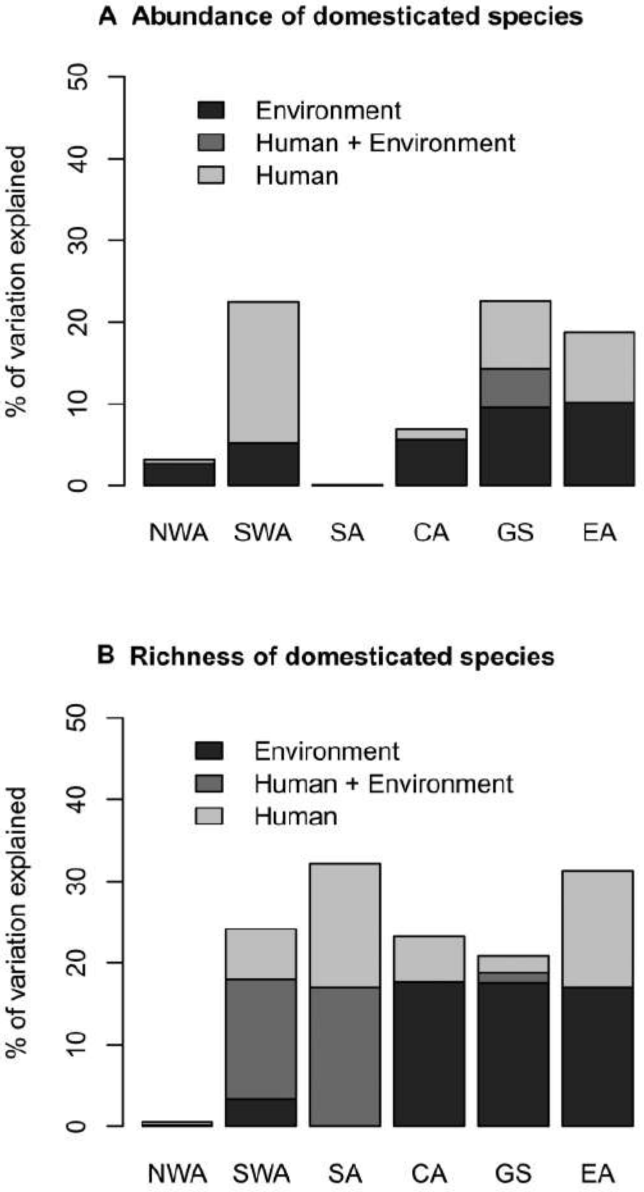
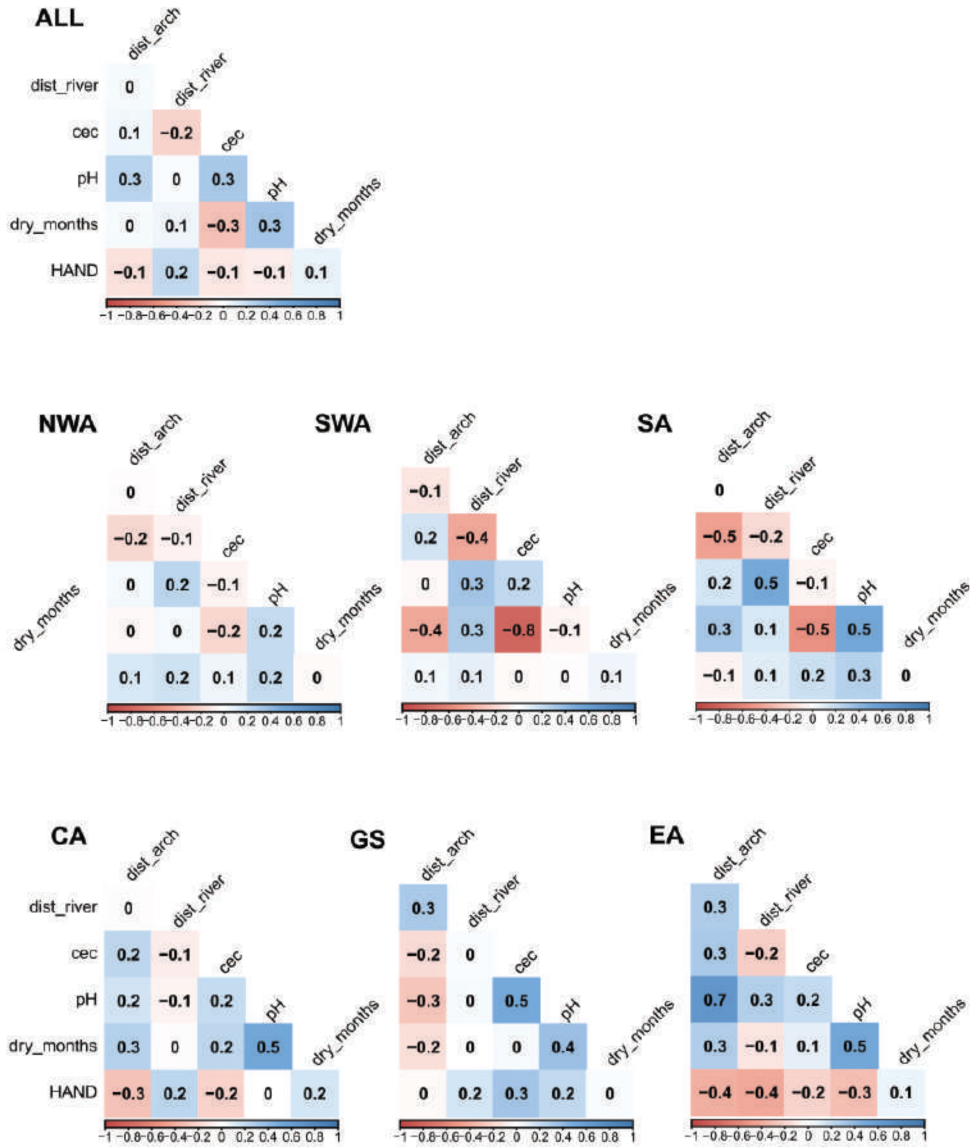


Figure A3.12. Relative contributions of human and environmental variables for explaining variation in abundance and richness of domesticated species in Amazonian forests. The figure shows the partitioning of variation in abundance (A) and richness (B) of domesticated species uniquely explained by environmental (dark gray) or human factors (light gray), and the variation jointly explained by both (gray). Variance partitioning was conducted over the results of multiple regression analyses presented in Figure 3.3. Amazonia was divided in six geological regions (NWA, north-western Amazonia; SWA, south-western Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia).



ALL	dist_arch	dist_river	cec	pH	dry_months
dist_river	0				
cec	0.1	−0.2			
pH	0.3	0	0.3		
dry_months	0	0.1	−0.3	0.3	
HAND	−0.1	0.2	−0.1	−0.1	0.1

NWA	dist_arch	dist_river	cec	pH	dry_months
	0				
	−0.2	−0.1			
	0	0.2	−0.1		
dry_months	0	0	−0.2	0.2	
	0.1	0.2	0.1	0.2	0

SWA	dist_arch	dist_river	cec	pH	dry_months
	−0.1				
	0.2	−0.4			
	0	0.3	0.2		
	−0.4	0.3	−0.8	−0.1	
	0.1	0.1	0	0	0.1

SA	dist_arch	dist_river	cec	pH	dry_months
	0				
	−0.5	−0.2			
	0.2	0.5	−0.1		
	0.3	0.1	−0.5	0.5	
	−0.1	0.1	0.2	0.3	0

CA	dist_arch	dist_river	cec	pH	dry_months
dist_river	0				
cec	0.2	−0.1			
pH	0.2	−0.1	0.2		
dry_months	0.3	0	0.2	0.5	
HAND	−0.3	0.2	−0.2	0	0.2

GS	dist_arch	dist_river	cec	pH	dry_months
	0.3				
	−0.2	0			
	−0.3	0	0.5		
	−0.2	0	0	0.4	
	0	0.2	0.3	0.2	0

EA	dist_arch	dist_river	cec	pH	dry_months
	0.3				
	0.3	−0.2			
	0.7	0.3	0.2		
	0.3	−0.1	0.1	0.5	
	−0.4	−0.4	−0.2	−0.3	0.1

Figure A3.13. Matrices of Spearman's correlation coefficients between pairs of explanatory variables used in the multiple regression models in Amazonia and each region. Amazonia was divided in six geological regions (NWA, north-western Amazonia; SWA, south- western Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia). dist_arch = log-transformed distance to archaeological sites, dist_river = log-transformed distance to navigable rivers, cec = soil cation exchange capacity, pH = soil pH, dry_months = number of dry months, HAND = log-transformed Height Above the Nearest Drainage.

Table A3.1. List of the 73 hyperdominant species studied. Three groups of 20 non-domesticated species with estimated population sizes (ter Steege et al., 2013) comparable to those of the 20 hyperdominant domesticated species are presented. The first group contains species primarily dispersed by non-human primates, the second consists of species selected based on specific criteria described in the Appendix 3A, and the third of species selected at random.

Species	Estimated population	Domesticated species	Dispersed by primates	Specific selection	Random selection
Euterpe precatoria	5.21 x 109	yes	no	no	no
Euterpe oleracea	3.78 x 109	yes	no	no	no
Oenocarpus bataua	3.71 x 109	yes	no	no	no
Astrocaryum murumuru	2.41 x 109	yes	no	no	no
Hevea brasiliensis	1.91 x 109	yes	no	no	no
Mauritia flexuosa	1.43 x 109	yes	no	no	no
Theobroma cacao	1.32 x 109	yes	yes	no	no
Theobroma subincanum	1.26 x 109	yes	yes	no	no
Oenocarpus bacaba	1.24 x 109	yes	no	no	no
Theobroma speciosum	1.20 x 109	yes	yes	no	no
Attalea maripa	9.65 x 108	yes	no	no	no
Attalea phalerata	5.91 x 108	yes	no	no	no
Pouteria caimito	5.79 x 108	yes	yes	no	no
Astrocaryum aculeatum	5.39 x 108	yes	no	no	no
Caryocar glabrum	5.22 x 108	yes	no	no	no
Spondias mombin	4.95 x 108	yes	yes	no	no
Garcinia macrophylla	4.65 x 108	yes	yes	no	no
Inga ynga	4.29 x 108	yes	yes	no	no
Pourouma cecropiifolia	4.25 x 108	yes	yes	no	no
Bertholletia excelsa	4.17 x 108	yes	no	no	no
Pseudolmedia laevis	4.30 x 109	no	yes	no	no
Brosimum lactescens	2.28 x 109	no	yes	no	yes
Helicostylis tomentosa	1.79 x 109	no	yes	no	no
Micropholis guyanensis	1.35 x 109	no	yes	no	no
Ecclinusa guianensis	1.18 x 109	no	yes	no	no
Brosimum guianense	1.04 x 109	no	yes	no	no
Brosimum rubescens	1.03 x 109	no	yes	no	yes
Chrysophyllum sanguinolentum	1.02 x 109	no	yes	no	no
Leonia glycycarpa	1.02 x 109	no	yes	no	no
Minquartia guianensis	9.87 x 108	no	yes	no	no
Pourouma minor	9.68 x 108	no	yes	no	no
Quararibea wittii	5.94 x 108	no	yes	no	no
Inga thibaudiana	5.77 x 108	no	yes	no	no
Manilkara bidentata	5.59 x 108	no	yes	no	no
Pouteria cuspidate	5.31 x 108	no	yes	no	no
Brosimum utile	4.89 x 108	no	yes	no	no
Bocageopsis multiflora	4.62 x 108	no	yes	no	no
Pouteria reticulate	4.51 x 108	no	yes	no	no
Pourouma bicolor	4.47 x 108	no	yes	no	yes
Apeiba tibourbou	4.14 x 108	no	yes	no	no
Protium altissimum	5.21 x 109	no	no	yes	no
Iriartea deltoidea	4.07 x 109	no	no	yes	no
Trattinnickia burserifolia	2.78 x 109	no	no	yes	no
Socratea exorrhiza	2.68 x 109	no	no	yes	no
Attalea butyracea	1.78 x 109	no	no	yes	no
Eperua leucantha	1.84 x 109	no	no	yes	yes
Clathrotropis macrocarpa	1.35 x 109	no	no	yes	yes
Pentaclethra macroloba	1.34 x 109	no	no	yes	no
Dicymbe corymbosa	1.26 x 109	no	no	yes	no
Virola calophylla	1.22 x 109	no	no	yes	no
Micrandra spruceana	9.57 x 108	no	no	yes	yes
Protium decandrum	5.87 x 108	no	no	yes	no
Cenostigma tocantinum	5.76 x 108	no	no	yes	no
Ocotea aciphylla	5.19 x 108	no	no	yes	no
Conceveiba guianensis	5.17 x 108	no	no	yes	no
Protium trifoliolatum	4.93 x 108	no	no	yes	no
Eschweilera tessmannii	4.68 x 108	no	no	yes	no
Ocotea cernua	4.31 x 108	no	no	yes	no
Trichilia pleeana	4.25 x 108	no	no	yes	no
Cedrelinga cateniformis	4.17 x 108	no	no	yes	yes
Aspidosperma excelsum	1.13 x 109	no	no	no	yes
Goupia glabra	9.88 x 108	no	no	no	yes
Lecythis idatimon	9.09 x 108	no	no	no	yes
Sagotia brachysepala	8.67 x 108	no	no	no	yes
Inga alba	7.82 x 108	no	no	no	yes
Iryanthera laevis	6.82 x 108	no	no	no	yes
Aparisthmium cordatum	6.18 x 108	no	no	no	yes
Scleronema micranthum	6.12 x 108	no	no	no	yes
Eperua grandiflora	5.41 x 108	no	no	no	yes
Leonia crassa	4.77 x 108	no	no	no	yes
Laetia procera	4.73 x 108	no	no	no	yes
Hura crepitans	4.21 x 108	no	no	no	yes
Pouteria procera	3.61 x 108	no	no	no	yes

Table A3.2. Results of the multiple regression models of the relative abundance and richness of domesticated species as functions of human and environmental variables using Bonferroni correction. Standardized regression coefficients for the relative abundance of domesticated species and the relative richness of domesticated species as a function of human factors (dist_arch = log-transformed distance to archaeological sites, dist_river = log-transformed distance to navigable rivers) and environmental conditions (cec = soil cation exchange capacity, pH = soil pH, dry_months = number of dry months, HAND = log-transformed Height Above the Nearest Drainage). Standardized coefficients are shown at the Amazonia-wide level (All) and region-level regression models (NWA, north-western Amazonia; SWA, south-western Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia) and presented only for significant relations analysed in the models before Bonferroni correction ($p \leq 0.05$). Significant codes are presented for each variable using Bonferroni correction: ($p \leq 0.0001$ '***'; ≤ 0.0014 '**'; ≤ 0.0071 '*') are presented for the effect of human factors and environmental conditions at the Amazonia-wide level (All; using mixed-effect models and region as random factors), and at the region level (using multiple regression models).

		Relative abundance		**Relative richness**	
Region (nº of plots)	**Variables**	**Standardized coefficient**	**Correction -value**	**Standardized coefficient**	**Correction -value**
All (1091)	dist_arch	-0.13	***	-0.10	**
	cec				
	pH			-0.12	*
	dry months	0.11	*	0.25	***
	HAND	-0.17	***	-0.14	***
NWA (197)	dist_arch				
	cec				
	pH				
	dry months			0.22	*
	HAND				
SWA (158)	dist_arch	-0.49	***	-0.35	***
	dist_rivers				
	pH				
	dry months	-0.38	**		
	HAND				
SA (86)	dist_arch				
	dist_rivers				
	cec				
	pH				
	dry months				
	HAND				
CA (250)	dist_arch				
	cec			0.17	*
	pH	-0.41	***	-0.62	***
	dry months	0.29	**	0.58	***
	HAND	-0.27	**	-0.32	***
GS (317)	dist_arch	0.22	***		
	cec				
	pH			-0.28	***
	dry months			0.51	***
	HAND			-0.17	*
EA (83)	dist_arch	-0.50	*	-0.63	***
	dist_rivers				
	cec				
	pH				
	dry months			0.39	*
	HAND				

Table A3.3. Results of the multiple regression models with data from the plots on archaeological sites and eco-archaeological regions and without these data. Standardized coefficients (Beta coefficients) and p values are presented for the relative abundance of domesticated species and the relative richness of domesticated species as a function of human factors (dist_arch = log-transformed distance to archaeological sites, dist_river = log-transformed distance to navigable rivers) and environmental conditions (cec = soil cation exchange capacity, pH = soil pH, dry_months = number of dry months, HAND = log-transformed Height Above the Nearest Drainage) at the Amazonia-wide level (All) and region-level regression models (SWA, south-western Amazonia and EA, eastern Amazonia) where plots on eco-archaeological regions are located. Standardized coefficients are presented only for significant relations analysed in the models ($p \leq 0.05$). Significant codes (p values: ≤ 0.001; '***'; ≤ 0.01 '**'; ≤ 0.05 '*'; > 0.05 'ns') are presented for the effect of human factors and environmental conditions at the Amazonia-wide level (All; using mixed-effect models and region as random factors), and at the region level (using multiple regression models).

		Relative abundance				**Relative richness**			
Region (nº of plots)	**Variables**	**Beta coefficient with plots**	**p**	**Beta coefficient without plots**	**p**	**Beta coefficient with plots**	**p**	**Beta coefficient without plots**	**p**
All (1091)	dist_arch	-0.13	***			-0.10	***		
	dist_river			-0.06	*	-0.09	**		
	cec								
	pH			-0.16	***	-0.12	**	-0.15	***
	dry months	0.11	**	0.14	***	0.25	***	0.27	***
	HAND	-0.17	***	-0.16	***	-0.14	***	-0.13	***
SWA (158)	dist_arch	-0.49	***	-0.21	*	-0.35	***	-0.23	*
	dist_river			0.22	*				
	cec	-0.31	**			-0.33	**	-0.37	*
	pH								
	dry months	-0.38	***	-0.31	*				
	HAND			-0.26	**				
EA (83)	dist_arch	-0.50	**	-0.36	*	-0.63	***	-0.54	***
	dist_river			-0.49	***			-0.23	*
	cec			-0.22	*				
	pH			0.61	***	0.39	*	0.55	**
	dry months	0.32	*			0.39	**	0.29	*
	HAND								

DATABASE A3

List of 85 species with populations that were likely domesticated, semi-domesticated or incipiently domesticated by pre-Columbian peoples in Amazonia and elsewhere in the Americas. The main use of each species, the degree of domestication (6), the rank of dominance according to ter Steege et al. (2013), the relative frequency of the species in each region (%), the number of regions where the species occurs and information about cultivation are provided. Numbers provided below each region correspond to the number of forest plots inventoried in each region (NWA, north-western Amazonia; SWA, south-western Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia). Species that were not present in Clement (1999) were classified here as incipiently domesticated species. References for evidence of domestication of each species are presented in this table. The information about cultivation was obtained from Mansfeld's World Database of Agricultural and Horticultural Crops (2001) and other sources described in the table. Species are listed based on the rank of dominance according to ter Steege et al. (2013). All species with ranking ≤ 227 are considered "hyperdominant" species.

Species	**Family**	**Main use(s)**	**Degree of Domestication**	**Rank**	**Regions**	**Reference of domestication**	**Information about cultivation**
Euterpe precatoria	Arecaceae	Oily fruit	Incipient	1	5	Perrut de Lima (2014)	Cultivated in Brazil, Bolivia and probably other countries because deliberate planting or sowing is an old management practice (Smith, 2015).
Euterpe oleracea	Arecaceae	Oily fruit	Incipient	6	3	Clement (1999)	Cultivated in all tropical and subtropical regions as a fruit and ornamental tree. May have been a staple crop of the Marajoara society on Marajó Island at the mouth of the Amazon River.
Oenocarpus bataua	Arecaceae	Oily fruit	Incipient	7	6	Clement (1999)	Wild stands are utilized. Experimentally cultivated in Venezuela, Colombia and Bolivia. At Peña Roja, Colombia, archaeological sequences suggest local management over several millennia, with use starting by 9,000 BP (Morcote-Ríos and Bernal, 2001).
Astrocaryum murumuru	Arecaceae	Oily fruit	Incipient	10	6	Clement (1999)	Cultivated in Bolivia. Abundant in forests covering artificial mounds in the seasonally-flooded savannas of the northern Bolivian Amazon (Erickson and Balée, 2006) and an indicator species for anthropogenic soils in Central Amazonia (Junqueira et al., 2010).
Hevea brasiliensis	Euphorbiaceae	Nut/Latex	Incipient	14	6	Clement (1999)	Cultivated in many tropical countries. Rubber has long been used by indigenous populations for making boots, water bottles, syringes, elastic bands etc. Siebert (1948) thought it might be semi-domesticated to use the seed as food.
Mauritia flexuosa	Arecaceae	Oily fruit	Incipient	23	5	Clement (1999)	Cultivated in Venezuela, Colombia, Ecuador, Peru, and Brazil. At Peña Roja, Colombia, use started by 9,000 BP (Morcote-Ríos and Bernal, 2001).
Theobroma cacao	Malvaceae	Stimulant/ Fruit	Semi	29	5	Clement (1999)	Cocoa is an old American cultivated plant. It started to be used and probably cultivated more than 2,500 BP in Ecuador. The traditional cultivation area is the American tropics, including Amazonia.
Theobroma subincanum	Malvaceae	Fruit	Incipient	31	6	Clement (1999)	Sometimes cultivated.
Oenocarpus bacaba	Arecaceae	Oily fruit	Incipient	33	6	Clement (1999)	Mainly wild stands are exploited, but also cultivated (e.g., French Guiana, Brazil). At Peña Roja, Colombia, use started by 9,000 BP (Morcote-Ríos and Bernal, 2001).
Theobroma speciosum	Malvaceae	Fruit	Incipient	35	6	Clement (1999)	Sometimes grown in house gardens.
Attalea maripa	Arecaceae	Oily fruit	Incipient	59	6	Clement (1999)	Cultivated in French Guiana, Surinam, Brazil, and Peru.
Attalea phalerata	Arecaceae	Thatch/Fruit	Incipient	122	3	Sosnowska et al. (2015)	Cultivated in home gardens and swiddens in the Tambo region in Peruvian Amazonia, absent in the surrounding forest where incipient domesticated species were found (Sosnowska et al., 2015). Abundant in forests covering artificial mounds in the seasonally-flooded savannas of the northern Bolivian Amazon (Erickson and Balée, 2006) and an indicator species for anthropogenic soils in Central Amazonia (Junqueira et al., 2010).
Pouteria caimito	Sapotaceae	Fruit	Semi	124	6	Clement (1999)	Cultivated as a fruit tree in tropical parts of America.
Astrocaryum aculeatum	Arecaceae	Fruit	Incipient	139	6	Clement (1999)	The cultivation of this palm in the past has been hypothesized because it occurs frequently around current settlements and villages. In Brazil it is cultivated by some indigenous populations.
Caryocar glabrum	Caryocaraceae	Edible nut	Incipient	145	6	Clement (1999)	Cultivated for the tasty kernels of the fruit, rich in oil.
Spondias mombin	Anacardiaceae	Fruit	Semi	154	6	Clement (1999)	Frequently cultivated as a fruit tree in the tropics, found in association with anthropogenic soils along the Madeira River (Junqueira et al., 2010).
Garcinia macrophylla	Clusiaceae	Fruit	Incipient	167	6	Clement (1999)	Cultivated as a fruit tree in Brazil.
Inga ynga	Fabaceae	Fruit	Semi	181	6	Clement (1999)	Cultivated widely in tropical South America.
Pourouma cecropiifolia	Urticaceae	Fruit	Semi	182	6	Clement (1999)	Often cultivated in western Amazonia and its occurrence often indicates previous human occupation.
Bertholletia excelsa	Lecythidaceae	Edible nut	Incipient	188	5	Clement (1999)	Widely cultivated inside and also outside its natural range, e.g., in Cuba, Sri Lanka and SW Asia. In use at the Caverna Pedra Pintada, Monte Alegre, Pará, before 9,800 BP (Roosevelt et al., 1996).
Pouteria macrophylla	Sapotaceae	Fruit	Semi	233	6	Clement (1999)	Cultivated as a fruit tree in the Amazon basin and Cuba.
Manilkara huberi	Sapotaceae	Fruit/Latex	Incipient	254	4	Clement (1999)	Cultivated within its natural distribution range.

Species	Family	Main use(s)	Degree of Domestication	Rank	Regions	Reference of domestication	Information about cultivation
Sterculia speciosa	Malvaceae	Fruit	Incipient	331	5	Clement (1999)	Cultivated in Guiana and in northern Brazil.
Matisia cordata	Malvaceae	Fruit	Semi	355	3	Clement (1999)	Cultivated in eastern Peru, Ecuador and Colombia, and western Amazonian Brazil as a fruit tree.
Hymenaea courbaril	Fabaceae	Starchy fruit	Incipient	370	6	Clement (1999)	The tree is cultivated for its fruits (e.g., in Cuba, Bolivia, Brazil). A close relative, H. parvifolia, was in use at the Caverna da Pedra Pintada, Monte Alegre, Pará, before 9,800 BP (Roosevelt et al., 1996).
Theobroma grandiflorum	Malvaceae	Fruit	Incipient	439	4	Clement (1999)	Cultivated from Pará and Maranhão to Manaus (Brazil), also in Colombia, Venezuela, Ecuador, and Costa Rica.
Chrysophyllum venezuelanense	Sapotaceae	Fruit	Incipient	466	6	Mansfeld's World Database (2001)	Cultivated as a fruit tree in the Brazilian Amazonia. Introduced and possibly naturalized in Brazil.
Dipteryx odorata	Fabaceae	Flavoring	Incipient	479	6	Mansfeld's World Database (2001)	The use of this tree by South American indigenous populations is known for centuries; flavouring for tobacco, liqueurs and other foodstuffs. Plantations of the species may be found in Venezuela, Brazil, on Trinidad and other Caribbean islands.
Grias neuberthii	Lecythidaceae	Fruit	Incipient	531	6	Clement (1999)	A component of home-gardens in the Peruvian Amazon region, where it is cultivated for its fruits. The disjunctive distribution in Ecuador may be the result of fruit dispersal by humans.
Inga laurina	Fabaceae	Fruit	Incipient	558	1	Mansfeld's World Database (2001)	Presumably cultivated by the Mayas.
Brosimum alicastrum	Moraceae	Edible nut	Incipient	566	5	Mansfeld's World Database (2001)	Cultivated in Mexico in orchards and experimental stations. Cultivated by the Mayas.
Campsiandra comosa	Fabaceae	Fruit	Incipient	608	3	Clement (1999)	-
Pouteria multiflora	Sapotaceae	Fruit	Semi	617	4	Clement (1999)	Cultivated as a fruit tree within its natural distribution range.
Lecythis pisonis	Lecythidaceae	Edible nut	Incipient	716	6	Clement (1999)	Often cultivated in home-gardens in the Amazonian region. Also cultivated in Central America, the Caribbean area and Peru.
Inga cinnamomea	Fabaceae	Fruit	Semi	722	6	Clement (1999)	Frequently cultivated as a fruit tree in the Brazilian Amazon.
Oenocarpus distichus	Arecaceae	Oily fruit	Incipient	760	3	Clement (1999)	Cultivated in eastern Amazonia.
Astrocaryum chambira	Arecaceae	Fiber	Incipient	810	3	García et al. (2015)	Cultivated in manioc fields and home-gardens by indigenous groups in the Colombian Amazon (García et al., 2015).
Couepia bracteosa	Chrysobalanaceae	Fruit	Incipient	840	5	Clement (1999)	Occasionally cultivated in the Amazon basin for its edible fruit.
Psidium acutangulum	Myrtaceae	Fruit	Incipient	849	3	Clement (1999)	Cultivated in eastern Ecuador in indigenous orchards. In Brazil it is cultivated as a fruit and ornamental tree.
Couepia longipendula	Chrysobalanaceae	Edible nut	Incipient	879	3	Clement (1999)	Cultivated around Manaus, Brazil for its edible cotyledons (fresh or cooked).
Couma utilis	Apocynaceae	Fruit/Latex	Incipient	982	2	Clement (1999)	Cultivated in central Amazonia.
Genipa americana	Rubiaceae	Fruit/Colorant	Full	1010	6	Clement (1999)	Cultivated for its edible fruits in tropical America and occasionally in the Philippines.
Inga macrophylla	Fabaceae	Fruit	Semi	1023	6	Clement (1999)	Frequently cultivated for its edible sweet fruit pulp.
Myroxylon balsamum	Fabaceae	Balsam	Incipient	1056	2	Mansfeld's World Database (2001)	'Peruvian balsam trees' were cultivated in the imperial gardens of the Aztecs.
Macoubea guianensis	Apocynaceae	Fruit	Semi	1065	6	Clement (1999)	Cultivated in the Amazonian regions of Colombia, Ecuador, Peru and western Brazil.
Talisia esculenta	Sapindaceae	Fruit	Incipient	1073	2	Clement (1999)	Cultivated for its fruits in many parts of Amazonia. In use at the Caverna da Pedra Pintada, Monte Alegre, Pará, before 9,800 BP (Roosevelt et al., 1996).

Species	Family	Main use(s)	Degree of Domestication	Rank	Regions	Reference of domestication	Information about cultivation
Alibertia edulis	Rubiaceae	Fruit	Incipient	1147	4	Clement (1999)	Cultivated in Colombia and frequently cultivated in home-gardens in Brazilian Amazon.
Pouteria macrocarpa	Sapotaceae	Fruit	Semi	1164	4	Clement (1999)	Cultivated as a fruit tree within its natural distribution area.
Caryocar villosum	Caryocaraceae	Fruit	Incipient	1204	6	Clement (1999)	The wild trees in the Amazonian region are promoted by local populations and cultivated in home-gardens of eastern Amazonia.
Caryodendron orinocense	Euphorbiaceae	Edible nut	Incipient	1325	2	Clement (1999)	Experimentally cultivated in Colombia, Ecuador, and Venezuela. At present mainly wild stands are harvested.
Annona montana	Annonaceae	Fruit	Semi	1370	6	Clement (1999)	Cultivated in Brazil, Colombia, Florida, Antilles and Philippines.
Platonia insignis	Clusiaceae	Fruit	Semi	1418	3	Clement (1999)	Cultivated in eastern Amazonia and adjacent Maranhão and Piauí as a fruit tree.
Astrocaryum vulgare	Arecaceae	Fruit	Incipient	1431	3	Mansfeld's World Database (2001)	Given its frequent occurrence in the neighbourhood of settlements and villages in Surinam, a former cultivation of this palm was hypothesized. Use started around 11,000 BP in Caverna da Pedra Pintada, Monte Alegre, Pará, Brazil (Roosevelt et al., 1996).
Bixa urucurana	Bixaceae	Colorant	Full	1518	3	Moreira et al. (2015)	Bixa urucurana is considered the wild progenitor of Bixa orellana (Moreira et al., 2015) that has been used since pre-Columbian times and often cultivated in the whole tropical America.
Poraqueiba sericea	Icacinaceae	Fruit	Semi	1519	3	Clement (1999)	Cultivated in the Amazonian region as a fruit tree.
Bactris gasipaes	Arecaceae	Fruit	Full	1530	3	Clement (1999)	This important useful palm is cultivated in many parts of Central and South America. Fully domesticated populations are only known cultivated.
Garcinia brasiliensis	Clusiaceae	Fruit	Incipient	1539	3	Clement (1999)	Cultivated by Kuikuro Indians in the upper Xingu River and in central Brazil for the edible fruits with a high content of oil, protein and vitamins.
Sapindus saponaria	Sapindaceae	Fish poison	Incipient	1586	5	Mansfeld's World Database (2001)	Occasionally cultivated as a fruit tree in Brazil. Known since pre-Columbian times and possibly an ancient domesticate.
Trema micrantha	Ulmaceae	Medicine /Paper	Incipient	1685	4	Mansfeld's World Database (2001)	Cultivated by the Kayapó Indians in Amazonia (Brazil) and used as a medicine. In Northern Puebla (Mexico) planted by the Otomi Indians to make bark paper (pre-Hispanic technology).
Cassia leiandra	Fabaceae	Fruit	Semi	1695	5	Clement (1999)	Frequently cultivated in Brazil since pre-Columbian times.
Erisma japura	Vochysiaceae	Fruit	Incipient	1737	1	Clement (1999)	Managed and harvested from forests in north-western Amazonia for its seeds (Cavalcante, 2010). The Tatuyo peoples of Vaupes-Colombia make a butter called Mantequilla de Batí, and Baniva peoples of Venezuela make a cheese called Queso de Jabua.
Grias peruviana	Lecythidaceae	Fruit	Incipient	1842	2	Clement (1999)	Occasionally cultivated from southern Ecuador to Peru in house-gardens as a fruit tree and ornamental tree. The disjunctive distribution in Ecuador may be the result of fruit dispersal by humans.
Lonchocarpus utilis	Fabaceae	Poison	Semi	1873	2	Clement (1999)	Cultivated since pre-Columbian times by indigenous populations and used as fish poison.
Caryocar nuciferum	Caryocaraceae	Edible nut	Incipient	1990	2	Clement (1999)	Widely cultivated within the range of its natural distribution.
Couepia subcordata	Chrysobalanaceae	Fruit	Semi	2011	2	Clement (1999)	Cultivated as a fruit and shade tree in the vicinity of Manaus.
Byrsonima crassifolia	Malpighiaceae	Oily fruit	Semi	2186	2	Clement (1999)	Cultivated for its fruit in Mexico by Mayan populations since pre-Columbian times.
Acrocomia aculeata	Arecaceae	Fruit	Incipient	2282	2	Clement (1999)	Probably introduced by people from South America into Central America in pre-Colombian times (Morcote-Ríos and Bernal, 2001). Cultivated on the Philippines and Cuba. It is associated with anthropogenic soils in Amazonia (Junqueira et al., 2010).
Annona squamosa	Annonaceae	Fruit	Full	2385	1	Mansfeld's World Database (2001)	Only cultivated with domesticated populations.

Species	Family	Main use(s)	Degree of Domestication	Rank	Regions	Reference of domestication	Information about cultivation
Anadenanthera peregrina	Fabaceae	Fruit	Semi	2510	2	Clement (1999)	The beginning of domestication took place through competition between Indian peoples for obtaining this stimulant.
Eugenia uniflora	Myrtaceae	Fruit	Incipient	2699	2	Clement (1999)	Cultivated in all tropical and subtropical regions as a fruit and ornamental tree.
Ilex guayusa	Aquifoliaceae	Stimulant	Full	2797	1	Clement (1999)	Frequently cultivated in Peru, Ecuador and Colombia, rarely found in non-cultivated contexts.
Psidium guineense	Myrtaceae	Fruit	Incipient	2884	1	Clement (1999)	Cultivated occasionally at medium elevations in tropical America, India, Indonesia and the Pacific islands.
Theobroma bicolor	Malvaceae	Fruit	Semi	2953	1	Clement (1999)	Cultivated in eastern Andean foothills and adjacent Amazonian lowlands.
Poraqueiba paraensis	Icacinaceae	Fruit	Semi	3040	1	Clement (1999)	Cultivated as a fruit tree in the Brazilian Amazon.
Eugenia stipitata	Myrtaceae	Fruit	Semi	3161	2	Clement (1999)	Occasionally cultivated as fruit tree in Brazil and more frequently in Peru.
Annona muricata	Annonaceae	Fruit	Full	3167	1	Clement (1999)	Cultivated from sea level to 1,000 m above sea level in the Antilles and from Southern Mexico to Peru and Northern Argentina.
Annona mucosa	Annonaceae	Fruit	Full	3271	3	Clement (1999)	Cultivated in the Neotropics, also planted in tropical SE Asia.
Anacardium occidentale	Anacardiaceae	Fruit	Semi	3450	3	Clement (1999)	Cultivated and sub-spontaneous in many parts of the tropical regions.
Phytelephas macrocarpa	Arecaceae	Thatch	Incipient	3571	2	Sosnowska et al. (2015)	Cultivated in fields and home gardens by Asháninka Indians in the Tambo region in Peruvian Amazon. In this region it occurs only in forests where incipiently domesticated populations were found (Sosnowska et al., 2015).
Campomanesia lineatifolia	Myrtaceae	Fruit	Incipient	3778	3	Mansfeld’s World Database (2001)	Ancient crop in Peru, cultivated there for its edible fruits.
Pouteria lucuma	Sapotaceae	Fruit	Semi	4319	1	Clement (1999)	Cultivated in the central Andes, in Mexico and Hawaii as a fruit tree. Old crop plant of the Inka empire.
Acioa edulis	Chrysobalanaceae	Edible nut	Incipient	4435	3	Clement (1999)	Synonym of Couepia edulis and occasionally cultivated in homegardens along the Solimões and lower Purus Rivers.
Caryocar brasiliense	Caryocaraceae	Fruit	Semi	4491	1	Smith, Fausto (2016)	Cultivated by indigenous populations in central Brazil for its edible fruits with a high content of oil, protein and vitamins.
Crescentia cujete	Bignoniaceae	Gourd	Full	4632	1	Clement (1999)	Cultivated in tropical America and other continents. Native perhaps only from Mexico to northern Central America, however widely introduced and naturalized in tropical Americas and other areas.
Elaeis oleifera	Arecaceae	Oily fruit	Incipient	-	1	Clement (1999)	Cultivated in Central America, frequently associated with anthropogenic soils in Central Amazonia (Junqueira et al., 2010).

CUSTOM R SCRIPTS

```
##### map scripts #####
##### function to add countries and rivers to maps of Amazon #####
#load the shapefiles
countries = readOGR(“D:/Documents/GIS Data/ESRIDATA/WORLD”, “CNTRY92”)
rivers = readOGR(“D:/Documents/GIS Data/ESRIDATA/WORLD”, “RIVERS”)
#if higher resolution needed
#countries = readOGR(“D:/Documents/GIS Data/ESRIDATA/WORLD”, “CNTRY98”)
#rivers = readOGR(“D:/Documents/GIS Data/ESRIDATA/WORLD”, “rivers98”)
forestborder = readOGR(“D:/Documents/GIS Data/neotropics”, “forestborder”)
#regions
regions = readOGR(“D:/Documents/GIS Data/neotropics/RAINFOR”, “itsct1”)
add.geography = function(draw.countries = T, draw.rivers = T, draw.forestborder = F,
                         draw.regions = F, r.color = “black”, border = “black”,
                         add.arrow = T, add.scale = T){
  force(border)
  if (draw.countries == T)    plot(countries, xlim = c(-80,-45), ylim = c(-20,10), border = border, add = T, asp = 1)
  if (draw.rivers == T)       plot(rivers, xlim = c(-80,-45), ylim = c(-20,10), col = ‘blue’, add = T, asp = 1)
  if (draw.forestborder == T) plot(forestborder, xlim = c(-80,-45), ylim = c(-20,10),
                                   col = ‘0’, border = border,add = T, lwd = 2, asp = 1)
  if (draw.regions == T){
    plot(regions, xlim = c(-80,-45), ylim = c(-20,10), col = ‘0’,
         border = border, add = T, lwd = 2)
    text(-58,2.5,”GS”, col = r.color)
    text(-48,-3,”EA”, col = r.color)
    text(-55,-8,”SA”, col = r.color)
    text(-63,-2.5,”CA”, col = r.color)
    text(-65,-13.5,”SWA”, col = r.color)
    text(-73.5, 1,”NWA”, col = r.color)
  }
  if(add.arrow == T) SpatialPolygonsRescale(layout.north.arrow(), offset = c(-80, 9) , scale = 2,
                                            fill = c(“black”, “black”), plot.grid = F)
  if(add.scale == T){
    SpatialPolygonsRescale(layout.scale.bar(), offset = c(-80, -20) , scale = 10/1.11,
                           fill = c(“transparent”, “black”), plot.grid = F)
    text(-77.8, -18.5 ,”1000 km”)
  }
}
##### End function add countries and rivers to maps of Amazon #####
##### map characteristics in loess map #####
map.loess = function(z, Longitude, Latitude, res = 1,
                     span = 0.75, degree = 2, se = T,
                     predict = T, surface = “direct”,
                     co = 0, draw.regions = F, r.color = “black”,
                     name = “”, draw.legend = T,
                     blocks = T, dots = T, c.col = “white”,
                     grid.color = c(“white”, “black”),
                     n.colors = 251999, pal = 0){
  force(span); force(degree); force(se);
  force(predict); force(surface)
  force(draw.regions); force(r.color)
  grid.pal = colorRampPalette(grid.color)(n.colors ) ## (n)
  if(pal == 1) grid.pal = heat.colors(n.colors, alpha = 1)
  if(pal == 2) grid.pal = terrain.colors(n.colors, alpha = 1)
```

```
if(pal == 3) grid.pal = topo.colors(n.colors, alpha = 1)
if(pal == 4) grid.pal = cm.colors(n.colors, alpha = 1)
if (res == 0.1){
  cex_pred = 0.1;  data2pred = AmazonForestGrid
} else if (res == 0.5){
  cex_pred = 1.25; data2pred = data_to_pred05
} else {
  cex_pred = 2.5;  data2pred = data_to_pred
}
z.loess = loess(z ~ Longitude * Latitude,
                span = span, degree = degree, se = se,
                normalize = TRUE, family = “gaussian”,
                surface = surface) #!surface is direct to be able to extrapolate
#calculate explained variation
SSq = sum((z-mean(z))^2)
SSqres = sum((z - z.loess$fit)^2)
expl_var = 100*(SSq-SSqres)/SSq
#give output for loess regression model and expl variation
cat(“explained variation :”,expl_var,”%”,”\n”)
#calculate the predicted values for the Amazon grid
grid.z.predict = predict(z.loess, data2pred, se = T)
#replace all fits < co by zero
grid.z.predict$fit[grid.z.predict$fit < co] = 0
if (blocks != T){
  plot(data2pred$Longitude,data2pred$Latitude,
       main = name,
       xlab = “Longitude”, ylab = “Latitude”,
       xlim = c(-80, -45), ylim = c(-20,10), asp = 30/30,
       xaxp = c(-80, -45, 7), yaxp = c(-20, 10, 6),
       pch  = 22, cex = 3,
       col  = rgb(0.85,0.95,0.85),
       bg   = rgb(0.85,0.95,0.85))
}
#show map of expected DCA scores and actual plot locations
if (blocks == T){
  grid.col   = vector(length = length(data2pred$Longitude))
  grid.min   = min(grid.z.predict$fit, na.rm = TRUE)
  grid.max   = max(grid.z.predict$fit, na.rm = TRUE)
  grid.range = grid.max - grid.min
  grid.col   = 1 -(grid.z.predict$fit - grid.min)/grid.range
  grid.col   = grid.pal[1+round((n.colors-1)*(grid.z.predict$fit - grid.min)/grid.range)]
  plot(data2pred$Longitude,data2pred$Latitude,
       main = name,
       xlab = “Longitude”, ylab = “Latitude”,
       xlim = c(-80, -45), ylim = c(-20, 10), asp = 30/30,
       xaxp = c(-80, -45, 7), yaxp = c(-20, 10, 6),
       pch = 22, cex = cex_pred,
       col = grid.col, bg = grid.col)
  }
if (dots == T){
  zmin   = min(z)
  zmax   = max(z)
  zrange = zmax - zmin
  zcex   = 0.1 + round((4*(z - zmin)/zrange),1)
  points(Longitude, Latitude, cex = zcex, pch = 21, bg = “black”, col = c.col)
  }
```

```
  if (draw.regions == T){
    add.geography(draw.forestborder = T, draw.regions = draw.regions, r.color = r.color)
  } else {
    add.geography(draw.forestborder = T)
  }
  if (draw.legend == T){
    if (blocks == T){
      n.round = 0
      if (grid.max <=10) n.round = 1
      if (grid.max <= 1) n.round = 2
      legend.n   = seq(grid.min, grid.max, by = grid.range/4)
      legend.pch = rep(2,length(legend.n))
      legend.col   = grid.pal[1+round((n.colors-1)*(legend.n - grid.min)/grid.range)]
      legend.fill = legend.col
      legend(x = -49, y = -13,
             legend = round(legend.n, n.round),
             fill = legend.fill,
             bg = “white”)
    }
    if (dots == T){
      legend.n   = round(seq(zmin,zmax,zrange/4),0)
      legend.pch = rep(21,length(legend.n))
      legend.cex = 0.1 + round((4*(legend.n - zmin)/zrange),1)
      legend(x = -48, y = 11,
             legend = legend.n,
             pch = legend.pch,
             pt.bg = “black”,
             col = c.col,
             pt.cex = legend.cex,
             bg = “white”)
      }
    }
  return(z.loess)
}
##### end map characteristics in loess map #####
##### map archaeological density#####
dens.arq<-rasterize(outp[,c(10,11)], amaz.r, fun=’count’, background=0)
dens.arq<-dens.arq*amaz.r
plot(dens.arq,col = terrain.colors(10), breaks = c(0,1,2,4,8,10,50,100,200))
##### end map archaeological density#####

##### generate balloon plot with default scaling #####
library(gplots)
balloonplot(dframe1$Region,dframe1$Variables, abs(tm),
            cum.margins=FALSE, rowmar=10.0, colmar=0.5, scale.range=”absolute”,
            zlab = “”, xlab = “”, ylab = “”, label=FALSE, dotsize=4,
            dotcolor = c(“blue”, “red”)[(c(tm5) < 0) + 1],
            show.margins=FALSE, sorted=FALSE, label.lines=FALSE,
            main=” “, cex.main=1)

##### non-linear relationships between abundance and richness #####
ytemp<-log((y - min(y)) + 0.1)
resu<-lm(ytemp~x)
summary(resu)
coef<-resu$coefficients
b<--as.vector(coef[2])
a<-as.vector(exp(coef[1]))
```

```
yo<-as.vector(min(y))
var<-c(yo,a,b);
names(var)<-c(“yo”,”a”,”b”)
# non-linear models
eq<-as.formula(y ~  yo + a*exp(b*x))
nlmod.2<-nls(eq, start=var,trace=TRUE)
resid<-residuals(nlmod.2)
# output
resu2<-summary(nlmod.2)
# summary
coef<-as.matrix(resu$coefficients)
df<-as.matrix(resu$df)
# statistics
dfregr<-df[1]-1
dfresid<-df[1]
dftotal<-length(y)-1
yest<-as.vector(fitted.values(nlmod.1)) # y estimado
ymed<-mean(y)
Rsqr<-sum((yest-ymed)^2)/sum((y-ymed)^2)
Rsqr<-round(Rsqr,2)
Radj<-1-(1-Rsqr)*(dftotal/dfresid)
Radj<-round(Radj,2)
F<-(sum((yest-ymed)^2)/dfregr)/(sum((y-yest)^2)/dfresid)
F<-round(F,2)
p<-df(F, dfregr, dfresid)
p<-round(p,2)
# plot
plot(y,x, pch=16, cex.lab=1.5, cex.axis=1.5, ylab=”Relative abundance of all domesticated spp. (%)”, xlab =
“Relative richness of domesticated spp. (%)”)
xest<-seq(round(min(x),1),round(max(x),2),length=101)
lines(xest,predict(nlmod.1,list(x=xest)))
```

CHAPTER 4

Disentangling pre-Columbian from recent human influence in old-growth Amazonian forests

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ABSTRACT

McMichael et al. (2017b) state that we overlooked the effects of post-Columbian human activities in shaping current floristic patterns in Amazonian forests. We formally show that post-Columbian human influences on Amazonian forests are indeed important, but they have played a smaller role when compared to the persistent effects of pre-Columbian human activities on current forest composition.

In our paper (Levis et al., 2017a – **Chapter 3**) we link pre-Columbian archaeological sites in Amazonia to current forest composition. We conclude that pre-Columbian human influences are still noticeable in the forest's composition today. The main issue that McMichael et al. (2017b) address is the effect of post-Columbian peoples on modern forests. Although they present distribution maps of modern and pre-Columbian human populations, they did not evaluate the effects of these populations on modern forests. All over the world, humans tend to live where people did before, and Amazonia is no exception. We argue, however, that a visualization of spatial trends between modern and ancient human occupation patterns and forest plots is insufficient to "show that the observed patterns of tree species distributions […] may be better explained by the influence of post-Columbian rather than pre-Columbian human activities" as stated by McMichael et al. (2017b). Although most other points raised by McMichael et al. (2017b) could be answered with a careful reading of our paper, we here address some of them and provide further analyses aiming to move forward in this debate.

McMichael et al. (2017b) criticize our list of domesticated species. In order to circumscribe this list, we used of a "broad" concept of plant domestication based on Darwin (1859), Rindos (1984) and Clement (1999), who argue that domestication is a process in which propagation and selection by humans yield a variety of outcomes over time. Forest management by Native Amazonians often resulted in changes in population structure and distribution of trees and palms without necessarily resulting in populations with clear signs of morphological selection (Rindos, 1984; Clement, 1999; Kennedy, 2012). In our list of 85 domesticated species we included 51 "incipiently domesticated" species, for which there is ample evidence for their management and cultivation through time. Although our list is extensive, it is still conservative, given that 301 of the species found in our plots are useful and have been documented under cultivation (see Hanelt, 2001; http://mansfeld.ipk-gatersleben.de/) and that there are at least 3500 plant species with documented uses in Amazonia (Revilla, 2002).

McMichael et al. (2017b) state that we "downplay the past 500 years of colonization by European settlers and the recovering indigenous population." We explicitly acknowledged the potential role of post-Columbian plant management on current floristic patterns (see p. 930 of Levis et al., 2017a – **Chapter 3**). It is indeed likely that the distribution and abundance of some economically important species (e.g., Hevea brasiliensis) have been modified during the past two centuries. We recognize as well that disentangling recent from pre-Columbian human impacts on forests is an important next step requiring approaches different from those used so far. We have started to explicitly address the issue of present and past human effects at a landscape scale. We found that old-growth forests along the middle Madeira River located on archaeological sites maintain a higher abundance and richness of domesticated species, even when they have not been intensively managed in the past 120 to 150 years (Figure 4.1). This shows that human impacts older than the rubber boom can persist in forests without recent management, and that recent forest management by modern people has an effect similar to that of forest management by ancient peoples. Thus, ancient and recent forest management continuously shapes the forests we see today.

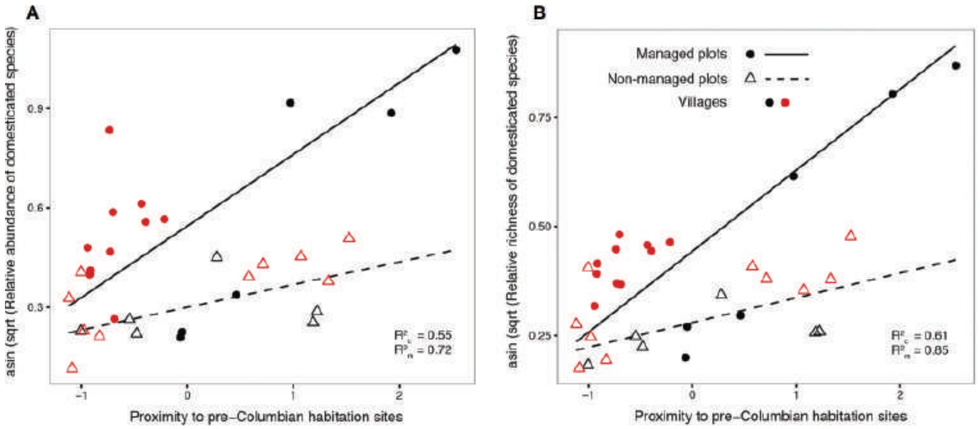

Figure 4.1. Post- and pre-Columbian human impacts on forests along the middle Madeira River, Central Amazonia. Effect of post- and pre-Columbian management activities on (A) the relative abundance and (B) the relative richness of domesticated species in 32 0.1-ha forest plots. Proximity to pre-Columbian habitation sites was assessed based on the degree of soil modification, assuming that soils with highest fertility and density of ceramic fragments were ancient habitation sites (Glaser and Birk, 2012). The *x* axis was obtained from a Principal Components Analysis (PCA), summarizing the variation in soil chemical and physical parameters. Information on current management was obtained from interviews with local residents. Regression lines are the result of linear mixed-effect models [response variable ~ proximity to pre-Columbian habitation sites x current management + (1|village)]. "Village" was included as a random factor because our plots were distributed in two different sites ("villages") with contrasting soil properties; plots in the village denoted by black symbols were in general located in more fertile soils (i.e., closer to pre-Columbian habitation sites) than those in the village denoted by red symbols (especially in the "non-managed" treatment). In both models, the probabilities (p) of all fixed factors are < 0.001. R^2_m and R^2_c refer to the fit of the fixed factors and of the whole model (fixed + random), respectively.

The distributions of modern and past human populations and of forest plots are indeed concentrated in accessible areas (see Figure A3.2 of **Chapter 3**; McMichael et al., 2017a). Still, the correlation between the distance of our plots to archaeological sites and the distance of our plots to modern population centres is weak (Spearman rank correlation = 0.27), because numerous archaeological sites and forest plots in our database are far from modern population centres. We added distance to modern population centres (Sorichetta et al., 2015) as a variable in an expanded model, in addition to the variables used in Levis et al. (2017a – **Chapter 3**). We found that distance to modern population centres has a small positive effect on relative abundance of domesticated species (particularly in the Guiana Shield; Figure 4.2A) and no effect on relative richness of domesticated species at the Amazon-wide level (although it has contrasting effects depending on the geographical region, positive for northwestern Amazonia and negative for southern Amazonia; Figure 4.2B). The effect of distance to archaeological sites on both relative richness and abundance of domesticated species is much stronger and consistently negative (particularly in southwestern and eastern Amazonia), similar to the results of our previous model (Levis et al., 2017a – **Chapter 3**). These results indicate that post-Colombian activities are indeed relevant, but contrary to McMichael et al.'s claim (2017b), these play a smaller role than pre-Columbian ones in shaping current forest compositions.

The transformation of Amazonian forests by humans is an ongoing process, and the current flora holds signatures of the interplay of ecological and anthropogenic processes in both pre- and post-Colombian times. Despite the complexity of this process, we disagree with McMichael et al.'s observation (2017b) that it is impossible to quantify human influence on forests "without identifying species natural (non-human influenced) abundance patterns". The use of well-designed plant inventories combined with paleoecological, archaeological, ecological and other human-related variables, is shedding light on basin-scale patterns that show substantial past human impacts on forests (Levis et al., 2017a – **Chapter 3**), mirroring patterns found at local and landscape scales (e.g., Figure 4.1; Watling et al., 2017a). Although the effects of post-Columbian human influences are important and deserve to be investigated in detail, our expanded analysis shows that they are insufficient to downplay the persistent effects of pre-Columbian peoples in shaping Amazonian forests.

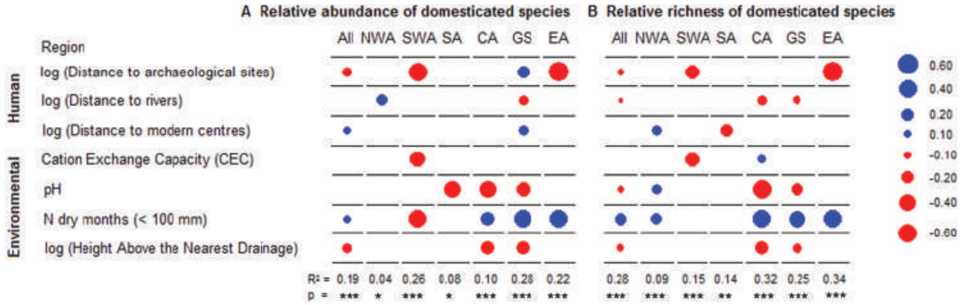

Figure 4.2. Relative abundance and richness of domesticated species as a function of human (pre- and post-Columbian) and environmental variables. Standardized regression coefficients for (A) the relative abundance and (B) the relative richness of domesticated species as a function of pre-Columbian human factors (distance to archaeological sites, distance to navigable rivers), modern human occupation (distance to modern population centres) and environmental conditions (soil cation exchange capacity, soil pH, number of dry months and height above the nearest drainage). Red circles indicate negative effects and blue circles positive effects. Circle size indicates the relative contribution of each predictor to the regression model (presented only for significant relations analysed in the models, p ≤ 0.05). Adjusted coefficient of determination (R^2) and significant codes (p values: ≤ 0.001 '***'; ≤ 0.01 '**'; ≤ 0.05 '*') are presented for all regression models. For details of the models see (Levis et al., 2017a – **Chapter 3**). Modern population centres are equal to grid cells of ≥ 25 persons/km^2 for the year 2000 (Sorichetta et al., 2015). Abbreviations for geological regions: NWA, northwestern Amazonia; SWA, southwestern Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia.

ACKNOWLEDGEMENTS

Data on the distribution of modern population centres available from Sorichetta et al. (2015).

AUTHOR CONTRIBUTIONS

All authors conceived the study and designed the analyses; A.B.J. and C.L. carried out the analyses; all authors wrote the manuscript.

CHAPTER 5

How people domesticated Amazonian forests

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ABSTRACT

For millennia, Amazonian peoples have managed forest resources, modifying the natural environment in subtle and persistent ways. Legacies of past human occupation are striking near archaeological sites, yet we still lack a clear picture of how human management practices resulted in the domestication of Amazonian forests. The general view is that domesticated forests are recognizable by the presence of forest patches dominated by one or a few useful species favored by long-term human activities. Here, we used three complementary approaches to understand the long-term domestication of Amazonian forests. First, we compiled information from the literature about how indigenous and traditional Amazonian peoples manage forest resources to promote useful plant species that are mainly used as food resources. Then, we developed an interdisciplinary conceptual model of how interactions between these management practices across space and time may form domesticated forests. Finally, we collected field data from 30 contemporary villages located on and near archaeological sites, along four major Amazonian rivers, to compare with the management practices synthesized in our conceptual model. We identified eight distinct categories of management practices that contribute to form forest patches of useful plants: (1) removal of non-useful plants, (2) protection of useful plants, (3) attraction of non-human animal dispersers, (4) transportation of useful plants, (5) selection of phenotypes, (6) fire management, (7) planting of useful plants, and (8) soil improvement. Our conceptual model, when ethnographically projected into the past, reveals how the interaction of these multiple management practices interferes with natural ecological processes, resulting in the domestication of Amazonian forest patches dominated by useful species. Our model suggests that management practices became more frequent as human population increased during the Holocene. In the field, we found that useful perennial plants occur in multi-species patches around archaeological sites, and that the dominant species are still managed by local people, suggesting long-term persistence of ancient cultural practices. The management practices we identified have transformed plant species abundance and floristic composition through the creation of diverse forest patches rich in edible perennial plants that enhanced food production and food security in Amazonia.

The notion of pristine rainforests has been questioned by increasing archaeological and ecological evidence suggesting long-term human activities across even the most intact forests worldwide (Denevan, 1992; Van Gemerden et al., 2003; Willis et al., 2004; Ross, 2011; Boivin et al., 2016; Roberts et al., 2017). Amazonia is no exception – over thousands of years with humans living in the region, forest composition has been altered significantly (Clement et al., 2015a; Levis et al., 2017a – **Chapter 3**). Many dominant species in Amazonian forests are widely used as food resources by native indigenous peoples (ter Steege et al., 2013), and at least 85 tree and palm species were domesticated to some degree during pre-Columbian times (Clement, 1999; Levis et al., 2017a – **Chapter 3**). Plant domestication is a long-term process that results from the capacity of humans to overcome environmental selection pressures with the purpose of managing and cultivating useful plants (Kennedy, 2012; Boivin et al., 2016; Levis et al., 2017a – **Chapter 3**), leading to significant changes in natural ecosystems and plant communities across landscapes (Clement, 1999; Terrell et al., 2003). First, useful individuals are managed in situ (Rindos, 1984; Wiersum, 1997a) and later humans select the best varieties with more desirable morphological traits for cultivation (Darwin, 1859; Rindos, 1984; Clement, 1999). Over time, humans create a mosaic of domesticated landscapes to favor numerous useful plant populations, each domesticated with different intensities and outcomes (Wiersum, 1997b). In modern Amazonian forests, legacies of past human societies are evident in the surroundings of archaeological sites, where humans enriched the forest with useful, especially edible, and domesticated plants (Balée, 1989; Erickson and Balée, 2006; Junqueira et al., 2010; Levis et al., 2017a – **Chapter 3**). These pre-Columbian legacies suggest that Native Amazonians interacted with natural ecological processes and shaped the distribution of plants and entire forest landscapes across the region (Balée, 2013).

In Amazonia, as in any other ecosystem, natural ecological processes drive the formation of plant assemblages and communities (Keddy, 1992; Zobel, 1997; Lortie et al., 2004; ter Steege et al., 2006). The first ecological process described to structure plant communities is the plant's capacity to disperse its seeds across landscapes (Ricklefs, 1987; Lortie et al., 2004), which depends on the regional species pool and multiple dispersal strategies, including occasional events of long distance dispersal (Ricklefs, 1987; Nathan et al., 2008). In wet Neotropical forests, animal dispersal is used by 75-98 % of the tree species (Howe and Smallwood 1982; Muller-Landau et al., 2008) and mammals disperse large-seeded species over long distances (Jordano, 2017). Once a propagule arrives in a given location, the second ecological process is related to how plants are able to overcome local environmental filters to successfully germinate and survive (Lortie et al., 2004). Plants compete with their neighbors for limited amounts of resources, such as light, nutrients and water (Moles and Westoby, 2006). The understory of a tropical forest is typically light-limited, forcing trees to either grow tall or survive in shady conditions (Poorter et al., 2003). Soils are also limited in water and nutrients, and plants need to compete in the rooting zone (Barberis and Tanner, 2005; Schnitzer et al., 2005). The third ecological process structuring plant assemblages is interaction with other organisms, such as herbivores and pathogens (Lortie et al., 2004; Bagchi et al., 2014). These multiple environmental and biological filters act simultaneously, resulting in trade-offs. For instance, species that grow fast under high light conditions tend to produce leaves that are less protected from herbivores, compared to the tougher and more resistant leaves of shade-tolerant species (Coley, 1983). In the long run, these ecological processes result in the selection of numerous adaptive plant traits (Reich et al., 2003), allowing species to thrive in complex and highly diverse systems, such as Amazonian forests. The high diversity of tropical ecosystems is in part maintained by natural disturbances and local biotic interactions, sometimes promoted by herbivores and pathogens that reduce the abundance of the most effective competitors, creating space for other species (Connell, 1978; LaManna et al., 2017).

Nonetheless, a few tree species often dominate plant assemblages forming oligarchic forests in diverse tropical forests (Connell and Lowman, 1989; Peh et al., 2011), including Amazonia (Peters et al., 1989; Pitman et al., 2001, 2013; ter Steege et al., 2013), Africa (Hart et al., 1989; Hart, 1990; Peh et al., 2011), Mesoamerica (Campbell et al., 2006), and Asia (Connell and Lowman, 1989; Peh et al., 2011). Natural and anthropogenic origins for the hyperdominance of tree species in Amazonian forests have been proposed. Aggregated patches of a few pioneer species occur after human or natural disturbance, while aggregated patches of a few shade-tolerant species may occur due to dispersal limitations (Valencia, 2004). Other hypotheses to explain why some species dominate large areas of Amazonian forests include: the species' ability to tolerate multiple environmental conditions, and to disperse over long distances (Pitman et al., 2001, 2013); and, in the case of useful species, the intentional or non-intentional enrichment promoted by past and contemporary human societies (Balée, 1989, 2013; Peters et al., 1989; ter Steege et al., 2013; Levis et al., 2017a – **Chapter 3**).

During the Holocene, useful plant populations benefited from a new set of interactions when humans started to transform landscapes (Denevan, 1995; Smith, 2011; Boivin et al., 2016), and manage plant populations, consciously or not (Rindos, 1984; Wiersum, 1997a,b; Peters, 2000). Indigenous management practices were formally defined by Wiersum (1997a, p. 7) as "*the process of making and effectuating decisions about the use and conservation of forest resources within a local territory*". When humans consciously manage forest resources, the underlying intention of their actions is not to domesticate forests, but to achieve certain short-term objectives, for instance to favor individual plants in the forest and promote their regeneration. Although changes in forest composition may not be the main goal of human actions, management practices also modify forest composition and structure beyond the targeted species in a long-term process. In tropical and subtropical forests worldwide, native societies have managed plants and landscapes, promoting oligarchic forests dominated by useful plant species, also defined as cultural or domesticated forests (Balée, 1989, 2013; Peters et al., 1989; Campbell et al., 2006; Michon et al., 2007; Reis et al., 2014; Morin-Rivat et al., 2017).

Today, many indigenous and traditional peoples recognize the handprints of their ancestors in the landscape (Frikel, 1978). Indigenous people are defined here as the descendants of native ethnic groups and members of an indigenous community that retains historical and cultural connections with the social organization of pre-Columbian indigenous societies (https://pib.socioambiental.org[1]). Traditional peoples can be understood as culturally differentiated and recognizable groups that have their own forms of social organization using knowledge, innovations and practices generated and transmitted by tradition, but they are not recognized as a member of indigenous communities (Brazilian Federal Decree No. 6.040[2]). In Amazonia, traditional peoples are generally descendants of migrants who intermarried with local indigenous peoples and they often exchange practices, objects and knowledge with members of indigenous communities. Although contemporary indigenous and traditional societies both cultivate fruit trees in their territory, they also take advantage of the aggregated patches of fruit trees created by the practices of previous generations (Frikel, 1978; Balée, 1989, 2013). These ancient cultivated landscapes were probably created by integrated agroforestry systems that included homegardens, swiddens and managed fallows in which tree and non-tree crops were intertwined (Denevan et al., 1984; Stahl, 2015). Such integrated systems were likely more efficient, in terms of food production, than long-fallow shifting cultivation systems when only stone axes were used to clear the forest in the past (Denevan, 1992). This is supported by the fact that past indigenous tree cultivation (arboriculture) was a common and widespread practice covering large areas of forest-savanna transition zones in Amazonia (Frikel, 1978).

Because trees persist in the forest following management (Levis et al., 2017a – **Chapter 3**) and annual crops disappear after human abandonment (Clement,

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[1] https://pib.socioambiental.org/files/file/PIB_institucional/No_Brasil_todo_mundo_é_índio.pdf
[2] http://www.planalto.gov.br/ccivil_03/_Ato2007-2010/2007/Decreto/D6040.htm

1999), contemporary indigenous and traditional people commonly attribute the aggregated distribution of useful perennial plants to the action of their ancestors. Based on this knowledge, they sometimes select a new place to settle in the forest (Frikel, 1978; Rival, 2007; Politis, 2007; Zurita-Benevides, 2016). For instance, the Nukak Indians in Colombian Amazonia prefer camping around sororoca plants (*Phenakospermum guyannense*), because they believe that these plants were brought by their ancestors to 'their living world', and they discard a large quantity of seeds around their temporary camps, contributing to form new patches (Politis, 2007). Given that multiple human generations have moved around through time, places like riverine settings and archaeological sites were frequent dispersal routes of people and their cultures, and consequently of useful plants in pre- and post-Columbian times (Denevan, 1996; Hornborg, 2005; Heckenberger and Neves, 2009; Guix, 2009; Clement et al., 2010; Levis et al., 2017a – **Chapter 3**, Levis et al., 2017b). The intimate connections between Native Amazonians, their ancestors and their plants can reveal how persistent pre-Columbian forest management practices (Balée, 2000) contributed to the large-scale vegetation patterns we observe in modern forests (Pitman et al., 2011; Levis et al., 2017a – **Chapter 3**; Levis et al., 2017b).

Our study aimed to unravel how people interacted with natural ecological processes to transform pristine forests into domesticated forests with different degrees of human intervention through unintentional and intentional management practices. How indigenous and traditional peoples have used and shaped Amazonian forests is described in ethnographical, ethnobotanical, archaeological, paleoethnobotanical, paleoecological and ecological publications. Here we used a historical-ecological perspective to evaluate the available information about how Native Amazonians have affected the distribution of plant species used mainly as food resources. Based on the information gathered from the literature, we developed an interdisciplinary conceptual model of how multiple management practices transformed pristine forests into domesticated forests, considering temporal and spatial contexts. In the field, we collected data about management practices and the composition of forest patches dominated by useful plants surrounding 30 contemporary villages, settled on or near archaeological sites. We compared field and literature data by documenting the multiple management practices known by 33 informants from two villages along the lower Tapajós River, and by relating these practices to the distribution and composition of the forest patches surrounding all 30 villages.

MATERIAL AND METHODS

Construction of the conceptual model of forest domestication

We reviewed the scientific literature for evidence of management practices of 22 useful perennial species (mainly used as food resources) that occur in forest patches in different parts of the Amazon basin (see Table A5.1 for information about the species). These species were also chosen because the authors had previous field knowledge about them and they include a variety of useful plants with wild, cultivated and domesticated populations. Although our review focused on edible perennial plants, we used the general concept of useful plants to define plant species that are currently used for any purpose or have been used by any human group in the past. Eighty-one studies in ethnographical, ethnobotanical, archaeological, paleoethnobotanical, paleoecological and ecological publications, including books, scientific articles and dissertations, were analyzed (Appendix 5). The literature review was conducted using the scientific name, English name and Portuguese name of each species as keywords in Web of Science and as title in Google Scholar.

Based on the information gathered for the 22 species, we classified the multiple management practices into eight categories that consist of a summary of all practices reported in the literature (Table 5.1): (1) removal of non-useful plants, (2) protection of useful plants, (3) attraction of non-human dispersers of useful plants, (4) human transportation of useful plants, (5) selection of phenotypes useful to humans, (6) fire management, (7) planting, and (8) soil improvement. The literature review provides examples to identify the role of - in many cases - multiple management practices in the formation and persistence of domesticated forests in Amazonia.

We combined different management practices into a category depending on: 1) what people want to achieve; 2) whether the effects of the practice are directional or not in the way they fundamentally shape plant species assemblages; and 3) whether the practices result in similarities in terms of forest composition, abundance and distribution of useful species. For instance, practices that remove non-useful plants in the forest, such as opening the canopy, clearing the understory, weeding and cutting lianas, are used to selectively benefit useful species or enhance their growth rate by reducing the competition of non-useful plants around the targeted plants. As a side effect, humans increase light availability in the forest and tend to favor light demanding species that may therefore be protected if useful. More similarities are expected inside each category than between them because each category leads to a unique type of interference in natural ecological processes. Nonetheless, their interactions may result in a diverse composition of useful species with different or even contrasting adaptations. Below we detail each of these eight categories, providing a definition, interaction with ecological processes and some examples.

1. Removal of non-useful plants

The most common practices used to remove non-useful plants in the forest are: opening the canopy; clearing the understory; weeding; cutting lianas; and removing unproductive individuals of useful species. These practices are used to selectively benefit useful species by reducing the costs of competition, and are expected to increase the performance of the selected useful plants. Competition can be reduced either by controlling the abundance of non-useful species (directly excluding them), or increasing the amount of available resources (*e.g.*, light or space). Practices that reduce leaf and root density of lianas, for example, can release the growth of some trees (Schnitzer et al., 2005), and increase fruit production (Kainer et al., 2014). Similar to other small-scale natural disturbances (Connell, 1978), these long-term management practices may increase the diversity of plants between plant communities at a regional scale (beta-diversity) (Balée, 2006). The Hotï Indians from northern Amazonia act as ecological disturbance agents by constantly creating and managing gaps that increase the amount of light inside the forest necessary to cultivate light-demanding useful plants (Zent and Zent, 2004). In southern Amazonia, the Kayapó Indians create forest islands by managing savanna landscapes, increasing the heterogeneity of the landscape and the resource abundance for humans, game animals and plants (Posey, 1985). The Nukak Indians from western Amazonia constantly move between old camps for hunting and gathering activities; when returning to old camps, they selectively clear the understory and canopy, altering plant composition and benefiting useful and domesticated plants by promoting their growth and reproduction (Politis, 1996).

2. Protection of useful plants

Humans protect plant seedlings, juveniles, adults and their fruits by keeping them alive through several practices: taking care of fruits, seedlings and adult plants; using non-destructive extractive practices; avoiding fire near useful trees; pruning; and repelling leaf-cutting ant species. Protection can be targeted to individuals with specific traits or to whole plant populations, by reducing the abundance of herbivores, predators, and natural disturbances. For instance, the Kayapó Indians in southern Amazonia use Azteca ants to repel leaf-cutting ants that eat useful species' leaves (Posey, 1987). The Huaorani Indians in western Amazonia and Hotï Indians in northern Amazonia increase the abundance of several useful plant species by keeping fruit trees alive in their territory (Rival, 1998; Zent and Zent, 2012). Aggregated patches of many useful plants are spared when clearing the forest for crop cultivation (Shanley et al., 2016), increasing the survival rates of these plants. This practice protects useful plant populations of Amazon nut trees (*Bertholletia excelsa*), uxí trees (Endopleura uchi), tucumã palms (*Astrocaryum aculeatum*) and açaí palms (*Euterpe oleracea*) in different parts of Amazonia (Shanley et al., 2016). Babaçu palms (*Attalea speciosa*) with more inflorescences are also protected in agroforestry systems of eastern Amazonia (Anderson et al., 1991).

3. Attraction of non-human dispersers of useful plants

The natural process of seed dispersal can be enhanced by human practices. Leaving some fruits under the mother tree for animals in domesticated landscapes and cultivating large-seeded species to attract game are common practices in traditional communities of Amazonia (Shanley and Medina, 2010). Although humans were responsible for population declines, and even local extinctions of large vertebrates across Neotropical forests (Guimarães et al., 2008), humans have also positively interacted with terrestrial animals by increasing their food availability via cultivation and protection of fruit trees in domesticated landscapes (Balée, 1993), thus increasing the dispersal capacity and distribution of useful plant species. Dispersal strategies among large-seeded species and their dispersers may result in aggregated distributions of Amazonian plant species. For instance, forest patches of inajá palm (*Attalea maripa*) are associated with tapir latrines, suggesting that tapirs are partly responsible for the aggregated distribution of this palm in Amazonian forests (Fragoso et al., 2003). Seeds of bacaba palm (*Oenocarpus distichus*) persist in secondary forests of Ka'apor Indians after abandonment, because game is attracted to these food resources and disperse even more seeds within these forests (Balée, 1993, 2013). Attracting animals to domesticated landscapes may indirectly contribute to form and maintain multi-species patches of useful plants from ancient homegardens and swiddens (Balée, 2013).

4. Human transportation of useful plants

Human transportation is the intentional or non-intentional movement of seeds and plants by humans from one place to another, outside or within the geographical limits of the plant population. For instance, planting seedlings or dispersing seeds intentionally and non-intentionally along forest trails, in swiddens and homegardens. During the Holocene, humans may have acted as primary long-distance dispersal vectors by transporting seeds of useful plants over long distances, often surpassing natural evolutionary barriers (Hodkinson and Thompson, 1997; Nathan et al., 2008). Past humans intentionally transported seeds, seedlings and clones of useful plants over long distances across the world (Boivin et al., 2016). As a consequence, the expansion of sedentary farming populations in Amazonia is associated with the dispersal of important native crops across the basin, such as manioc (*Manihot esculenta*) (Arroyo-Kalin, 2012), Amazon nut trees (Shepard and Ramirez, 2011; Thomas et al., 2015), and cacao trees (*Theobroma cacao*) (Thomas et al., 2012). Over short distances, human seed dispersal occurs when plants are exchanged among groups (Eloy and Emperaire, 2011), during periodic movements of groups to new areas (Posey, 1993), systematic movements between forests and settlements (Ribeiro et al., 2014), and between temporary camps (Politis, 2007). Short distance dispersal within a plant population's range is also reported, when seeds are scattered along trails during hunting and gathering activities, often non-intentionally (Zent and Zent, 2004; Ribeiro et al., 2014). The Hotï spend days in the forest to collect large quantities of umirí (*Humiria balsamifera*) fruits, many of which drop from baskets on the way back to the village, explaining its high abundance surrounding their villages (Zent and Zent, 2004). Similarly, the Kayapó transport large amounts of Amazon nut seeds, suggesting that the high density of seedlings along trail margins results from seeds accidentally dropped during transport (Ribeiro et al., 2014). Extensive trail systems were described in the Kayapó territory where they intentionally plant, transplant and spread useful species (Posey, 1993), forming landscapes full of useful plant species.

5. Phenotypic selection of useful plants

Trait selection practices are motivated by human preferences for specific phenotypes, for instance, fruits with larger sizes or larger contents of desirable properties, such as sugar, starch and oil. Humans often protect individuals previously selected for their preferred traits and they propagate these individuals outside their original population (see 2.1.4), resulting in plant domestication (Rindos, 1984; Clement, 1999). Phenotypic selection promotes morphological and genetic divergence from the ancestral population based on human criteria (Clement, 1999). The set of phenotypic traits that distinguish domesticated from wild plant populations is called the domestication syndrome (Hammer, 1984; Harlan, 1992; Meyer et al., 2012). Selection does not necessarily imply intentionality; however, if unconscious practices lead to changes in plant traits, followed by selection and propagation, these actions start to be systematically repeated (Rindos, 1984; Zeder, 2006). Human criteria for selecting plant traits vary across geographical regions, through time and with cultural interests (Meyer et al., 2012), and depend on the availability of useful populations in the landscape and the knowledge to interpret and manage morphological variation (Terrell et al., 2003). In Amazonia, some studies have described domestication syndromes for useful plants: variation in the toxicity of manioc roots that were selected for different soil types (McKey et al., 2010a; Fraser et al., 2012); peach palm (*Bactris gasipaes*) may have been first selected for its small oily fruits or wood, and later for large starchy fruits with better fermentation qualities (Clement et al., 2009); the selection of annatto (*Bixa orellana*) with increased pigment yield from its seeds, and changed fruit dehiscence (Moreira et al., 2015); the high morphological variation of pequí fruit (*Caryocar brasiliense*) varieties selected by the Kuikuro Indians of the upper Xingu River (Smith and Fausto, 2016); selection of varieties of Virola elongata with exudates of different hallucinogenic qualities, and varieties of *Cyperus articulatus* with rhizomes having different medicinal properties selected by Yanomami groups in Northwestern Brazil (Albert and Milliken, 2009). Along the lower Tapajós River, traditional people selected non-bitter fruits of *Caryocar villosum*, domesticating them accidentally or intentionally (Alves et al., 2016). The importance of selection for promoting agrobiodiversity in Amazonia is underscored in ethnographies of cultivated plants, such as manioc (Boster, 1984; Rival & McKey, 2008) and pequí (Smith and Fausto, 2016).

6. Fire management

Fire has been a land management tool since pre-historical times (Pausas and Keeley, 2009). People have used prescribed fire in forests or swiddens mainly for cultivation, and also highly controlled fire for waste management near their houses. People manage fire for hunting activities, group communication, rituals, and to prevent uncontrollable fires (Mistry et al., 2016). Fire was intensely managed by pre-Columbian peoples in homegardens or settlement areas for domestic activities, such as cooking and burning waste. This domestic use may have contributed in the long run to fertilize the soil, producing Amazonian Dark Earth (ADE or *Terra Preta de Índio* - TPI) (Smith, 1980; Schmidt et al., 2014) found throughout the Amazon basin (McMichael et al., 2014). Fire was also managed in swiddens to improve soil fertility with intensive cultivation techniques in ancient times, forming fertile dark brown soils, a soil slightly less fertile than ADE (Denevan, 2001; Woods et al., 2013). Management practices involving fire also increase availability of other resources, such as light, by reducing the abundance of competitors, and promoting useful species that are more nutrient demanding, such as chili peppers (*Capsicum* spp.) (Junqueira et al., 2016a). Patches of buriti palms (*Mauritia flexuosa*), for instance, are associated with fire history in the Gran Savana, where people have used fire to prevent forest re-expansion into savannas (Montoya et al., 2011). When people manage fire to reduce competition for cultivated plants, fire-adapted species are often selected (Jakovac et al., 2016a). Many plants, useful or not, have evolved to tolerate contact with fire, allowing them to persist through time in frequently burnt places (Bond and Midgley, 2001). Some examples are the light-demanding sororoca

(P. *guyanense*) that resprout after fire, cumatí trees (*Myrcia splendens*) that form patches in gaps managed with fire (Elias et al., 2013) and babaçu palms that persist in burnt sites due to cryptogeal germination (Jackson, 1974). The ancient connection between fire and humans (Bowman et al., 2011) and the intense fire history in Amazonian forests is revealed by the high charcoal abundance in forests around old settlements (Bush et al., 2015), which are expected to be dominated by fire-adapted species.

7. Planting

Planting is defined here as the intentional planting, sowing and transplanting of seeds and seedlings to cultivated landscapes. It is important to note that when seeds and seedlings are transported by humans (see **4. Human transportation of useful plants**) with the intention of planting, these categories overlap. When humans disperse seed without this intention (e.g., when gathering fruits in the forest) the overlap between planting and human transportation doesn't exist, which justifies separating these categories of practices. Planting practices may increase a useful plant's performance, survival and reproduction because people usually take care of seedlings after planting. In Amazonia, several tree and palm species are planted mostly in agroforestry systems, forest gardens and forest gaps surrounding settlements (Denevan et al., 1984; Balée, 1993; Zent and Zent, 2012). In the past, indigenous groups also planted several perennial species, originating patches of useful trees and palm species across the basin (Frikel, 1978). Therefore, the presence and abundance of edible trees and palms in Amazonian forests and their proximity to ancient settlements may indicate past indigenous planting activities (Balée, 2013; Levis et al., 2017a – **Chapter 3**). Some examples in Amazonia are forest patches of *Poraqueiba sericea* (Padoch and Jong, 1987, Franco-Moraes, 2016) in western Amazonia, C. *brasiliense* in the upper Xingu River (Smith and Fausto, 2016), C. *villosum* in the lower Tapajós River (Alves et al., 2016), and B. *excelsa* in Amapá (Paiva et al., 2011) that are all associated with past indigenous planting.

8. Soil improvement

In some parts of the Amazon basin, *terra-firme* forests are poor in nutrients, which selected for plants with efficient nutrient-conservation mechanisms (Herrera et al., 1978). Amerindians, however, interfered with these processes by changing soil structure and increasing soil fertility (Kleinman et al., 1995). Soil improvement involves several practices, such as the addition of charcoal and ashes that release nutrients and carbon in the soil; the use of organic additives, such as human and animal wastes, ash, garbage, crop residues, leaves, compost, cleared weeds, seaweed, mulch, urine, ant nest refuse, turf, muck and water; and also by building mounds in floodable landscapes (Denevan, 1995, 2001). The improvement of soil conditions was observed for piquiá trees inside the forest, in which local people accumulate leaf litter under the trees (Alves et al., 2016), and for açaí, uxí, and peach palm through organic additives (Shanley et al., 2016). Also, extremely fertile ADE were probably created in pre-Columbian refuse heaps in which ash and charcoal, human and animal wastes, and ceramics accumulated (Woods and McCann, 1999; Schmidt et al., 2014). Although ADE soils were a product of sedentary human settlement and cannot be classified as a management practice, modern people usually take advantage of these fertile soils to cultivate crops (Junqueira et al., 2016b). Brown soils were probably formed in cultivation zones with ash and charcoal that originated from frequent burning, and by composting and mulching the soil (Denevan, 1995). Unintentional and sometimes intentional soil improvement practices that resulted in the creation of ADE and brown soils were probably common in the past, since anthropogenic soils occur across most of the Amazon basin (Woods et al., 2013). The improvement of soil structure and fertility creates a new environmental filter that favors plants of interest and excludes species not adapted to the new soil conditions. Species with adaptations to resist or tolerate fire or to benefit from fertile soils may become dominant in improved soils. As a consequence, useful species adapted to fertile soils can form aggregated patches in ADE sites across the basin (Balée, 1989). This is may be case H. balsamifera trees, dominant in soils previously burned in the upper Negro River (Franco-Moraes, 2016), and palm species, such as *Elaeis oleifera*, *Attalea phalerata* and *Astrocaryum murumuru*, which are indicators of anthropogenic soils along the Madeira River (Junqueira et al., 2011).

Synthesis

As a synthesis of the information obtained about these eight management practices, their interactions and how each practice affects natural ecological processes, we present a new conceptual model that explains the process of Amazonian forest domestication. Following Goldberg et al. (2016), we describe a temporal continuum from the late Pleistocene until today. We also present spatial gradients from settlements through swiddens to domesticated forests, and from old-growth forests to domesticated forests, illustrating at which distances from settlements these different practices operate to form domesticated forests with different degrees of human intervention. Although Goldberg et al. (2016) modeled human population dynamics during the Holocene without data from Central Amazonia, this model is the only one available describing a temporal continuum of past human population in South America. We considered a temporal dynamic that starts in the Pleistocene when humans arrived, and follows human population growth rates during the Holocene (Goldberg et al., 2016). In our conceptual model, we considered pristine forests to exist when humans had not yet altered natural ecological processes (Denevan, 1992). Pristine forests were the norm during the Pleistocene and, with at least 13,000 years of growing human populations across the Amazon basin, pristine forests gradually disappeared (Clement et al., 2015a) and old-growth forests – mature forests without recent human interference, but not necessarily pristine (Wirth et al., 2009) – cover most of the basin today.

Field surveys

All authorizations to conduct the study were obtained before field work. The study was approved by the Brazilian Ethics Committee for Research with Human Beings (Process n°10926212.6.3001.5020, 2013), the Federation of the Indigenous Organizations of the Negro River – FOIRN and the Regional Coordinator of the Brazilian National Indigenous Foundation - FUNAI, and the Brazilian System of Protected Areas (SISBIO, process n°47373-1, 2014). In each village, we obtained the informed consent of each local traditional or indigenous leadership at the beginning of the study.

In the field, we studied 30 contemporary villages settled on river banks distributed in nine sub-basins of four major rivers (Madeira, Solimões, Negro, Tapajós) across Brazilian Amazonia (see Table A5.2 for names of the villages visited and their distances to archaeological sites). We visited from two to ten villages in each sub-basin and selected villages located on or near archaeological sites with ADE. Archaeological sites with anthropogenic soils are ancient sedentary settlements (Neves et al., 2003), and they were chosen for our study because they indicate long-term human occupation, where rich soils, new landforms and domesticated plants accumulated through time in response to human agency (Clement et al., 2015a). In each village, from March 2013 until March 2015 (three months per year during the rainy season), we searched for indigenous and traditional ecological knowledge about the forest patches dominated by useful plant species in the surroundings of these villages.

Of the 30 contemporary villages along river banks, 27 are currently inhabited by traditional peoples (*ribeirinhos*) that have lived there for at least one generation; most of them are descendants of migrants who intermarried with local indigenous peoples. Their daily activities include farming, fishing, hunting, timber and non-timber forest product extraction, and two villages are involved in community-based tourism. Three villages in the upper Negro River are inhabited by members of the Baré indigenous group, descendants of Arawak speaking groups, who lost their original language and adopted the Tupi-based Nheengatu, taught by the missionaries.

In each village, we searched for patches of native forest species used mainly as food resources. We focused on edible fruits because previous studies showed that these resources accumulated around ancient indigenous villages (Frikel, 1978; Balée, 1989, 1993). We interviewed 56 local people (on average 2 per village) regarding the occurrence and distribution of these forest patches, and used participatory mapping techniques (Gilmore and Young, 2012) to locate these patches around the villages. We used the suffix “zal” or “al”, which means abundance, aggregation or patches in Portuguese, and “tíwa” (in the Nheengatu language) to communicate with local people. These terms are used by contemporary people that associate the suffix with the name of the dominant species and identify a forest patch of useful species based on their traditional knowledge. For instance, a patch of bacaba palm (*Oenocarpus bacaba* / *O. distichus*) is named a *bacabal* in Portuguese and a *iwakátíwa* in Nheengatu.

All patches of useful species were mapped with participatory mapping and complemented with the information collected during guided tour (Gilmore and Young, 2012; Albuquerque et al., 2014). Participatory mapping techniques are used to map local knowledge about the landscape, and to translate indigenous and local representations into techno-scientific language (Chapin et al., 2005; Heckenberger, 2009; Gilmore and Young, 2012). All local residents were invited to participate in a participatory mapping workshop that occurred during one morning or afternoon in each village. People were encouraged to draw and identify first the main local rivers, second ADE sites, and third different patches of useful species on maps made with georeferenced grids on top of recent cloud-free LANDSAT TM images of the area. With participatory mapping, we obtained the approximate location and size of ADE sites, and patches of useful species surrounding the villages. With guided tour we validated the location of at least one ADE site and/or one patch of useful species per village. Village members chose one person to guide us and visit the most accessible forest and ADE site. During the guided tour, we collected geographical coordinates of ADE sites and useful forest patches, and documented all useful species observed according to local knowledge. The botanical species were pre-identified in the field using some books of fruit trees and palms (Cavalcante, 2010; Henderson, 1995), and when possible, botanical material was also collected for final identification. The botanical identification was confirmed by José Ramos, a parataxonomist at INPA (Instituto Nacional de Pesquisas da Amazônia). Some plants were only identified to genus level in the field due to logistical limitations.

The distribution of all forest patches identified around the villages was documented during the interviews, participatory mapping and guided tour. In total, we studied 21 patches visited with local informants dominated by 14 different useful species, as some patches visited concentrate the same dominant species. Forest patches are located up to 5 km from archaeological sites, and we documented a minimum of four useful species, a maximum of 21, and median of seven useful species per patch. In each of the nine sub-basins visited in the field, we documented a minimum of six useful forest patches dominated by different species, a maximum of fourteen and a median of nine patches.

We compared our results obtained from field surveys and the literature review with field data from two villages along the right margin of the lower Tapajós River, where we documented all management practices performed by local people with the species that dominate local forest patches. This comparison served as ground-truth for our conceptual model. During free listing interviews and guided tour (Albuquerque et al., 2014) local informants described practices with which they benefit useful species found in patches of this sub-basin. In January and February of 2015, we interviewed 33 informants who know and use forest species in Maguarí and Jamaraquá villages in the Tapajós National Forest (FLONA). We also walked approximately 80 km along trails in the FLONA Tapajós with the seven most experienced informants to identify useful species in the forest. During these guided tour, the informants explained how they manage the useful species found in forest patches. With information about how local residents manage useful species, we compared the number and frequency of the practices obtained in the field with the same information obtained from the literature review.

We used ArcGis software to map the information collected in the field with participatory mapping and GPS. The closest (minimum distance) and longest (maximum distance) linear distances from each patch of useful species to the closest ADE were calculated manually using a digital ruler. We calculated the frequency of forest patches that occur at intervals of a minimum distance of 1 km to the nearest ADE. Using the minimum distance from forest patches to the closest ADE sites, we compared the spatial gradient of our conceptual model (settlements, swiddens or old-growth forests) with the location of the forest patches found in the field: patches on top of ADE sites were associated with pre-Columbian settlements, those located in fallows close to ADE sites were associated with past swiddens, and forest patches more distant from ADE sites were associated with old-growth forests, and confirmed by local knowledge and the presence of large trees.

RESULTS

A conceptual model of forest domestication in Amazonia

Our conceptual model shows how pristine forests were converted into domesticated forests by a long-term process involving the interaction between eight human management practices (Figure 5.1). The conceptual model presents three general aspects of the forest domestication process: 1) a time span since the Pleistocene (Figure 5.1A); 2) interactions among human practices (arrows in Figure 5.1B); and 3) a spatial zone of influence for each management practice (arrows in Figure 5.1C). First, our model proposes that the frequency of these management practices increases with human population in South America (Goldberg et al., 2016), resulting in more extensive domestication of Amazonian forests through the Holocene (Figure 5.1A). Second, each arrow presented in our conceptual model indicates interactions among a pair of categories of management, showing that one practice can positively affect others (Figure 5.1B). For instance, humans remove non-useful plants (Practice 1 – P1) while often selectively protecting useful individuals with desirable phenotypes (P5), or plant selected individuals (P5) in forest gaps (natural or created by humans – P1), swiddens and homegardens (P7). Native Amazonians protect plants (P2) as sources of seeds for future planting (P7) and selection (P5), and also to attract animal dispersers (P3). A gradual transformation of the forest is expected to occur by the interaction between humans (P4) and non-human dispersers (P3). Seeds and seedlings of selected useful plants (P5) are transported by humans from natural to domesticated landscapes (P4), guaranteeing their planting and propagation (P7). Fire management (P6) is often used in association with protection of species (P2) with plants previously selected for traits of interest (P5). The combination of fire management (P6) with the protection of certain species (P2) in domesticated landscapes may allow even useful fire-sensitive plants to form patches in ancient cultivated systems. Ancient planting practices (P7) attract dispersers (humans and non-humans; P3 and P4) and improve soil conditions (P8). The planting of useful edible trees (P7) attracts game animals that may disperse their seeds throughout the area (P3), thus increasing the abundance of the species locally. Indigenous people disperse seeds of plants (P4) and plant them in agroforestry systems and along forest trails (P7) when they move from one place to another, increasing food availability during long walks in the forests. Trees planted in agroforestry systems (P7) may enrich soil fertility (P8), reproducing the nutrient-conservation mechanism observed in the forest. By improving naturally nutrient-poor soils (P8), pre-Columbian societies enhanced food production in Amazonian landscapes, also allowing their population expansion.

Third, the gradient of soil improvement is illustrated in the spatial representation in our conceptual model (Figure 5.1C). Five practices, removal of non-useful plants (P1), protection of useful plants (P2), attraction of non-human dispersers of useful plants (P3), human transportation of useful plants (P4), and selection of phenotypes useful to humans (P5) occur across the entire gradient of human influence from settlements, through swiddens, to domesticated forests to old-growth forests. Fire management (P6), direct planting (P7) and soil improvement (P8) are practices mainly used in swidden/fallows and settlements, giving rise to domesticated forests with useful plants related to these activities.

Relationships among management practices: evidence from the literature and field

We found that all eight categories of management practices described in the literature (Table 5.1) are also known by traditional people in the two villages along the lower Tapajós River that we studied (Figure 5.2). Transportation of plants by humans, planting of useful plants and selection of desirable phenotypes were the most frequent practices in the literature, whereas clearing the understory, cutting lianas and weeding (P1 - removal of non-useful plants) and not cutting useful plants (P2 - protection of the useful) were the most cited practices in field interviews (Figure 5.2). Attraction of dispersers and soil improvement were the least frequent practices in the literature and field interviews, documented for less than 40 % of the species investigated.

More than half of the useful plant species investigated in the literature and the field are managed with at least five practices. Based on the literature, four species (*A. maripa*, *C. villosum*, *M. flexuosa*, *T. cacao*) are managed with seven practices, and for these species at least five different uses were reported (Table A5.1). Based on field data, two species (*C. villosum* and *E. uchi*) are managed with seven practices and used for several purposes, such as food, medicine and hunting (Table A5.1). Local people reported that they do not clear the land or use fire in places where aggregated patches of these species occur, with the purpose of protecting the whole population. One species, *M. splendens*, with only two uses reported in the literature (manufacturing and fuel), is managed with only one practice (P6 - fire management) based on the literature.

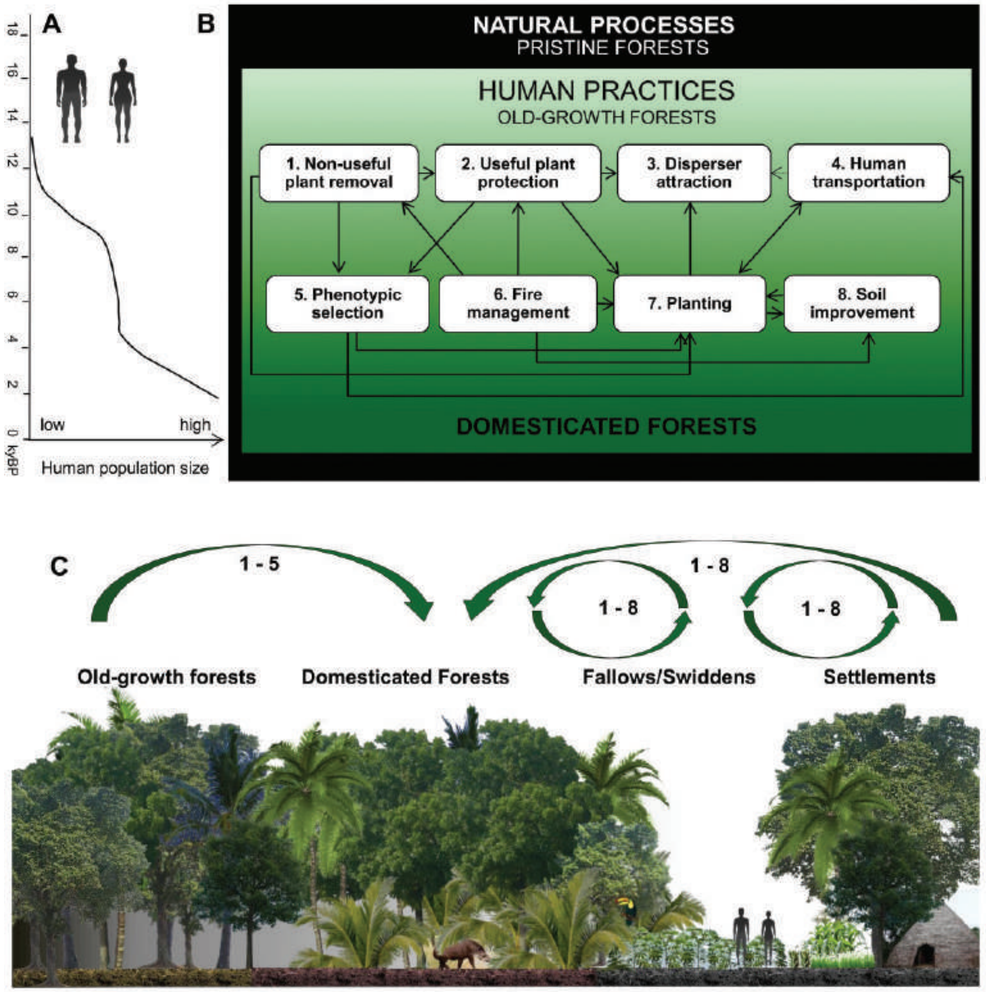

Figure 5.1. Conceptual model illustrating the interaction of eight management practices and their effects on the domestication of forests through time. (A) Expected trends in human population growth rate in Amazonia from fourteen to two thousand years ago before present (kyBP) based on published data for South America outside of Amazonia (adapted from Goldberg et al., 2016). (B) Management practices (1-8), their interactions and their effects on the forest domestication process through time [from top (16 kyBP) to bottom (0 kyBP)]. Natural ecological processes operate during all moments in time and along a domestication gradient from pristine to domesticated forests. Management practices may have a positive direct effect (dark arrows) or hypothetical positive effect (light arrow) on other practices that intensify as human population increases (from light green to dark green). (C) The forest domestication process in a spatial context of human influence from settlements, through swiddens, domesticated forests to old-growth forests, which may have been domesticated in the past, but lack recent human intervention. Domesticated forests can originate (arrows) from settlements and swiddens, or from old-growth forests. Our model describes an open-ended process.

Table 5.1. Examples of all management practices classified into eight categories. Lines refer to the eight categories of management practices. Columns present examples of management practices from the literature for each category, the useful species that were involved in each example of a practice and the references used in the literature review. See Appendix 5 for the complete reference list corresponding to each number and Table A5.1 for the complete scientific names of all species.

Examples of practices	Useful species	References
1. Removal of non-useful plants: people benefit useful species by reducing the costs of competition		
clearing the understory	*E. oleracea, B. excelsa, E. uchi*	72
weeding	*A. aculeatum, A. speciosa, C. villosum, E. oleracea, E. precatoria, M. flexuosa, T. cacao*	2, 3, 4, 12, 22, 37, 55, 74, 77
liana cutting	*B. excelsa, C. villosum, E. oleracea*	2, 24, 77
cutting male individuals	*M. flexuosa*	12
cutting older individuals	*A. maripa, E. oleracea, O. bataua, O. bacaba*	15, 43, 74, 80
girdling neighboring large trees	*E. oleracea, M. flexuosa*	4
cutting other trees	*A. aculeatum, E. oleracea, E. precatoria, M. flexuosa, O. bataua, P. sericea, T. cacao*	3, 12, 27, 57, 77, 78
cutting stems in a clump	*E. oleracea*	12, 77
cutting unproductive individuals	*A. aculeatum, E. uchi, E. oleracea*	72
opening forest canopy	*A. speciosa, B. excelsa, O. distichus, P. guyannense*	5, 9, 65, 70
opening forest paths	*H. brasiliensis*	69
2. Protection of useful plants: people protect plant seedlings, juveniles, adults and their fruits by keeping them alive through several practices		
keeping plants alive during fruit harvest	*C. villosum*	2
rotating harvest	*A. aculeatum, E. precatoria, O. bacaba, O. bataua*	12, 15
keeping when clearing the land	*A. aculeatum, A. maripa, A. speciosa, B. excelsa, E. precatoria, O. bacaba, O. bataua, O. distichus, P. guyannense, P. sericea*	5, 12, 21, 24, 37, 50, 65, 74, 81
not cutting	*A. aculeatum, B. excelsa, C. villosum, E. uchi, E. oleracea*	2, 58, 72
protecting seedlings	*E. precatoria*	74
pruning	*A. maripa, A.speciosa, E. oleracea, M. flexuosa, O. bacaba, O. bataua, T. cacao*	3, 12
selective harvesting of certain individuals based on age, size or sex	*E. oleracea, E. precatoria, M. flexuosa, O. bataua*	12
using other ants to repel leaf-cutting ant species	*T. cacao*	60
using non-destructive extractive practices to keep plants alive during harvest activities	*C. villosum , M. flexuosa, O. bataua, O. distichus*	2, 12, 32, 36, 45, 56
3. Disperser attraction: people attract non-human dispersers of useful plants by promoting the natural process of seed dispersal		
attracting game by keeping fruits in the swiddens	*A. maripa, O. distichus*	6, 8
leaving some fruits for animals	*C. villosum*	2
protecting fruits for animals	*M. flexuosa*	32
4. Human transportation: people disperse seeds and transplant seedlings intentionally or non-intentionally from one place to another increasing their distribution		
accidental dropping of seeds	*A. aculeatum, B. excelsa, H. balsamifera, H. parvifolia, M. flexuosa, O. bataua, O. distichus, P. guyannense, T. cacao*	6, 7, 8, 12 17, 59, 63, 74, 80
dispersing seeds and/or collecting seedlings for transplanting elsewhere	*A. aculeatum, A. maripa, B. excelsa, C. villosum, E. oleifera, E. oleracea, E. precatoria, E. uchi, H. brasiliensis, H. balsamifera, M. carana, M. flexuosa, M. saccifera O. bacaba, O. bataua, O. distichus, P. sericea, T. cacao*	2, 3, 11, 12, 20, 29, 31, 47, 49, 58, 60, 61, 69, 72, 73, 74, 75, 77
5. Phenotypic selection: people select for specific phenotypes of useful plants promoting morphological and genetic divergence from the ancestral population based on human criteria		
hybridization of the best individuals	*O. bacaba*	10
human selection and intervention in plant populations	*A. aculeatum, A. maripa, A. speciosa, B. excelsa, C. villosum, E. speciosa, E. uchi, E. oleracea, E. precatoria, H. brasiliensis, H. balsamifera, M. flexuosa, O. bacaba, O. bataua, O. distichus, P. sericea, T. cacao*	1, 2, 5, 16, 41, 49, 60, 66, 71, 76
6. Fire management: people manage fire as land management tool increasing availability of other resources, such as light and soil nutrients		
controlled burning	*A. aculeatum, T. cacao*	60, 67
selecting species through fire	*A. maripa, A. speciosa, H. balsamifera, M. flexuosa, M. splendens, O. bacaba, P. guyannense*	5, 9, 28, 29, 43, 52, 74, 80
7. Planting: people plant seeds and seedlings in cultivated landscapes intentionally increasing the plant's performance, survival and reproduction		
intentional sowing and planting of seedlings	*A. aculeatum, A. maripa, B. excelsa, C. villosum, E. oleifera, E. uchi, E. oleracea, E. precatoria, M. flexuosa, M. carana, H. brasiliensis, H. balsamifera, O. bacaba, O. bataua, O. distichus, M. saccifera, P. guyannense, P. sericea, T. cacao*	1, 2, 3, 5, 12, 11, 18, 19, 20, 22, 23, 24, 25, 26, 29, 30, 31, 33, 34, 35, 39, 40, 47, 48, 49, 50, 51, 54, 57, 58, 60, 61,62, 68, 69, 72, 74, 75, 77, 79

Examples of practices	Useful species	References
8. Soil improvement: people improve soil structure and fertility creating a new environmental filter that favors plants of interest		
burning of refuse	*H. balsamifera*	29
adding organic material and mulch	*C. villosum, E. oleracea, T. cacao, M. flexuosa*	2, 5, 12, 77
combining termite and ant nests with mulch	*T. cacao*	60
spreading mulch fertilizers	*E. uchi, E. oleracea*	72

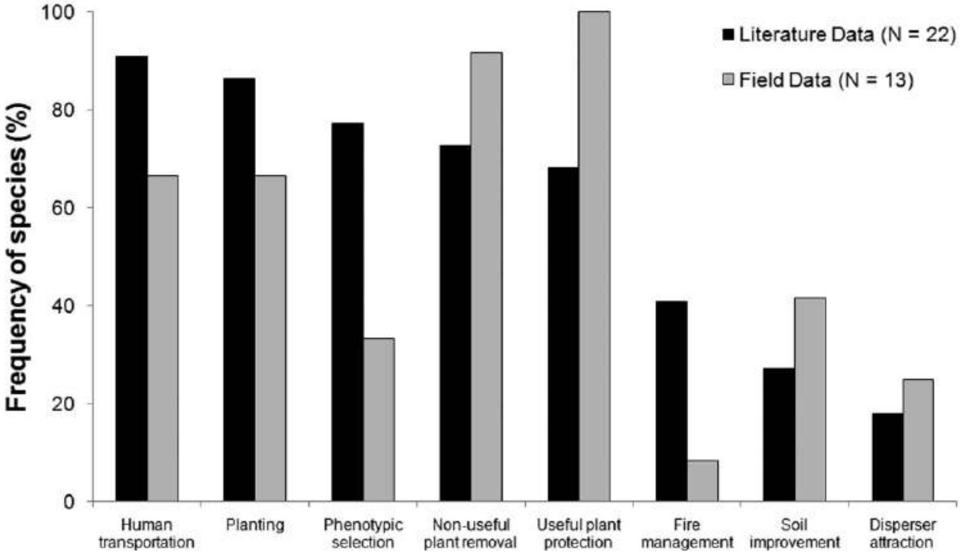

Figure 5.2. Frequency of useful species involved in each management practice based on the literature (black bars) and field interviews (gray bars). Information for 22 species was obtained from the literature and for 13 species in the field in two villages.

Multi-species patches of useful plants

We found multiple forest patches of useful species surrounding the 30 contemporary villages visited in Amazonia (Figure 5.3). In total, people cited 35 patches with different names and corresponding to 38 useful species (Table A5.1). The most common patches were açaízal (*E. precatoria*), babacal (*O. bacaba*), castanhal (*B. excelsa*), piquiázal (*C. villosum*), patauázal (*O. bataua*), and uxízal (*E. uchi*) (Figure 5.4). Most patches are common in more than one sub-basin visited and a few patches are only common in one sub-basin visited; some examples of localized patches are cf. *Neoxythece elegans* in the lower Madeira River basin, *Duguetia stenantha* in the upper Solimões River basin, *H. balsamifera* in the upper Negro River basin, and *Hymenea parvifolia* in the lower Tapajós River basin. Detailed information of the regional differences of forest patches across Amazonia is given in Table A5.1 and Table A5.3. Of all species that dominate the patches, 90 % are used for more than one purpose (Figure 5.3).

Although forest patches are dominated by one species after which they are named, they concentrated multiple useful species that dominate forest patches in different sub-basins of Brazilian Amazonia (Table 5.2). We visited 21 patches that are dominated by 14 out of 38 useful species that form patches across the basin. Palm species of the genus Oenocarpus occur in 75 % of the 21 forest patches visited across the basin. We found regional differences in the composition of useful palm species that occur in the forest patches: A. maripa were found in most patches of the Madeira River basin, E. precatoria of the Solimões River basin, O. bataua of the Negro River basin and O. distichus of the Tapajós River basin. Forest patches dominated by B. excelsa species are the most common and the most diverse patches: they concentrate 5 to 8 useful species that also are dominant species in other forest patches in different parts of the basin (Figure 5.4 and Table 5.2). In total, 87 useful species were cited in the patches visited (Table 5.3) and the number of useful species cited increases with the number of patches visited (Figure 5.1).

Most patches are small in size (less than 1 km^2), and occur at various distances from archaeological sites (0 to 40 kilometers), implying that they may have originated from all spatial contexts: settlements, old swiddens or old-growth forests (Figure 5.5). Few patches are restricted to ADE sites and old villages. Half of all patches are located up to 1 km from the archaeological sites, although some patches can be found up to 40 km away from these sites (Figure 5.5 and Figure A5.2). As a common pattern and according to local people, patches dominated by useful palm species are more common in valley forests, whereas patches dominated by tree species occur commonly in other environmental settings, such as plateau forests and white-sand forests (campinaranas).

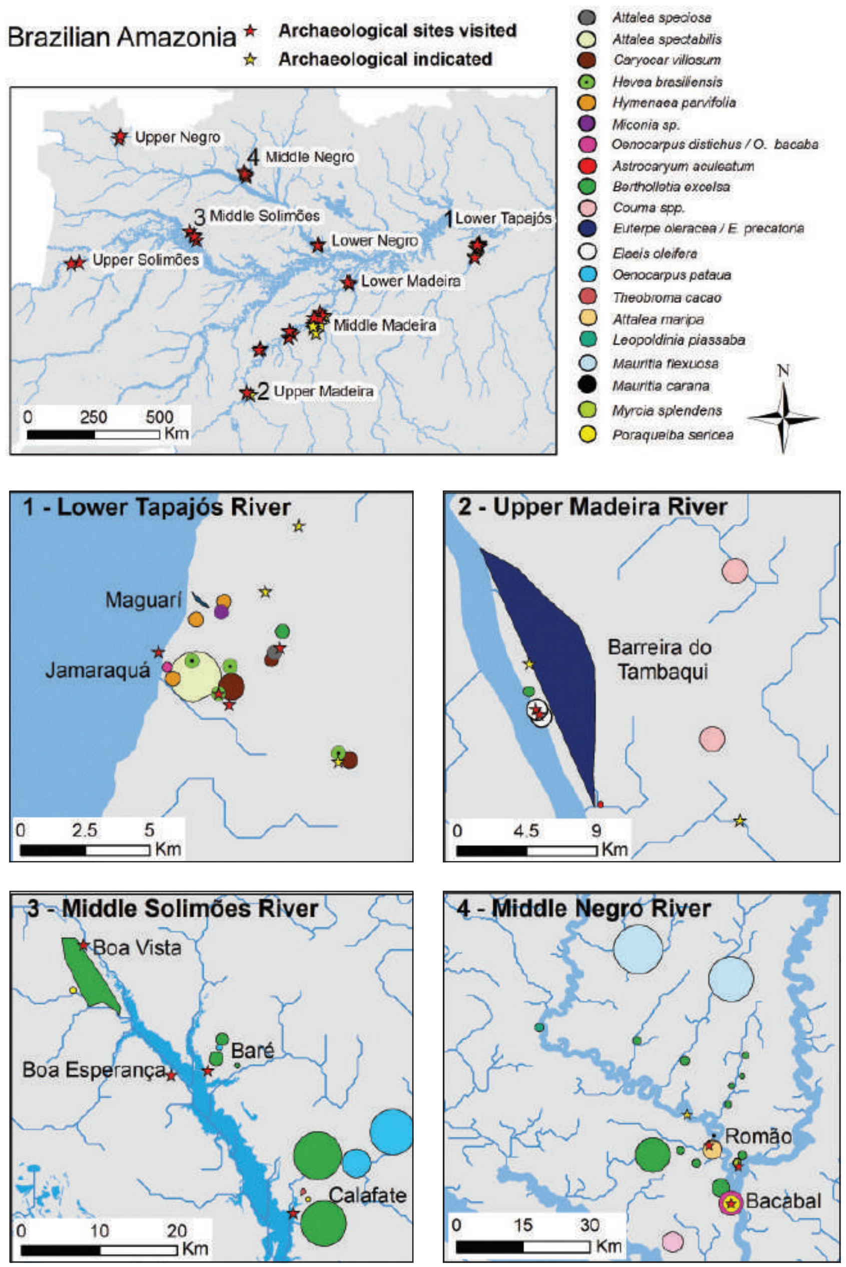

Figure 5.3. Maps of examples of useful forest patches around archaeological sites in four sub-basins of Brazilian Amazonia. Different sizes and shapes of forest patches presented in the figures are based on local knowledge descriptions and local drawings. See Table A5.1 for more information about the forest patches presented in this figure. Archaeological sites are ancient sedentary settlements with anthropogenic soils (Amazonia Dark Eath - ADE) and have been re-occupied by contemporary peoples.

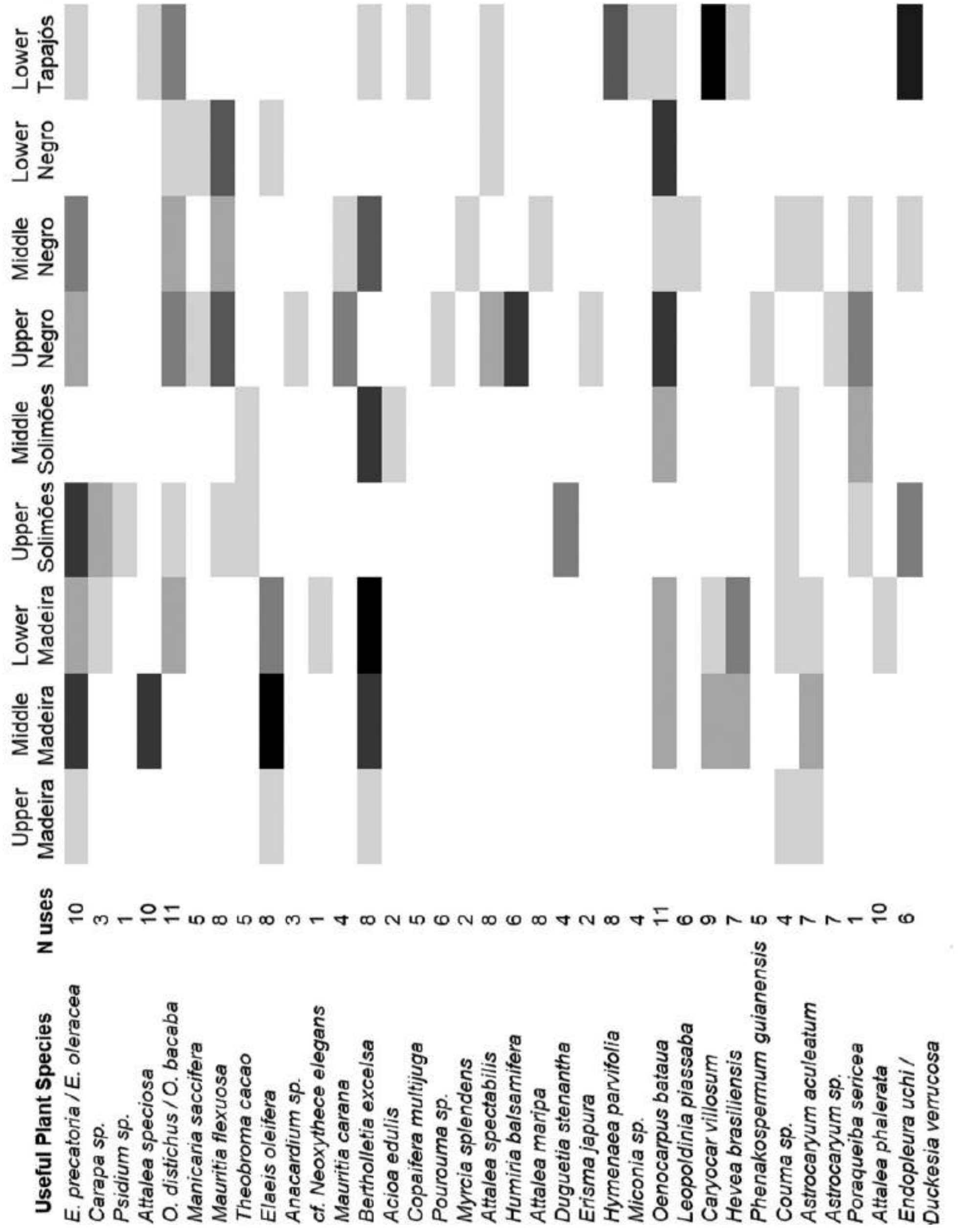

Figure 5.4. Forest patches of useful species found in nine Amazonian sub-basins. Shades of gray indicate the frequency of citation in each sub-basin (very light gray – 1 to black – 7 citations). The total number of uses was obtained from both the literature review and field interviews. See Table A5.1 for more information on the forest patches and uses attributed to each species.

Table 5.2. List of useful species that occur in the 21 forest patches visited during guided tour. The name of the forest patches, sub-basins visited, dominant species, number of individuals of the dominant species per kilometer walked during the tours, uses of the dominant species (*information from the literature review), management practices of the dominant species (*numbers from the literature review), botanical name of useful species that form patches and were found in the tour, spatial context according to our conceptual model (settlements, swiddens or old-growth forests) are described in this table. Use category: (F) Food. (C) Construction, (T) Thatch, (Fu) Fuel, (M) Medicinal, (Ma) Manufacturing or Technology, (Co) Commerce, (A) Attractive for game, (Af) Animal food, (R) Ritualistic, and (O) Other. Management practices: (1) removal of non-useful plants, (2) protection of useful plants, (3) attraction of non-human dispersers of useful plants, (4) human transportation of useful plants, (5) selection of phenotypes useful to humans, (6) fire management, (7) planting, and (8) soil improvement. See Table A5.3 for the complete scientific name of all species.

Local name	Sub-Basin	Dominant species	N ind/ km	Uses*	Manage-ment*	Other useful species in the patches	Spatial context
Caiuézal São Félix	Middle Madeira	*Elaeis oleifera*	10 / 0.5	F, C, T, M, Ma, Co, Fu, Af	4,5,7	*A. aculeatum; A. phalerata*	Settlements
Babaçual São Felix	Middle Madeira	*Attalea speciosa*	68 / 0.55	F, C, T, Fu, M, Ma, Co, Af, O	1,2,5,6	*A. aculeatum; A. maripa; Copaifera sp.; cf Neoxythece elegans; Couma sp.; E. precatoria; O. bacaba; O. bataua; O. mapora; H. parvifolia*	Swiddens/ Old-growth
Castanhal Terra Preta	Middle Madeira	*Bertholletia excelsa*	3 / 0.35	F, C, M, Fu, Ma, Co	1,2,4,5,7	*A. speciosa; A. maripa*	Swiddens/ Old-growth
Castanhal Mata Alta	Lower Madeira	*Bertholletia excelsa*	32 / 1.3	F, C, M, Fu, Ma, Co	1,2,4,5,7	*A. aculeatum; A. maripa; A. speciosa; C. villosum; E. precatoria; H. brasiliensis; O. mapora*	Swiddens/ Old-growth
Castanhal Talento	Lower Madeira	*Bertholletia excelsa*	23 / 1.59	F, C, M, Fu, Ma, Co	1,2,4,5,7	*A. maripa; C. villosum; E. precatoria; E. uchi; O. bataua; O. mapora*	Swiddens/ Old-growth
Jabutipúzal da Ponta	Upper Solimões	*Duguetia stenantha*	10 / 0.1	F,Af	Planted in the villages	*A. aculeatum; B. excelsa; E. precatória; O. mapora; P. sericea*	Swiddens
Jabutipúzal da Terra Preta	Upper Solimões	*Duguetia stenantha*	10 / 0.1	F,Af	Planted in the villages	*H. parvifolia*	Swiddens
Castanhal Boa Vista	Middle Solimoes	*Bertholletia excelsa*	3 / 0.13	F,C,M, Fu,Ma,Co	1,2,4,5,7	*A. edulis; A. aculeatum; C. villosum; Couma sp.; O. bacaba*	Swiddens/ Old-growth
Castanhal Finado Tavares	Middle Solimoes	*Bertholletia excelsa*	10 / 2.27	F,C,M, Fu,Ma,Co	1,2,4,5,7	*A. maripa; E. uchi; C. villosum; Couma sp.; E. precatoria*	Swiddens/ Old-growth
Patauátíwa	Upper Negro	*Oenocarpus bataua*	7 / 0.05	F, C, T, M, Ma, Co, Fu, R, A, Af, O	1,2,4,5,7	*E. precatoria; M. flexuosa*	Old-growth
Japuratíwa	Upper Negro	*Erisma japura*	17 / 0.13	F	Protected in the village	*E. precatoria; Hevea sp.; O. bacaba; O. bataua*	Swiddens
Tucumtíwa	Upper Negro	*cf Astrocaryum chambira*	6 / 0.05	F,Ma	Protected in the villages	*E. precatoria; I. deltoidea; O. bataua; P. sericea*	Swiddens
Castanhal Tapuruquara	Middle Negro	*Bertholletia excelsa*	15 / 1.3	F,C,M, Fu,Ma,Co	1,2,4,5,7	*Anacardium sp.; A. maripa; A. aculeatum; C. villosum; E. uchi; E. precatória; O. bacaba; O. bataua*	Swiddens/ Old-growth

Local name	Sub-Basin	Dominant species	N ind/ km	Uses*	Manage-ment*	Other useful species in the patches	Spatial context
Inajázal Tapuruquara	Middle Negro	*Attalea maripa*	19 / 0.23	F, C, T, M, Ma, A, Af, O	1,2,3,4,5,6,7	*A. aculeatum; O. bacaba*	Swiddens
Patauázal Sítio São Francisco	Lower Negro	*Oenocarpus bataua*	9 / 0.5	F, C, T, M, Ma, Co, Fu, R, A, Af, O	1,2,4,5,7	*M. flexuosa; O. bacaba*	Old-growth
Picada do Buritízal	Lower Negro	*Mauritia flexuosa*	12 / 0.5	F, C, T, M, Ma, Co, A, O	1,2,3,4,5,6,7,8	*Couma sp.; O. bataua*	Old-growth
Jutaízal Jamaraquá	Lower Tapajos	*Hymenea parvifolia*	10 / 0.39	F, M, Co, Af	4		Swiddens
Uxízal Prainha	Lower Tapajos	*Endopleura uchi / Duckesia verrucosa*	11 / 0.73	F,C,M,Co,A,Af	1,2,4,5,7,8	*Anacardium sp.; C. villosum; H. parvifolia; O. bataua*	Old-growth
Seringal Jamaraquá	Lower Tapajos	*Hevea brasiliensis*	100 / 0.1	F,C,Ma, Co,A	1,4,5,7 Planted in the swiddens	*A. spectabilis; A. vulgare; A. aculeatum; O. distichus*	Swiddens
Piquiázal Jamaraquá	Lower Tapajos	*Caryocar villosum*	16 / 1.2	F,C,M, Fu,Ma,Co,A, Af,O	1,2,3,4,5,7,8	*A. aculeatum; A. spectabilis; Miconia sp.; O. distichus*	Swiddens/ Old-growth
Bacabal Prainha	Lower Tapajos	*Oenocarpus distichus*	30 / 0.11	F,C,T,Ma	1,2,3,4,5,7	*A. maripa; H. brasiliensis; Miconia sp.*	Swiddens

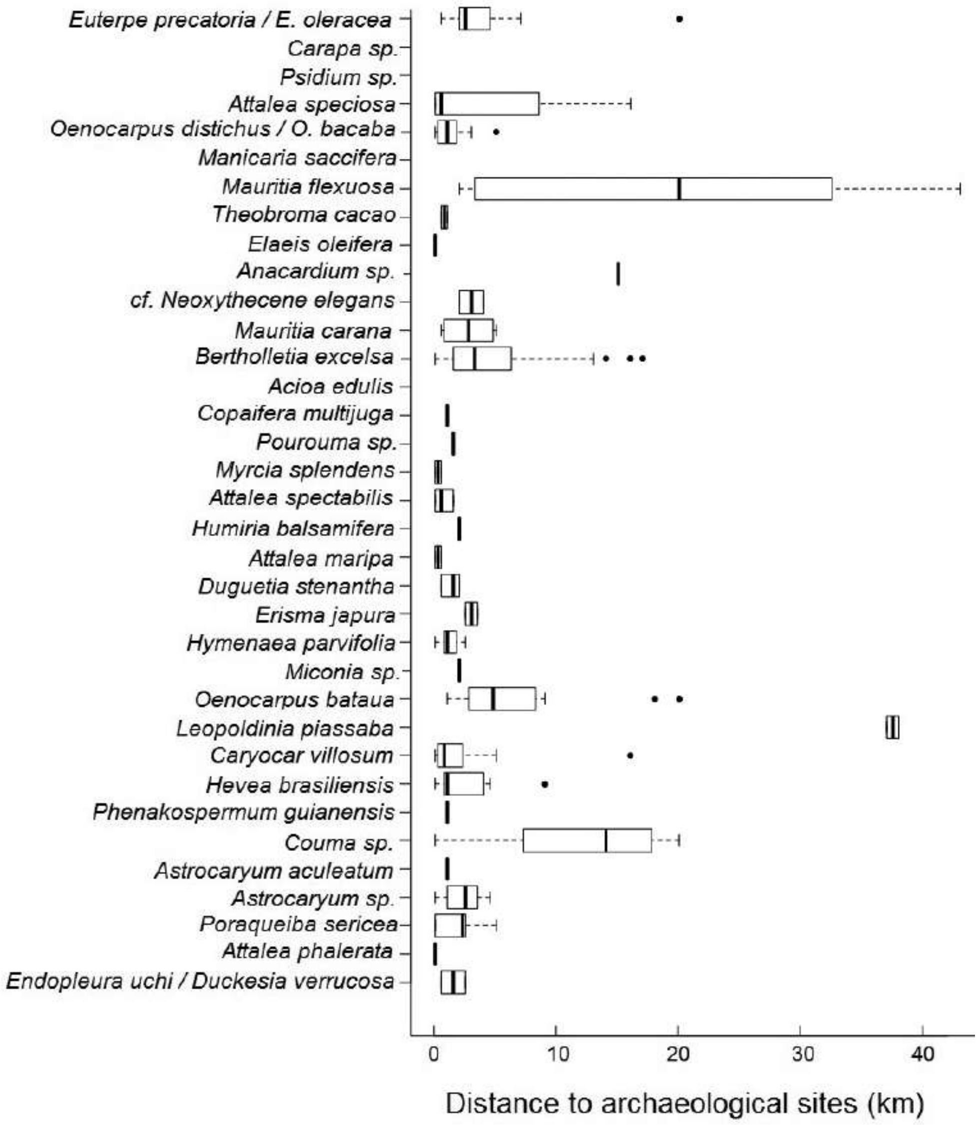

Figure 5.5. Occurrences of patches of useful species along a distance gradient from archaeological sites. Median (dark line), first and third quartile (rectangles), minimum and maximum distances (dotted line) from the forest patches to the closest archaeological sites are presented. Archaeological sites are ancient sedentary settlements with anthropogenic soils (Amazonia Dark Eath - ADE) and have been re-occupied by contemporary peoples. Black dots are extreme values (outliers). No data is available for four species because people couldn’t determine the location of these patches in the maps we used.

DISCUSSION

Based on our multidisciplinary approach, we provide a framework for understanding how human practices have led to the formation of patches of useful perennial plant species across Amazonian forests. Our conceptual model portrays how Amazonian peoples manage forests in multiple ways through eight categories of management practices that interfere with natural ecological processes and promote domesticated forests around human settlements. The similarities between ethnographic descriptions of management practices across the basin and our field observations of two villages indicate the commonness of these practices, suggesting that pre-Columbian and contemporary peoples transformed forest composition at varying distances from their settlements by multiple management practices. In the field, we confirmed that multiple diverse patches of useful species, currently managed by indigenous and traditional peoples, occur mainly near these settlements. Overall, our results support the view that these diverse patches of useful plant species were created and maintained by human actions.

Our conceptual model also reflects positive long-term interactions between humans and plants (Smith, 2011), as described in other tropical regions worldwide (Wiersum, 1997a; Michon, 2005; Kennedy, 2012; Reis et al., 2014; Boivin et al., 2016; Roberts et al., 2017). Previous models had suggested that the plant and forest domestication processes are associated with the cultivation of domesticated tree crops (Wiersum, 1997a,b). Although our model is inspired by previous studies, we present a new framework to understand the domestication of Amazonian forests that simplifies the complex network of interactions between human actions and natural ecological processes. Because these interactions cannot be understood by separately assessing only individual management practices or species, the intricate groups of management practices shown in our model illustrate how multiple human actions interact to shape Amazonian forests. Species-specific details are scattered in the literature, and here we synthesized this information into a single model that can be tested with individual site-specific situations.

In our model, forest domestication is defined as an open-ended process (Rival, 2007; Kennedy, 2012), in which domesticated forests can originate through varying degrees of human intervention from settlements and swiddens, and also from old-growth forests. This perspective makes the typical distinction between hunter-gatherers vs. farming groups inappropriate for the Amazonian context (Terrell et al., 2003; Kennedy, 2012), as most ancient Native Amazonians (often characterized as hunter-gatherers) were actually practicing many activities, including planting tree species (Frikel, 1978). Amazonian forests that were once cultivated and domesticated are often transformed into swiddens or settlements as a cyclic pattern that has also been observed in Indonesian forests (Michon, 2005). Because early successional species usually depend on forest gaps for recruiting, they are maintained with management practices, similar to fully domesticated plant populations that require human care for survival and reproduction (Clement, 1999).

Although it is likely that current management practices maintain the legacy of past societies (Junqueira et al., 2017 – **Chapter 4**), the effects of past forest domestication have been detected in forests even without recent management activities (Van Gemerden et al., 2003; Dambrine et al., 2007; Ross, 2011; Levis et al., 2017a – **Chapter 3**). The persistent effect of pre-Columbian plant domestication on modern forest composition has been revealed in Amazonian old-growth forests (Levis et al., 2017a – **Chapter 3**; Junqueira et al., 2017 – **Chapter 4**), secondary forests (Junqueira et al., 2010) and even in highly dynamic home-gardens growing in archaeological sites (Lins et al., 2015). Domesticated species adapted to stable soil conditions created by management practices, such as ADE, may persist for a long time after abandonment (Quintero-Vallejo et al., 2015). This may explain why domesticated palms dominate modern forests growing on pre-Columbian mounds, anthropogenic soils and geoglyphs abandoned more than 400 years ago (Erickson and Balée, 2006; Quintero-Vallejo et al., 2015; Watling et al., 2017a). Another possible explanation for this persistence is the continuous recruitment of useful and domesticated plants present in the forest seed bank (Lins et al., 2015). Pre-Columbian peoples may also have played a major role in disseminating large multi-seeded fruits within and across Neotropical biomes during the Holocene, resulting in the spread of diverse patches of useful plants associated with human settlements and trails (Guix, 2005). Human-mediated dispersal of invasive plants is well-documented (Hodkinson and Thompson, 1997; Nathan et al., 2008); however, ecological studies frequently overlook this mechanism when considering native species (Levis et al., 2017b).

Modern Amazonian peoples who live on pre-Columbian settlements seem to have inherited indigenous knowledge, including these management practices that benefit useful and domesticated plant populations. Our field data show that most useful species dominant in forest patches occur in more than one sub-basin visited, suggesting a widespread use and management of forest resources by past and contemporary peoples. The forest domestication process was assimilated by contemporary societies through the transmission of indigenous knowledge from one generation to another, as described for indigenous groups from Ecuadorian Amazonia (Zurita-Benevides et al., 2016) and traditional people in Brazilian Amazonia (Alves et al., 2016). Villages with home-gardens that were occupied by several pre-Columbian cultures contain a higher beta diversity of useful plants compared to villages with home-gardens occupied by a single culture (Lins et al., 2015), suggesting that previously existing useful plants were incorporated into new agroforestry systems when old villages are re-occupied (Miller and Nair, 2006). Some practices, however, have changed in intensity and extension through time. Slash-and-burn agriculture, for instance, has increased since the arrival of European societies that introduced metal tools to cut down the forest (Denevan, 2001). In pre-Columbian times, sedentary societies frequently improved soil conditions by managing fire in their habitation and cultivation zones (Denevan, 2001; Neves et al., 2003; Woods et al., 2013). Sedentary societies with high human population densities were responsible for the formation of anthropogenic soils that are no longer being created on a broad scale (Neves et al., 2003). These same anthropogenic soils, however, are widely used by modern societies to cultivate crops, allowing the diversification and intensification of food production in Amazonia (Woods et al., 2013; Junqueira et al., 2016b).

Amazonian societies managed fire, planted useful species and improved soils that resulted in substantial transformation in forests close to their homes. Although some scholars argue for a localized impact involving these three practices in pre-Columbian Amazonia, associating them with the margins of the main rivers (McMichael et al., 2012a; McMichael et al., 2014; Piperno et al., 2015; Bush et al., 2015), the impact of long-term management practices has been detected in the forests of interfluvial areas (Levis et al., 2012; Franco-Moraes, 2016; Watling et al., 2017a) and across the Amazon basin (Levis et al., 2017a – **Chapter 3**). These findings suggest that even in remote areas, far from known archaeological sites, contemporary people also manage the forest, protecting useful species and removing the non-useful, which are the most frequent practices reported by contemporary societies. Logistical limitations constrain our ability to detect the long-term effects of these practices away from current human settlements (Stahl, 2015), and even the participatory techniques used in this study are based on current knowledge about the forest, requiring ethnographic projection to infer the impact of past peoples. For instance, patches of rubber tree (*Hevea brasiliensis*) have been managed by modern societies driven by economic interest since the mid-19th century (Schroth et al., 2003), but were probably managed differently before that time. Although several socio-economic factors push contemporary peoples to concentrate their activities on market-oriented forest resources (Jakovac et al., 2016b), they occasionally use and manage forest patches located up to 40 km from their villages for hunting animals and gathering fruits (Figure 5.5; Franco-Moraes, 2016). As an alternative approach, the abundance and richness of useful plants, especially of domesticated species, might be used to predict the location of ancient human settlements in these remote Amazonian areas (Levis et al., 2017a – **Chapter 3**).

Future multidisciplinary studies that combine alternative methods may help to reconstruct forest composition dynamics (Stahl, 2015), as Watling et al. (2017a) did in the geoglyph region of Acre, revealing more details of the influence of past peoples in Amazonian forests. The integration of paleoecology, archaeology, archaeobotany and forest ecology is a promising combination (Mayle and Iriarte, 2014; Iriarte, 2016; Watling et al., 2017a,b). In southwestern Amazonia, archaeobotanical remains have revealed that past peoples consumed a rich diet, including many palm fruits (Dickau et al., 2012). The increase in palm abundance is also visible in soil profiles of archaeological sites across the region (McMichael et al., 2015a; Watling et al., 2017a), suggesting that past societies enriched the forest with useful palms to improve food production. Today, useful and domesticated palms are dominant in southwestern Amazonian forests (Levis et al., 2017a – **Chapter 3**), growing on abandoned pre-Columbian mounds, anthropogenic soils and geoglyphs created by past management practices (Erickson and Balée, 2006; Quintero-Vallejo et al., 2015; Levis et al., 2017a – **Chapter 3**; Watling et al., 2017a). Many palm species were found in most of the forest patches investigated here, suggesting long-term human management. Regional contrasts in palm and other plant species composition across Amazonia may reveal different human practices or specific environmental conditions that should be investigated in detail.

We conclude that our literature review, conceptual model and field results contribute to explain how domesticated forests were formed in Amazonia, in part by revealing how integrated categories of management practices interfere with natural ecological processes that shape plant communities in tropical forests. Different degrees and types of management, cultural preferences and environmental conditions may lead to a wide variety of outcomes and explain why diverse combinations of useful species were found in Amazonian forest patches. Insights from agroforestry systems in tropical and sub-tropical regions confirm that indigenous management practices have been used worldwide to domesticate plant species and entire forest landscapes (Wiersum, 1997a,b; Michon, 2005; Kennedy, 2012; Reis et al., 2014). Learning about indigenous knowledge of forest management is important not only to understand the plant and landscape domestication processes, but also to guide policies for forest conservation, local people's empowerment, and food production (Michon et al., 2007; Roberts et al., 2017). In Amazonia today, millions of people live in rural landscapes, with partial dependence on forest resources for their well-being, and with profound local knowledge that should be incorporated in environmental conservation and management plans.

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AUTHOR CONTRIBUTIONS

C.L. conceived the study; C.L.,B.M.F.,P.A.M.,B.G. L.,R.P.A.,J.F-M.,J.L.,E.K. collected data and carried out the analyses; C.L.,B.M.F.,P.A.M.,B.G.L.,R.P.A. ,J.F-M.,J.L.,F.B.,M.P-C.,F.R.C.C.,C.R.C. wrote the manuscript; all authors designed and discussed the analyses, and commented on various versions of the manuscript.

SUPPLEMENTARY MATERIALS FOR CHAPTER 5

How people domesticated Amazonian forests

Appendices 5

Appendix 5A - References used in the literature review

Figures A5.1 and A5.2

Tables A5.1 and A5.3

APPENDIX 5A - MATERIALS

References used in the literature review of the 22 useful species

01. Abraao, M. B., Shepard, G. H., and Nelson Jr., B. W. (2010). “Baniwa vegetation classification in the white-sand Campinarana habitat of the northwest Amazon, Brazil,” in *Landscape ethnoecology. Concepts of biotic and physical space*, eds. L. M. Johnson and E. S. Hunn (New York: Berghahn Books), 83–115.

02. Alves, R. P., Levis, C., and Clement, C. R. (2016). Use and management of piquiá suggest in situ domestication a long the lower Tapajós river, Brazilian Amazonia. *Econ. Bot.* 70, 198–202.

03. Anderson, A. B., and Ioris, E. M. (1992). Valuing the rain forest: economic strategies by small-scale forest extractivists in the Amazon estuary. *Hum. Ecol.* 20, 337–369.

04. Anderson, A. B., Magee, P., Gely, A., and Gonçalves Jardim, M. A. (1995). Forest management patterns in the floodplain of the Amazon estuary. *Conserv. Biol.* 9, 47–61.

05. Anderson, A. B., May, P. H., and Balick, M. J. (1991). The subsidy from nature: *Palm forests, peasantry, and development on an Amazon frontier.* Columbia University Press.

06. Balée, W. (1993). Indigenous Transformation of Amazonian Forests: An Example from Maranhão, Brazil. *L’Homme*, 231–254.

07. Balée, W. (2010). Contingent diversity on anthropic landscapes. *Diversity* 2, 163–181.

08. Balée, W. (2013). *Cultural forests of the Amazon: a historical ecology of people and their landscapes.* Tuscaloosa: The University of Alabama Press.

09. Balée, W., Schaan, D. P., Whitaker, J. A., and Holanda, R. (2014). Florestas antrópicas no Acre: inventário florestal no geoglifo Três Vertentes, Acrelândia. *Amaz. Antropol.* 6, 140–169.

10. Balick, M. J. (1988). *The palm-tree of life: biology, utilization and conservation.*, ed. M. J. Balick New York: New York Botanical Garden.

11. Begossi, A., Hanazaki, N., and Peroni, N. (2000). Knowledge and use of biodiversity in Brazilian hot spots. *Environ. Dev. Sustain.* 2, 177–193.

12. Bernal, R., Torres, C., García, N., Isaza, C., Navarro, J., Vallejo, M. I., et al. (2011). Palm Management in South America. *Bot. Rev.* 77, 607–646.

13. Brum, H. D., Nascimento, H. E., Laurance, W. F., Andrade, A. C., Laurance, S. G., and Luizão, R. C. (2008). Rainforest fragmentation and the demography of the economically important palm Oenocarpus bacaba in central Amazonia. *Plant Ecol.* 199, 209–215.

14. Cámara-Leret, R., Copete, J. C., Balslev, H., Gomez, M. S., and Macía, M. J. (2016). Amerindian and Afro-American Perceptions of Their Traditional Knowledge in the Chocó Biodiversity Hotspot. *Econ. Bot.* 70, 160–175.

15. Choo, J., Zent, E. L., and Simpson, B. B. (2009). The importance of traditional ecological knowledge for palm-weevil cultivation in the Venezuelan Amazon. *J Ethnobiol.* 29, 113-128.

16. Clement, C. R. (1999). 1492 and the loss of Amazonian crop genetic resources. II. Crop biogeography at contact. *Ecomonic Bot.* 53, 203–216.

17. Comberti, C., Thornton, T. F., de Echeverria, V. W., and Patterson, T. (2015). Ecosystem services or services to ecosystems? Valuing cultivation and reciprocal relationships between humans and ecosystems. Glob. *Environ. Chang.* 34, 247–262.

18. Davidson-Hunt, I. J., and Berkes, F. (2001). “Changing Resource Management Paradigms, Traditional Ecological Knowledge, and Non-timber Forest Products,” in *Forest Communities in the Third Millennium: Linking Research, Business, and Policy Toward a Sustainable Non-Timber Forest Product Sector*, eds. I. Davidson-Hunt, L. C. Duchesne, and J. C. Zasada (St. Paul: North Central Research Station), 78–92.

19. Davis, E. W., and Yost, J. A. (1983). The ethnomedicine of the Waorani of Amazonian Ecuador. *J. Ethnopharmacol.* 9, 273–297.

20. De Jong, W. (2001). Tree and forest management in the floodplains of the Peruvian Amazon. *For. Ecol. Manage.* 150, 125–134.

21. Denevan, W. M., Treacy, J. M., Alcorn, J. B., Padoch, C., Denslow, J., and Paitan, S. F. (1984). Indigenous agroforestry in the Bora Indian management of swidden fallows. *Interciencia* 9, 346–357.

22. DeWalt, B. (1994). Using indigenous knowledge to improve agriculture and natural resource management. *Hum. Organ.* 53, 123–131.

23. Dubois, J. C. L. (1996). Uses of wood and non-wood forest products by Amazon forest dwellers. *Unasylva - FAO* 47, 8–15.

24. Duchelle, A. E., Kainer, K. A., & Wadt, L. H. (2014). Is certification associated with better forest management and socioeconomic benefits? A comparative analysis of three certification schemes applied to Brazil nuts in Western Amazonia. *Society & Natural Resources*, 27, 121-139.

25. Ducke, A. (1946). Plantas de cultura precolombiana na Amazônia brasileira: notas sobre as espécies ou formas espontâneas que supostamente lhes teriam dado origem. *Bol. Técnico do Inst. Agronômico do Norte* 8, 3–24.

26. Duke, J. A., and Vasquez, R. (1994). *Amazonian Ethnobotanical Dictionary.* New York: CRC Press.

27. Eden, M. J., McGregor, D. F. M., and Vieira, N. A. Q. (1990). Pasture development on cleared forest land in northern Amazonia. *Geogr. J.* 156, 283–296.

28. Elias, F., Marimon, B. S., de Almeida Reis, S. M., Forsthofer, M., Gomes, L., Morandi, P. S., et al. (2013). Dinâmica da distribuição espacial de populações arbóreas, ao longo de uma década, em cerradão na transição Cerrado-Amazônia, Mato Grosso. *Biota Amaz.* 3, 1–14.

29. Franco-Moraes, J. (2016). Ecologia histórica de florestas da Bacia do Rio Içana, alto rio Negro, Amazonas: um legado Baniwa nas paisagens. [dissertation/master’s thesis]. [Manaus (AM)]: INPA

30. Fujisaka, S., Escobar, G., and Veneklaas, E. J. (2000). Weedy fields and forests:

interactions between land use and the composition of plant communities in the Peruvian Amazon. *Agric. Ecosyst. Environ.* 78, 175–186.

31. Garí, J. (2001). Biodiversity and indigenous agroecology in Amazonia: the indigenous people of Pastaza. Etnoecologica 5, 21–37.

32. Gilmore, M. P., Endress, B. A., and Horn, C. M. (2013). The socio-cultural importance of Mauritia flexuosa palm swamps (aguajales) and implications for multi-use management in two Maijuna communities of the Peruvian Amazon. *J. Ethnobiol. Ethnomed.* 9, 1–23.

33. Goeschl, T., and Igliori, D. C. (2006). Property rights for biodiversity conservation and development: extractive reserves in the Brazilian Amazon. *Dev. Change* 37, 427–451.

34. Hammond, D. S., Dolman, P. M., and Watkinson, A. R. (1995). Modern Ticuna swidden-fallow management in the Colombian Amazon: ecologically integrating market strategies and subsistence-driven economies? *Hum. Ecol.* 23, 335–356.

35. Holm, J. A., Miller, C. J., and Cropper, W. P. (2008). Population dynamics of the dioecious Amazonian palm Mauritia flexuosa: simulation analysis of sustainable harvesting. *Biotropica* 40, 550–558.

36. Horn, C. M., Gilmore, M. P., and Endress, B. A. (2012). Ecological and socio-economic factors influencing aguaje (Mauritia flexuosa) resource management in two indigenous communities in the Peruvian Amazon. *For. Ecol. Manage.* 267, 93–103.

37. Jakovac, C. C., Peña-Claros, M., Mesquita, R. C., Bongers, F., and Kuyper, T. W. (2016). Swiddens under transition: Consequences of agricultural intensification in the Amazon. *Agric. Ecosyst. Environ.* 218, 116–125.

38. Junqueira, A. B., Shepard, G. H., and Clement, C. R. (2010). Secondary forests on anthropogenic soils in Brazilian Amazonia conserve agrobiodiversity. *Biodivers. Conserv.* 19, 1933–1961.

39. Kawa N. C. (2008). Use and Management of Amazonian Dark Earth in Borba, Amazonas, Brazil. [dissertation/PhD thesis].

40. Kawa, N. C., Michelangeli, J. A. C., and Clement, C. R. (2015). Household agrobiodiversity management on Amazonian dark earths, oxisols, and floodplain soils on the lower Madeira river, Brazil. *Hum. Ecol.* 43, 339–353.

41. Levis, C., Costa, F. R. C., Bongers, F., Peña-Claros, M., Clement, C. R., Junqueira, A. B., et al. (2017). Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science (80-.)*. 355, 925–931.

42. Lopez-Zent, E. (1998). A Creative Perspective of Environmental Impacts by Native Amazonia Human Populations. *Interciencia* 23, 232–240.

43. Lopez-Zent, E. M. (1999). Hoti ethnobotany: Exploring the interactions between plants and people in the Venezuelan Amazon. [dissertation/PhD thesis].

44. Major, J., Ditommaso, A., German, L. A., and Mccann, J. M. (2003). "Weed population dynamics and management on Amazonian Dark Earths," in *Amazonian dark earths: origin, properties, management*, eds. J. Lehmann, D. C. Kern, B. Glaser, and W. I. Woods (Springer Netherlands), 2003.

45. Manzi, M., and Coomes, O. T. (2009). Managing Amazonian palms for community use: a case of aguaje palm (Mauritia flexuosa) in Peru. *For. Ecol. Manage.* 257, 510–517.

46. Markley, K. S., and Jenkins, D. W. (1949). Oil palm resources of the American Hemisphere. *J. Am. Oil Chem. Soc.* 26, 257–267.

47. Marquardt, K., Milestad, R., and Salomonsson, L. (2013). Improved fallows: a case study of an adaptive response in Amazonian swidden farming systems. *Agric. Human Values* 30, 417–428.

48. Marquardt, K., Salomonsson, L., and Brondizio, E. (2010). Small-scale farmers' management strategies in the upper Amazon: an action research case study. *Interciencia* 35, 421–429.

49. Menezes, A. J. E. A. de, and Homma, A. K. O. (2014). "Recomendações para o plantio de uxizeiro," in *Extrativismo Vegetal na Amazônia: história, ecologia, economia e domesticação*, ed. A. K. O. Homma (Brasília: Embrapa), 321–328.

50. Miller, R., J. P., and Leeuwen, J. van (2006). "Amazonian homegardens: their ethnohistory and potential contribution to agroforestry development," in *Tropical Homegardens: A Time-Tested Example of Sustainable Agroforestry*, eds. B. M. Kumar and P. K. R. Nair (Springer), 43–60.

51. Miller, C. (2002). Fruit production of the ungurahua palm (Oenocarpus bataua subsp. bataua, Arecaceae) in an indigenous managed reserve. *Econ. Bot.* 56, 165–176.

52. Montoya, E., Rull, V., Stansell, N. D., Abbott, M. B., Nogué, S., Bird, B. W., et al. (2011). Forest–savanna–morichal dynamics in relation to fire and human occupation in the southern Gran Sabana (SE Venezuela) during the last millennia. *Quat. Res.* 76, 335–344.

53. Morcote-Ríos, G., and Bernal, R. (2001). Remains of palms (Palmae) at archaeological sites in the New World: A review. *Bot. Rev.* 67, 309–350.

54. Müller-Schwarze, N. K. (2006). Antes and Hoy Día: plant knowledge and categorization as adaptations to life in Panama in the twenty-first century. *Econ. Bot.* 60, 321–334.

55. Muñiz-Miret, N., Vamos, R., Hiraoka, M., Montagnini, F., and Mendelsohn, R. O. (1996). The economic value of managing the açaí palm (Euterpe oleracea Mart.) in the floodplains of the Amazon estuary, Pará, Brazil. *For. Ecol. Manage.* 87, 163–173.

56. Nascimento, A. R., Amaral dos Santos, A., Martins, R. C., and Borges Dias, T. A. (2009). Comunidade de palmeiras no território indígena Krahò, Tocantins, Brasil: biodiversidade e aspectos etnobotânicos. *Interciencia* 34, 182–188.

57. Padoch, C., and De Jong, W. (1987). "Traditional agroforestry practices of native and ribereno farmers in the lowland Peruvian Amazon," in *Agroforestry: Realities, Possibilities and Potentials. Martinus Nijhoff Publisher, Dordrecht*, ed. H. L. GHOLZ (Dordrecht: Martinus Nijhoff Publishers).

58. Paiva, P. M., Guedes, M. C., and Funi, C. (2011). Brazil nut conservation through shifting cultivation. *For. Ecol. Manage.* 261, 508–514.

59. Politis, G. G. (2007). *Nukak: Ethnoarchaeology of an Amazonian People.* Walnut Creek: Left Coast Press.

60. Posey, D. A. (1985). Indigenous management of tropical forest ecosystems: the case of the Kayapo Indians of the Brazilian Amazon. *Agrofor. Syst.* 3, 139–158.

61. Posey, D. A. (1987). Ethnoentomological survey of Brazilian indians. *Entomol. Gen.*, 191–202.

62. Prance, G. T. (1992). The resource of useful tree species: identification of priorities for domestication: Amazonian tree diversity and the potential for supply of non-timber forest products. in *Tropical trees: the potential for domestication and the rebuilding of forest resources*, eds. R. R. B. Leakey and A. C. Newton (Edingburgh: Heriot-Watt University).

63. Ribeiro, M. B. N., Jerozolimski, A., de Robert, P., Salles, N. V., Kayapó, B., Pimentel, T. P., et al. (2014). Anthropogenic landscape in southeastern Amazonia: contemporary impacts of low-intensity harvesting and dispersal of Brazil nuts by the Kayapó Indigenous people. *PLoS One* 9, e102187. doi: 10.1371/journal.pone.0102187

64. Roosevelt, A. C. (2014). *Parmana: prehistoric maize and manioc subsistence along the Amazon and Orinoco.* New York: Academic Press.

65. Salm, R. (2004). Tree species diversity in a seasonally-dry forest: the case of the Pinkaití site, in the Kayapó Indigenous Area, southeastern limits of the Amazon. *Acta Amaz.* 34, 435–443.

66. Santos, M. F., Damasceno-Silva, K. J., Carvalhaes, M. A., and Lima, P. S. C. (2015). Genetic variation detected by RAPD markers in natural populations of babassu palm (Attalea speciosa Mart.). *Genet. Mol. Res.* 14, 6124–6135.

67. Schroth, G., Da Mota, M. S. S., Lopes, R., and De Freitas, A. F. (2004). Extractive use, management and in situ domestication of a weedy palm, Astrocaryum tucuma, in the central Amazon. *For. Ecol. Manage.* 202, 161–179.

68. Schroth, G., Mota, M. S. S., and Jerozolimski, A. (2006). “Agroforestry and the conservation of forest cover and biodiversity in tropical landscapes–on–site and off–site effects and synergies with environmental legislation,” in *Sistemas Agroflorestais: Bases Científicas para o desenvolvimento sustentável*, eds. A. C. da G. Rodrigues, N. F. de Barros, E. F. da Gama-Rodrigues, M. M. S. Freitas, A. P. Viana, J. M. Jasmin, et al. (Campos dos Goytacazes: Embrapa Informação Tecnológica), 67–86.

69. Schroth, G., and Maria do Socorro, S. D. (2013). Technical and institutional innovation in agroforestry for protected areas management in the Brazilian Amazon: opportunities and limitations. *Environ. Manage.* 52, 427–440.

70. Scoles, R., and Gribel, R. (2015). Human Influence on the Regeneration of the Brazil Nut Tree (Bertholletia excelsa Bonpl., Lecythidaceae) at Capanã Grande Lake, Manicoré, Amazonas, Brazil. *Hum. Ecol.* 43.

71. Seibert, R. J. (1948). The uses of Hevea for food in relation to its domestication. *Ann. Missouri Bot. Gard.* 35, 117–121.

72. Shanley, P., Clement, C. R., Carvalho, J. E. U. de, Homma, A. K. O., and Menezes, A. J. E. A. de (2016). “Amazonian fruits: How farmers nurture nutritional diversity on farm and in the forest,” in *Tropical Fruit Tree Diversity: Good Practices for in situ and on-Farm Conservation*, eds. B. Sthapit, H. A. H. Lamers, V. R. Rao, and A. Bailey (Routledge), 147–160.

73. Shepard JR, G., and Ramirez, H. (2011). “Made in Brazil”: human dispersal of the Brazil nut (Bertholletia excelsa, Lecythidaceae) in ancient Amazonia. *Econ. Bot.* 65, 44–65. doi: 10.1007/s12231-011-9151-6

74. Smith, N. (2015). *Palms and People in the Amazon.* Springer.

75. Sosnowska, J., Walanus, A., and Balslev, H. (2015). Asháninka palm management and domestication in the Peruvian Amazon. *Hum. Ecol.* 43, 451–466.

76. Thomas, E., Alcázar Caicedo, C., McMichael, C. H., Corvera, R., and Loo, J. (2015). Uncovering spatial patterns in the natural and human history of Brazil nut (Bertholletia excelsa) across the Amazon Basin. *J. Biogeog.* 42, 1367-1382. doi: 10.1111/jbi.12540

77. Weinstein, S., and Moegenburg, S. (2004). Acai palm management in the Amazon Estuary: Course for conservation or passage to plantations? *Conserv. Soc.* 2, 315–346.

78. Woomer, P. L., Palm, C. A., Alegre, J., Castilla, C., Cordeiro, D. G., Hairiah, K., et al. (1999). “Slash-and-burn effects on carbon stocks in the humid tropics,” in *Global Climate Change and Tropical Ecosystems*, eds. R. Lal, J. M. Kimble, and B. A. Stewart (New York: CRC Press), 99–115.

79. Yamakuri, A. C. (2011). ‘Guacamayo azul’: palabras del ritual de las frutas que llega a nosotros como comida en abundancia, de parte de los okaina. *Mundo Amaz.*, 307–327.

80. Zent, E. L., and Zent, S. (2004). “Amazonian Indians as Ecological Disturbance Agents: The Hotï of the Sierra de Maigualida, Venezuelan Guayana,” in *Etnobotany and Conservation of Biocultural Diversity*, eds. T. S. Carlson and L. Maffi (Advances in Economic Botany), 79–112.

81. Zent, S., and Zent, E. (2012). Jodï horticultural belief, knowledge and practice: incipient or integral cultivation? *Bol. do Mus. Para. Emílio Goeldi. Ciências Humanas* 7, 293–338.

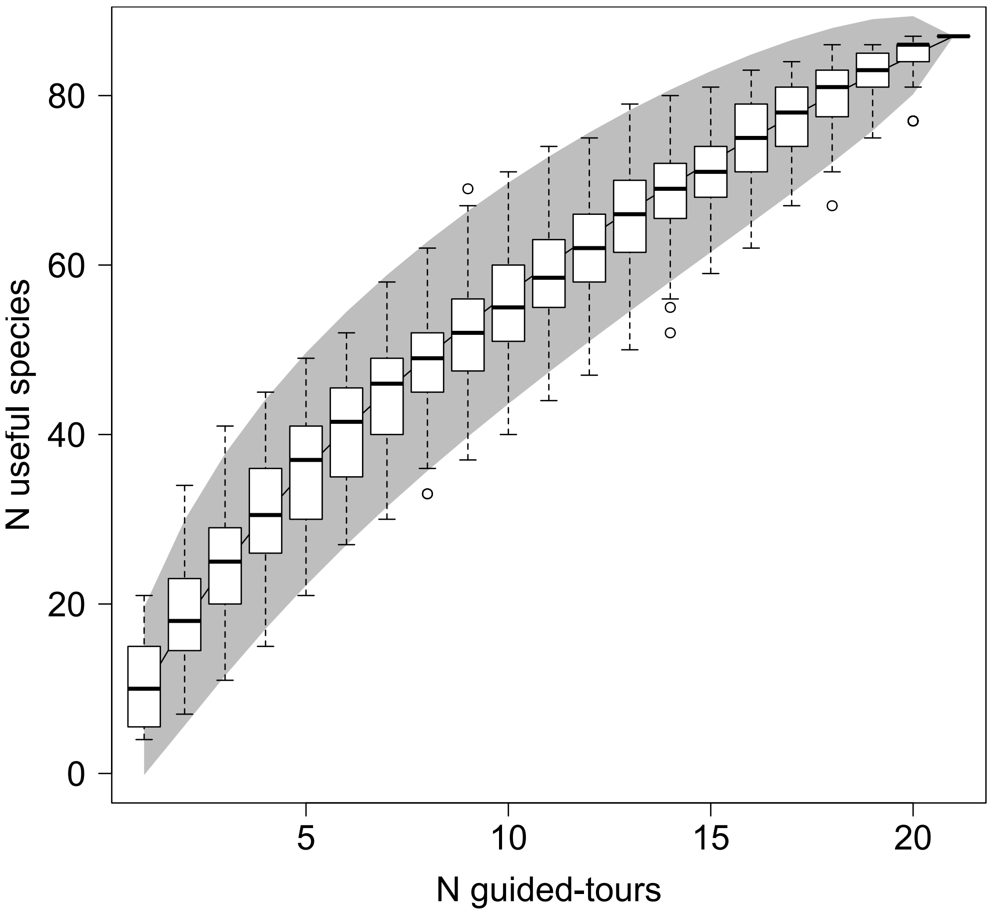

Figure A5.1. Species accumulation curve as function of the number of guided-tours. List of useful species that occur in the forest patches visited during guided-tours is presented in the Supplementary Table 3 (separate Excel file). We used the function "specaccum" and method "random", that finds a species accumulation curves and their standard deviations from random permutations of the data, using R. This method shown each random simulation separately (boxplots in the figure). The confidence interval shown was obtained from the standard method "partial match", also using R program.

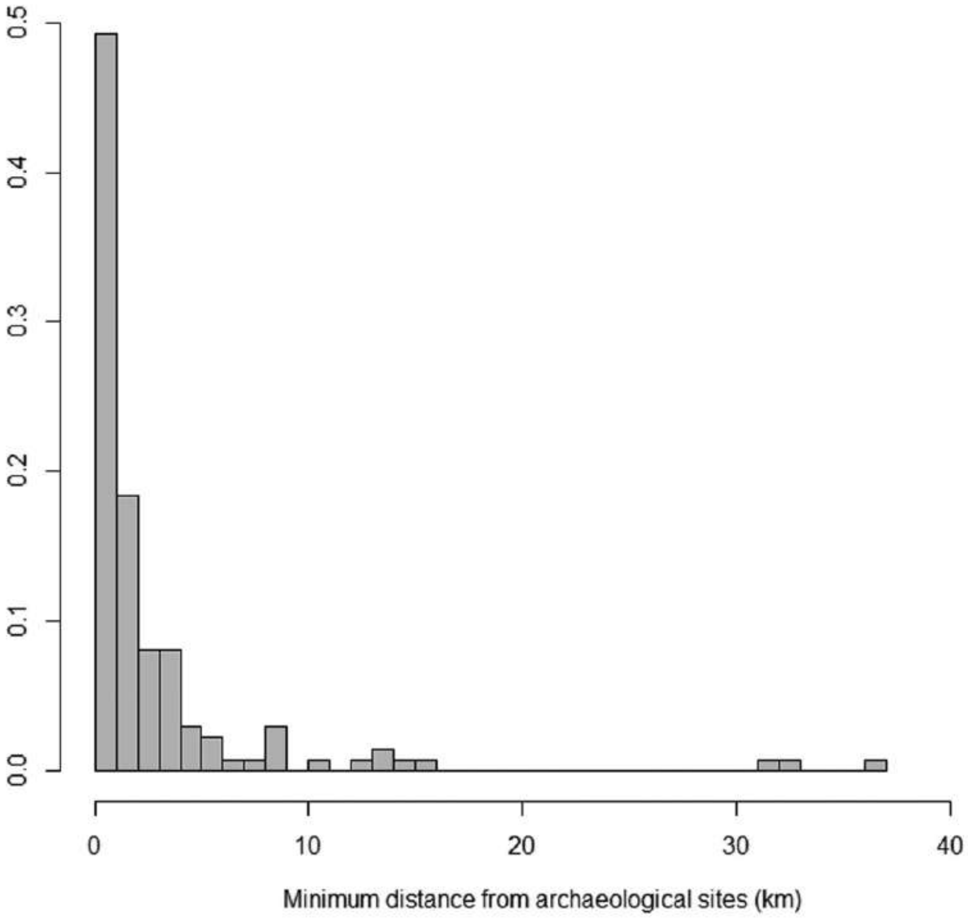

Figure A5.2. The frequency of forest patches of useful species along a distance gradient from archaeological sites. Density of forest patches was calculated in relation to the minimum straight-line distance from the closest archaeological site. Number of forest patches analyzed is equal to 136.

Table A5.1. List of the 38 native useful species found in the 35 forest patches surrounding the 30 villages surveyed across Brazilian Amazonia. The number of sub-basins where a specific forest patch was identified, number of forest patches mapped in the field, their uses, management practices, spatial context according to our conceptual model (settlements, swiddens or old-growth forests), distribution around the villages (environments according to local informants) are described in this table. Use category: (F) Food; (C) Construction; (T) Thatch; (Fu) Fuel; (M) Medicinal; (Ma) Manufacturing or Technology; (Co) Commerce; (A) Attractive for game; (Af) Animal food; (R) Ritualistic; and (O) Other.

Scientific name	Common name of patch	Sub-Basin (N=9)	Number of patches	Use Category (literature)	Use Category (field)	Management practices (literature)	Management practices (field data in two villages)	Spatial context	Distribution of patches around villages
Euterpe precatoria Mart.	Açaízal	6	7	F, C, T, M, Ma, Co, A, O	F	1, 2, 4, 5, 7	-	Old-growth	Valley
Euterpe oleracea Mart.	Açaizal	1	1	F, C, T, M, Ma, Co, A, R, O	F, C, M, Ma, Co, Af, R	1, 2, 4, 5, 7, 8	1,2,4,7,8	Old-growth	Valley
*Carapa sp.*Aubl.	Andirobal	2	0	-	M	-	-	-	White-sand
Psidium sp. L.	Araçazal	1	0	-	F	-	-	-	-
Attalea speciosa Mart. ex Spreng.	Babaçual	3	2	F, C, T, Fu, M, Ma, Co, Af, O	F, T, Fu, M, Ma, A, Af, O	1, 2, 5, 6	1,2,5,6	Swiddens/ Old-growth	Plateau
Oenocarpus distichus Mart.	Bacabal	1	5	F, C, T, Ma	F, C, Ma, M, A	1,2,3,4,5,7	1,2,4,7	Swiddens	Fallow
Oenocarpus bacaba Mart.	Bacabal	6	3	F, C, T, M, Ma, Co, A	F, C, M, Ma, A	1, 2, 4, 5, 6, 7	1,2,4,7	Swiddens	Fallow
Manicaria saccifera Gaertn.	Buçuzal	2	0	F, C, T, M, Ma	F	4, 7	-	-	Valley
Mauritia flexuosa L.f.	Buritizal	4	6	F, C, T, M, Ma, Co, A, O	F	1,3,4,5,6,7,8		Old-growth	Valley
Theobroma cacao L.	Cacoal	2	1	F,C,M,Co,Af	F	1, 2, 4, 5, 6, 7, 8		Settlements	Old villages
Elaeis oleífera (Kunth) Cortés	Caiauézal	4	12	F, C, T, M, Ma, Co, Fu, Af	F	4, 5, 7		Settlements	TPI
*Anacardium sp.*L.	Cajutíwa	1	1	-	F	-	-	Old-growth	Headwaters
cf. Neoxythece elegans (A.DC.) Aubrév.	Caramurizal	1	1	-	F	-	-	Old-growth	Plateau
Mauritia carana Wallace	Caranãzal	2	2	F, C, T, Ma	F	4, 7		Old-growth	Floodplains
Bertholletia excelsa Bonpl.	Castanhal	6	28	F, C, M, Fu, Ma, Co	F, C, Ma, A, Af, Co	1, 2, 4, 5, 7	1,2,4,7,8	Swiddens/ Old-growth	Plateau
Acioa edulis Prance	Castanhal de cutia	1	0	F, Ma	F	-	-	-	Plateau
Copaifera multijuga Hayne	Copaibal	1	1	M, C	M, C, Co, A, Af	-	1,2,4,7,8	Old-growth	Plateau
Pourouma sp. Aubl.	Cururaítíwa	1	1	-	F	-	-	Swiddens	Plateau
Myrcia splendens (Sw.) DC.	Cumatizal	1	1	Ma, Fu	Ma	6	-	Swiddens	Fallow
Attalea spectabilis Mart.	Curuázal	3	3	F,T,M,Ma,A,Af	F,T,M,Ma,A,Af	-	1,2,3	Swiddens	Plateau
Humiria balsamifera (Aubl.) A.St.-Hil.	Humiritíwa	1	1	F,C,Fu,M,R,O	F	4,5,6,7,8	-	Swiddens	White-sand

Scientific name	Common name of patch	Sub-Basin (N=9)	Number of patches	Use Category (literature)	Use Category (field)	Management practices (literature)	Management practices (field data in two villages)	Spatial context	Distribution of patches around villages
Attalea maripa (Aubl.) Mart.	Inajazál	1	1	F,C,T,M,Ma,A,Af,O	F	1,2,4,5,6,7	-	Swiddens	Fallow
Duguetia stenantha R.E.Fr.	Jabutipúzal	1	3	F,Af	F	-	-	Swiddens	Plateau
Erisma japura Spruce ex Warm.	Japuratíwa	1	1	F	F	-	-	Swiddens	Plateau
Hymenaea parvifolia Huber	Jutaízal	1	4	F,M,Co,Af	F,C,Fu,Ma,M,Co,A,Af	4	1,2,4,7	Swiddens	Fallow
Miconia sp. Ruiz & Pav.	Muubal	1	1	-	F,C,M,A		2	Swiddens	Fallow
Oenocarpus bataua Mart.	Patauázal	7	10	F,C,T,M,Ma,Co,Fu,R,A,Af,O	F,C,M,A,Af	1,2,4,5,7	1,2	Old-growth	Valley
Leopoldinia piassaba Wallace	Piaçabal	1	1	F,T,M,Ma,Co	F	-	-	Old-growth	Headwaters
Caryocar villosum (Aubl.) Pers.	Piquiázal	3	6	F,C,M,Fu,Ma,Co,A,Af,O	F,C,M,Fu,Ma,Co,A,Af,O	1,2,3,4,5,7,8	1,2,3,4,5,7,8	Swiddens/ Old-growth	Plateau
Hevea brasiliensis (Willd. ex A.Juss.) Müll.Arg.	Seringal	3	9	F,C,Ma,Co,A	F,C,Fu,Ma,Co,A,O	1,4,5,7	1,2,4,5,7	Swiddens/ Old-growth	Fallow / Valley
Phenakospermum guianensis (A.Rich.) Endl. ex Miq.	Sororocatíwa	1	1	F,C,M,Ma,O	F	1,2,4,6,7	-	Swiddens	Plateau
Couma sp. Aubl.	Sorval	4	6	-	F	-	-	Old-growth	White-sand
Astrocaryum aculeatum G.Mey.	Tucumãzal	4	1	F,C,Ma,Co,R,A,O	F	1,2,4,5,6,7	-	Swiddens	Fallow
Astrocaryum sp. G.Mey.	Tucumtiwa	1	7	-	F	-	-	Swiddens	Fallow
Attalea phalerata Mart. ex Spreng.	Urucurizal	1	1	F,C,T,M,Ma,O	F	-	-	Settlements	TPI
Poraqueiba sericea Tul.	Umarizal	4	5	F	F	1,2,4,5,7	-	Swiddens	White-sand
Endopleura uchi (Huber) Cuatrec.	Uxízal	4	2	F,C,M,Co,A,Af	F,C,M,A	1,2,4,5,7,8	1,2,3,4,5,7,8	Old-growth	Plateau
Duckesia verrucosa (Ducke) Cuatrec.	Uxízal	1	1	F,A,Af	F	-	-	Old-growth	Plateau

Table A5.2. Name of the 30 villages studied along four major rivers and their distance to archaeological sites.

Sub-basin	Villages	Distance to archaeological sites (km)
Lower Madeira	São Félix	0
Lower Madeira	Santa Rita	0
Lower Madeira	Puruzinho	0
Lower Madeira	Vila Gomes	0
Lower Negro	Terra Preta	0
Lower Negro	São Sebastião	0
Lower Negro	Canaã	0
Lower Tapajós	Jaguarari	0
Lower Tapajós	Jamaraquá	0
Lower Tapajós	Maguarí	1
Lower Tapajós	Prainha	0
Middle Madeira	São João	0
Middle Madeira	Boca do Rio	0
Middle Madeira	Barro Alto / Liberdade	0
Middle Madeira	São Francisco	0
Middle Madeira	Terra Preta	0
Middle Madeira	Santa Cívica	0
Middle Negro	Bacabal	0
Middle Negro	Romão	0
Middle Solimões	Calafate	0
Middle Solimões	Boa Esperança	0
Middle Solimões	Baré	0
Middle Solimões	Boa Vista	0
Upper Madeira	Barreira do Tambaqui	0
Upper Negro	São Francisco	7
Upper Negro	São Marcelino	0
Upper Negro	Tabocal dos Pereiras	0
Upper Solimões	São Raimundo Universo	0
Upper Solimões	Bom Sucesso	5
Upper Solimões	Monte Tabô	5

Table A5.3. List of all useful species that occur in the 21 forest patches visited during guided-tours. Sub-basin visited: (MM) Middle Madeira; (LM) Lower Madeira; (US) Upper Solimões; (MS) Middle Solimões; (UN) Upper Negro; (MN) Middle Negro; (LN) Lower Negro; and (LT) Lower Tapajós.

Local name	Scientific name	MM	MM	MM	LM	LM	US	US	MS	MS	UN	UN	UN	MN	MN	LN	LN	LT	LT	LT	LT	LT
abacaxi-do-mato	*Ananas sp.*	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
abiorana	*Pouteria sp.*	0	0	0	0	0	0	0	1	1	0	0	0	7	0	0	0	1	0	8	0	0
açaí	*Euterpe precatoria*	0	2	0	5	25	3	0	0	7	1	1	4	28	0	0	0	0	0	0	0	0
açaí chumbinho	*Euterpe catinga*	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
amapá	*Brosimum sp.*	0	2	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	4	0	0	0
anoirá	*Indet*	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
arumã	*Ischnosiphon sp.*	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
atarana	*Annona sp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
babaçu	*Atallea speciosa*	0	68	90	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
bacaba	*Oenocarpus bacaba*	0	6	0	2	0	0	0	1	0	0	2	0	31	2	1	0	0	0	0	0	0
bacaba	*Oenocarpus distichus*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	22	30
bacabinha	*Oenocarpus mapora / O. minor*	0	1	0	1	6	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
bacurí	*Garcinia sp.*	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
bacuri coroa	*Garcinia sp.*	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
bambuzinho	*Guadua sp.*	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
burití	*Mauritia flexuosa*	0	0	0	0	0	0	0	0	0	14	0	0	0	0	1	12	0	0	0	0	0
cacau jacaré/cacuí	*Theobroma marie*	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0
cacau-do-mato/cacauarana	*Theobroma speciosum*	0	0	0	2	2	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0
caiaué	*Elaies oleifera*	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
caju-açu	*Anacardium sp.*	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
carapanaúba	*cf Aspidosperma nitidum*	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
castanha	*Bertholletia excelsa*	0	0	3	32	23	1	0	3	10	0	0	0	15	0	0	0	0	0	0	0	0
castanha de cutia	*Acioa edulis*	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
copaíba	*Copaifera sp.*	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
cucura-do-mato	*Pourouma sp.*	0	0	0	0	0	0	0	0	0	0	0	0	3	5	0	0	0	0	0	0	0
cumarú	*Dipterix odorata*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
cumatê	*cf Saccoglotis guyanensis*	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
cupu cabeça-de-macaco	*Theobroma sp.*	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
cupu cabeça-de-urubu	*Theobroma obovatum*	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
cupuí	*Theobroma subincanum*	0	1	0	0	0	1	0	3	3	0	0	0	2	0	2	4	0	0	0	0	0

Local name	Scientific name	MM	MM	MM	LM	LM	US	US	MS	MS	UN	UN	UN	MN	MN	LN	LN	LT	LT	LT	LT	LT
curuá	*Attalea spectabilis*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
cutite	*Pouteria sp.2*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
faveira	*Parkia sp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
fruta amarela	*Indet*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
garroteiro	*cf Bagassa guianiensis*	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
genipapo	*Genipa americana*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
guajará	*cf Neoxythece elegans*	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
inajá	*Attalea maripa*	0	3	1	20	19	0	0	0	2	0	0	0	20	19	0	0	0	0	0	0	15
inga	*Inga sp.*	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
inga rabo de guariba	*Inga sp.*	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
ingá wariaruaia	*Inga sp.*	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
inharé	*cf Helicostylis tomentosa*	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
jabotí/jabotipú	*Duguetia stenantha*	0	1	0	0	0	10	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0
japurá	*Erisma japura*	0	0	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0	0	0
jatobá	*Hymenea courbaril*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
jutaí	*Hymenea parvifolia*	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	10	2	0	0	0
mamorana	*Jacaratia spinosa*	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
mapatí do mato	*Pourouma sp.*	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
massaranduba	*Manilkara huberi*	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	1	0	0	0
mata-mata	*Eschweilera sp.*	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
morototó	*Schefflera morototoni*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
mumbaca	*Astrocaryum sp.*	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
muru-muru	*Astrocaryum muru-muru*	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
muuba	*Miconia sp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
palheira	*Attalea sp.*	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
patauá	*Oenocarpus bataua*	0	1	0	0	1	0	0	0	0	7	1	1	1	0	9	31	0	1	0	0	0
paxiúba	*Socratea exorrhiza*	0	0	0	1	1	0	10	0	2	0	0	0	0	0	0	5	0	0	0	0	0
paxiubão	*Iriartea deltoidea*	0	0	0	0	0	0	0	7	5	0	1	1	0	0	0	0	0	0	0	0	0
pé de gato	*Indet*	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
pepino	*Ambelania acida*	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
piquiá	*Caryocar villosum*	0	0	0	4	2	0	0	2	4	0	0	0	1	0	0	0	0	3	0	16	0
piquiarana	*cf Caryocar glabrum*	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
pirirema	*Syagrus coccoides*	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0
pitomba	*Talisia sp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0

Local name	Scientific name	MM	MM	MM	LM	LM	US	US	MS	MS	UN	UN	UN	MN	MN	LN	LN	LT	LT	LT	LT	LT
pororoca	*cf. Dialium guianense*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
puraquekaa	*Indet*	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
puruí	*Alibertia edulis*	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
samaúma	*Ceiba pentandra*	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
sapucaia	*Lecythis sp.*	0	3	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	0
seringa do igapó	*Hevea sp.*	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
seringueira plantada	*Hevea brasiliensis*	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	0	2
sorva / sorva grande	*Couma sp.*	0	1	0	0	0	0	0	1	2	0	0	0	0	0	0	2	0	0	0	0	0
sucuuba	*Hymatantus sucuuba*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
taperebá	*Spondias mombin*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0
tauarí	*Couratari sp.*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
tucum	*cf Astrocaryum chambira*	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0
tucumã	*Astrocaryum aculeatum*	1	1	0	2	0	1	0	1	0	0	0	0	14	5	0	0	0	0	1	2	0
tucumã piranga	*Astrocaryum vulgare*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
ubim açu	*Geonoma oldemannii*	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
ubim branco	*Geonoma sp.*	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
ucuuba	*Virola sp.*	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
umarí	*Poraqueiba sericea*	0	0	0	0	0	5	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
urucú do mato	*Carpotroche longifolia*	0	0	0	0	0	0	10	1	0	0	0	0	0	0	0	0	0	0	0	0	0
urucurí	*Attalea phalerata*	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
uxi	*Endopleura uchi*	0	0	0	0	1	0	0	0	1	0	0	0	3	0	0	0	0	7	0	0	0
uxi curuba/uxi coroa	*Duckesia verrucosa*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0
xurú	*Cariniana micranta*	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0

CHAPTER 6

Extensive pre-Columbian soil improvement maintains human legacies in old-growth Amazonian forests

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ABSTRACT

Most habitable ecosystems on Earth have been domesticated to some extent during human history. Even apparently untouched forests in Amazonia, far from major rivers, were to a certain degree altered by ancient societies. However, the extent and persistence of pre-Columbian human influences in old-growth forests are still controversial, partly because modern societies may have modified ancient legacies when they re-occupied past settlements. Here, we quantified and compared the effects of pre-Columbian and recent landscape domestication processes on old-growth forests at different distances from ancient and modern villages located inside protected areas (indigenous lands and national forests). We evaluated the effect of ancient and recent management practices on Amazonian forest soils and vegetation in 27 plots in the lower Tapajós River and upper-middle Madeira River basins. We found that pre-Columbian villages were more densely distributed in interfluves of both river basins than modern villages settled inside protected areas. Soil nutrients, especially total soil phosphorus (P), increased with the proximity to ancient villages but did not increase with the intensity of recent management activities. Soil charcoal is frequent in all forest plots, suggesting widespread fires in the past. Plant composition was influenced by recent management practices, but also by pre-Columbian soil improvement. Ancient soil improvement, measured as P, increased the density and basal area of managed and cultivated plants in forest plots. Overall, our results support the hypothesis that ancient management practices influenced soils of old-growth forests more than modern practices. By enriching soil nutrients in and around their villages, pre-Columbian peoples domesticated forest landscapes surrounding their settlements, promoting forest species of great interest to modern Amazonian societies. Our results indicate that forests inside protected areas hold legacies of past societies that are partly maintained by local management practices. To develop effective conservation and management plans for forest resources in these areas, we must consider how they adapted to long-term human actions.

Human societies expanded across most terrestrial ecosystems, domesticating landscapes in multiple ways (Kareiva et al., 2007; Boivin et al., 2016; Roberts et al., 2017). Landscapes can be analysed as a durable record of the activities practiced by past human generations (Ingold, 1993; Balée, 2006). Landscape domestication is a process in which human manipulation of species populations and soil composition result in more secure and productive landscapes (Clement, 1999; Kareiva et al., 2007; Erickson, 2008). This process depends on cumulative cultural and material inheritances and the energy invested in ecosystem transformation (Ellis, 2015). Natural ecological conditions, such as terrain, also influence the potential productivity of an area for sustaining a given society (Ellis, 2015). In fact, landscape domestication is a continuum of transformations extending from semi-natural landscapes with subtle changes in the original ecosystems to cultivated lands and densely settled areas with major alterations associated with clearing and burning of the original ecosystem (Clement, 2014; Ellis, 2015). This extraordinary capacity of humans to modify landscapes has promoted global alterations in natural ecological processes, ecosystems and species distributions (Kareiva et al., 2007; Boivin et al., 2016).

Evidence of ancient human transformations has been found in extensive areas that, to the untrained eye, seem natural, showing the antiquity of past landscape domestication (Heckenberger et al., 2003; 2008; Van Gemerden et al., 2003; Dambrine et al., 2007; Ross, 2011; Levis et al., 2017a – **Chapter 3**). For instance, modern tree species composition in Central African forests is driven by historical human disturbances of three centuries ago (Van Gemerden et al., 2003). In France, species richness and soil nutrients increase with the proximity to ancient Roman settlements abandoned millennia ago (Dambrine et al., 2007). In Mesoamerican forests, a higher abundance of plant species used by Maya people for daily needs still persists in densely-settled forest areas even after centuries of human abandonment (Ross, 2011). In Amazonia, a mosaic of domesticated landscapes was detected in an area of approximately 50,000 km2 in the Upper Xingu River basin, indicating intensive and semi-intensive land use strategies in pre-Columbian times (Heckenberger et al., 2008). Across the Amazon basin, the abundance and richness of plants traditionally used, managed, cultivated and domesticated are concentrated in and around past human settlements due to numerous historical management practices (Levis et al., 2017a – **Chapter 3**; Levis et al. 2018 – **Chapter 5**).

Since multiple practices have been used to domesticate landscapes, wide-ranging evidence of this process has been found across the Amazon basin (Clement et al., 2015a). The most common signatures left by pre-Columbian peoples in densely settled areas are patches of Amazonian Dark Earths (ADE or Terra Preta de Índio - TPI). These anthropogenic soils are rich in nutrients, ceramics and domesticated plants

(Smith, 1980; Clement et al., 2003). Charcoal records have been used to identify ancient cultivated landscapes across Amazonia (Bush et al., 2008; Mayle and Power, 2008; McMichael et al., 2012a), as fire was the main tool used by indigenous people to transform forest landscapes around their villages (Erickson, 2008). Although fire regimes are often linked with past human disturbance (Mayle and Power, 2008), the length and severity of dry seasons, due to changes in precipitation regimes during the early Holocene, were likely the main drivers of past fires (Maezumi et al., 2017). Signs of past landscape domestication can also be detected by assessing the distribution and abundance of useful and/or domesticated species (Clement, 2014), as observed in Central Amazonia and across the basin (Levis et al., 2012; Levis et al., 2017a – **Chapter 3**).

However, the persistence of ancient landscape domestication processes beyond densely settled areas is still controversial for several reasons. First, ecological and archaeological studies have mostly investigated human impacts along the margins of major Amazonian rivers in areas expected to have been heavily modified (Bush and Silman, 2007; Piperno et al., 2015; McMichael et al., 2017a). Second, scholars are using different methods and datasets, although each method detects specific kinds of human activities (Piperno et al., 2015; Stahl, 2015). Third, the effects of pre-Columbian activities in forests may disappear after their abandonment due to natural processes (Bush et al., 2015; McMichael et al., 2017b). Fourth, and equally important, many archaeological sites were re-occupied by modern societies, challenging the distinction between pre-Columbian and post-conquest management practices (McMichael et al., 2017b), but see (Junqueira et al., 2017 – **Chapter 4**). By comparing the effects of ancient and recent people on modern forests, we can evaluate if the influence of pre-Columbian activities persists on landscapes after their abandonment (Junqueira et al. 2017 – **Chapter 4**).

With the demographic collapse of Amerindian societies during European conquest and colonization (O'Fallon and Fehren-Schmitz, 2011), many pre-Columbian villages were abandoned and hidden by forest re-growth (Denevan, 1992). By reconstructing the history of indigenous land use in interfluvial environments, studies have shown that forest clearing for small-scale agriculture activities has become more concentrated with time (Siren, 2014; Riris, 2018), suggesting that past human impacts were more extensive than previously assumed (Riris, 2018). Although human occupation patterns have changed in the interval between European conquest and today, current Amazonian societies often decide to settle in archaeological sites or places that they had lived before (Rival, 2007; Politis, 2009).

Because both past and present villages tend to be associated with riverine environments, and modern forest conversion and degradation rates are extremely high, some scholars argue that Amazonian forests were much more altered by modern societies than by pre-Columbian societies (Peres et al., 2010; McMichael et al., 2017b). Conversely, the effects of pre-Columbian peoples on plant composition of old-growth forests were found to be stronger than those of modern peoples (Junqueira et al., 2017 – **Chapter 4**). To shed light on this debate, we explore the effects of landscape domestication by pre-Columbian and modern Amazonian societies on old-growth forests, by quantifying their influences in two forest landscapes located inside protected areas (National Forests and Indigenous Lands). We chose to work within protected areas because these are less impacted by modern urbanization and market pressures, making the comparison between pre-Columbian and current traditional and indigenous societies more realistic, and relevant to future conservation programs. We must understand how forests that evolved in intimate association with humans have reacted to long-term impact to develop efficient conservation actions (Ross, 2011).

In this study, we first describe the spatial patterns of occupation between pre-Columbian and modern peoples to understand the scale of impact, and then evaluate the effects of management practices by both societies on forest soils and vegetation. Since knowledge is continuously transmitted within and between human generations (Balée, 2000; Odling-Smee and Laland, 2011), we expected a cumulative effect of past and current management on forest soils and plants used, managed and cultivated today. To test this hypothesis, we addressed two main questions: 1) were pre-Columbian and modern villages equally distributed across riverside and interfluvial areas? and 2) how have ancient and current management practices influenced forest soils, forest structure and composition?

METHODS

Data Collection

We studied six villages in two river basins: two villages in the lower Tapajós River basin and four villages in the upper-middle Madeira River basin (Figure 6.1). Environmental conditions vary among these two river basins. A minimum of three dry months occurs along the upper-middle Madeira and five dry months along the lower Tapajós (Figure 6.1A). Altitude also varies among sites in the Madeira River basin (80-110 m) and in the Tapajós River basin (150-200 m). Despite these variations, all villages are located in protected areas (National Forests and Indigenous Lands). In the Tapajós River basin, villages are inhabited by traditional societies and located along this river's banks in the Tapajós National Forest. In the Madeira River basin, two villages are also inhabited by traditional societies and located along this river's banks in the Humaitá National Forest. The other two villages are inhabited by indigenous societies settled along the Transamazon Highway (BR-230) in the Madeira-Tapajós interfluve, approximately 70 km from the Madeira River in the Jiahui Indigenous Land.

Riverine traditional societies (*ribeirinhos*) in both basins have lived for at least a generation at each locality; most of them are descendants of migrants who intermarried with local indigenous peoples and they are not members of an indigenous group. Their daily activities include farming, fishing, hunting, timber and non-timber forest product extraction, and, in the case of the Tapajós National Forest, the villages are involved in community-based tourism. Current indigenous villages in the Madeira River are inhabited by members of the Jiahui indigenous group, and speak a Tupi-Guarani language (Peggion, 2007).

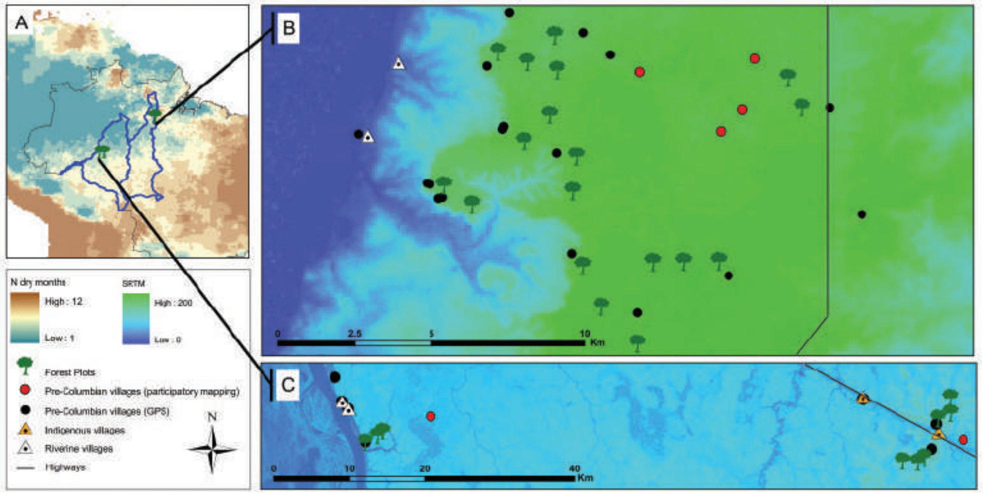

Figure 6.1. Maps of the Tapajós River and Madeira River basins. (A) Map showing the variation in rainfall seasonality across Amazonia in relation to the location of the two basins in Brazil (Madeira to the west of Tapajós). Other maps show topographic variation across the landscapes studied and the location of forest plots (trees), pre-Columbian villages mapped with participatory techniques (red circles) and GPS (black circles), current riverside and indigenous villages (triangles) (B) in the lower Tapajós River basin, and (C) in the upper-middle Madeira River basin. Pre-Columbian villages were sedentary settlements with anthropogenic soils (ADE sites). Topographic variation was detected using SRTM (Shuttle Radar Topography Mission) images. Rainfall seasonality was calculated as the maximum cumulative number of months with < 100 mm of rainfall using the monthly data from 1998 to 2004 from the Tropical Rainfall Measuring Mission (TRMM) satellite product 3B43 V6 at a 0.25° resolution (Kummerow, et al. 1998). Some pre-Columbian villages were mapped by Schann et al. (2015).

According to Brazilian law, all authorizations to conduct the study were obtained before fieldwork. The study was approved by the Brazilian Ethics Committee for Research with Human Beings (Process n°10926212.6.3001.5020 and n°1.396.762/2016), the Regional Coordinator of the Brazilian National Indigenous Foundation (FUNAI – CR Madeira, n°001/APIJ/2016), the Brazilian System of Protected Areas (SISBIO, process n°47373-1, n°45094-1 and n°53041-2) and National Institute of Historic and Artistic Heritage (nº01494.000171/2011-78). In each village, we obtained the informed consent of the local traditional or indigenous leadership at the beginning of the study, and all informants signed informed consent terms when they participated in our activities.

Although all archaeological sites mapped in both regions contain ADE sites with ceramics, which indicate sedentary pre-Columbian occupation (Neves et al., 2003), the ancient history of the regions differ. Tapajó or Santarém Phase pottery covers an area of 10,000 km^2 across riverine and interfluvial lands in the lower Tapajós River basin (e.g., Gomes, 2017; Schaan et al., 2015; Schaan, 2016; Stenborg et al., 2018). Before this study, 148 archaeological sites were recorded around the Tapajós National Forest and 13 sites were mapped inside this protected area (Figueiredo, personal communication). Almost 70% of all archaeological sites are located on the interfluve (53.4% in the plateau) and only 20% are located along the Tapajós River and lakes. Despite the abundance of archeological sites in interfluvial areas, riverine settings have a longer occupation history, starting around 3,200 BP (years Before the Present) (Stenborg, 2016). Pre-Columbian activities intensified around 700 BP and remained until the arrival of the Europeans. After European conquest, another period of intensification began during the rubber boom (in the late 19th century), when the region was re-occupied by its current inhabitants. In contrast to the lower Tapajós, the ancient history of the upper Madeira is much older, started by 12,000 BP (Miller, 1992) and intensified 1,000 BP when the Polychrome Tradition pottery expanded along the Madeira (Moraes and Neves, 2012). The expansion of this Tradition has been associated with the expansion of Tupi speaking groups (Barreto et al., 2016). Although most riverside villages in the Humaitá National Forest are inhabited by traditional societies associated with the rubber boom, the interfluvial areas are still populated by Jiahui peoples. Archeological sites in riverine and interfluvial areas of the upper-middle Madeira near Humaitá city have been overlooked and we mapped the archaeological sites identified in this study.

Here we defined current villages if they are occupied today; recent villages were established approximately 120 years ago and were abandoned 40 years ago in the Flona Tapajós; ancient villages are pre-Columbian villages with ADE sites older than 350 years ago. Inside the Flona Tapajós, the extension of the ADE soils, in the majority of the sites, was measured with the assistance of a member of the community and handheld Global Positioning System (GPS). In addition, in two ADE sites, shovel test pits were excavated in two transects in order to delimit the extension of these sites. Handheld GPS and Google Earth images were also used to map the area occupied by current houses and homegardens in the Maguarí and Jamaraquá villages we worked with. In the Madeira basin, we couldn't measure the size of the ADE sites, because of logistical limitations.

In each village we conducted the following activities: (1) free listing interviews with key informants about the trees and palms useful for them, and the forest management activities related to these plants (Albuquerque et al., 2014); (2) participatory mapping and guided tours to describe the extension of their activities in the forest and the location of recent and ancient villages, and to identify the plants they currently manage in the forest (Gilmore and Young, 2012; Albuquerque et al., 2014); and (3) 27 forest inventory plots at different distances from current, recent and pre-Columbian villages. We used snowball sampling techniques to find informants who know and use forest species (Albuquerque et al., 2014), We conducted free-listing interviews with 33 informants in the Tapajós National Forest, 24 informants in the Humaitá National Forest and 12 informants in the Jiahui Indigenous Lands. We walked approximately 80 km along trails in the Tapajós with the seven most experienced informants to identify useful species in the forest and approximately 115 km along trails in the Madeira with the 15 most experienced informants. During the guided-tours, we collected the GPS points of ADE sites and of useful plants cited in the interviews.

Based on local knowledge and our previous study (Levis et al., 2017a – **Chapter 3**), we created four categories of useful plants. First, we classified all plants used by local informants into two categories: 1) useful plant species that are not managed today; and 2) useful plant species that are managed today (see Levis et al., 2018 – **Chapter 5** for more details about the management categories). Within the managed species, we categorized another group that is more intensively managed, because people occasionally plant them in cultivated landscapes, called cultivated species. We also created a fourth category of useful plants, called domesticated species, when a currently useful plant has some degree of domestication somewhere in Amazonia and was included in the list elaborated by Levis et al. (2017a) – **Chapter 3**. It is important to know that these categories overlap, because all cultivated species are managed in multiple ways and some domesticated species are managed and cultivated by locals. This classification was used to create a gradient of different management intensities of useful species. In the Tapajós villages, we identified 203 useful plants, of which 145 are managed plants, of which 54 are occasionally cultivated plants. In the Madeira villages, we identified 167 useful plants, of which 126 are managed plants, of which 49 are cultivated plants. Fifteen percent of the 203 useful plants in the Tapajós and 15 % of the 167 useful plants in the Madeira were domesticated by pre-Columbian people somewhere in Amazonia, not necessarily in the lower Tapajós or upper-middle Madeira, but based on the list elaborated by Levis et al. (2017a) –**Chapter 3**.

To evaluate the effects of management practices on old-growth forests and to compare these effects between pre-Columbian and current societies we carried out forest inventories in 27 0.5 hectare plots. Forest plots were allocated in old-growth forest on terra-firme terrain located on the top of the plateau along the Tapajós River and Madeira River basins (Figure 6.1B and 6.1C). Because people often use forests for hunting and gathering more intensively near their villages (Heckenberger et al., 2008; Read et al., 2010), we set up forest plots at different distances from pre-Columbian (0 – 4.1 km) and current villages (0 – 15.4 km). We did not sample forests located more than 4 km from pre-Columbian sites, because the maximum distance we found between two sites is 5 km. To establish the plots at different distances from pre-Columbian villages, we created buffers around the ADE sites, differing in size (0-1, 1-2, 2-4 km). We used these buffer classes to randomly select one location in each buffer for our inventory plot, based on Heckenberger et al.'s (2008) pre-Columbian land use zones. We selected a location for the plot where the buffers did not overlap more than 50 % from a neighbouring buffer class. Distances and buffers were established based on the information gathered from participatory mapping and with GPS along guided tours and mapped with ArcGIS 9.3 software.

To assign an index for the intensity of recent forest activity in each plot, we asked local informants (one informant of each village who helped us during the inventories) the following questions before the plot inventory: 1) what management activities have you recently performed in this area? and 2) what management activities did you perform before the protected areas were created (approximately 40 years ago)? Nine types of activities were mentioned in the interviews: hunting; gathering fruits; gathering medicinal plants; gathering other forest products; subsistence logging; opening pathways; construction of dirt roads; tourism; and opening of campsites. We calculated an index of the intensity of recent activity for each plot using the sum of all recent activities and those practiced before the creation of the protected areas, divided by the total number of activities (Total = 9 activities x 2 (today = 1 + past = 1) = 18).

During the plot inventories, trees and palms with diameters at breast height (dbh) ≥ 1 cm were sampled in sub-plots of 0.01 ha, trees and palms with dbh ≥ 10 cm were sampled in sub-plots of 0.25 ha, and trees and palms with dbh ≥ 30 cm were sampled in the full 0.5 ha plot. We counted and measured the diameter of all living trees and palms present in the plot, but we only identified and collected botanical vouchers for useful species with vernacular names listed in the interviews. Some vernacular names refer to single botanical species, but others refer to a group of botanical species that share similar traits, and which often belong to the same botanical family or even genus (Berlin, 2014). We used the vernacular names given by informants in this study as these are the units that people actually use and manage. The botanical material was pre-identified in the field and collected for comparison with herbarium collections. The botanical identification was conducted by José Ramos, parataxonomist at INPA (Brazilian National Institute for Amazonian Research), and confirmed by taxonomists, and by comparing the vouchers collected to specimens at the INPA Herbarium (Manaus, Brazil). Fertile specimens were deposited at the INPA Herbarium and the UFOPA Herbarium (Herbarium of the Federal University of Western Pará State). Sterile materials will be deposited at the EAFM Herbarium (Herbarium of the Federal Institute of Amazonas State).

To detect the effects of ancient and current management on forest soils and to identify fire events, we used a post-hole digger to collect soils in three locations along the central plot line. We quantified the charcoal visible to the naked eye from 0 to 40 cm, and every 10 cm depth in each of the three locations; frequency of charcoal is the charcoal presence in each point at each depth, so 100 % frequency is charcoal presence at all 12 points per plot. We also calculated the frequency of soil charcoal below 20 cm and above 20 cm, because charcoal above 20 cm is associated with modern fires and below this layer is mainly associated with pre-Columbian fires (McMichael et al., 2012a).

Soil samples were dried and analyzed in the Plant and Soil Thematic Laboratory at INPA. Exchangeable Ca, Mg, K, Na and Al were determined by the silver thiourea method (Ag-TU; Pleysier and Juo, 1980); with this method, a complete cation exchange value is obtained (Quesada et al., 2010). Total phosphorus was determined by acid digestion using concentrated sulphuric acid (Quesada et al., 2010). Available phosphorus was determined by Mehlich I. The percentage of sand, silt and clay was also measured in the laboratory. Effective cation exchange capacity, ECEC, was calculated as a sum of all exchangeable concentrations of each element (Ca, Mg, K, Na and Al in cmolc/kg). Three forest plots in the Madeira basin are located on Plintosols and the other plots in the Madeira basin and all in the Tapajós basin are located on Ferrasols (Quesada et al., 2010); for more details of differences in soil variables per basin, see Figure A6.1 and A6.2.

Data analyses

To evaluate if pre-Columbian and modern villages were equally distributed along the rivers and across interfluvial areas, we measured the minimum linear distances between villages and from villages to rivers using the “near distance” tool of ArcMap version 9.3. We also calculated the density of pre-Columbian and current villages that occur in the study area in both basins. We used all upcells of HydroSHEDS data to define streams and upcell values greater than 15,000 to define perennial rivers of approximately 30 meters width, following the study of McMichael et al. (2014).

We compared the effects of pre-Columbian (hereafter ancient) and recent management practices on soils and vegetation. To confirm if people use and manage more intensively forests closer to their villages in both regions, we measured the walking distance from forest plots to the current villages and found this distance gradient to be negatively correlated with the intensity of recent activities in the Tapajós and Madeira forest plots (Spearman’s rank correlation = - 0.58 and - 0.76, p = 0.013 and 0.017, respectively). Given the association of forest management intensity and walking distance from villages to plots in recent times, and because we cannot ask ancient people how intensively they managed the forests surrounding their villages, we used the proximity of forest plots from pre-Columbian villages (in kilometers), as a proxy for ancient management. The index of intensity of recent activities in each plot was used as a proxy for recent management. To evaluate the possible correlation between recent and ancient management practices, we used Spearman’s correlation analyses. The index of the intensity of recent activities is not correlated with the proximity to pre-Columbian villages (Spearman’s rank correlation = 0.28, p = 0.159), indicating that some forests closer to pre-Columbian villages are not intensively used by current people. However, before the creation of the FLONA Tapajós approximately 40 years ago, people often resided in the interfluvial areas. The distance from plots to these abandoned villages correlates with the distance from plots to ancient villages within this basin (Spearman’s rank correlation = 0.53, p = 0. 021). Therefore, pre-Columbian management practices in the Tapajós area may also reflect some of the recent management activities that occurred before the creation of the FLONA Tapajós.

We explored the variability of soil chemical and physical variables across forest plots using Principal Component Analysis (PCA) based on a correlation matrix. Soil chemical variables were log-transformed to increase normality. We only included silt and clay in the PCA because sand and clay were highly correlated. The PCA was used to reduce the number of soil variables in our analysis and to select the soil variable that is most associated with the ADE site. We selected total phosphorus for our models, because it has a high loading value in the first PCA axis, indicating its association with soil nutrients, therefore reflecting soil fertility. Soil phosphorus is also recognized as an indicator of anthropogenic soils (Glaser and Birk, 2012), and predictor of forest biomass and composition across Amazonia (Quesada et al., 2010). We also included clay in our analysis to represent natural soil conditions, as we expected that texture is less affected by past management in modern forest soils (Quintero-Vallejo et al., 2015).

To understand how ancient and current management practices have influenced forest soils, forest structure and composition we used SEM (Structural Equation Modelling) and performed all statistical analyses in the R (version 3.4.1) environment (2012). We tested the direct effects of ancient (pre-Columbian) and recent management on forest structure and composition, and their indirect effects on forest structure and composition mediated by three soil variables: soil phosphorus as a proxy of soil fertility; soil clay as a proxy of natural soil conditions; and soil charcoal as a proxy of past fires. We generated a tentative model for evaluating these effects, and adjusted it when necessary (Grace et al., 2010). We developed one conceptual structural equation model for three forest structure variables (stand basal area, density of canopy stems and density of sub-canopy stems) and another one for four forest composition variables (relative basal area and relative density of useful non-managed plants, useful managed plants, useful cultivated plants, and useful domesticated plants) (Figure 6.2). Our model included five fixed predictor variables: ancient management, recent management, soil phosphorus, soil clay and soil charcoal (0-40 cm). Each forest structure or composition variable was used as a response variable. SEM models were created using mixed-linear models, which were evaluated using the lme function of the nlme package (Kuznetsova et al., 2017), and we used the MuMIn package for obtaining conditional and marginal r squares (Barton and Barton, 2017). SEM was performed using the sem function of the piecewiseSEM package (Lefcheck, 2016). The PCA analysis was run using the prcomp function and visualized using the autoplot function of the ggfortify package (Tang et al., 2016). The correlation matrix of all soil variables was created using the corrplot function of the psych package (Revelle and Revelle, 2017). Contrast plots were used to visualize the mixed-effect models using the visreg package (Breheny and Burchett, 2012). Basin was incorporated as random factor and other predictor variables as fixed factors in the models. All conceptual models were supported when we incorporated the correlation between soil phosphorus and soil clay (Fisher C = 0.15, p = 0.997), indicating they described the data with sufficient accuracy.

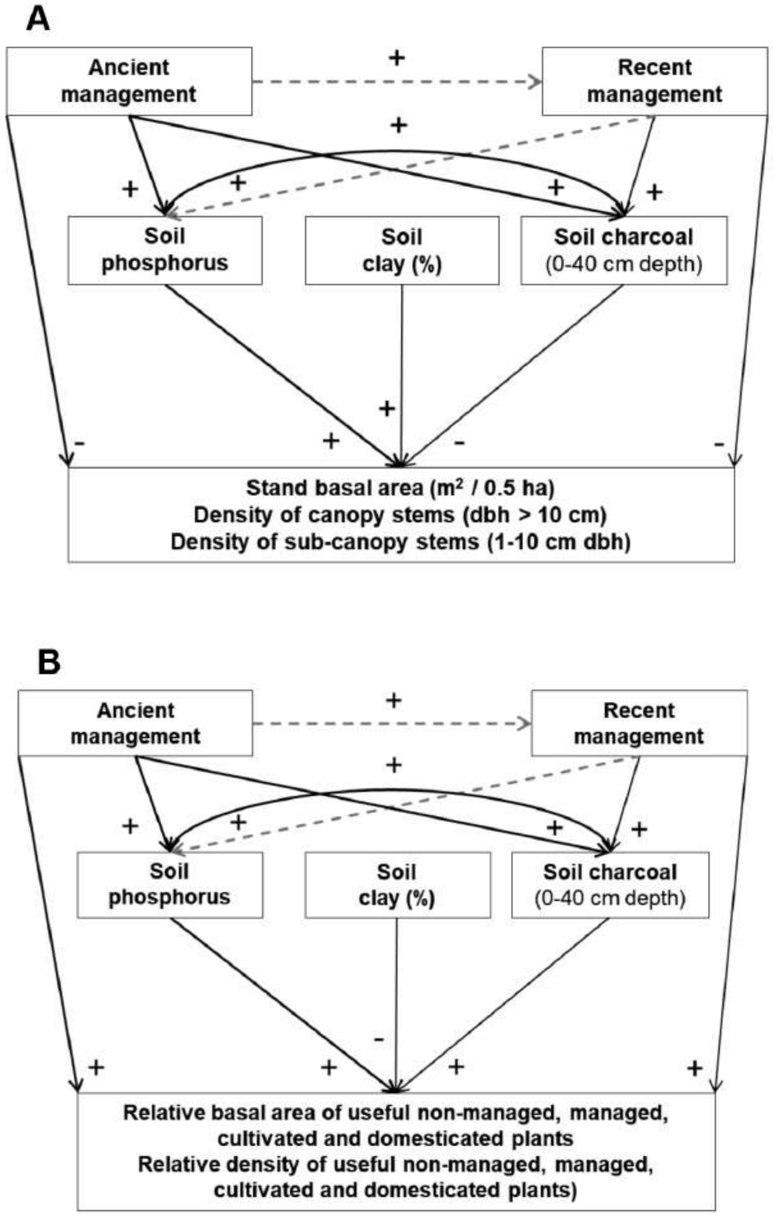

Figure 6.2. Conceptual models. Models show how ancient and recent management may affect forest soils (soil nutrients – total phosphorus) and fire events (soil charcoal), and how forest soils (soil phosphorus and clay), fires and management together may affect (A) forest structure and (B) forest composition. Black continuous arrows show hypothetically significant effects, grey dotted arrows show hypothetically less significant effects and two direction arrows show hypothetical correlations.

RESULTS

Spatial patterns of pre-Columbian and modern human occupations

Pre-Columbian villages were more densely distributed across the landscape than current villages located in protected areas (Table 6.1). We mapped 17 ancient villages around two current villages in the Tapajós River basin and 9 ancient villages around four current villages in the Madeira River basin. In general, the straight-line distance between pre-Columbian villages varies from 2 to 5 km, whereas the distance between the current villages varies from 1 to 11 km (Table 6.1). In the Tapajós River basin, current villages are located along this river's banks, whereas pre-Columbian villages were spread across the study area, up to 15 km from this river's margin (Figure 6.1). In the Madeira River basin, ancient and current villages were found along this river's banks and approximately 70 km from this river's margin near small streams. Pre-Columbian villages were smaller in estimated size, but densely distributed across the landscape. The total area occupied by 12 pre-Columbian riverside and interfluvial villages in the Tapajós River basin is 93 hectares (mean size = 8 ha), while the estimated area occupied by houses and homegardens of the two current riverside villages is 50 hectares.

The effects of ancient and current landscape domestication on forest soils and vegetation

Effects on soil fertility

We found that ancient forest management activities left a significant positive effect on soil fertility, mostly represented by soil phosphorus (Figure A6.3A). The first axis of the PCA based on soil chemical and physical variables separated plots with high values of total phosphorus (P total), available phosphorus (P available), exchangeable magnesium (Mg), exchangeable calcium (Ca) from plots with lower values of these variables (Figure A6.3C). The second axis of the PCA separated plots with high concentrations of silt in the Madeira River basin from plots with high concentrations of exchangeable sodium (Na) and clay in the Tapajós River basin. The forest plot sampled exactly over a pre-Columbian village (ADE site) has a considerably higher value of soil nutrients than all other plots. Since this site has an extremely high value of total phosphorus, we decided to exclude it from the structural equation models used to evaluate the direct and indirect effects of ancient and current management practices on forest soils and vegetation (Figure 6.3 and 6.4).

We found a significant increase in soil phosphorus with proximity to pre-Columbian villages (from 0.3 up to 4.1 km), even after removing the ADE site from the analysis (Figure 6.4A, $p = 0.008$). Surprisingly, we found that the natural amount of clay in soils had a negative association with the intensity of recent management activities in forests plots (Figure 6.3) and phosphorus tended to decrease with the intensification of recent management activities (Figure 6.4B).

Effects on soil charcoal

Although forests closer to current villages and ancient villages have been more used and managed than remote forests, we found charcoal in all forest plots of the two river basins indicating that fire events were widespread. We did not find an effect of the proximity to pre-Columbian villages nor of the intensity of recent activities on the frequency of charcoal in forest soils (Figure 6.3).

We also found a significantly higher frequency of charcoal below 20 cm of soil depth than above this soil layer ($p = 0.002$, Figure 6.5), which suggests that fire was more frequent in pre-Columbian than in modern times. The frequencies of charcoal in these two soil layers are highly correlated (Spearman's rank correlation = 0.71, $p < 0.001$). Charcoal is more common in the Tapajós forest plots that are exposed to longer dry seasons than in the Madeira plots

Table 6.1. Distribution of villages, archaeological sites and rivers in the two study areas. Major rivers are the Tapajós River and Madeira River.

Basin	Time and location of villages	Number of villages	Density of villages (km^2)	Distance between villages (km)	Distance from villages to major rivers (km)	Distance from villages to perennial rivers (km)	Distance from villages to streams (km)
Tapajós	Pre-Columbian National Forest	17	0.14	2.06 ± 0.88	5.93 ± 4.22	5.93 ± 4.22	2.87 ± 1.59
	Current National Forest	2	0.02	1.75	0	0	0
Madeira	Pre-Columbian Jiahui Land	4	0.02	5.29 ± 3.29	70 ± 4	21.54 ± 6.24	1.19 ± 0.97
	Pre-Columbian National Forest	5	0.03	5.03 ± 2.21	0	0	0
	Current Jiahui Land	2	0.01	11.11	65 and 76	26.94 and 15.81	0.38 and 1.60
	Current National Forest	2	0.01	1.29	0	0	0

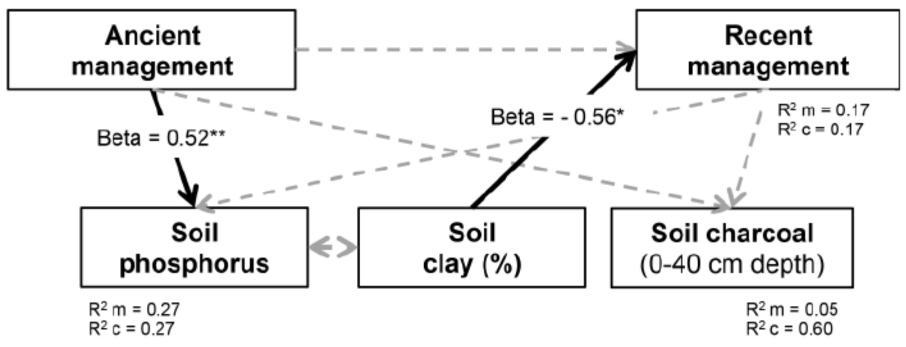

Figure 6.3. Upper part of the structural equation model that shows the direct effects of ancient and recent management on soils. Black continuous arrows show significant pathways, grey dotted arrows show non-significant pathways, and double-sided arrows show correlations. The standardized regression coefficient (Beta) and significance probabilities (p values: ≤ 0.01 '**'; ≤ 0.05 '*') are shown. R^2's indicate the total variation in a dependent variable that is explained by the combined fixed variables (R^2 marginal - R^2 m) and together with the random factor (R^2 conditional - R^2 c). Detailed information of all structural equation models is presented in Table S2.

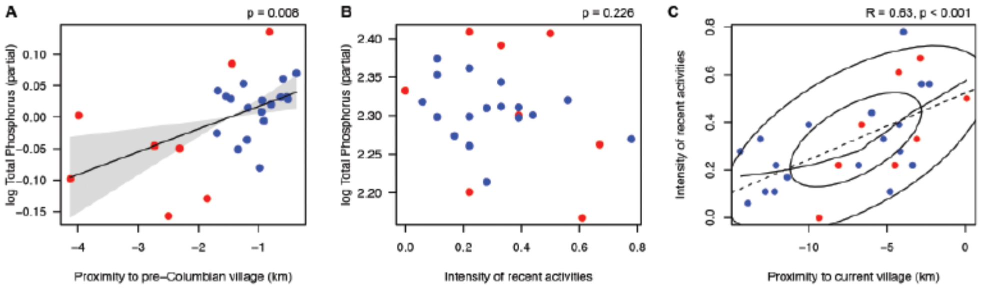

Figure 6.4. Partial regression plots obtained from the mixed-models presented in the structural equation models. Models evaluated the effects of (A) the proximity to pre-Columbian villages as a proxy of ancient management activities on total soil phosphorous and (B) the intensity of recent activities as a proxy of recent management on total soil phosphorus. (C) The correlation plot between the intensity of recent activities and the proximity to current villages. Red dots are forest plots located in the Madeira River basin (8 plots) and blue dots are forest plots in the Tapajós River basin (18 plots). Fitted line in A indicates significant fixed-effects of linear mixed-model analysis detailed in Table S2 ($R^2m = 0.27$ and $R^2c = 0.27$). Mixed models fit by t-tests use Satterthwaite approximations: lme (soil variable ~ proximity to pre-Columbian villages + intensity of recent activities + (1 | Basin)).

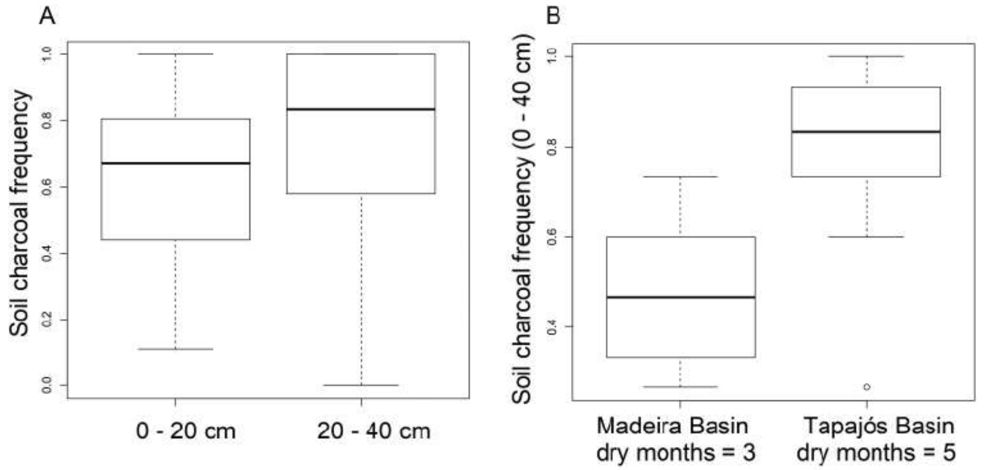

Figure 6.5. Frequency of charcoal in forest soils. Boxplots show A) the frequency of charcoal in the 0 to 20 cm and the 20 to 40 cm soil layers on the two basins (fixed-effects of linear mixed-model analyses is equal to t = 3.55 (p = 0.002) with basin considered a random factor, and B) the frequency of charcoal in the Madeira River (N = 9) and Tapajós River basins (N = 18).

Effects on forest structure

We found an extremely high value of stand basal area (50.6 m^2/ ha) in the plot located on the ADE site in the Madeira River basin compared to other plots (Table A6.1). In all our structural models, we did not find any effect (direct or indirect) of ancient and current management on the total basal area, the total density of canopy and sub-canopy plants (Table A6.2). We only found a significant indirect effect of ancient management on forest structure, through soil improvement, when the ADE site was included in the model due to two large sumaúma trees (*Ceiba pentandra*): the total basal area significantly increased in forests growing on this highly fertile anthropogenic soil (see Table A6.1 and Table A6.3). Although we did not find any effect of management on forest structural variables, we found that twenty useful plant species dominate half of the basal area across plots in both regions and at least a quarter of the total density of individuals (for more details of dominant species see Table 6.1). Current people have managed at least 15 and cultivated 9 out of the 20 dominant useful species in both basins. Thus, the structure of these forests and likely ancient and recent management effects on the vegetation are mostly driven by these useful dominant species.

Table 6.2. List of the 20 useful plant species with the highest basal area in forest plots of the Tapajós River and Madeira River basins. One useful plant can refer to more than one scientific species (sometimes more than one genus) and was classified based on local knowledge. The relative basal area and density are shown as percentages of the total basal area and total density (all stems with dbh ≥ 1 cm measured). The categories of management are described per species as managed (Man.), cultivated (Cult.) and domesticated (Dom.). The most cited use (described by the majority of people) is presented. Useful domesticated species were classified according to Levis et al. (2017a) – **Chapter 3**.

Tapajós River Basin

Scientific names	Local names	Basal Area (%)	Density (%)	Man.	Cult.	Dom.	Most cited use
Erisma uncinatum	cedro guaruba; guaruba	12.4	2.7	yes	yes	no	Construction
Tachigali eriopetala;	tachí; tachí vermelho	9.7	6.8	no	no	no	Construction
T. micropetalum	tachí; tachí preto/ branco						
Attalea speciosa	babaçu	3.1	3.3	yes	yes	no	Food
Caryocar villosum	piquiá	3.1	0.1	yes	yes	yes	Food, Medicine
Virola venosa	ucuúba, ucuúba da terra-firme	2.7	2.8	yes	no	no	Construction
Chamaecrista apoucoutta	coração-de-nego; muirapixuna; mirapixuna	2.4	1.3	yes	no	no	Construction
Lecythis spp.	sapucaia; castanha sapucaia	2.3	0.4	yes	no	no	Food
Eschweilera spp.	murrão branco	2.3	2.2	no	no	no	Fiber for canoes
Lecythis prancei	jarana branca	1.9	0.6	yes	no	no	Construction
Dipteryx odorata	cumarú	1.9	0.4	yes	yes	yes	Medicine
Hymenea courbaril	jatobá	1.6	0.3	yes	yes	yes	Food, Medicine
Couratari stellata	tauarí	1.6	1.5	yes	yes	no	Manufacture
Lecythis lurida	jarana	1.5	0.6	yes	yes	no	Construction
Aspidosperma oblongum	carapanaúba	1.4	0.3	yes	no	no	Medicine
Vochysia obidensis	cedrorana	1.3	0.3	yes	yes	no	Construction
Dialium guianensis	pororoca; jutaí pororoca	1.2	0.6	no	no	no	Food
Terminalia amazonia	mirindiba; cuiarana	1.1	0.4	yes	no	no	Game attractive
Mezilaurus itauba	itaúba	1.0	0.3	yes	yes	no	Construction
Jacaranda copaia	parapara	1.0	0.4	yes	no	no	Firewood
Fabaceae (Indet)	sucupira	1.0	0.5	yes	no	no	Construction
Bertholletia excelsa	castanha do pará, castanha	1.0	0.2	yes	yes	yes	Food
All species		55.5	25.8				

Madeira River Basin

Scientific names	Local names	Basal Area (%)	Density (%)	Man.	Cult.	Dom.	Most cited use
Ceiba pentandra	sumaúma	11.2	0.1	yes	yes	no	Construction
Moraceae (11 spp.)	pama; pama grande	4.5	4.8	yes	yes	no	Food
Bertholletia excelsa	castanha	4.4	0.3	yes	yes	yes	Food
Cariniana micranta	castanha sapucaia	3.7	0.3	yes	no	no	Food
Sapotaceae (25 spp.)	abiu	3.6	4.4	yes	no	no	Food
Annonaceae (10 spp.)	envira	3.5	6.3	yes	no	no	Manufacture
Lecythidaceae (5 spp.)	envira						
Protium (5 spp.)	breu branco	2.3	2.8	yes	no	no	Manufacture
Attalea speciose	babaçu	2.2	4.5	yes	yes	no	Food
Burseraceae (18 spp.)	breu; breu grande	1.7	5.3				
Sapindaceae (4 spp.)	breu; breu grande						
Trichilia schomburgkii	breu; breu grande						
Micropholis guyanensis; M.venulosa	caramuri	1.6	1.6	no	no	no	Food
Pouteria opposite	caramuri						
Swietenia macrophylla	cedro agoano; mogno	1.5	0.1	no	no	no	Construction
Caryocar villosum	piquiá	1.4	0.1	yes	yes	yes	Food
Theobroma subincanum	cupuí; cupuaçu do mato	1.1	0.7	yes	no	yes	Food
T. obovatum	cupuí; cupuaçu do mato						
T. microcarpa	cupuí; cupuaçu do mato						
Chrysobalanaceae (17 spp.)	macucu	1.1	3.1	no	no	no	Construction
Caryocar glabrum	piquiarana	1.0	0.1	yes	yes	yes	Game attractive
Aspidosperma schultesii	carapanaúba	0.9	0.3	no	no	no	Medicine, Manufacture
Couratari stellate	tauarí	0.9	0.5	yes	yes	no	Construction
Cecropia sciadophylla	embaúba	0.8	1.1	no	no	no	Game attraction
Pourouma (5 spp.)	embaúba						
Inga spp.	inga chichica; inga de macaco	0.8	0.9	yes	yes	no	Food
Hymenolobium modestum	angelim	0.8	0.2	yes	yes	no	Construction
All species		49.2	37.4				

Effects on forest composition

We evaluated the effect of ancient and current management on the relative basal area and relative density of four categories of useful plant species: useful non-managed plants, useful managed plants, useful cultivated plants, and useful domesticated plants. The variation explained by fixed factors (soil variables, ancient and current management) ranged from 11% to 52% (for more statistical details see Table A6.2).

Soil variables generally had strong positive and negative effects on most plant groups (Figure 6.6). The percentage of soil clay had a negative and direct effect on the relative basal area of useful non-managed and managed plants, and on the relative density of cultivated plants (Figure 6.6, β = - 2.29, - 1.89 and - 1.99, respectively). Total soil phosphorus had a positive and direct effect on the relative basal area of managed and cultivated plants, and on the relative density of cultivated plants (β = 0.51, 0.61 and 0.73, respectively). Soil charcoal had a negative and direct effect on the relative basal area of cultivated plants (β = - 0.63). Only when we included the ADE site in the model did the relative density of domesticated plants significantly increase with soil phosphorus, enriched by ancient human management practices (indirect effect = 0.74), and decrease with the natural amount of soil clay (β = - 0.94, Table A6.3).

Managed plants were affected by both pre-Columbian and recent management practices, whereas cultivated plants were only affected by ancient management (Figure 6.6). Ancient management had a direct negative effect on the relative density of managed (β = - 0.46) and cultivated plants (β = - 0.61) and a positive indirect effect, through soil phosphorus, on the relative basal area of managed and cultivated plants (indirect effect = 0.27 and 0.34, respectively), and on the relative density of cultivated plants (indirect effect = 0.38). Recent management activities had a positive effect on the relative basal area and density of managed plants (direct effect = 0.43 and 0.42, respectively).

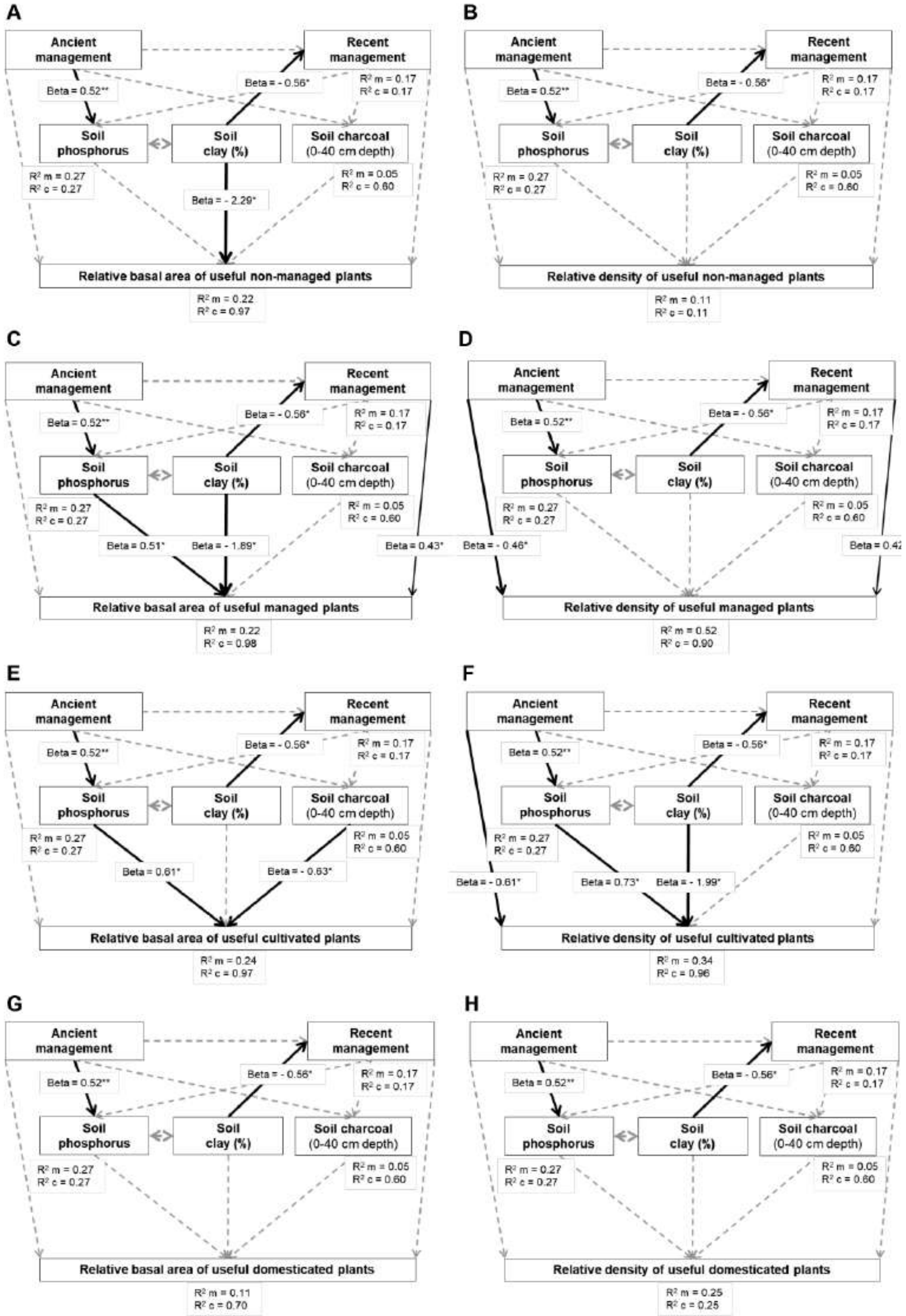

Figure 6.6. Results of the structural equation models. Models show the direct and indirect effects of ancient and recent management on (A) relative basal area of useful non-managed plants, (B) relative density of useful non-managed plants, (C) relative basal area of useful managed species, (D) relative density of useful managed plants, (E) relative basal area of useful cultivated species, (F) relative density of useful cultivated species, (G) relative basal area of useful domesticated plants, (H) relative density of useful domesticated species. Black continuous arrows show significant pathways, grey dotted arrows show non-significant pathways, and double-sided arrows show correlations. The standardized regression coefficient (Beta) and significance probabilities (p values: ≤ 0.001 '***'; ≤ 0.01 '**'; ≤ 0.05 '*') are shown. R^2's are given to indicate the total variation in a dependent variable that is explained by the combined fixed variables (R^2 marginal) and together with the random factor (R^2 conditional). Detailed information of all structural equation models is presented in Table S1.

DISCUSSION

We found that pre-Columbian villages are not located only on the most suitable landscape features, such as on bluffs of major rivers (Denevan, 1996; Levis et al., 2014 – **Chapter 2**), and in regions with highly seasonal climates, as previously thought (Bush and Silman, 2007; Bush et al., 2015), but they are distributed across interfluvial and less seasonal areas also. In comparison with current traditional villages in protected areas, ancient villages were more densely distributed both in the lower Tapajós and in the upper-middle Madeira river basins. Around ancient villages, pre-Columbian societies extensively enriched soil nutrients resulting in a widespread distribution of anthropogenic brown soils up to 4 km from archaeological sites, as predicted by Denevan (2004). Areas of heavy human influence up to 2.5 km from ancient settlements were also found in the upper Xingu River basin, indicating that pre-Columbian societies had developed intensive land use systems across Amazonia (Heckenberger et al., 2008). In contrast, we did not find a significant effect of recent management activities on soils of forests managed today and soil phosphorus tended to decrease with the intensification of these activities. By enriching soil nutrients in and around their villages, ancient peoples created new environmental conditions that favored mainly managed and cultivated species in forests of both basins. Therefore, Amazonian soil and vegetation in both riverine and interfluvial areas have been modified by long-term landscape domestication more than by current use.

Ancient and modern spatial occupation patterns along environmental gradients

Environmental settings along the major Amazonian rivers and in seasonal areas are considered suitable locations for sustaining high population densities in ancient times (Denevan, 1996; 2014; Bush et al., 2015; Piperno et al., 2015; McMichael et al., 2017a). Bluffs and plateaus up to 10 km inland from river margins and seasonally flooded lowland savannas sustained large human populations, estimated around 10 people per km^2 and 2 people per km^2 at the European conquest, respectively (Denevan, 2014). Today, the density generally varies between 1 to 5 people per km^2 (Cincotta et al., 2000). Interfluvial areas in *terra-firme* forests are usually considered to have sustained low population densities due to environmental limitations (Bush et al., 2015); therefore, human disturbance intensity is hypothesized to decrease exponentially up to 15 km from major Amazonian rivers. In contrast, we did not find a decay of past human occupation as we move away from major rivers. ADE sites were found in both riverine and interfluvial areas near small streams or depressions, sometimes up to 70 km from the Madeira River, and 15 km from the Tapajós River, suggesting that the probability of finding sedentary occupation sites in interfluvial areas is higher than predicted by Bush et al. (Bush et al., 2015). Indeed, a widespread network of 40-ha pre-Columbian towns with populations around 1,000 was found in the upper Xingu River basin (Heckenberger et al., 2008) and historical documents reported large indigenous villages with populations of 1,000 or more across interfluvial areas (e.g., Carvajal, 1934 [1542]; Acuña, 1639). Thus, it may be too simplistic to expect that the influence of pre-Columbian people in Amazonian landscapes is mostly predicted by the distance to major rivers, since perennial and temporary rivers are abundant across the basin (Junk et al., 2011).

Tributary rivers were likely densely occupied by pre-Columbian peoples (see maps of McMichael et al., 2014; Levis et al., 2012; Levis et al. 2014 – **Chapter 2**; and Palace et al., 2017). These rivers offer aquatic resources that support population expansion into the interfluves (Levis et al., 2014 – **Chapter 2**). In places where temporary rivers were scarce, e.g., east of the Tapajós River where we worked, people used the natural depressions of the land and built artificial ponds (Stenborg, 2016; Stenborg et al., 2018), expanding even more their territories.

By investigating the distribution of current village inside these protected areas, we found that modern villages are more concentrated along river margins than pre-Columbian ones. Ancient villages are spatially correlated with recent villages along Amazonian rivers (McMichael et al., 2017b), but they are not correlated in interfluvial areas. Past human societies overcame the environmental limitations of interfluvial landscapes by improving soil fertility and creating water reservoirs (Stenborg, 2016; Stenborg et al., 2018). Current traditional people do not manage these lands and soil properties in the same way as past societies did, either due to land use restrictions imposed by protected areas (Amaral et al., 2013) or because people migrated to Amazonian towns (Parry et al., 2010). As a consequence, the domestication of forest landscapes by contemporary societies is more restricted to major river margins in protected areas, while past domestication was widespread before restrictions and migrations.

Effects of management on soils

We found strong effects of past activities on forest soils towards the core of pre-Columbian villages, but no significant effect of recent management on soil fertility, or maybe some evidence that current use is depleting soil nutrients. A possible explanation for this persistent effect of past societies on modern forest soils is the combination of long-term human occupation with intense land use systems and efficient practices of soil management (Denevan, 2004). Small patches of dark and fertile soils rich in ceramics - ADE sites - have been found across the basin and attributed to pre-Columbian sedentary habitation zones (Smith, 1980; Woods and McCann, 1999; Neves et al., 2003). These soils originated from refuse disposal areas in middens around habitation zones and routes of movement (Schmidt et al., 2014). Dark brown forms of anthropogenic soils rich in charcoal, but without ceramics, have been observed in much more extensive areas, not only around ADE cores in Central and Eastern Amazonia (Sombroek, 1966; Woods and McCann, 1999; Denevan, 2004), but also in naturally rich soils of Western Amazonia (Quintero-Vallejo et al., 2015). The widespread distribution of these brown soils (known as *terra mulata*) across anthropogenic landscapes suggests they originated through intensive cultivation and soil management activities associated with agroforestry crop production (Denevan, 2004). Even though most studies have defined ADE and non-ADE sites as discrete categories due to sharp contrasts in soil nutrients between these soils, Fraser et al. (2011) proposed a continuum of soil improvement from the core of ADE sites towards the adjacent soils in Central Amazonia. Schmidt et al. (2014) confirmed these observations, showing a widespread pattern of anthropogenic soil formation surrounding domestic areas across the basin. Our results support this pattern and suggest that pre-Columbian peoples increased essential nutrient concentrations in Amazonian soils, such as phosphorus, not only in their village middens and homegardens, but across a larger scale than measured by these studies (Fraser et al., 2011; Schmidt et al., 2014; Figure A6.4).

Across the basin, the fertility of *terra-firme* forest soils is correlated with a natural gradient of pedogenic development (Quesada et al., 2010). Soils rich in nutrients mainly occur on young terrains of western Amazonian forests, while old soils poor in nutrients are commonly found in Eastern and Central Amazonian forests. By increasing the heterogeneity of soils surrounding their villages, pre-Columbian societies reproduced the basin-wide natural soil variation in their domesticated landscapes, creating a wide range of environmental conditions to cultivate plant species adapted to different levels of soil nutrients (Junqueira et al., 2016).

Effects of soils and management practices on forest structure

The basal area and stem density of old-growth forests in both basins were apparently not affected by ancient and recent human activities, in contrast to our initial expectation that the higher nutrient availability common in anthropogenic soils would influence forest structure. Using indices from satellite imagery, Palace et al. (2017) found that biomass, tree height and tree cover are lower in forests located within 50 km of a ADE site than random forest sites. Since we worked no more than 4 km from an ADE site, we did not find a forest without any human intervention for comparison. However, when we included the ADE site in the analyses, we did find an effect of pre-Columbian soil improvement on stand basal area of the forest (Table A6.4). This site has an extremely high value of stand basal area (50.6 m^2/ha) compared to other plots and studies across the basin (Baker et al., 2004), driven mainly by two individuals of sumaúma (*Ceiba pentandra*) that are an indicator of ADE sites across Amazonia (Clement et al., 2003) and in the Madeira River basin (Junqueira et al., 2011). Forest soils with high nutrient availability across Amazonia promote species with high diameter increments and low wood density (Quesada et al., 2012), such as sumaúma. This broad-scale pattern also helps explain why nutrient-demanding species were only found in anthropogenic soils (Paz-Rivera and Putz, 2009), and suggest that some good colonizers may persist in old-growth forests after human abandonment due to changes in soil conditions rather than extensive cultivation during pre-Columbian occupation.

Effects of soils and management on forest composition

We found that the basal area of useful but non-managed plants was only affected by natural soil variation, while managed and cultivated plants were also influenced by ancient soil fertilization. As modern people have moved to live along the major rivers, they are no longer cultivating plants in interfluvial enriched soils, explaining why we did not find any effect of recent management on the basal area and density of this plant group. Today people are planting these species in homegardens and swiddens near their villages where they may improve soil conditions (Alves et al., 2016), but not in old-growth forests cultivated in the pre-Columbian times. These results support the hypothesis that old-growth forests in Amazonia were more strongly influenced by pre-Columbian activities than modern analogues of these practices, as shown by Junqueira et al. (2017) – **Chapter 4**.

Indigenous and traditional peoples have benefited useful plants by multiple management practices around their villages (Posey, 1985; Balée, 1993; Zent and Zent, 2004; Balée, 2013; Levis et al. 2018 – **Chapter 5**). Although the basal area of managed and cultivated plants increased with pre-Columbian soil improvement, we found that the density of these plants decreased with proximity to ancient villages. Historical removal of construction materials and some other plants may explain the decline of these species densities near past settlements. Ethnographic and paleoecological studies focusing on this category of useful species may help to understand how long people have been removing plants used for construction surrounding their villages. For instance, fossil pollen history of an Amazonian species often used for construction can be reconstructed in lake sediments near archaeological sites and compared with human activities during the Holocene (Bush and McMichael, 2016). Whereas species currently used for construction are often trees with higher wood density and lower growth rates (Fearnside, 1996), other categories of useful plants selected by humans may cope better with more soil nutrients (e.g., species that have resource acquisition traits; Milla et al., 2015), and therefore persist in soils improved by ancient management practices. For instance, modern understory palm species respond strongly to variations in soil nutrients caused by past modifications (Quintero-Vallejo et al., 2015).

Useful plants that we classified as domesticated were neither affected by past management nor recent management activities that occurred outside habitation zones. Domesticated species were only abundant in the ADE site, indicating their strong association with these sites in Central Amazonia, as observed by Junqueira et al. (2010). Many domesticated species people cultivate today (e.g., *Spondias mombin*) were shown to be abundant in very fertile anthropogenic soils (Junqueira et al., 2016), suggesting that only with very high nutrient levels found in ADE sites we find higher abundances of domesticated species across the basin. Indeed, the abundance of domesticated species is higher on archaeological sites across Amazonia and mainly in geological regions where fertile soils predominate, e.g., Southwestern Amazonia (Levis et al., 2017a – **Chapter 3**). Incipiently domesticated species dominate large areas, but fully domesticated species are rare in forests across the basin (Levis et al., 2017a – **Chapter 3**), as fully domesticated populations cannot survive in mature forests without intensive management (Clement, 1999). In Amazonian landscapes with naturally poor soils (Quesada et al., 2010), semi and especially fully domesticated species may only persist on ADE sites and even there will require continuing management (Clement, 1999). In contrast, studies in Amazonian landscapes with naturally and anthropogenically fertile soils demonstrated that fully, semi and incipiently domesticated species occur over large forest areas (216 ha) even centuries after they were abandoned (Paz-Rivera and Putz, 2009).

Implications for management plans

Although we do not know exactly when and where ancient management practices occurred, the influence of humans on forest landscapes likely started 13,000 BP when earliest people arrived in the region (Roosevelt, 2013). Management practices probably intensified when human populations expanded around 2,500 BP (Goldberg et al,. 2016; Levis et al., 2018 – **Chapter 5**), matching the timing of anthropogenic soils formation in Amazonia (Neves et al., 2004). Particularly in the lower Tapajós River basin, archaeological dates indicate that occupation of interfluvial sites started only in 700 BP and continued to 300 BP (Schaan, 2016; Stenborg, 2016). This legacy attracted current people who now manage these forests. During the rubber boom (in the late 19th century), both the Tapajós and Madeira basins were re-occupied by the current inhabitants (Harris, 2011). Management activities that occurred during this period may have influenced forest structure and composition since local people mentioned they used forests more extensively in that time than they do today. In the last century, people have favoured the development of rubber agroforests by actively planting rubber trees (*Hevea brasiliensis*) in their manioc fields and managing them in fallows that became agroforests (Schroth et al., 2003). Patches of rubber trees were only found in secondary forests in both study areas, confirming their affiliation with recently cultivated landscapes.

Although recent land-use histories are considered an important factor to predict successional pathways in secondary forests in Amazonia (Mesquita et al., 2001; Chazdon, 2003; Arroyo-Rodríguez et al., 2017), ancient land use histories are often overlooked when old-growth forests are investigated (Dambrine et al., 2007). The analysis of land-use histories across a much longer time scale is crucial to understand the heterogeneity of forests and soils in Amazonia, and to guide effective management plans that aim to conserve important forest resources in protected areas. Our study shows that the distribution of some forest species of great importance to modern societies was affected by ancient management practices and depends on current activities to be maintained.

CONCLUSIONS

Ancient and recent management practices increased the spatial heterogeneity of forest soils and modified the composition of forests across interfluvial landscapes surrounding pre-Columbian and modern villages. We found that the influence of ancient peoples is stronger than previously assumed and has persisted in forest soils no longer enriched by contemporary peoples. The effects of pre-Columbian management practices are still detectable in Amazonian old-growth forests mainly because of the long-lasting influence of ancient soil fertilization. Pre-Columbian soil fertilization has maintained useful plant species of great interest to current Amazonian societies in old-growth forests of Brazilian protected areas. Knowing this, it seems unrealistic to manage forest landscapes without considering how humans have domesticated them over time and across space.

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AUTHOR CONTRIBUTIONS

C.L., M.P-C., F.R.C.C., C.R.C., and F.B. conceived the study and designed the analyses; C.L., R.P.A., M.J.F., C.G.F. collected data, C.L. carried out most analyses and wrote the manuscript; all authors discussed further analyses, and commented on various versions of the manuscript.

SUPPLEMENTARY MATERIALS FOR CHAPTER 6

Extensive pre-Columbian soil improvement maintains human legacies in old-growth Amazonian forests

Appendices 6

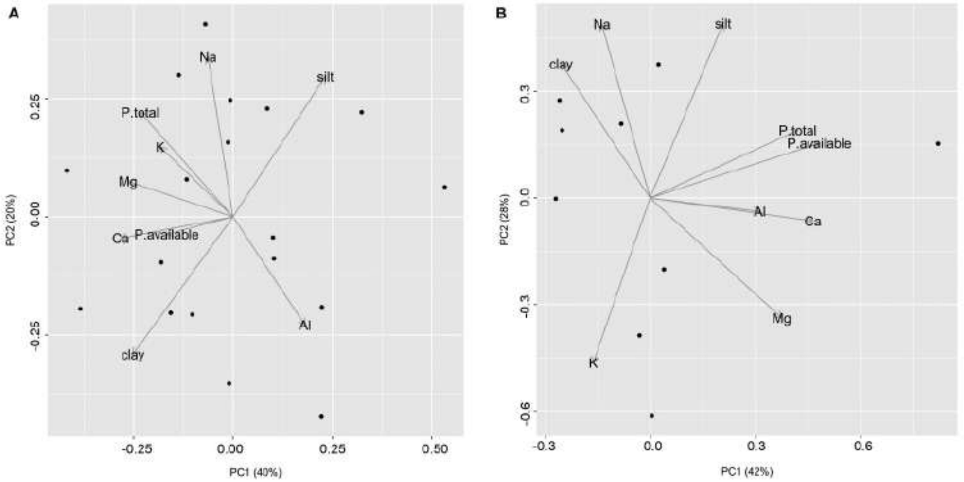
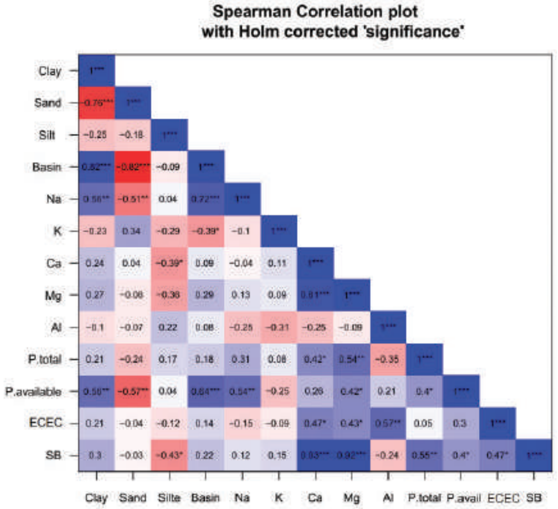


Figure A6.1. Principal Component Analysis (PCA) of soil variables for plots in the (A) Tapajós River and (B) Madeira River basins. Arrows indicate the magnitude of the influence of the soil variables used and their angles are the relationships with each axis. Soil chemical variables were log-transformed before the analysis to increase normality and the correlation matrix was used because variables were measured in different units.


Spearman Correlation plot
with Holm corrected 'significance'

	Clay	Sand	Silte	Basin	Na	K	Ca	Mg	Al	P.total	P.avail	ECEC	SB
Clay	1***												
Sand	−0.76***	1***											
Silt	−0.25	−0.18	1***										
Basin	0.82***	−0.82***	−0.09	1***									
Na	0.56**	−0.51**	0.04	0.72***	1***								
K	−0.23	0.34	−0.29	−0.39*	−0.1	1***							
Ca	0.24	0.04	−0.39*	0.09	−0.04	0.11	1***						
Mg	0.27	−0.08	−0.36	0.29	0.13	0.09	0.81***	1***					
Al	−0.1	−0.07	0.22	0.08	−0.25	−0.31	−0.25	−0.09	1***				
P.total	0.21	−0.24	0.17	0.18	0.31	0.08	0.42*	0.54**	−0.35	1***			
P.available	0.56**	−0.57**	0.04	0.84***	0.54**	−0.25	0.26	0.42*	0.21	0.4*	1***		
ECEC	0.21	−0.04	−0.12	0.14	−0.15	−0.09	0.47*	0.43*	0.57**	0.05	0.3	1***	
SB	0.3	−0.03	−0.43*	0.22	0.12	0.15	0.93***	0.92***	−0.24	0.55**	0.4*	0.47*	1***

Figure A6.2. Matrix of Spearman correlation coefficients between pairs of soil variables with Holm corrected significance. Red indicates negative correlations and blue positive correlations. Soil variables were log-transformed before the analysis to increase normality. Significance codes (p values: ≤ 0.001 '***'; ≤ 0.01 '**'; ≤ 0.05 '*') are presented.

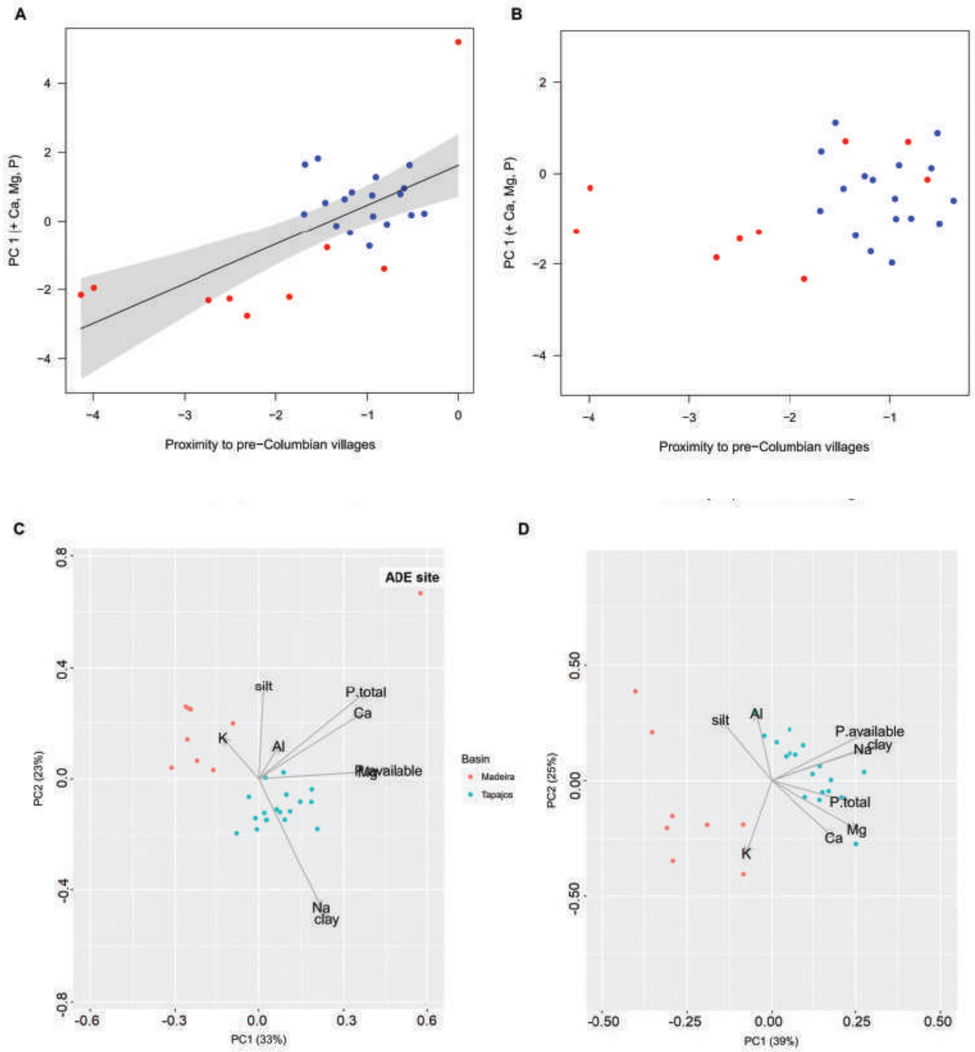


Figure A6.3. Principal Component Analysis (PCA) of soil variables for plots in the Tapajós (blue dots) and Madeira river basins (red dots) and the proximity to pre-Columbian villages. (A) the first PCA axis with the ADE site and the proximity to pre-Columbian villages in kilometers ($p < 0.001$), (B) the first PCA axis without the ADE site and the proximity to pre-Columbian villages, (C) PCA with the ADE site, (D) PCA without ADE site. Arrows indicate the magnitude of the influence of the soil variables used and their angles are the relationships with each axis. Soil chemical variables were log-transformed before the analysis to increase normality and the correlation matrix was used because variables were measured in different units. Fitted lines indicate significant fixed-effects of linear mixed-model analyses. Mixed models fit by t-tests use Satterthwaite approximations: lme (PC1 ~ proximity to pre-Columbian villages + (1 | Basin)).

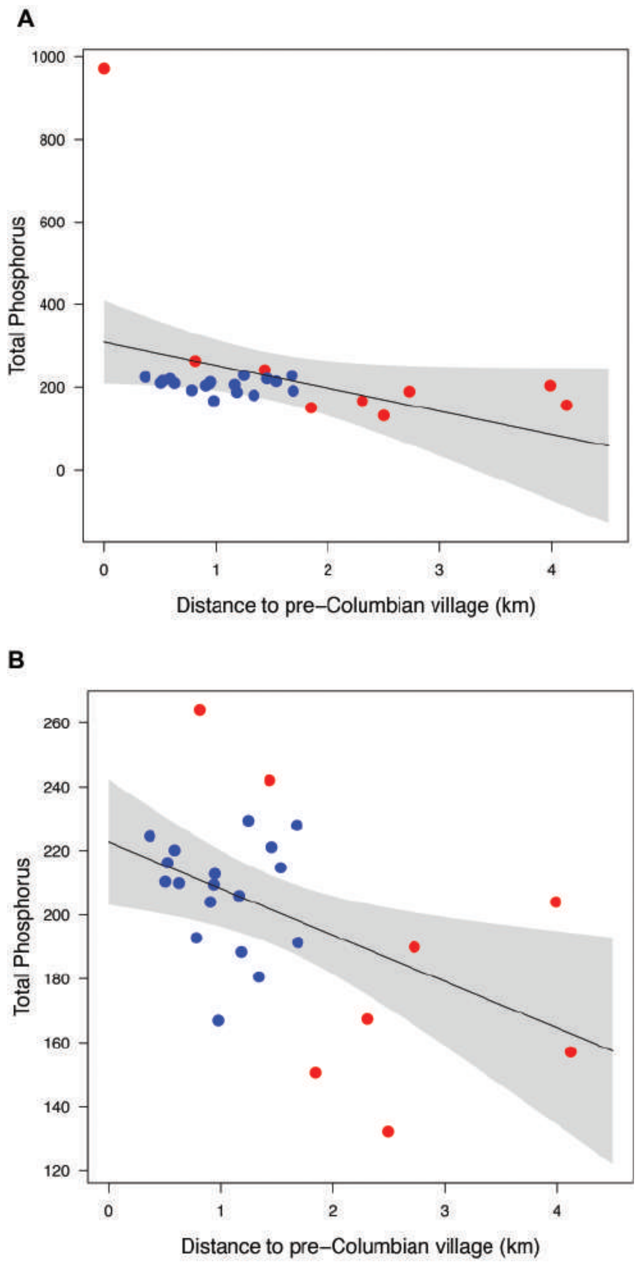


Figure A6.4. Relationship between total soil phosphorus and the distance to pre-Columbian villages. Simple linear regressions (A) with ADE site ($r^2 = 0.10$, $p = 0.059$) and (B) without ADE site ($r^2 = 0.20$, $p = 0.013$), note differences in the scale of y-axis between these two figures. Red dots are forest plots located in the Madeira River basin (9 plots) and blue dots are forest plots in the Tapajós River basin (18 plots).

Table A6.1. Stand basal area and density of stems of 27 forest plots located in the Tapajós River and Madeira River basins, and their distances from ancient villages (ADE) and current villages (Actual) in kilometers. Stand basal area (BA) and density (Dens) of all live stems with dbh ≥ 10 cm and 1 cm were estimated for 1-hectare plots based on information from 0.5-ha, 0.25-ha and 0.01-ha subplots. The percentages of basal area and density in the forest plots for useful non-managed (Use), useful managed (Man), useful cultivated (Cult) and useful domesticated plants (Dom) are presented.

Basin	**Dist.**	**Dist.**	**BA**	**Dens**	**Dens**	**BA**	**BA**	**BA**	**BA**	**Dens**	**Dens**	**Dens**	**Dens**
	ADE (km)	Actual (km)	(m^2)	dbh ≥ 10	dbh ≥ 1	Use (%)	Man (%)	Cult (%)	Dom (%)	Use (%)	Man (%)	Cult (%)	Dom (%)
Tapajos	0.4	3.8	31.6	330	3430	17	70	30	26	14	44	7	2
Tapajos	0.5	11.0	32.2	470	5170	6	72	38	14	8	34	13	3
Tapajos	0.5	15.4	27.2	396	4196	5	62	30	16	13	40	17	5
Tapajos	0.6	3.3	36.8	466	4066	1	64	39	1	10	30	12	2
Tapajos	0.6	7.0	31.3	572	5072	11	55	30	6	13	38	15	7
Tapajos	0.8	5.0	38.3	494	5694	11	53	17	6	9	40	9	3
Tapajos	0.9	13.8	34.4	452	2152	1	54	40	14	4	36	19	6
Tapajos	0.9	5.2	26.3	388	2988	4	66	43	9	6	53	26	3
Tapajos	1.0	14.9	28.5	444	4844	5	64	34	17	10	28	7	4
Tapajos	1.0	5.2	26.7	434	2834	16	54	30	24	13	36	9	5
Tapajos	1.2	6.2	45.9	412	4312	7	74	52	1	12	46	17	5
Tapajos	1.2	12.4	31.9	394	4894	6	66	30	5	5	38	13	2
Tapajos	1.3	4.4	31.5	428	3428	2	61	18	7	6	37	13	8
Tapajos	1.3	7.8	40.6	458	5458	3	54	19	6	8	30	6	3
Tapajos	1.5	5.8	34.0	514	4414	2	59	24	5	9	32	9	3
Tapajos	1.5	14.1	36.1	438	5038	3	80	46	2	9	40	16	1
Tapajos	1.7	13.2	35.2	372	5672	0	71	45	18	4	42	26	5
Tapajos	1.7	13.1	22.9	556	3556	8	54	15	8	11	32	14	4
Mean	1.0	9.0	32.8	446	4290	6	63	32	10	9	38	14	4
Madeira	0.0	7.0	50.6	558	2958	1	69	60	8	2	38	18	26
Madeira	0.8	0.9	30.6	512	5412	14	48	21	2	6	45	21	3
Madeira	1.4	4.1	30.4	512	4412	7	52	35	14	7	50	25	8
Madeira	1.9	9.1	32.9	658	8958	7	36	12	5	7	49	7	2
Madeira	2.3	3.9	25.6	500	6700	12	48	24	10	16	50	14	7
Madeira	2.5	5.2	36.3	478	5378	2	66	29	2	2	58	26	6
Madeira	2.7	10.4	30.5	608	6308	17	29	5	2	16	39	7	5
Madeira	4.0	5.5	32.6	520	9820	16	42	25	12	2	55	19	9
Madeira	4.1	7.6	27.0	418	6018	6	74	45	26	4	64	34	7
Mean	2.2	6.0	32.9	529	6218	9	51	28	9	7	50	19	8

Table A6.2. Results of the structural equation models without the ADE site. Models test the direct and indirect effects of ancient and current management on forest structure and forest composition variables excluding the forest plot located on the ADE site. The regression coefficient (Coef.), standardized coefficients (Std. Coef.), standard error (SE), and p-value are given for all regression models. The variations explained only by the fixed effects (marginal R^2) and together with random effect (conditional R^2) are given in the mixed-models. Total phosphorus was log-transformed to increase normality. Basin was included as a random factor.

Analyses	Response Variable	Predictor variable	Coef.	Std. Coef.	SE	P-value
Mixed-model	$\log_{10}$ total P	Ancient management	0.04	0.52	0.18	0.008
		Recent management	-0.08	-0.22	0.18	0.226
R^2 conditional			0.27			
R^2 marginal			0.27			
Mixed-model	Soil charcoal (0-40 cm)	Recent management	0.28	0.25	0.17	0.15
		Ancient management	0.02	0.08	0.22	0.709
R^2 conditional		0.6				
R^2 marginal		0.05				
Mixed-model	Recent management	Ancient management	0.11	0.54	0.27	0.054
		Soil clay	-0.004	-0.56	0.26	0.048
R^2 conditional			0.17			
R^2 marginal			0.17			
Correlation	Soil clay	$\log_{10}$ total P	0.14			0.259
Mixed-model	Stand basal area (m^2/ 0.5 ha)	$\log_{10}$ total P	-4.11	-0.11	0.25	0.67
		Recent management	3.05	0.24	0.24	0.336
		Soil charcoal (0-40 cm)	-4.32	-0.38	0.27	0.178
		Ancient management	-0.07	-0.03	0.33	0.94
		Soil clay	0.05	0.53	0.37	0.162
R^2 conditional		0.12				
R^2 marginal		0.12				
Mixed-model	Density of subcanopy individuals (dbh < 10 cm/0.5 ha)	$\log_{10}$ total P	-3699	-0.3	0.23	0.218
		Recent management	368	0.09	0.17	0.616
		Soil charcoal (0-40 cm)	-325	-0.09	0.2	0.671
		Ancient management	-324	-0.38	0.24	0.13
		Soil clay	50	1.53	0.78	0.063
R^2 conditional		0.94				
R^2 marginal		0.13				
Mixed-model	Density of canopy individuals (dbh ≥ 10 cm/0.5 ha)	$\log_{10}$ total P	-174.53	-0.31	0.28	0.271
		Recent management	-50.79	-0.27	0.21	0.22
		Soil charcoal (0-40 cm)	1.18	0.01	0.25	0.978
		Ancient management	14.31	0.37	0.29	0.22
		Soil clay	0.77	0.52	0.87	0.557
R^2 conditional		0.87				
R^2 marginal		0.09				
Mixed-model	Relative basal area of useful non-managed species (%)	$\log_{10}$ total P	-9.19	-0.33	0.29	0.262
		Recent management	4.41	0.15	0.21	0.477
		Soil charcoal (0-40 cm)	2.87	0.16	0.25	0.527
		Ancient management	0.23	0.07	0.29	0.808
		Soil clay	0.35	2.29	0.97	0.030
R^2 conditional			0.97			
R^2 marginal			0.22			
Mixed-model	Relative basal area of managed species (%)	$\log_{10}$ total P	92.56	0.51	0.24	0.044
		Recent management	26.89	0.43	0.17	0.019
		Soil charcoal (0-40 cm)	-19.70	-0.36	0.20	0.087
		Ancient management	-6.07	-0.48	0.24	0.054
		Soil clay	-0.91	-1.89	0.80	0.029
R^2 conditional			0.98			
R^2 marginal			0.22			
Mixed-model	Relative basal area of cultivated species (%)	$\log_{10}$ total P	107.16	0.62	0.27	0.032
		Recent management	22.33	0.38	0.19	0.064
		Soil charcoal (0-40 cm)	-32.91	-0.63	0.23	0.012
		Ancient management	-5.03	-0.42	0.27	0.134
		Soil clay	-0.87	-1.88	0.9	0.05
R^2 conditional			0.97			
R^2 marginal			0.24			
Mixed-model	Relative basal area of domesticated species (%)	$\log_{10}$ total P	16.19	0.14	0.31	0.658
		Recent management	-0.7	-0.02	0.25	0.946
		Soil charcoal (0-40 cm)	-1.03	-0.03	0.29	0.921
		Ancient management	-1.66	-0.21	0.35	0.563
		Soil clay	-0.17	-0.54	0.86	0.538
R^2 conditional			0.71			
R^2 marginal			0.11			

Analyses	Response Variable	Predictor variable	Coef.	Std. Coef.	SE	P-value
Mixed-model	Relative density of useful non-managed species (%)	$\log_{10}$ total P	-10.58	-0.06	0.25	0.810
		Recent management	0.54	0.02	0.24	0.929
		Soil charcoal (0-40 cm)	2.14	0.13	0.27	0.650
		Ancient management	1.54	0.38	0.33	0.260
		Soil clay	-0.01	-0.12	0.37	0.748
R^2 *conditional*			0.90			
R^2 *marginal*			0.52			
Mixed-model	Relative density of managed species (%)	$\log_{10}$ total P	3.35	-0.19	0.18	0.303
		Recent management	19.06	0.42	0.14	0.008
		Soil charcoal (0-40 cm)	9.24	0.26	0.16	0.126
		Ancient management	-4.04	-0.46	0.20	0.031
		Soil clay	0.07	0.83	0.54	0.138
R^2 *conditional*			0.90			
R^2 *marginal*			0.52			
Mixed-model	Relative density of cultivated species (%)	$\log_{10}$ total P	79.91	0.73	0.27	0.013
		Recent management	12.25	0.33	0.19	0.108
		Soil charcoal (0-40 cm)	-10.66	-0.32	0.23	0.175
		Ancient management	-4.58	-0.6	0.27	0.038
		Soil clay	-0.58	-1.99	0.88	0.036
R^2 *conditional*			0.97			
R^2 *marginal*			0.34			
Mixed-model	Relative density of domesticated species (%)	$\log_{10}$ total P	11.12	0.33	0.24	0.184
		Recent management	1.18	0.1	0.21	0.635
		Soil charcoal (0-40 cm)	-0.58	-0.06	0.24	0.817
		Ancient management	-1.24	-0.53	0.29	0.084
		Soil clay	-0.03	-0.39	0.54	0.481
R^2 *conditional*			0.25			
R^2 *marginal*			0.25			

Table A6.3. Results of the structural equation models with the ADE site. Models test the direct and indirect effects of ancient and recent management on forest structure and forest composition variables including the forest plot located on the ADE site. The regression coefficient (Coef.), standardized coefficients (Std. Coef.), standard error (SE), and p-value are given for all regression models. The variations explained only by the fixed effects (marginal R^2) and together with random effect (conditional R^2) are given in the mixed-models. Total phosphorus was log-transformed to increase normality. Basin was included as a random factor.

Analyses	Response Variable	Predictor variable	Coef.	Std. Coef.	SE	P-value
Mixed-model	$\log_{10}$ total P	Ancient management	0.12	0.81	0.21	>0.001
		Recent management	-0.21	-0.28	0.16	0.09
R^2 *conditional*			0.70			
R^2 *marginal*			0.34			
Mixed-model	Soil charcoal (0-40 cm)	Recent management	0.33	0.28	0.15	0.08
		Ancient management	-0.01	-0.05	0.18	0.803
R^2 *conditional*			0.68			
R^2 *marginal*			0.04			
Mixed-model	Recent management	Ancient management	0.06	0.30	0.23	0.210
		Soil clay	-0.01	-0.32	0.23	0.187
R^2 *conditional*			0.08			
R^2 *marginal*			0.08			
Correlation	Soil clay	log10 (total P)	-0.60			0.999
Mixed-model	Stand basal area (m2/ 0.5 ha)	$\log_{10}$ total P	10.97	0.53	0.27	0.037
		Recent management	3.11	0.20	0.20	0.338
		Soil charcoal (0-40 cm)	-4.69	-0.36	0.25	0.161
		Ancient management	-0.1	-0.03	0.29	0.913
		Soil clay	-0,31	-0.26	0.44	0.624
R^2 *conditional*			0.72			
R^2 *marginal*			0.26			
Mixed-model	Density of subcanopy individuals (dbh < 10 cm/0.5 ha)	$\log_{10}$ total P	-1233	-0.22	0.20	0.29
		Recent management	410	0.09	0.17	0.58
		Soil charcoal (0-40 cm)	-474	-0.13	0.21	0.533
		Ancient management	-350	-0.41	0.24	0.103
		Soil clay	29.93	0.93	0.53	0.093
R^2 *conditional*			0.88			
R^2 *marginal*			0.14			

Analyses	Response Variable	Predictor variable	Coef.	Std. Coef.	SE	P-value
Mixed-model	Density of canopy individuals (dbh ≥ 10 cm/0.5 ha)	log$_{10}$ total P	-37.81	-0.15	0.25	0.552
		Recent management	-47.40	-0.24	0.21	0.256
		Soil charcoal (0-40 cm)	-10.08	-0.06	0.25	0.808
		Ancient management	12.16	0.32	0.30	0.293
		Soil clay	-0.60	-0.42	0.47	0.381
R^2 conditional			0.45			
R^2 marginal			0.08			
Mixed-model	Relative basal area of useful non-managed species (%)	log$_{10}$ total P	-9.19	-0.25	0.24	0.313
		Recent management	4.41	0.16	0.20	0.449
		Soil charcoal (0-40 cm)	2.87	0.12	0.25	0.631
		Ancient management	0.23	0.04	0.30	0.887
		Soil clay	0.35	1.69	0.67	0.021
R^2 conditional			0.94			
R^2 marginal			0.24			
Mixed-model	Relative basal area of managed species (%)	log$_{10}$ total P	43.45	0.53	0.20	0.017
		Recent management	26.19	0.42	0.17	0.024
		Soil charcoal (0-40 cm)	-17.08	-0.33	0.21	0.137
		Ancient management	-5.63	-0.46	0.25	0.076
		Soil clay	-0.53	-1.15	0.57	0.058
R^2 conditional			0.96			
R^2 marginal			0.22			
Mixed-model	Relative basal area of cultivated species (%)	log$_{10}$ total P	58.56	0.67	0.21	0.004
		Recent management	21.61	0.32	0.17	0.076
		Soil charcoal (0-40 cm)	-30.24	-0.54	0.21	0.020
		Ancient management	-4.58	-0.35	0.25	0.175
		Soil clay	-0.49	-0.99	0.57	0.099
R^2 conditional			0.95			
R^2 marginal			0.28			
Mixed-model	Relative basal area of domesticated species (%)	log$_{10}$ total P	2.09	0.04	0.3	0.893
		Recent management	-1.3	-0.03	0.25	0.898
		Soil charcoal (0-40 cm)	0.83	0.03	0.3	0.934
		Ancient management	-1.28	-0.17	0.36	0.649
		Soil clay	0.03	0.1	0.36	0.791
R^2 conditional			0.02			
R^2 marginal			0.02			
Mixed-model	Relative density of useful non-managed species (%)	log$_{10}$ total P	-10.58	-0.38	0.27	0.174
		Recent management	0.54	0.03	0.23	0.913
		Soil charcoal (0-40 cm)	2.14	0.12	0.27	0.665
		Ancient management	-0.01	-0.03	0.32	0.922
		Soil clay	1.54	0.37	0.32	0.267
R^2 conditional			0.17			
R^2 marginal			0.17			
Mixed-model	Relative density of managed species (%)	log$_{10}$ total P	3.35	0.05	0.17	0.748
		Recent management	19.06	0.41	0.14	0.010
		Soil charcoal (0-40 cm)	9.24	0.24	0.17	0.181
		Ancient management	-4.04	-0.45	0.20	0.041
		Soil clay	0.07	0.22	0.20	0.300
R^2 conditional			0.64			
R^2 marginal			0.64			
Mixed-model	Relative density of cultivated species (%)	log$_{10}$ total P	14.69	0.30	0.25	0.254
		Recent management	10.86	0.29	0.22	0.196
		Soil charcoal (0-40 cm)	-5.92	-0.19	0.26	0.474
		Ancient management	-3.70	-0.51	0.31	0.114
		Soil clay	0.02	0.08	0.31	0.793
R^2 conditional			0.24			
R^2 marginal			0.24			
Mixed-model	Relative density of domesticated species (%)	log$_{10}$ total P	28.99	0.91	0.12	>0.001
		Recent management	1.47	0.06	0.10	0.561
		Soil charcoal (0-40 cm)	-1.63	-0.08	0.13	0.530
		Ancient management	-1.42	-0.30	0.15	0.056
		Soil clay	-0.18	-0.95	0.33	0.006
R^2 conditional			0.96			
R^2 marginal			0.54			

CHAPTER 7

General discussion

Amazonia is frequently perceived as an untouched natural paradise. The astonishing biodiversity found in the largest tropical rainforest on Earth has fascinated environmentalists and scientists worldwide. Recent archaeological findings revealed that Amazonia also holds an old history of interactions with humans, who actively managed forest resources since at least 13,000 years ago (Roosevelt, 2013). Over time, Amazonian societies accumulated cultural innovations that lead to the domestication of landscapes and plants across the basin (Clement, 1999; Clement et al., 2015a). Modern landscapes contain histories of human-nature interactions that have been gradually unveiled in places previously seen as pristine (Heckenberger et al., 2003).

Until very recently, apparently unsuitable environments (e.g., poor soils, lack of animal protein, climatic oscillations) were interpreted as limiting for cultural development compared to neighbouring Andean areas (Meggers, 1954). Indeed, centralized and highly hierarchical societies are less visible in Amazonian archaeological records across the basin that lack monumental buildings left by pre-Columbian societies (Neves, 2013). On the other hand, archaeological studies show several domesticated landscapes in different parts of the basin that include large deposits of anthropogenic soils (ADE), extensive earthworks, such as canals, ditches, mounds and road networks (Erickson, 2008; Heckenberger and Neves, 2009; Clement et al., 2015a). Such legacies of landscape domestication have challenged the idea that Amazonian forests were largely untouched by pre-Columbian societies. It is likely that at least 138 plant species - mostly trees and other perennial species - were domesticated by peoples before European conquest (Clement, 1999). Even more were managed in forest landscapes (Balée, 1989; Peters, 2000; Levis et al., 2012).

During the last decades, scientists have been debating to what extent pre-Columbian peoples altered Amazonian landscapes. To date, the only consensus is that past human disturbance was spatially heterogeneous across the basin (Clement et al., 2015a; Bush et al., 2015). While evidence of large and complex settlements were found in some parts of the basin (Erickson, 2000; Heckenberger et al., 2003; Heckenberger et al., 2008), areas with high precipitation levels and away from aquatic resources are considered by some scholars to have been sparsely occupied by past societies (Bush and Silman, 2007; McMichael et al., 2012a). This thesis addresses this debate by generating a broad scale assessment of the long-term effects of past human activities on modern Amazonian forests.

For this, I combined multiple datasets from the social and natural sciences, and analysed detailed field data across the basin to understand how past peoples transformed forest landscapes at different spatial scales (see Figure 1.4 – **Chapter 1**).

Instead of classifying Amazonia as "pristine nature" or "cultural parkland" (Heckenberger et al., 2003), I studied the forest as a mosaic of patches domesticated to different degrees by human-nature interactions. In this chapter, I synthesise and discuss the main findings of my thesis (see Box 7.1). I also expand the landscape domestication model (Figure 1.3 – **Chapter 1**), proposing new approaches for better evaluating the influence of past (and contemporary) peoples in Amazonian landscapes. Finally, I discuss some implications of my results for conservation planning and argue why the so common dichotomy between nature and culture is inappropriate for understanding, managing and conserving complex systems such as Amazonia.

EVIDENCE OF PAST HUMAN INFLUENCE ON AMAZONIA

Persistent effects of ancient domestication

Denevan (1996) hypothesized that sedentary pre-Columbian societies were concentrated on bluffs along major rivers where people could exploit a wide variety of resources from the floodplains and *terra-firme* forests throughout the year. Rivers were used by these societies as routes for transporting people, materials, resources and plants (Hornborg et al., 2005). Terrestrial routes were also used for connecting indigenous peoples, such as Arawak societies, that developed extensive exchange systems while expanding their influence (Hornborg et al., 2005; Eriksen, 2011). These regional exchange systems were essential not only for intensifying trade of goods and services, but also as a fast route for dissemination and exchange of culture (Hornborg et al., 2005; Eriksen, 2011). For instance, Amazonian Dark Earth (ADE) sites - good markers of pre-Columbian sedentary villages - became abundant from 2.500 to 500 years Before Present (BP) along the margins of major rivers, suggesting an increase of human population density (Neves et al., 2004). In Chapter 2 and 6 we show that sedentary habitation sites are also common along tributary rivers and temporary streams, sometimes up to 70 km from the major Amazonian floodplains. Along the margins of these smaller rivers, the distance between ancient villages tended to be less than 5 km, suggesting that interfluvial landscapes were also extensively occupied by past societies, challenging previous predictions about the occupation of interfluvial areas (e.g., McMichael et al., 2012a; Piperno, 2015; Bush, 2015).

To understand whether the effects of ancient societies persist in modern-day plant communities, we combined data from 1,091 forest inventory plots across the Amazon

BOX 7.1.
Answers to the main questions of this thesis:

1) What are the relative roles of human and environmental factors in shaping the distribution of useful and domesticated plants across Amazonian forests? In Chapter 3, we studied 85 domesticated plant species across Amazonia and found that they are five times more likely to dominate the forest than non-domesticated species. Domesticated species are more diverse and abundant in forests near archaeological sites and rivers, on poorly drained soils, and in regions with higher rainfall seasonality. Whereas environmental conditions explained up to 30 % of the variation in the distribution of these species, our proxies for past human activity explained up to 20 % of this variation in some Amazonian regions, refuting the idea that forests are largely untouched by humans.

2) How do management practices and natural ecological processes interact to form forest patches dominated by useful plants? In Chapter 5, we show how Amazonian people have interacted with natural ecological processes that shape plant communities, resulting in the formation of forest patches dominated by useful plant species. Through multiple management practices, people transformed, for instance: 1) plants' dispersal capacity; 2) local environmental filters; and 3) biological interactions. Ancient cultural practices have been transmitted by tradition and maintained through time, contributing to maintain the legacies of past peoples.

3) How do ancient and current effects of human activities vary across forest landscapes? In Chapters 2 and 6 we show that pre-Columbian sedentary habitation sites are common along tributary rivers or temporary streams, sometimes up to 70 km from major Amazonian floodplains. Along smaller rivers, the distance between ancient villages tended to be less than 5 km, suggesting that interfluvial landscapes were also extensively occupied by past societies. In Chapters 4 and 6, we show that forest landscapes re-occupied by contemporary societies hold signatures of both the pre- and post-Columbian occupation periods, but ancient effects were stronger than recent effects on old-growth forests due to extensive soil improvement. Thus, ancient and modern peoples have transformed Amazonian forests through time.

basin and the Guiana Shield with the location of more than 3,000 archaeological sites in the same area (see details about these databases in Levis et al., 2017a – **Chapter 3**). Our analysis also incorporated environmental data to distinguish the relative importance of environmental and human factors in modern plant communities. Our results revealed that the richness and abundance of 85 domesticated plant species were spatially correlated with archaeological sites and rivers (Levis et al., 2017a – **Chapter 3**). These domesticated plants are more diverse and abundant in forests near archaeological sites, on poorly drained soils, and in regions with higher rainfall seasonality. Although most of the variation in the relative richness and abundance of domesticated species remains unexplained by either human or environmental factors in most of the regions, the proxies for past human influence (distance to archaeological sites and rivers) explained up to 20 % of this variation in some regions. Across Amazonia, domesticated species were found to be up to five times more dominant than non-domesticated ones, suggesting that modern-day plant communities have been structured to some degree by past domestication, and not only by environmental conditions. Other studies have also detected the influence of past societies in old-growth and secondary forests on archaeological sites, even centuries after the demographic collapse of pre-Columbian populations (Erickson and Balée, 2006; Junqueira et al., 2010; Quintero-Vallejo et al., 2015). Recent archaeobotanical studies are revealing that such changes in plant composition are associated with the intensification of human management practices during the Holocene (McMichael et al., 2015a; Watling et al., 2017a). Our findings show that the species composition of old-growth forests, often assumed to be undisturbed (Peres et al., 2010; Barlow et al., 2012), actually reflects both natural and historical human processes (**Chapters 3-6**).

Despite such evidence, the persistence of ancient human effects in modern forests continues to be questioned. McMichael et al. (2017a) argue that most changes in the vegetation relate to the 500 years of human history after European conquest rather than to the pre-Columbian period, given the spatial correlation between ancient and recent villages. To disentangle the roles of ancient and recent management, we reanalysed our data incorporating the potential effects of recent human activities on our study sites. We found that forests managed by contemporary societies hold signatures of both occupation periods, yet ancient effects were stronger than recent effects on plant composition (Junqueira et al., 2017 – **Chapter 4**).

In **Chapter 6**, we show that the influence of ancient peoples on old-growth forests is stronger than previously assumed in part because they enriched soil nutrients around their villages. Contemporary societies are more concentrated along river margins than ancient ones due to many reasons, such as land use restrictions (Amaral et al., 2013), migration to Amazonian towns (Parry et al., 2010) and changes in land use practices. Consequently, forest soils further away from river margins are no longer extensively improved by contemporary peoples that are mostly living along rivers. We found that current societies have transformed old-growth forests by actively managing useful plants, not by modifying soil conditions. These results indicate that human activities before and during the last 500 years of history have left their signatures on modern forests, and reinforce the need for further investigation of past and current impacts and the consequences thereof on Amazonian forests.

Why do pre-Columbian legacies persist in modern forests?

To explain why ancient legacies persist in modern landscapes, we gathered data from the literature and in the field about how indigenous and traditional people manage tree and palm species. With this information, we developed a model of forest domestication (Levis et al., 2018 – **Chapter 5**) in which we describe how people interacted with natural ecological processes that shape plant communities. For instance, people transformed: 1) plant species' dispersal capacity by dispersing seeds intentionally or non-intentionally over short and long distances, and by transplanting seedlings from one place to another; 2) local environmental filters, by improving soil conditions; and 3) biological interactions by planting seeds to attract game animals, enhancing the long-lasting effects of seed dispersal (Levis et al., 2018 – **Chapters 5**; **Chapter 6**). These ancient cultural practices have been transmitted by tradition and maintained through time (Levis et al., 2018 – **Chapter 5**). Today, current management practices have additive effects in forests that were historically managed, which shows the importance of local people in maintaining past legacies (**Chapter 4-6**).

Monumental trees as legacies of ancient societies

Throughout this thesis, I showed that the distribution of some useful plants across Amazonia is associated with past human occupation (**Chapter 3-6**). Some of these useful living plants are emblematic trees with very large stature. A classic example is the Amazon nut, also called Brazil nut (*Bertholletia excelsa*), frequent in the vicinity of Amazonian Dark Earths (Thomas et al., 2015; Levis et al., 2018 – **Chapter 5**). Another example is the high frequency of sumaúma (*Ceiba pentandra*) - a giant light-demanding species commonly found in floodplains - on Amazonian Dark Earth sites (Clement et al., 2003; **Chapter 6**). Interestingly, indigenous peoples used to bury their dead in urns among the large buttress roots (*sapopemas*) of sumaúma trees (Nimuendajú, 2004). This species is perceived in Amazonia and by the Maya peoples in Central America as sacred, which shows the widespread manifestation of sumaúma trees in indigenous mythological narratives (Figure 7.1). The cultural importance of certain plant species (dos Santos and Aparicio, 2016; de Oliveira, 2016) and their affiliation with archaeological sites (e.g., Amazonian Dark Earths) elucidates which species can be classified as indicators of pre-Columbian activities or indigenous cultures across Amazonia (Clement et al., 2003; Junqueira et al., 2010), and likely in the Neotropics.

Given the historical association between plants and peoples (Balée, 1989; Balée, 2013; Peters, 2000; Stahl, 2015; **this thesis**), the distribution of the many useful plants, especially domesticated ones, could be interpreted as evidence of past human activities across tropical ecosystems. This may be especially useful in remote areas, where archaeological artefacts (e.g., ceramics) and structures (e.g., mounds) are hidden under (the soil of) the forest, whereas these monumental trees are standing and even towering above the forest canopy.

Sixteen thousand tree species are estimated to occur in Amazonia (ter Steege et al., 2013), more than 3,000 plant species are known to be used (Revilla, 2002), and at least 301 trees are known to be cultivated by indigenous peoples (Hanelt, 2001; http://mansfeld.ipk-gatersleben.de/). Amazonian ethnic groups (e.g., the Tupi-Guarani linguistic family) expanded from southwestern and possibly eastern Amazonia to southern parts of the Atlantic coast of Brazil in the late Holocene (Almeida and Neves, 2015; Iriarte et al., 2017). It is likely that some cultivated trees accompanied these migrations. For instance, we found that the probable origin of domestication of some widespread species does not match the location where these plants are most abundant, probably due to past human dispersal (Levis et al., 2017a – **Chapter 3**). Surprisingly, cultivated and domesticated species found to occur in Amazonian forests are also widespread across seasonally dry forests (see Box 7.2) suggesting that plant distributions in these ecosystems may be also influenced by past human activities.

Figure 7.1. Sumaúma tree (*Ceiba pentandra*) growing on an Amazonian Dark Earth site in Jamaraquá village, along the lower Tapajós River, Pará, Brazil. Author: Carolina Levis

BOX 7.2.

Forest conservation: Humans' handprints

(Levis et al. Science, 355: 466-467. 2017)

Neotropical forests have been home to humans since the end of the Pleistocene, and large pre-Columbian societies emerged in tropical dry forests in Central and South America and in wetter forests of the Amazon basin during the past several millennia. The role of humans in shaping species distributions, however, tends to be overlooked in ecological studies. For example, in their Research Article analyzing the largest data set of floristic inventories in neotropical dry forests ("Plant diversity patterns in neotropical dry forests and their conservation implications," 23 September 2016, p. 1383), Banda et al. (2016) mentioned humans occasionally, but not as a potential driver of the patterns observed. Although Banda et al. (2016) showed neotropical dry forests to be dominated by woody plant species with geographically restricted distributions, 17 of the 4660 species recorded were widespread across dry forests, occurring in at least 9 of 12 floristic groups. Interestingly, 8 of these 17 widespread species are known to be cultivated today (Hanelt, 2001), and two of those have populations that were cultivated and probably domesticated by pre-Columbian societies (*Sapindus saponaria* and *Trema micrantha*) (Hanelt, 2001). Surprisingly, all eight widespread species of the dry biome that were cultivated by past or modern Amerindians also occur in Amazonian forests (ter Steege et al., 2013). Amazonian forests are partly dominated by useful species, a pattern that might result from past management activities (ter Steege, 2013; Levis et al., 2017a – **Chapter 3**). The widespread distribution of cultivated and/or domesticated species across wet and dry biomes suggests that human-plant interactions transcend ecological boundaries and supports the hypothesis of a substantial effect of past human societies in shaping plant distributions across the Neotropics. Accordingly, it is important that ecological studies take into account the potential role of prehistorical and historical human dispersal as a driver of plant distributions within and among neotropical biomes.

FRONTIERS FOR HISTORICAL ECOLOGICAL STUDIES

Reassessing the spatial extent of past human influence

Revealing the spatial distribution of past peoples in tropical forests remains challenging. As the bluffs along major Amazonian rivers are considered the most suitable locations for sustaining high population densities (Denevan, 1996; Denevan, 2014), Bush et al. (2015) proposed that the influence of past people in Amazonian landscapes decreases exponentially up to 15 km from major river floodplains. This prediction assumes that most interfluvial areas between these rivers were not affected by past human disturbance. However, a previous study done in Central Amazonia found signatures of past human activities on the vegetation up to 40 km from major rivers in areas previously described as pristine (Levis et al., 2012). McMichael et al. (2012) modelled the distribution of archaeological sites using environmental databases, and predicted that most of these anthropogenic soils occur within 10 km from perennial rivers in interfluves of major rivers. Similarly, we observed a decrease of domesticated species in forests up to 10 km from perennial rivers, but also up to 25 km when the distance from archaeological sites was considered (Levis et al., 2017a – **Chapter 3**). These results suggest that our knowledge of the distribution of archaeological sites is far from complete, especially in remote areas.

In well-surveyed regions, the mean distance between archaeological sites is less than 5 km (Levis et al., 2014 – **Chapter 2**; **Chapter 6**). In **Chapter 5** we show that 80 % of the patches of useful species are located up to 4 km from archaeological sites, although some patches extend up to 40 km from ancient and current villages. In **Chapter 6**, we demonstrate that ancient societies increased soil nutrients around their villages, independent of the distance from their villages to major and perennial rivers. Therefore, our findings suggest that remote and apparently undisturbed areas are not pristine, and should be the main targets for further studies (Clement et al., 2015a), rather than just assumed to be untouched (cf. Bush et al., 2015).

Expanding the conceptual model of landscape domestication

Bluff zones adjacent to extensive floodplains, rich soils and areas with high rainfall seasonality have been previously described as the most suitable places for sustaining large population densities at the Amazon basin scale (Denevan, 1996; Bush and Silman, 2007; Bush et al., 2015). The combination of abundant aquatic resources from floodplains with stable terrains to live sedentarily and cultivate perennial plants may have formed a perfect scenario for the development of long-duration settlements across Amazonia (Denevan, 1996). Also, the rich soils and open areas commonly found in southern and southwestern parts of the basin may have supported large settlements because these environments are appropriate for producing annual crops (Piperno, 2011). Areas with low altitudes (0-100 m) and within 10 km of perennial rivers have also been shown as suitable environments for humans in central and eastern regions of the basin (McMichael et al., 2014; McMichael et al., 2017a). At the landscape scale, rich soils, abundant aquatic resources and stable topographic conditions (such as flat terrain and low elevation) are probably the most suitable environments for humans (Figure 7.2A).

In this thesis, we showed that pre-Columbian peoples occupied all Amazonian regions in both suitable and areas considered to be unsuitable, as humans changed the environment according to their needs. It seems likely that humans identified suitable environments for living and later expanded their living environment (niche) into less suitable areas by actively domesticating their landscapes, as illustrated in Figure 2B. Around their villages people domesticated landscapes and plant populations. Over time, humans expanded their distribution into the interfluves, occupying areas near lakes, streams or natural depressions where water could be stored (Figure 7.2B). This expansion involved various human niche construction activities (referred to in Levis et al., 2018 – **Chapter 5** as management practices) that modified soil fertility and plant composition, increasing the diversity and abundance of some palm and tree species and increasing soil nutrients. Consequently, humans created forest landscapes domesticated to varying degrees from highly modified (homegardens in settled areas), through intermediate (cultivated areas), to less modified landscapes (managed forests). The forest domestication process involved multiple management practices that we organized into eight categories: 1) removal of non-useful plants, 2) protection of useful plants, 3) attraction of non-human dispersers of useful plants, 4) human transportation of useful plants, 5) selection of phenotypes useful to humans, 6) fire management, 7) direct planting, and 8) soil improvement (see Levis et al., 2018 – **Chapter 5** for more information about these practices). In homegardens and cultivated areas near their settlements, all eight practices are widely used. In managed forests further away from settlements, active and energy demanding human activities that involve fire management, direct planting and soil improvement are less common than the other practices. By managing soils, forests and water resources, past societies expanded their niches and created domesticated landscapes in environments previously described as unsuitable for sedentary human occupation.

In the lower Tapajós River and upper-middle Madeira River basin, we observed that pre-Columbian societies occupied landscapes that are no longer occupied by contemporary traditional societies (**Chapter 6**). Today, traditional villages are mostly located near river floodplains or perennial rivers (Figure 7.2C), whereas pre-Columbian villages were widespread in both riverine and interfluvial landscapes

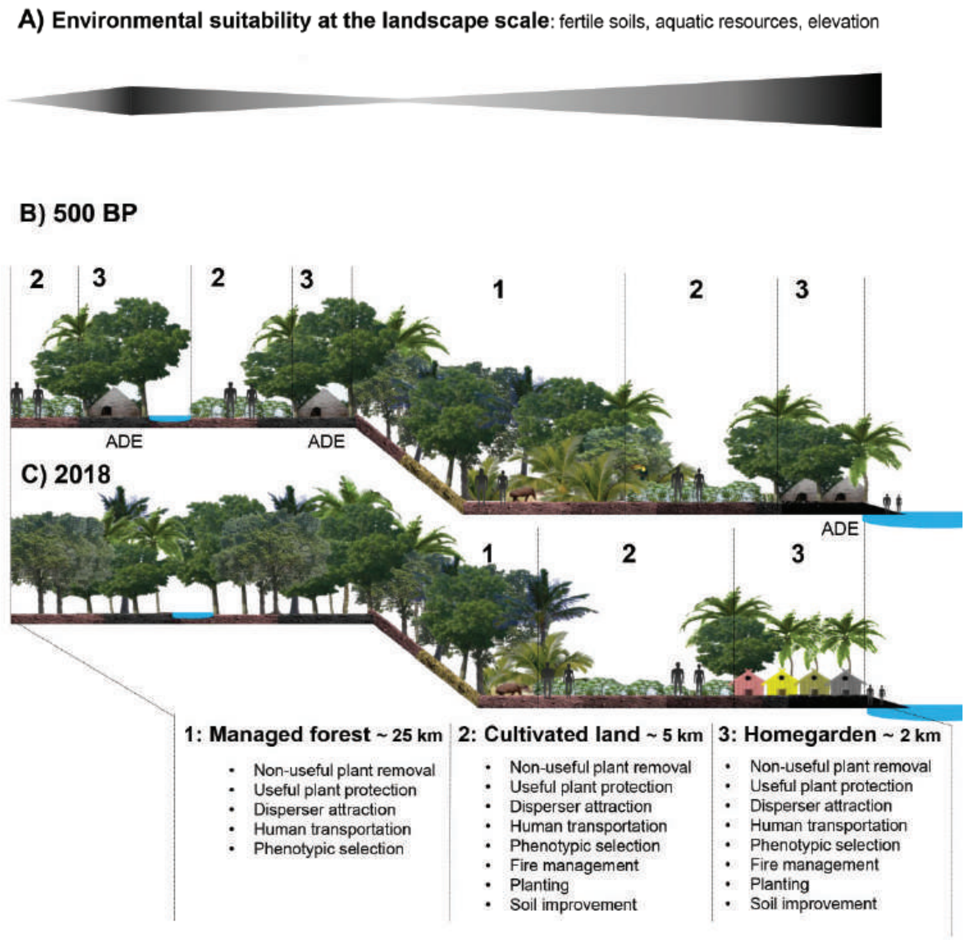


Figure 7.2. Conceptual model of Amazonian landscape domestication that shows how humans expanded their niches across suitable and unsuitable environments. A) Gradients from suitable (black) to unsuitable (white) environments for humans at the landscape scale. Landscape domestication process in two time periods: B) 500 years Before Present (BP) and C) today (2018). Human influence is detected in the soils (differences in soil colours) and in the vegetation (differences in plant species). Amazonian Dark Earth (ADE) sites are anthropogenic soils and good markers of pre-Columbian sedentary villages. This model also illustrates how humans have constructed new niches for living in suitable (near major and perennial rivers) and also apparently unsuitable habitats (interfluves near small streams or natural depressions). Pre-Columbian societies expanded their niches and occupied landscapes that contemporary traditional societies do not occupied (**Chapters 5 and 6**). For more details of how humans domesticated forests through time, see the conceptual model of Levis et al., 2018 – **Chapter 5**.

(Figure 7.2B). This difference has implications for the landscape domestication. In the past, people extensively domesticated Amazonian landscapes. Today, current villages are more concentrated in towns or along major and perennial rivers, sometimes imposed by land use restrictions in protected areas, implying that forests on ancient homegardens and cultivate areas further away from current villages are likely managed, but not intensively domesticated.

Considering the long-term and widespread presence of humans and their capacity to transform plant communities, Balée (1989) estimated that past societies modified 11.8 % of Amazonian forests. After two decades of scientific advances in Amazonian Archaeology, Clement et al. (2015a) proposed that all sorts of pre-Columbian cultures domesticated landscapes to different degrees. In this thesis, I found that the Amazon forest is a mosaic of numerous and diverse forest patches with different degrees of human intervention, and that the most domesticated forests are found where humans have lived sedentarily for centuries or millennia, as illustrated in Figure 7.2. This mosaic is the result of different sorts of environmental factors, past and current human activities and cultures.

The need for a multi-proxy approach

The intensity, duration and spatial distribution of past human activities have been investigated by multiple disciplines. However, the interpretation of the data and the methods used can differ completely among studies (Clement et al., 2015a; McMichael et al., 2015b; Clement et al., 2015b; Watling et al., 2017a; Piperno et al., 2017; Watling et al., 2017b; Levis et al., 2017a – **Chapter 3**; McMichael et al., 2017b; Junqueira et al., 2017 – **Chapter 4**). This divergence happens because assessments of past human activities often make use of a single dataset (proxy). To take a step forward in estimating the impact of human activities across Amazonia, we are developing a multi-proxy approach that would allow us to correlate multiple datasets (McMichael, Levis et al. 2018, in preparation). For example, without correlating plant distributions with archaeological and environmental databases we would not have been able to determine to what extent the distribution of domesticated plants is related to (past and recent) human activities, environmental conditions or both factors (Levis et al., 2017a – **Chapter 3** and Junqueira et al., 2017 – **Chapter 4**).

A multi-proxy approach should cover all spatial and temporal scales of human activities. For instance, Mayle and Iriarte (2014) have already demonstrated how the integration of paleoecological datasets (i.e., pollen records from lakes close to archaeological sites) with archaeology and archaeobotany datasets (i.e., plant remains from past habitation sites) can shed light on pre-Columbian land use systems. While pollen records from lake sediments provide information about past vegetation shifts, archaeological data reconstructs the chronology of past cultures and archaeobotany identifies part of their diets; together they reveal how pre-Columbian cultures interacted with their environments over time (Mayle and Iriarte, 2014). Another way to strengthen the investigation of human activities across temporal scales is determining whether plant communities observed in pollen records persist in modern forests on archaeological sites, as in the inferences about the sustainability of the ancient Maya city of Tikal (Lentz et al., 2014). To estimate the spatial extent of past land use systems in Amazonia, other methods may be useful, such as remote sensing techniques (e.g., the very high spatial resolution LiDAR) that revealed archaeological sites under the forest canopy (Khan et al., 2017; Stenborg et al., 2018).

IMPLICATIONS FOR CONSERVATION

Amazonia as a natural-cultural heritage of humanity

The romantic view of Amazonian and other tropical forests worldwide as having no history has led to misguided conservation priorities that set aside protected areas from local human needs, completely ignoring human legacies (West et al., 2006). Imprudent protection policies can alter the ways local people see and interact with their surroundings and their traditions, and may even result in the relocation of indigenous people from their territories (Holt, 2005). For instance, Brazilian law (n° 3.924, 1961) considers archaeological sites as property of the Nation, sometimes disconnecting indigenous peoples from their cultural heritage. At the same time, national and international organizations are setting priorities to protect cultural values and natural resources in Amazonia in different ways and rarely together. For example, according to the International Union for the Conservation of Nature (IUCN) categories of protected areas, Strictly Protected Areas, such as Natural Reserves, exclude humans from living with their "nature" whereas Suitable Use Reserves include traditional societies, their cultural practices and management systems in nature conservation[1]. Similarly, Indigenous Lands are also created to allow indigenous peoples to occupy their historical lands in Brazil (Brazilian Constitution, 1988 Art. 231, § 1). So far the idea that Amazonia has been shaped by interactions between cultural and natural processes, however, has not been acknowledged in conservation planning.

The IUCN has developed another category to protect landscapes "*where the interaction of people and nature over time has produced an area of distinct character*

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[1] https://www.iucn.org/theme/protected-areas/about/protected-area-categories

with significant, ecological, biological, cultural and scenic value". Since 1992, the United Nations Educational, Scientific and Cultural Organization (UNESCO) has recognized these cultural landscapes and created a mixed category of natural-cultural heritage in which both natural resources and cultural values are conserved in the same place[2]. In Neotropical ecosystems, perhaps the most iconic example is the Tikal National Park, created to conserve its high biodiversity and important archaeological sites of the Maya culture. Based on the findings of this thesis, Amazonia should also be understood as a mixed natural-cultural heritage of humanity that deserves urgent conservation actions.

Archaeological sites and forests with a strong historical component are at risk of disappearing due to deforestation, degradation, roadbuilding, mining, river dams and other threats, essentially driven by the demands of a market-oriented society. The agro-industrial frontier of exotic crops is expanding (Soares-Filho et al., 2006) and threatening the conservation of about half of all Amazonian tree species, mainly in the southwestern, southern and eastern Amazonian regions (ter Steege et al., 2015). These Amazonian forests are not usually seen as biodiversity hotspots. However, these locations should be top conservation priorities, because these are exactly the areas where we found the highest diversity of native domesticated species (Levis et al., 2017a – **Chapter 3**), implying that they are hotspots of agrobiodiversity and ancient cultures. Several important crops were first domesticated in southwestern Amazonia, such as manioc, peach palm, *Capsicum* peppers and peanut (Clement et al., 2016), indicating the importance of this region for maintaining the genetic diversity of globally important crops. If well managed, these landscapes may represent reservoirs of agrobiodiversity for future human generations (Junqueira et al., 2010) and provide options for increasing food security.

REUNIFYING NATURE AND SOCIETY

Historically, western scientists have divided the study of nature and human society into separate disciplines with very little dialogue between them. Archaeologists have focused their research on ancient human artefacts and ecologists on evolutionary and environmental drivers of natural populations, communities and ecosystem functions. More recently, the discipline of forest ecology has merged with human ecology and human history (Balée, 2006; Roosevelt, 2013), resulting in novel research frameworks both in ecology and anthropology, and their related fields (Redman et al., 2004; Ostrom, 2009; Balée, 2006). A considerable scientific effort has already been expended in studies of socio-ecological systems that aim to integrate knowledge from different disciplines into one complex framework in which the interactions among the parts of the system are more important than each part alone (Redman et al., 2004; Ostrom, 2009). Socio-ecological systems have also been described in indigenous ethnographies (Egleé, 2013) in which human and non-human domains are in a constant dialogue and movement (de Oliveira, 2016). If "*the terms "nature" and "society" do not designate domains of reality*" (Latour, 2004, p. 53), then we as scientists need to avoid this dichotomous view and understand that we are all part of the same system (Ostrom, 2009).

In this thesis, I investigated the historical human influence on the world's largest tropical rainforest (**Chapter 3-5**), and provided an interdisciplinary model to explain how Amazonian forests are formed by interactions between natural and cultural processes (**Chapter 5**). I suggest that living plants associated with archaeological sites can be used as indicators of past human activities in any Amazonian areas including those remote from modern societies (**Chapter 3-6**), and perhaps should be considered as monuments of past societies. With my work, I hope to motivate social scientists to incorporate an ecological view, and natural scientists to consider the long-term effects of humans.

To conclude, the results of this thesis reveal that the Amazonian flora is in part a surviving heritage of its past inhabitants that depends on current local management practices to persist. Native peoples managed forest landscapes, their biodiversity, and cultivated and domesticated a wide variety of plants during at least 13,000 years. Their practices created a mosaic of forest patches that offer varying resources, such as food, medicine, construction materials, water and fertile soils. I hope that one day these forests will be understood, managed and conserved as a natural-cultural heritage of global importance.

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[2] http://whc.unesco.org/en/criteria/

REFERENCES

Acuña, C. (1641). *Relacción del Nuevo Descubrimiento del rio de las Amazonas*. Quito: Imprenta del Reyno.

Albert, B., and Milliken, W. (2009). *Urihi A: a terra-floresta Yanomami*. São Paulo: Instituto Socioambiental.

Albuquerque, U. P., Ramos, M. A., Lucena, R. F. P. de, and Alencar, N. L. (2014). "Methods and techniques used to collect ethnobiological data," in *Methods and Techniques in Ethnobiology and Ethnoecology*, eds U. P. Albuquerque, L. V. F. C. da Cunha, R. F. P. de Lucena, and R. R. N. Alves (New York: Springer), 15–37.

Alden, D. (1976). The significance of cacao production in the Amazon region during the late colonial period: An essay in comparative economic history. *Proc. Am. Philos. Soc.* 120, 103-135.

Almeida, F. O. d., and Neves, E. G. (2015). Evidências arqueológicas para a origem dos Tupi-Guarani no leste da Amazônia. *Mana* 21, 499-525.

Alves, R. M., Sebbenn, A. M., Artero, A. S., Clement, C., and Figueira, A. (2007). High levels of genetic divergence and inbreeding in populations of cupuassu (*Theobroma grandiflorum*). *Tree Genet. Genomes* 3, 289-298.

Alves, R. P., Levis, C., and Clement, C. R. (2016). Use and management of piquiá suggest in situ domestication along the lower Tapajós river, Brazilian Amazonia. *Econ. Bot.* 70, 198–202.

Amaral, S. A. P., Dal'Asta, N., Brigatti, C. M. D., de Pinho, L. C., de Castro Medeiros, P. R., de Andrade, T. F., et al. (2013). Comunidades ribeirinhas como forma socioespacial ddfge expressão urbana na Amazônia: uma tipologia para a região do Baixo Tapajós (Pará-Brasil). *REBEP* 30, 367-399.

Anderson, A. B., May, P. H., and Balick, M. J. (1991). *The subsidy from nature: Palm forests, peasantry, and development on an Amazon frontier*. New York: Columbia University Press.

Armstrong, C. G., Shoemaker, A. C., McKechnie, I., Ekblom, A., Szabó, P., Lane, P. J., et al. (2017). Anthropological contributions to historical ecology: 50 questions, infinite prospects. *PLoS One* 12, e0171883.

Arroyo-Kalin, M. (2012). Slash-burn-and-churn: Landscape history and crop cultivation in pre-Columbian Amazonia. *Quat. Int.* 249, 4–18.

Arroyo-Kalin, M. (2017). Human Niche Construction and Population Growth in Pre-Columbian Amazonia. *Archaeology International* 20, 122-136.

Arroyo-Rodríguez, V., Melo, F. P., Martínez-Ramos, M., Bongers, F., Chazdon, R. L., Meave, J. A., et al. (2017). Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. *Biol. Rev.* 92, 326-340.

Bagchi, R., Gallery, R. E., Gripenberg, S., Gurr, S. J., Narayan, L., Addis, C. E., et al. (2014). Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature* 506, 85-88.

Baker, T. R., Phillips O. L., Malhi Y., Almeida S., Arroyo L., Di Fiore A., et al. (2004). Variation in wood density determines spatial patterns inAmazonian forest biomass. *Global Change Biol*. 10, 545-562.

Balée, W. (1989). "The Culture of Amazonian Forests," in *Resource Management in Amazonia: Indigenous and Folk Strategies*, eds D. A. Posey and W. Balée (NY: NYGB Press), 1–21.

Balée, W. (1993). Indigenous Transformation of Amazonian Forests: An Example from Maranhão, Brazil. *L'Homme* 33, 231–254.

Balée, W. (1998). "Historical ecology: premises and postulates," in *Advances in Historical Ecology*, ed W. Balée (New York: Columbia University Press), 13-29.

Balée, W. (2000). Antiquity of Traditional Ethnobiological Knowledge in Amazonia: The Tupí-Guaraní Family and Time. *Ethnohistory* 47, 399–422.

Balée, W. (2006). The Research Program of Historical Ecology. *Annu. Rev. Anthr.* 35, 75–98.

Balée, W. (2013). *Cultural forests of the Amazon: a historical ecology of people and their landscapes*. Tuscaloosa: The University of Alabama Press.

Banda, K., Delgado-Salinas, A., Dexter, K. G., Linares-Palomino, R., Oliveira-Filho, A., Prado, D., et al. (2016). Plant diversity patterns in neotropical dry forests and their conservation implications. *Science* 353, 1383-1387.

Barberis, I. M., and Tanner, E. V. J. (2005). Gaps and root trenching increase tree seedling growth in Panamanian semi-evergreen forest. *Ecology* 86, 667–674.

Barlow, J., Gardner, T. A., Lees, A. C., Parry, L., & Peres, C. A. (2012). How pristine are tropical forests? An ecological perspective on the pre-Columbian human footprint in Amazonia and implications for contemporary conservation. *Biol. Conserv.* 151, 45-49.

Barton, K., and M. K. Barton. (2017). *Package 'MuMIn'*; available online at https://cran.r-project.org/web/packages/MuMIn/index.html.

Beckerman, S (1994). "Hunting and fishing in Amazonia. Hold the answers, what are the questions?," in *Amazonian Indias from Prehistory to the Present: Anthropological Perspectives*, ed. A. C. Roosevelt (Tucson & London: Arizona University Press), 77-200.

Belletti, J. D. S. (2013). *Mapeamento arqueológico do Lago de Tefé, médio rio Solimões (Amazonas-Brasil)*. Master's Qualification, PPGA-MAE-USP, São Paulo.

Berlin, B. (2014). *Ethnobiological classification: Principles of categorization of plants and animals in traditional societies*. Princeton: Princeton University Press.

Boivin, N. L., Zeder, M. A., Fuller, D. Q., Crowther, A., Larsong, G., Erlandsonh, J. M., et al. (2016). Ecological consequences of human niche construction: Examining long-term anthropogenic shaping of global species distributions. *Proc. Natl. Acad. Sci. U.S.A.* 113, 6388–6396.

Bond, W. J., and Midgley., J. J. (2001). Ecology of sprouting in woody plants: the persistence niche. *Trends Ecol. Evol.* 16, 45–51.

Boster, J. S. (1984). "Classification, cultivation and selection of Aguaruna cultivars of Manihot esculenta (Euphorbiaceae)," in *Ethnobotany in the Neotropics*, eds G. T. Prance and J. A. Kallunki (Bronx, NY: NYBG Press), 34–47.

Bowman, D. M. J. S., Balch, J., Artaxo, P., Bond, W. J., Cochrane, M. A., D'Antonio, C. M., et al. (2011). The human dimension of fire regimes on Earth. *J. Biogeogr*. 38, 2223–2236.

Boyle, B., Hopkins, N., Lu, Z., Garay, J. A. R., Mozzherin, D., Rees, T., et al. (2013). The taxonomic name resolution service: an online tool for automated standardization of plant names. *BMC bioinformatics* 14, 16.

BRASIL (2007). *Manual de Construção da Base Hidrográfica Ortocodificada* (Brasília, ANA, SGI); available online at www.ana.gov.br.

Breheny, P., and W. Burchett. (2012). *Visualizing regression models using visreg* (Comprehensive R Archive Network); available online at https://cran.r-project.org/web/packages/visreg/index.html.

Bush, M. B., and McMichael, C. H. (2016). Holocene variability of an Amazonian hyperdominant. *J. Ecol*. 104, 1370-1378.

Bush, M. B., and Silman, M. R. (2007). Amazonian exploitation revisited: ecological asymmetry and the policy pendulum. *Front. Ecol. Environ.* 5, 457-465.

Bush, M. B., Silman, M., McMichael, C., Saatchi, S. (2008). Fire, climate change and biodiversity in Amazonia: a Late-Holocene perspective. *Proc. R Soc. B* 363, 1795-1802.

Bush, M. B., McMichael, C. H., Piperno, D. R., Silman, M. R., Barlow, J., Peres, C. A., et al. (2015). Anthropogenic influence on Amazonian forests in pre-history: An ecological perspective. *J. Biogeogr.* 42, 2277–2288.

Campbell, D. G., Ford, A., Lowell, K. S., Walker, J., Lake, J. K., Ocampo-Raeder, C., et al. (2006). "The feral forests of the eastern Petén," in *Time and complexity in historical ecology: Studies in the Neotropical Lowlands*, eds W. L. Balée and C. L. Erickson (New York: Columbia University Press), 21-55.

Carvajal, F. 1934 [1542]. "Discovery of the Orellana River: Account Written by Friar Gaspar de Carvajal," in *The Discovery of the Amazon According to the Account of Friar gaspar de Carvajal and other Documents*, eds J. T. Medina and H. C. Heaton (New York: American Geographical Society), 167-235.

Cavalcante, P.B. (2010). *Frutas comestíveis na Amazônia*. Belém: Museu Paraense Emílio Goeldi.

Chapin, M., Lamb, Z., and Threlkeld, B. (2005). Mapping indigenous lands. *Annu. Rev. Anthropol.* 34, 619-638.

Chazdon, R. L. (2003). Tropical forest recovery: legacies of human impact and natural disturbances. *Perspect. Plant Ecol. Evol. Syst.* 6, 51-71.

Cincotta, R. P., Wisnewski, J., Engelman, R. (2000). Human population in the biodiversity hotspots. *Nature* 404, 990-992.

Clark, D. B. (1996). Abolishing virginity. *J. Trop. Ecol.* 12, 735-739.

Clement, C. R. (1989). A center of crop genetic diversity in western Amazonia. *BioScience* 39, 624-631.

Clement, C. R. (1999). 1492 and the loss of Amazonian crop genetic resources. I. The relation between domestication and human population decline. *Econ. Bot.* 53, 188–202.

Clement, C. R. (2014). "Landscape domestication and archaeology," in *Encyclopedia of Global Archaeology*, ed C. Smith (New York: Springer), 4388-4394.

Clement, C. R., and Junqueira, A. B. (2010). Between a Pristine Myth and an Impoverished Future. *Biotropica* 42, 534-536.

Clement, C. R., de Cristo-Araújo, M., Coppens D'Eeckenbrugge, G., Alves Pereira, A., and Picanço-Rodrigues, D. (2010). Origin and domestication of native Amazonian crops. *Diversity* 2, 72-106.

Clement, C. R., Denevan, W. M., Heckenberger, M. J., Junqueira, A. B., Neves, E. G., Teixeira, W. G., et al. (2015a). The domestication of Amazonia before European conquest. *Proc. R Soc. B* 282, e20150813.

Clement, C. R., Denevan, W. M., Heckenberger, M. J., Junqueira, A. B., Neves, E. G., Teixeira, W. G., et al. (2015b) Response to comment by McMichael, Piperno and Bush. *Proc. R Soc. B* 282, e20152459.

Clement, C. R., Klüppel, M. P., German, L. A., Almeida, S. S. de, Major, J., Aragão, L. E. O. e C. de, et al. (2009). "Diversidade Vegetal em Solos Antrópicos da Amazônia," *in As Terras Pretas de Índio da Amazônia: Sua caracterização e uso deste conhecimento na criação de novas áreas*, eds W. G. Teixeira, D. C. Kern, B. E. Madari, H. N. Lima, and W. I. Woods (Manaus: Embrapa Amazônia Ocidental), 146–161.

Clement, C. R., McCann, J. M., & Smith, N. J. (2003). "Agrobiodiversity in Amazonia and its relationship with dark earths," in *Amazonian dark earths: origin, properties, management*, eds J. Lehmann, D. C. Kern, B. Glaser, and W. I. Woods (Berlin: Springer), 159-178.

Clement, C. R., Rodrigues, D. P., Alves-Pereira, A., Mühlen, G. S., Cristo-Araújo, M. d., Moreira, P. A., et al. (2016). Crop domestication in the upper Madeira River basin. *Bol. Mus. Para. Emílio Goeldi. Cienc. Hum.* 11, 193-205.

Coley, P. D. (1983). Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol. Monogr.* 53, 209–234.

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.

Connell, J. H., and Lowman, M. D. (1989). Low-diversity tropical rain forests: some possible mechanisms for their existence. *Am. Nat.* 134, 88-119.

Costa, B. L. S. D. (2008). Levantamento arqueológico na RDS Amanã. *Uakari* 4, 7-18.

Crevels, M., and Van der Voort, H. (2008). "The Guaporé-Mamoré region as a linguistic area," in *From Linguistic Areas to Areal Linguistics*, ed P. Muysken (Amsterdam: John Benjamins Press, 2008), 151–179.

Crowley, M. J. (2007). *The R Book*. Hoboken: John Wiley & Sons.

Crumley, C. (2007). "Historical Ecology: integrated thinking at multiple temporal and spatial scales," in *The World System and the Earth System: Global Socio-Environmental Change and Sustainability Since the Neolithic*, eds A. Hornborg and C. Crumley (Walnut Creek: Left Coast Press), 15–28.

Crutzen, P. J. (2006). "The anthropocene," in *Earth system science in the anthropocene*, eds E. Ehlers and T. Krafft (Berlin: Springer), 13-18.

Curry, A. (2013). The milk revolution. *Nature* 500, 20.

Dambrine, E., Dupouey, J. L., Laüt, L., Humbert, L., Thinon, M., Beaufils, T., et al. (2007). Present forest biodiversity patterns in France related to former Roman agriculture. *Ecology* 88, 1430-1439.

Darwin, C. (1859). On the Origin of Species. London: John Murray.

Dawson, I. K., Hollingsworth, P. M., Doyle, J. J., Kresovich, S., Weber, J. C., Montes, C. S., et al. (2008). Origins and genetic conservation of tropical trees in agroforestry systems: a case study from the Peruvian Amazon. *Conserv. Genet.* 9, 361-372 (2008).

de Mattos, P. F. J. (2011). Visões do paraíso: as expedições de Francisco de Orelhana e Pedro Teixeira na Amazônia. *Navigator* 7, 104-116.

de Oliveira, J. C. (2016). Mundos de roças e florestas. *Bol. Mus. Para. Emílio Goeldi. Cienc. Hum.* 11, 115-131.

de Paiva, J. R., Barros, L. D. M., and Cavalcanti, J. J. V. (2009). "Cashew (Anacardium occidentale L.) breeding: a global perspective," in *Breeding Plantation Tree Crops: Tropical Species*, eds S. M. Jain and P. M. Priyadarshan (New York: Springer), 287–324.

de Paula Moraes, C., and Neves, E. G. (2012). O ano 1000: adensamento populacional, interação e conflito na Amazônia Central. *Amazônica* 4, 122-148.

Dempewolf, H., Rieseberg, L. H., & Cronk, Q. C. (2008). Crop domestication in the Compositae: a family-wide trait assessment. *Genet. Resour. Crop Ev.* 55, 1141-1157.

Denevan, W. M., Treacy, J. M., Alcorn, J. B., Padoch, C., Denslow, J., and Paitan, S. F. (1984). Indigenous agroforestry in the Bora Indian management of swidden fallows. *Interciencia* 9, 346–357.

Denevan, W. M. (1992). The pristine myth: the landscape of the Americas in 1492. *Ann. Assoc. Am. Geogr.* 82, 369–385.

Denevan, W. M. (1995). 2 Prehistoric agricultural methods as models for sustainability. *Adv. Plant Pathol.* 11, 21-43.

Denevan, W. M. (1996). A bluff model of riverine settlement in prehistoric Amazonia. *Ann. Assoc. Am. Geogr.* 86, 654-681.

Denevan, W. M. (2001). *Cultivated landscapes of native Amazonia and the Andes*. New York: Oxford University Press.

Denevan, W. M. (2004). "Semi-intensive pre-European cultivation and the origins of anthropogenic dark earths in Amazonia," in *Amazonian Dark Earths: origin, properties, management*, eds J. Lehmann, D. C. Kern, B. Glaser, and W. I. Woods (Berlin: Springer), 135-143.

Denevan, W. M. (2014). Estimating Amazonian Indian numbers in 1492. *J. Lat. Am. Geogr.* 13, 207-221.

Descola, P. (2013). *Beyond nature and culture*. Chicago: University of Chicago Press.

Dickau, R., Bruno, M. C., Iriarte, J., Prümers, H., Betancourt, C. J., Holst, I., et al. (2012). Diversity of cultivars and other plant resources used at habitation sites in the Llanos de Mojos, Beni, Bolivia: evidence from macrobotanical remains, starch grains, and phytoliths. *J. Archaeol. Sci.* 39, 357–370.

dos Santos, G. M., and Aparicio, M. (2016). *Redes Arawa: ensaios de etnologia do Médio Purus*. Manaus: EDUA, Editora da Universidade Federal do Amazonas.

Dwyer, P. D. (1996). "The invention of nature," in *Redefining Nature: Ecology, Culture, and Domestication*, eds R. Ellen and K. Fukui (Oxford (UK)/Washington (DC): Berg Publishers), 157-186.

Egleé, E. L. (2013). Jotï ecogony, Venezuelan Amazon. *Environ. Res. Lett.* 8, e015008.

Elias, F., Marimon, B. S., de Almeida Reis, S. M., Forsthofer, M., Gomes, L., Morandi, P. S., et al. (2013). Dinâmica da distribuição espacial de populações arbóreas, ao longo de uma década, em cerradão na transição Cerrado-Amazônia, Mato Grosso. *Biota Amaz.* 3, 1–14.

Ellis, E. C. (2011). Anthropogenic transformation of the terrestrial biosphere. *Philos. Trans. Royal Soc. A* 369, 1010-1035.

Ellis, E. C. (2015). Ecology in an anthropogenic biosphere. *Ecol. Monograph.* 85, 287-331.

Eloy, L., and Emperaire, L. (2011). La circulation de l'agrobiodiversité sur les fronts pionniers d'Amazonie (région de Cruzeiro do Sul, état de l'Acre, Brésil). *L'esp. géographique* 40, 62–74.

Emilio, T., Quesada, C. A., Costa, F. R., Magnusson, W. E., Schietti, J., Feldpausch, T. R., et al. (2014). Soil physical conditions limit palm and tree basal area in Amazonian forests. *Plant Ecol. Divers.* 7, 215-229.

Erickson, C. L. (2000). An artificial landscape-scale fishery in the Bolivian Amazon. *Nature* 408, 190-193.

Erickson, C. L., and Balée, W. L. (2006). "The historical ecology of a complex landscape in Bolivia," in Time and complexity in historical ecology: Studies in the Neotropical Lowlands, eds. W. L. Balée and C. L. Erickson (New York: Columbia University Press), 187–233.

Erickson, C. L. (2008). "Amazonia: the historical ecology of a domesticated landscape," in *Handbook of South American Archaeology*, eds H. Silverman and W. Isbell (Berlin: Springer), 157-183.

Eriksen, L. (2011). *Nature and Culture in Prehistoric Amazonia Using GIS to reconstruct ancient ethnogenetic processes from archaeology, linguistics, geography, and ethnohistory*. PhD thesis, Human Ecology Division, Lund University.

Esquinas-Alcázar (2005). Protecting crop genetic diversity for food security: political, ethical and technical challenges. *Nat. Rev. Genet.* 6, 946-953.

Esquivel-Muelbert et al. (2016). Seasonal drought limits tree species across the Neotropics. *Ecography* 39, 001-012.

Fauset, S., Johnson, M. O., Gloor, M., Baker, T. R., Monteagudo, A., Brienen, R. J., et al. (2015). Hyperdominance in Amazonian forest carbon cycling. *Nat. Commun*. 6, 6857.

Fearnside, P. M. (1996). Amazonian deforestation and global warming: carbon stocks in vegetation replacing Brazil's Amazon forest. *For. Ecol. Manag. 80*, 21-34.

Fittkau, E. J. (1971). "Esboço de uma divisão ecológica da região amazônica," in *Proc. II Simpósio y Foro de Biologia Tropical Amazônica*, ed J. M. Idrobo (Bogotá: Editorial PAX), 363–372.

Ford, A., and Emery, K. F. (2008). Exploring the legacy of the Maya forest. *J. Ethnobiol.* 28, 147-153.

Fragoso, J., Silvius, K. M., and Correa, J. A. (2003). Long-distance seed dispersal by tapirs increases seed survival and aggregates tropical trees. *Ecology* 84, 1998–2006.

Franco-Moraes, J. (2016). *Ecologia Histórica De Florestas Da Bacia Do Rio Içana, Alto Rio Negro, Amazonas: Um Legado Baniwa Nas Paisagens*. Master's Thesis, INPA, Manaus.

Fraser, J. A., Alves-Pereira, A., Junqueira, A. B., Peroni, N., and Clement, C. R. (2012). Convergent adaptations: bitter manioc cultivation systems in fertile anthropogenic dark earths and floodplain soils in Central Amazonia. *PLoS One* 7, e43636.

Fraser, J. A., Teixeira W., Falcão N., Woods W., Lehmann J., and Junqueira, A. B. (2011). Anthropogenic soils in the Central Amazon: from categories to a continuum. *Area* 43, 264-273.

Frikel, P. (1978). Áreas de arboricultura pré agrícola na Amazônia: notas preliminares. *Rev. Antropol.* 21, 45–52.

Galloway, J. N., Aber, J. D., Erisman, J. W., Seitzinger, S. P., Howarth, R. W., Cowling, E. B., et al. (2003). The nitrogen cascade. *AIBS Bulletin* 53, 341-356.

García, N., Galeano, G., Mesa, L., Castaño, N., Balslev, H., and Bernal, R. (2015). Management of the palm Astrocaryum chambira Burret (Arecaceae) in northwest Amazon. *Acta Bot. Bras.* 29, 45-57.

Gilmore, M. P., and Young, J. C. (2012). The use of participatory mapping in ethnobiological research, biocultural conservation, and community empowerment: a case study from the Peruvian Amazon. *J. Ethnobiol.* 32, 6-29.

Glaser, B., and Birk, J. J. (2012). State of the scientific knowledge on properties and genesis of Anthropogenic Dark Earths in Central Amazonia (terra preta de Índio). Geochim. Cosmochim. *Acta* 82, 39-51.

Goldberg, A., Mychajliw, A. M., and Hadly, E. A. (2016). Post-invasion demography of prehistoric humans in South America. *Nature* 532, 232-235.

Gomes, D. (2017). Politics and ritual in large villages in Santarém, Lower Amazon, Brazil. *Camb. Archaeol. J.* 27, 275-293.

Gomes, J. (2011). É verdade que aqui já foi uma antiga aldeia de índio? Análise cerâmica e cronologia preliminar do sítio arqueológico Boa Esperança, RDS AMANÃ, médio Solimões, AM. *Uakari* 7, 7-20.

Grace, J. B., Anderson, T. M., Olff, H., and Scheiner, S. M. (2010). On the specification of structural equation models for ecological systems. *Ecol. Monograph.* 80, 67-87.

Guimarães Jr, P. R., Galetti, M., and Jordano, P. (2008). Seed dispersal anachronisms: rethinking the fruits extinct megafauna ate. *PLoS One* 3, e1745.

Guix, J. C. (2005). Evidence of Old Anthropic Effects in Forests at the Confluence of the Caurés and Negro Rivers, NW Amazonia: The Role of Indians and Caboclos. *Grup. Estud. Ecológicos* 8, 1–27.

Guix, J. C. (2009). Amazonian forests need Indians and Caboclos. *Orsis* 24, 33-40.

Hammer, K. (1984). Das domestikationssyndrom. *Die Kult.* 32, 11–34.

Hammer, K., and Khoshbakht, K. (2015). A domestication assessment of the big five plant families. *Genet. Resour. Crop Ev.* 62, 665–689.

Hanelt, R. (2001). *Mansfeld's Encyclopedia of Agricultural and Horticultural Crops: Except Ornamentals*. Berlin: Springer; available online at http://mansfeld.ipk-gaters.

Harlan, J. R. (1992). *Crops and man*. Madison: American Society of Agronomy.

Harris, D. R. (1989). "An evolutionary continuum of people-plant interaction," in *Foraging and farming: the evolution of plant exploitation*, eds D. R. Harris and G. Hilman (London: Unwin Hyman.), 11–26.

Harris, M. (2011). "The Floodplain of the Lower Amazon as a Historical Place," in *The Amazon Várzea: The Decade Past and the Decade Ahead*, eds M. Pinedo-Vasquez, M. L. Ruffino, C. Padoch, and E. S. Brondízio (Berlin: Springer), 125-134

Hart, T. B., Hart, J. A., and Murphy, P. G. (1989). Monodominant and species-rich forests of the humid tropics: causes for their co-occurrence. *Am. Nat.* 133, 613-633.

Hart, T. B. (1990). Monospecific dominance in tropical rain forests. *Trends Ecol. Evol.* 5, 6-11.

Heckenberger M. J., Russell J. C., Toney J. R., and Schmidt M. J. (2007). The legacy of cultural landscapes in the Brazilian Amazon: Implications for biodiversity. *Phil Trans R Soc* B 362, 197–208.

Heckenberger, M. J. (2009). Mapping indigenous histories: collaboration, cultural heritage, and conservation in the Amazon. *Collab. Anthropol.* 2, 9-32.

Heckenberger, M. J., Kuikuro, A., Kuikuro, U. T., Russell, J. C., Schmidt, M., Fausto, C., et al. (2003). Amazonia 1492: pristine forest or cultural parkland? *Science* 301, 1710-1714.

Heckenberger, M. J., Russell, J. C., Fausto, C., Toney, J. R., Schmidt, M. J., Pereira, E., et al. (2008). Pre-Columbian urbanism, anthropogenic landscapes, and the future of the Amazon*. Science* 321, 1214-1217.

Heckenberger, M., and Neves, E. G. (2009). Amazonian archaeology. *Annu. Rev. Anthropol.* 38, 251-266.

Henderson, A. (1995). *The palms of the Amazon*. Oxford: Oxford University Press.

Henderson, A. P., and Crampton, W. G. R. (1997) A comparison of fish diversity and abundance between nutrient-rich and nutrient-poor lakes in the upper Amazon. *J. Trop. Ecol.* 13, 175-198.

Hengl, T., de Jesus, J. M., MacMillan, R. A., Batjes, N. H., Heuvelink, G. B., Ribeiro, E., et al. (2013). SoilGrids1km-Global Soil Information based on automated mapping. *PLoS One* 9, e105992.

Herrera, R., Jordan, C. F., Klinge, H., and Medina, E. (1978). Amazon ecosystems. Their structure and functioning with particular emphasis on nutrients. *Interciencia* 3, 223–231.

Hodkinson, D. J., and Thompson, K. (1997). Plant dispersal: the role of man. *J. Appl. Ecol*. 34, 1484–1496.

Holt, F. L. (2005). The Catch-22 of conservation: indigenous peoples, biologists, and cultural change. *Hum. Ecol.* 33, 199-215.

Hoorn, C., Wesselingh, F. P., Ter Steege, H., Bermudez, M. A., Mora, A., Sevink, J., et al. (2010). Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science* 330, 927-931.

Hornborg, A., Gassn, R., Heckenberger, M., Hill, J., Neves, E., SantosGranero, F., et al. (2005). Ethnogenesis, regional integration, and ecology in prehistoric Amazonia: Toward a system perspective. *Curr. Anthropol.* 46, 589-620.

Howe, H. F., and Smallwood, J. (1982). Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* 13, 201–228.

Ingold, T. (1993). The temporality of the landscape. *World Archaeol.* 25, 152-174.

Iriarte, J., Glaser, B., Watling, J., Wainwright, A., Birk, J., Renard, D., et al. (2010). Agricultural landscapes of coastal Amazonia: Phytolith and carbon isotope analysis of raised fields from French Guiana savannah. *J. Archaeol. Sci.* 37, 2984-2994.

Iriarte, J. (2016). "Investigating Amazonian Dark Earths as Agro-Ecosystems and their Impact on the Regional Landscapes of the Lower Amazon," in *Beyond Waters Archaeology and Environmental History of the Amazonian Inland*, ed. P. Stenborg (Gothenburg: University of Gothenburg), 71–86.

Iriarte, J., Smith, R. J., Gregorio de Souza, J., Mayle, F. E., Whitney, B. S., Cárdenas, M. L., et al. (2017). Out of Amazonia: Late-Holocene climate change and the Tupi–Guarani trans-continental expansion. *The Holocene* 27, 967-975.

Jackson, G. (1974). Cryptogeal germination and other seedling adaptions to the burning of vegetation in savanna regions: The origin of the pyrophytic habit. *New Phytol.* 73, 771–780.

Jakovac C. C., Peña-claros M., Mesquita R., Bongers F., Kuyper T. W. (2016b) Swiddens under transition: consequences of agricultural intensification in the Amazon. *Agr. Ecosyst. Environ*. 218. 116–25.

Jakovac, C. C., Bongers, F., Kuyper, T. W., Mesquita, R. C., and Peña-Claros, M. (2016a). Land use as a filter for species composition in Amazonian secondary forests. *J. Veg. Sci.* 27, 1104–1116.

Jordano, P. (2017). What is long-distance dispersal? And a taxonomy of dispersal events. *J. Ecol.* 105, 75–84.

Junk W. J., Bayley P. B., Sparks R. E. (1989). "The flood pulse concept in river-floodplain systems," in *Proceedings of the International Large River Symposium*, ed D. P. Dodge (Ontario: Can. Spec. Publ. Fish. Aquat. Sci), 110-127.

Junk, W. J., M. T. F. Piedade, J. Schöngart, M. Cohn-Haft, J. M. Adeney, and F. Wittmann. (2011). A classification of major naturally-occurring Amazonian lowland wetlands. *Wetlands* 31, 623-640.

Junqueira, A. B., Shepard, G. H., and Clement, C. R. (2010). Secondary forests on anthropogenic soils in Brazilian Amazonia conserve agrobiodiversity. *Biodivers. Conserv.* 19, 1933–1961.

Junqueira, A. B., Shepard, G. H., and Clement, C. R. (2011). Secondary forests on anthropogenic soils of the middle Madeira river: valuation, local knowledge, and landscape domestication in Brazilian Amazonia. *Econ. Bot.* 65, 85–99.

Junqueira, A. B., Souza, N. B., Stomph, T. J., Almekinders, C. J., Clement, C. R., and Struik, P. C. (2016a). Soil fertility gradients shape the agrobiodiversity of Amazonian homegardens. *Agric. Ecosyst. Environ*. 221, 270–281.

Junqueira, A. B., Stomph, T. J., Clement, C. R., and Struik, P. C. (2016b). Variation in soil fertility influences cycle dynamics and crop diversity in shifting cultivation systems. *Agric. Ecosyst. Environ.* 215, 122–132.

Junqueira A. B., and Clement, R. C. (2013). Useful mature forests on terra preta: concentration and maintenance of plant resources in anthropogenic forests through human management. *3er Encuentro Internacional de Arqueología Amazónica*, Poster presentation.

Junqueira, A. B., Levis, C., Bongers, F., Peña-Claros, M., Clement, C. R., Costa, F. and ter Steege, H. (2017). Response to Comment on "Persistent effects of pre-Columbian plant domestication on Amazonian forest composition". *Science* 358, aan8837.

Kainer, K. A., Wadt, L. H., and Staudhammer, C. L. (2014). Testing a silvicultural recommendation: Brazil nut responses 10 years after liana cutting. *J. Appl. Ecol.* 51, 655–663.

Kareiva, P., Watts, S., McDonald, R., and Boucher, T. (2007). Domesticated Nature: Shaping Landscapes and Ecosystems for Human Welfare. *Science* 316, 1866-1869.

Keddy, P. A. (1992). A pragmatic approach to functional ecology. *Funct. Ecol.* 6, 621–626.

Kennedy, J. (2012). Agricultural systems in the tropical forest: a critique framed by tree crops of Papua New Guinea. *Quat. Int.* 249, 140–150.

Khan, S., Aragão, L., and Iriarte, J. (2017). A UAV–lidar system to map Amazonian rainforest and its ancient landscape transformations. *Int. J. Remote Sens.* 38, 2313-2330.

Kleinman, P. J. A., Pimentel, D., and Bryant, R. B. (1995). The ecological sustainability of slash-and-burn agriculture. *Agric. Ecosyst. Environ.* 52, 235–249.

Kummerow, C., Barnes, W., Kozu, T., Shiue, J., and Simpson, J. (1998). The tropical rainfall measuring mission (TRMM) sensor package. *J. Atmos. Ocean Tech.* 15, 809-817.

Kuznetsova, A., Brockhoff, P. B., and Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software 82, 1–26.*

Laland, K. N., Odling-Smee, F. J., and Feldman, M. W. (1999). Evolutionary consequences of niche construction and their implications for ecology. *Proc. Natl. Acad. Sci. U.S.A.* 96, 10242-10247.

Laland, K. N., Odling-Smee, J., and Feldman, M. W. (2001). Cultural niche construction and human evolution. *J. Evol. Biol.* 14, 22-33.

Laland, K. N., Kendal, J. R., and Brown, G. R. (2007). The niche construction perspective: Implications for evolution and human behaviour. *Evol. Psychol.* 5, 51-66.

LaManna, J. A., Mangan, S. A., Alonso, A., Bourg, N. A., Brockelman, W. Y., Bunyavejchewin, S., et al. (2017). Plant diversity increases with the strength of negative density dependence at the global scale. *Science* 356, 1389-1392.

Latour, B. (2004). *Politics of nature*. Cambridge: Harvard University Press.

Lefcheck, J. S. (2016). piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* 7, 573-579.

Legendre, P. (2008). Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. *J. Plant Ecol.* 1, 3-8.

Lehner, B., Verdin, K., and Jarvis, A. (2008). New global hydrography derived from spaceborne elevation data. *Eos, Trans. Amer. Geophys*. 89, 93-94.

Lentz, D. L., Dunning, N. P., Scarborough, V. L., Magee, K. S., Thompson, K. M., Weaver, E., et al. (2014). Forests, fields, and the edge of sustainability at the ancient Maya city of Tikal. *Proc. Natl. Acad. Sci. U.S.A.* 111, 18513-18518.

Leonardi, M., Gerbault, P., Thomas, M. G., and Burger, J. (2012). The evolution of lactase persistence in Europe. A synthesis of archaeological and genetic evidence. *Int Dairy J.* 22, 88-97.

Levis, C., de Souza, P. F., Schietti, J., Emilio, T., da Veiga Pinto, J. L. P., Clement, C. R., et al. (2012). Historical human footprint on modern tree species composition in the Purus-Madeira interfluve, Central Amazonia. *PLoS One* 7, e48559.

Levis, C., Clement, C. R., Ter Steege, H., Bongers, F., Junqueira, A. B., Pitman, N., et al. (2017b). Forest conservation: Humans' handprints*.* *Science* 355, 466–467.

Levis, C., Costa, F. R. C., Bongers, F., Peña-Claros, M., Clement, C. R., Junqueira, A. B., et al. (2017a). Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science* 355, 925–931.

Levis, C., Flores, B. M., Moreira, P. A., Luize, B. G., Alves, R.P., Franco-Moraes, J., et al. (2018). How people domesticated Amazonian forests. *Front. Ecol. Evol.* 5, 171.

Levis, C., Silva, M. S., Silva, M. A., Moraes, C. P., Neves, E. G., Tamanaha, E. K., et al. (2014). "What do we know about the distribution of Amazonian Dark Earth along tributary rivers in Central Amazonia?," in: *Antes de Orellana - Actas del 3er Encuentro Internacional de Arqueología Amazónica*, ed. S. Rostain (Lima, Peru: Instituto Francés de Estudios Andinos), 305-311.

Lewis, S. L., and Maslin, M. A. (2015). Defining the anthropocene. *Nature* 519, 171-180.

Lima, M. (2012). *Processos Naturais e Culturais na formação do registro arqueológico do baixo rio Negro (AM): Estudo de caso dos sítios Floresta e Lago das Pombas*. Master's Qualification, PPGA-MAE-USP, São Paulo.

Lima, M., Tamanaha, E. K. (2007). *Relatório parcial de atividades entregue ao PIATAM*. Manaus: PIATAM.

Lima, M., Tamanaha, E. K. (2008). *Relatório final de atividades entregue ao PIATAM*. Manaus: PIATAM.

Lins, J., Lima, H. P., Baccaro, F. B., Kinupp, V. F., Shepard Jr, G. H., and Clement, C. R. (2015). Pre-Columbian floristic legacies in modern homegardens of Central Amazonia. *PLoS One* 10, e0127067.

Lombardo, U., Canal-Beeby, E., Veit, H. (2011). Eco-archaeological regions in the Bolivian Amazon. *Geog. Helv.* 66, 173-182.

Lombardo, U., Denier, S., May, J.-H., Rodrigues, L., and Veit, H. (2013). Human–environment interactions in pre-Columbian Amazonia: The case of the Llanos de Moxos, Bolivia. *Quat. Int.* 312, 109-119.

Lortie, C. J., Brooker, R. W., Choler, P., Kikvidze, Z., Michalet, R., Pugnaire, F. I., et al. (2004). Rethinking plant community theory. *Oikos* 107 433-438.

Lüdecke, D. (2016). *sjPlot: Data Visualization for Statistics in Social Science* (The Comprehensive R Archive Network); available online at https://cran.r-project.org/package=sjPlot.

Maezumi, S. Y., Whitney, B. S., Mayle, F. E., de Souza, J. G., and Iriarte, J. (2017). Reassessing climate and pre-Columbian drivers of paleofire activity in the Bolivian Amazon. *Quat. Int.* 3, 1-14.

Mayle, F. E., and Iriarte, J. (2014). Integrated palaeoecology and archaeology–a powerful approach for understanding pre-Columbian Amazonia. *J. Archaeol. Sci.* 51, 54–64.

Mayle, F. E., and Power., M. J. (2008). Impact of a drier Early–Mid-Holocene climate upon Amazonian forests. *Phil. Trans. R. Soc. B* 363, 1829-1838.

McKey, D., Rostain, S., Iriarte, J., Glaser, B., Birk, J. J., Holst, I., et al. (2010a). Pre-Columbian agricultural landscapes, ecosystem engineers, and self-organized patchiness in Amazonia. *Proc. Natl. Acad. Sci. U.S.A.* 107, 7823-7828.

McKey, D., Elias, M., Pujol, B., and Duputié, A. (2010b). The evolutionary ecology of clonally propagated domesticated plants. *New Phytol.* 186, 318–332.

Mckey, D., Renard, D., Zangerlé, A., Iriarte, J., Montoya, K. L. A., Suarez Jimenez, L. S., et al. (2014). "New approaches to pre-Columbian raised-field agriculture: the ecology of seasonally flooded savannas, and living raised fields in Africa, as windows on the past and future" in *Antes de Orellana - Actas del 3er Encuentro Internacional de Arqueología Amazónica*, ed S. Rostain (Lima, Peru: Instituto Francés de Estudios Andinos), 91-136.

McMichael, C. H., Piperno, D. R., Bush, M. B., Silman, M. R., Zimmerman, A. R., Raczka, M. F., et al. (2012a). Sparse pre-Columbian human habitation in western Amazonia. *Science* 336, 1429–1431.

McMichael, C. H., Bush, M. B., Piperno, D. R., Silman, M. R., Zimmerman, A. R., and Anderson, C. (2012b). Spatial and temporal scales of pre-Columbian disturbance associated with western Amazonian lakes. *The Holocene* 22, 131-141.

McMichael, C. H., Palace, M. W., Bush, M. B., Braswell, B., Hagen, S., Neves, E. G., et al. (2014). Predicting pre-Columbian anthropogenic soils in Amazonia. *Proc. R Soc. B* 281, 20132475.

McMichael, C., Piperno, D., and Bush, M. (2015a). 'Comment on Clement et al. 2015 'The domestication of Amazonia before European conquest'' *Proc. R Soc. B* 282, 20151837 1821.

McMichael, C. H., Piperno, D. R., Neves, E. G., Bush, M. B., Almeida, F. O., Mongeló, G., et al. (2015b). Phytolith assemblages along a gradient of ancient human disturbance in western Amazonia. *Front. Ecol. Evol.* 3, 1–15.

McMichael, C. N., Matthews-Bird, F., Farfan-Rios, W., and Feeley, K. J. (2017a). Ancient human disturbances may be skewing our understanding of Amazonian forests. *Proc. Natl. Acad. Sci. U.S.A.* 114, 522-527.

McMichael, C. H., Feeley, K. J., Dick, C. W., Piperno, D. R., and Bush, M. B. (2017b). Comment on "Persistent effects of pre-Columbian plant domestication on Amazonian forest composition". *Science* 358, eaan8347.

Meggers B. J., and Evans C. (1957). *Archaeological investigations at the mouth of the Amazon*. Washington: Smithsonian Institution Press.

Meggers, B. J. (1954). Environmental limitation on the development of culture. *Am. Anthropol.* 56, 801-824.

Mellars, P. (2006). Why did modern human populations disperse from Africa 60,000 years ago? A new model. *Proc. Natl. Acad. Sci. U.S.A.* 103, 9381-9386.

Mesquita, R. C., Ickes, K., Ganade, G., and Williamson, G. B. (2001). Alternative successional pathways in the Amazon Basin. *J. Ecol.* 89, 528-537.

Meyer, R. S., DuVal, A. E., and Jensen, H. R. (2012). Patterns and processes in crop domestication: an historical review and quantitative analysis of 203 global food crops. *New Phytol.* 196, 29–48.

Michon, G. (2005). *Domesticating forests: how farmers manage forest resources*. Bogor: IRD/CIFOR/ICRAF.

Michon, G., De Foresta, H., Levang, P., and Verdeaux, F. (2007). Domestic forests: a new paradigm for integrating local communities' forestry into tropical forest science. *Ecol. Soc.* 12.

Milla, R., Osborne, C. P., Turcotte, M. M., and Violle, C. (2015). Plant domestication through an ecological lens. *Trends Ecol. Evol.* 30, 463-469.

Miller, R. P., and Nair, P. R. (2006). Indigenous agroforestry systems in Amazonia: from prehistory to today. *Agrofor. Syst.* 66, 151-164.

Mistry, J., Bilbao, B. A., and Berardi, A. (2016). Community owned solutions for fire management in tropical ecosystems: case studies from Indigenous communities of South America. *Phil. Trans. R. Soc. B* 371, 20150174.

Moles, A. T., and Westoby, M. (2006). Seed size and plant strategy across the whole life cycle. *Oikos* 113, 91–105.

Mongeló, G. (2015). *O formativo e os modos de produção: ocupações pré-ceramistas no Alto Rio Madeira-RO*. Master's Thesis, PPGA-MAE-USP, São Paulo.

Montoya, E., Rull, V., Stansell, N. D., Abbott, M. B., Nogué, S., Bird, B. W., et al. (2011). Forest–savanna–morichal dynamics in relation to fire and human occupation in the southern Gran Sabana (SE Venezuela) during the last millennia. *Quat. Res.* 76, 335–344.

Moraes, C. P., and Neves, E. G. (2012). O ano 1000: Adensamento populacional, interação e conflito na Amazônia Central. *Amazônica* 4, 122-148.

Morcote-Rios G., Bernal R. (2001). Remains of palms (Palmae) at archaeological sites in the New World: A review. *Bot. Rev.* 67, 309-350.

Moreira, P. A., Lins, J., Dequigiovanni, G., Veasey, E. A., and Clement, C. R. (2015). The domestication of annatto (Bixa orellana) from Bixa urucurana in Amazonia. *Econ. Bot.* 69, 127–135.

Morin-Rivat, J., Fayolle, A., Favier, C., Bremond, L., Gourlet-Fleury, S., Bayol, N., et al. (2017). Present-day central African forest is a legacy of the 19th century human history. *Elife* 6, e20343.

Muller-Landau, H. C., Wright, S. J., Calderón, O., Condit, R., and Hubbell, S. P. (2008). Interspecific variation in primary seed dispersal in a tropical forest. *J. Ecol.* 96, 653–667.

Myers, T. P. (2004). "Dark Earths in the Upper Amazon," in *Amazonian Dark Earths: Explorations in Space and Time*, eds. B. Glaser, and W. I. Woods (Berlin: Springer), 67-94.

Nathan, R., Schurr, F. M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., and Tsoar, A. (2008). Mechanisms of long-distance seed dispersal. *Trends Ecol. Evol.* 23, 638-647.

Neves, E. G., Petersen, J. B., Bartone, R. N., and Silva, C. D. (2003). "Historical and socio-cultural origins of Amazonian Dark Earths," in *Amazonian Dark Earths: origin, properties, management*, eds. J. Lehmann, D. C. Kern, B. Glaser, and W. I. Woods (Berlin: Springer), 29–50.

Neves, E. G., Petersen, J. B., Bartone, R. N., and Heckenberger, M. J. (2004). "The timing of terra preta formation in the central Amazon: archaeological data from three sites," in *Amazonian Dark Earths: Explorations in space and time*, eds B. Glaser and W. I. Woods (Berlin: Springer), 125-134.

Neves, E. G., and Peterson J. B. (2006). "The political economy of Pre-Columbian Amerindians: Landscape transformations in Central Amazonia," in *Time and Complexity in Historical Ecology: Studies in the Neotropical Lowlands*, eds W. Balée, and C. L. Erickson (New York: Columbia University Press), 279-309.

Neves, E. G. (2010). *Serviços de Estudos de Prospecção, Avaliação, Salvamento e Resgate de Patrimônio Arqueológico na Implantação de Faixa e Abertura de Valas no Gasoduto Coari-Manaus e no GLPDuto Urucu-Coari*. São Paulo: IPHAN.

Neves, E. G. (2012). *Sob os tempos do equinócio: oito mil anos de história na Amazônia Central (6.500 AC—1.500 DC)*. Post-doctoral dissertation, PPGA-MAE-USP, São Paulo.

Neves, E. G. (2013). "Was agriculture a key productive activity in pre-colonial Amazonia? The stable productive basis for social equality in the Central Amazon," in *Human-Environment Interactions*, E. S. Brondízio and E. F. Moran (Berlin: Springer), 371-388.

Nevle, R. J., and Bird, D. K. (2008). Effects of syn-pandemic fire reduction and reforestation in the tropical Americas on atmospheric CO2 during European conquest. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 264, 25-38.

Nimuendaju, C. (2004). *In pursuit of a past Amazon*. Archaeological researches in the Brazilian Guyana and in the Amazon region. Translated by S. Rydén and P. Stenborg. Ethnological Studies 45. Gothenburg: Världskulturmuseet.

Nobre, A. D., Cuartas, L. A., Hodnett, M., Rennó, C. D., Rodrigues, G., Silveira, A., et al. (2011). Height above the nearest drainage - a hydrologically relevant new terrain model. *J. Hydrol*. 404, 13-29.

Odling-Smee, F. J., Laland, K. N., and Feldman, M. W. (1996). Niche construction. *Am. Nat.* 147, 641-648.

O'Fallon, B. D., and Fehren-Schmitz, L. (2011). Native Americans experienced a strong population bottleneck coincident with European contact. *Proc. Natl. Acad. Sci. U.S.A.* 108, 20444-20448.

Oksanen J., Blanchet F., Kindt R., Legendre P., O'Hara R. (2016). *'vegan': Community ecology package*; available online at https://github.com/vegandevs/vegan.

Ostrom, E. (2009). A general framework for analyzing sustainability of social-ecological systems. *Science* 325, 419-422.

Padoch, C., and De Jong, W. (1987). "Traditional agroforestry practices of native and ribereno farmers in the lowland Peruvian Amazon," in *Agroforestry: Realities, Possibilities and Potentials*. Martinus Nijhoff Publisher, Dordrecht, ed. H. L.Gholz (Dordrecht: Martinus Nijhoff Publishers), 179-194.

Paiva, P. M., Guedes, M. C., and Funi, C. (2011). Brazil nut conservation through shifting cultivation. *For. Ecol. Manage.* 261, 508–514.

Palace, M., McMichael, C., Braswell, B., Hagen, S., Bush, M., Neves, E., et al. (2017). Ancient Amazonian populations left lasting impacts on forest structure. *Ecosphere* 8, e02035.

Parry, L., Peres, C. A., Day, B., and Amaral, S. (2010). Rural–urban migration brings conservation threats and opportunities to Amazonian watersheds. *Conserv. Lett.* 3, 251-259.

Pärssinen, M., Schaan, D., & Ranzi, A. (2009). Pre-Columbian geometric earthworks in the upper Purús: a complex society in western Amazonia. *Antiquity* 83, 1084-1095.

Pausas, J. G., and Keeley, J. E. (2009). A burning story: the role of fire in the history of life. *Bioscience* 59, 593–601.

Paz-Rivera, C., and F. E. Putz. (2009). Anthropogenic soils and tree distributions in a lowland forest in Bolivia. *Biotropica* 41, 665-675.

Peggion, E. A. (2007). Ritual e vida cotidiana no sul do Amazonas: os Tenharim do rio Marmelos. *Perspectivas* 29, 149-168.

Peh, K. S. H., Lewis, S. L., and Lloyd, J. (2011). Mechanisms of monodominance in diverse tropical tree-dominated systems. *J. Ecol.* 99, 891-898.

Peres, C., and Baider, C. (1997). Seed dispersal, spatial distribution and population structure of Brazil nut trees (Bertholletia excelsa) in southeastern Amazonia. *J. Trop. Ecol.* 13, 595-616.

Peres, C. A., Gardner, T. A., Barlow, J., Zuanon, J., Michalski, F., Lees, A. C., et al. (2010). Biodiversity conservation in human-modified Amazonian forest landscapes. *Biol. Conserv.* 143, 2314-2327.

Peres, C. A., Emilio, T., Schietti, J., Desmoulière, S. J., and Levi, T. (2016). Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proc. Natl. Acad. Sci. U.S.A.* 113, 892-897.

Perrut de Lima, P. (2014). *Caracterização da variabilidade genética, sistema de cruzamento e parâmetros de germinação e emergência de euterpe precatoria martius em populações do Baixo Rio Solimões*. Master's Thesis, INPA, Manaus.

Peters, C. M., Balick, M. J., Kahn, F., and Anderson, A. B. (1989). Oligarchic forests of economic plants in Amazonia: utilization and conservation of an important tropical resource. *Conserv. Biol.* 3, 341-349.

Peters, C. M. (2000). "Precolumbian silviculture and indigenous management of neotropical forests," in *Imperfect balance: Landscape transformations in the Precolumbian Americas*, ed D. L. Lentz (New York: Columbia University Press), 203–223.

Pinheiro J., Bates D., DebRoy S., Sarkar D. and R Core Team (2018). *nlme: Linear and Nonlinear Mixed Effects Models*; available online at https://CRAN.R-project.org/package=nlme.

Piperno, D. R. (2011). The origins of plant cultivation and domestication in the New World tropics: patterns, process, and new developments. *Curr. Anthropol.* 52, 453-470.

Piperno, D. R., McMichael, C., and Bush, M. B. (2015). Amazonia and the Anthropocene: What was the spatial extent and intensity of human landscape modification in the Amazon Basin at the end of prehistory? *The Holocene* 25, 1588–1597.

Piperno, D. R., McMichael, C., & Bush, M. B. (2017). Further evidence for localized, short-term anthropogenic forest alterations across pre-Columbian Amazonia. *Proc. Natl. Acad. Sci. U.S.A.*, 201705585.

Pitman, N. C. A., Terborgh, J. W., Silman, M. R., Núñez V., P., Neill, D. A., Cerón, C. E., et al. (2001). Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* 82, 2101–2117.

Pitman, N. C., Cecilio, M. P., Pudicho, M. P., Graham, J. G., Núñez V, M. P., Valenzuela, M., et al. (2011). Indigenous perceptions of tree species abundance across an upper Amazonian landscape. *J. Ethnobiol.* 31, 233–243.

Pitman, N. C., Silman, M. R., and Terborgh, J. W. (2013). Oligarchies in Amazonian tree communities: a ten-year review. *Ecography* 36, 114–123.

Pleysier, J., and Juo, A. (1980). A single-extraction method using silver-thiourea for measuring exchangeable cations and effective CEC in soils with variable charges. *Soil Sci.* 129, 205-211.

Politis, G. G. (1996). Moving to produce: Nukak mobility and settlement patterns in Amazonia. *World Archaeol*. 27, 492–511.

Politis, G. G. (2007). *Nukak: Ethnoarchaeology of an Amazonian People*. Walnut Creek: Left Coast Press.

Poorter, L., Bongers, F., Sterck, F. J., and Wöll, H. (2003). Architecture of 53 rain forest tree species differing in adult stature and shade tolerance. *Ecology* 84, 602-608.

Posey, D. A. (1985). Indigenous management of tropical forest ecosystems: the case of the Kayapo Indians of the Brazilian Amazon. *Agrofor. Syst.* 3, 139–158.

Posey, D. A. (1987). Ethnoentomological survey of Brazilian indians. *Entomol. Gen.* 12, 191–202.

Posey, D. A. (1993). "The importance of semi-domesticated species in post-contact Amazonia: effects of the Kayapo Indians on the dispersal of flora and fauna," in *Tropical Forests, People and Food: Biocultural interactions and applications to development*, eds C. M. Hladik, A. Hladik, O. F. Linares, H. Pagezy, A. Semple, and M. Hadley (Paris: UNESCO-Parthenon), 63–71.

Purugganan, M. D., and Fuller, D. Q. (2009). The nature of selection during plant domestication. *Nature* 457, 843-848.

Quesada, C., Lloyd, J., Schwarz, M., Patino, S., Baker, T., Czimczik, C., et al. (2010). Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences* 7, 1515-1541.

Quesada, C., Phillips, O., Schwarz, M., Czimczik, C., Baker, T., Patiño, S., et al. (2012). Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences* 9, 2203-2246.

Quintero-Vallejo, E., Klomberg, Y., Bongers, F., Poorter, L., Toledo, M., and Peña-Claros, M. (2015). Amazonian dark earth shapes the understory plant community in a Bolivian forest. *Biotropica* 47, 152–161.

R Core Team (2012). *A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna, Austria); available online at www.R-project.org.

Read, J. M., Fragoso, J. M., Silvius, K. M., Luzar, J., Overman, H., Cummings, A., et al. (2010). Space, place, and hunting patterns among indigenous peoples of the Guyanese Rupununi region. *J. Lat. Am. Geogr.* 9, 213-243.

Redman, C. L., Grove, J. M., and Kuby, L. H. (2004). Integrating social science into the long-term ecological research (LTER) network: social dimensions of ecological change and ecological dimensions of social change. *Ecosystems* 7, 161-171.

Reich, P. B., Wright, I. J., Cavender-Bares, J., Craine, J. M., Oleksyn, J., Westoby, M., et al. (2003). The evolution of plant functional variation: traits, spectra, and strategies. *Int. J. Plant Sci.* 164, S143–S164.

Reis, M., Ladio, A., and Peroni, N. (2014). Landscapes with Araucaria in South America: evidence for a cultural dimension. *Ecol. Soc.* 19, 43.

Revelle, W., and Revelle, M. W. (2017). *Package 'psych'*; available online at: http://org/r/psych-manual.pdf.

Revilla, J. (2002). *Plantas úteis da bacia amazônica*. Manaus, BR: Instituto Nacional de Pesquisas da Amazónia.

Ribeiro, M. B. N., Jerozolimski, A., de Robert, P., Salles, N. V., Kayapó, B., Pimentel, T. P., et al. (2014). Anthropogenic landscape in southeastern Amazonia: contemporary impacts of low-intensity harvesting and dispersal of Brazil nuts by the Kayapó Indigenous people. *PLoS One* 9, e102187.

Richards, T. (2008) "Survey strategies in landscape archaeology," in *Handbook of Landscape Archaeology*, eds. B. David and T. Julian (California: Left Coast Press), 551-561.

Ricklefs, R. E. (1987). Community diversity: relative roles of local and regional processes. *Science* 235, 167–171.

Rindos, D. (1984). *The Origins of Agriculture: An Evolutionary Perspective*. London: Academic Press.

Riris, P. (2018). Assessing the impact and legacy of swidden farming in neotropical interfluvial environments through exploratory modelling of post-contact Piaroa land use (Upper Orinoco, Venezuela). *The Holocene*, 0959683617752857. [first published online]

Rival, L. (1998). "Domestication as a historical and symbolic process: wild gardens and cultivated forest in the Ecuatorian Amazon," in *Advances in Historical Ecology*, ed W. Balée (New York: Columbia University Press), 232–250.

Rival, L. (2007). "Domesticating the landscape, producing crops and reproducing society in Amazonia," in *Convergence and Emergence: Towards a New Holistic Anthropology?*, eds. D. Parkin and S. Ulijaszek (Oxford: Berghahn Books), 72–90.

Rival, L., and McKey, D. (2008). Domestication and diversity in manioc (Manihot esculenta Crantz ssp. esculenta, Euphorbiaceae). *Curr. Anthropol.* 49, 1119– 1128.

Roberts, P., Hunt, C., Arroyo-Kalin, M., Evans, D., and Boivin, N. (2017). The deep human prehistory of global tropical forests and its relevance for modern conservation (Review Article). *Nat. Plants* 3, 17093.

Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin III, F. S., Lambin, E., et al. (2009). Planetary boundaries: exploring the safe operating space for humanity. *Ecol. Soc.* 14, 32.

Roosevelt, A. C. (1991). *Moundbuilders of the Amazon: geophysical archaeology on Marajo Island, Brazil*. San Diego: Acad. Press.

Roosevelt, A. C., Da Costa, M. L., Machado, C. L., Michab, M., Mercier, N., Valladas, H., et al. (1996). Paleoindian cave dwellers in the Amazon: the peopling of the Americas. *Science* 272, 373-384.

Roosevelt, A. C. (2013). The Amazon and the Anthropocene: 13,000 years of human influence in a tropical rainforest. *Anthropocene* 4, 69-87.

Ross, N. J. (2011). Modern tree species composition reflects ancient Maya "forest gardens" in northwest Belize. *Ecol. Appl.* 21, 75-84.

Rostain, S. (2008). "Agricultural earthworks on the French Guiana coast," in *Handbook of South American Archaeology*, eds H. Silverman and W. Isbell (Berlin: Springer), 217-233.

Salque, M., Bogucki, P. I., Pyzel, J., Sobkowiak-Tabaka, I., Grygiel, R., Szmyt, M., et al. (2013). Earliest evidence for cheese making in the sixth millennium BC in northern Europe. *Nature* 493, 522-525.

Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V., and Woolmer, G. (2002). The human footprint and the last of the wild: the human footprint is a global map of human influence on the land surface, which suggests that human beings are stewards of nature, whether we like it or not. *BioScience* 52, 891-904.

Santos, E. J. M. D., Silva, A. L. S. D., Ewerton, P. D., Takeshita, L. Y., & Maia, M. H. T. (2015). Origins and demographic dynamics of Tupí expansion: a genetic tale. *Bol. Mus. Para. Goeldi. Ciências Human.* 10, 217-228.

Schaan, D. P., Pärssinen, M., Ranzi, A., & Piccoli, J. C. (2007). Geoglifos da Amazônia ocidental: evidência de complexidade social entre povos da terra firme. *Revista de Arqueologia* 20, 67-82

Schaan, D., Figueiredo, C., Alves, D., Stenborg, P. (2015). *Selva Cultivada: Desenvolvimento Socio-econômico e Mudanças Ambientais na Amazônia Pré-Colombiana*. 3o Relatório Parcial-Outubro de 2013 a Dezembro de 2014, IPHAN.

Schaan, D. (2016). "Discussing center-periphery relations within the Tapajó domain, Lower Amazon," in *Beyond Waters Archaeology and Environmental History of the Amazonian Inland*, ed. P. Stenborg (Gothenburg: University of Gothenburg), 23-36.

Scheffer, M., van Bavel, B., van de Leemput, I. A., and van Nes, E. H. (2017). Inequality in nature and society. *Proc. Natl. Acad. Sci. U.S.A.* 114,13154–13157.

Schietti, J., Emilio, T., Rennó, C. D., Drucker, D. P., Costa, F. R., Nogueira, A., et al. (2014). Vertical distance from drainage drives floristic composition changes in an Amazonian rainforest. *Plant Ecol. Divers.* 7, 241-253.

Schmidt, M. J., Py-Daniel, A. R., Moraes, C. de P., Valle, R. B. M., Caromano, C. F., Texeira, W. G., et al. (2014). Dark earths and the human built landscape in Amazonia: a widespread pattern of anthrosol formation. *J. Archaeol. Sci*. 42, 152–165.

Schnitzer, S. A., Kuzee, M. E., and Bongers, F. (2005). Disentangling above-and below-ground competition between lianas and trees in a tropical forest. *J. Ecol.* 93, 1115–1125.

Schroth, G., Coutinho, P., Moraes, V. H., amd Albernaz, A. L. (2003). Rubber agroforests at the Tapajós river, Brazilian Amazon—environmentally benign land use systems in an old forest frontier region. *Agric. Ecosyst. Environ.* 97, 151-165.

Seibert, R. J. (1948). The uses of Hevea for food in relation to its domestication. *Ann. Missouri Bot. Gard.* 35, 117-121.

Shanley, P., Clement, C. R., Carvalho, J. E. U. de, Homma, A. K. O., and Menezes, A. J. E. A. de (2016). "Amazonian fruits: How farmers nurture nutritional diversity on farm and in the forest," in *Tropical Fruit Tree Diversity: Good Practices for in situ and on-Farm Conservation*, eds. B. Sthapit, H. A. H. Lamers, V. R. Rao, and A. Bailey (Abingdon: Routledge), 147–160.

Shanley, P., Serra, M., and Medina, G. (2010). *Frutíferas e plantas úteis na vida Amazônica*. Bogor: CIFOR.

Shepard JR, G., and Ramirez, H. (2011). "Made in Brazil": human dispersal of the Brazil nut (Bertholletia excelsa, Lecythidaceae) in ancient Amazonia. *Econ. Bot.* 65, 44–65.

Siren, A. (2014). History of natural resource use and environmental impacts in an interfluvial upland forest area in western Amazonia. *Fennia* 192, 36-53.

Smith, B. D. (2011). General patterns of niche construction and the management of ‘wild’ plant and animal resources by small-scale pre-industrial societies. *Philos. Trans. R. Soc. B* 366, 836-848.

Smith, B. D., and Zeder, M. A. (2013). The onset of the Anthropocene. *Anthropocene* 4, 8-13.

Smith, N. (2015). *Palms and People in the Amazon*. Berlin: Springer.

Smith, M., and Fausto, C. (2016). Socialidade e diversidade de pequis (Caryocar brasiliense, Caryocaraceae) entre os Kuikuro do alto rio Xingu (Brasil). *Bol. Mus. Para. Emílio Goeldi. Cienc. Hum.* 11, 87–113.

Smith, N. J. H. (1980). Anthosols and Human Carrying Capacity in Amazonia. *Ann. Assoc. Am. Geogr.* 70, 553–566.

Soares-Filho, B. S., Nepstad, D. C., Curran, L. M., Cerqueira, G. C., Garcia, R. A., Ramos, C. A., et al. (2006). Modelling conservation in the Amazon basin. *Nature* 440, 520-523.

Sombroek, W. G. (1966). *Amazon Soils – a reconnaissance of soils of the Brazilian Amazon region*. Wageningen: Centre for Agricultural Publications and Documentation.

Sorichetta, A., Hornby, G. M., Stevens, F. R., Gaughan, A. E., Linard, C., and Tatem, A. J. (2015). High-resolution gridded population datasets for Latin America and the Caribbean in 2010, 2015, and 2020. *Sci. Data* 2, 150045.

Sosnowska, A., Walanus, A., and Balslev, H. (2015). Asháninka palm management and domestication in the Peruvian Amazon. *Hum. Ecol.* 43, 1-16.

Stahl, P. W. (2015). Interpreting interfluvial landscape transformations in the pre-Columbian Amazon. *The Holocene* 25, 1598–1603.

Steffen, W., Crutzen, P. J., and McNeill, J. R. (2007). The Anthropocene: are humans now overwhelming the great forces of nature. *AMBIO* 36, 614-621.

Stenborg, P. (2016). *Beyond Waters: Archaeology and Environmental History of the Amazonian Inland*. Gothenburg: University of Gothenburg.

Stenborg, P., Schaan, D. P., and Figueiredo, C. G. (2018). Contours of the Past: LiDAR Data Expands the Limits of Late Pre-Columbian Human Settlement in the Santarém Region, Lower Amazon. *J. Field Archaeol.* 43, 1-14.

Sternberg, H. O. R. (1998). *A água e o homen na várzea do Careiro*. Belém: Museu Paraense Emílio Goeldi.

Sujii, P. S., Martins, K., de Oliveira Wadt, L. H., Azevedo, V. C. R., and Solferini, V. N. (2015). Genetic structure of Bertholletia excelsa populations from the Amazon at different spatial scales. *Conserv. Gen.* 16, 955-964.

Tamanaha, E. K. (2012). *Ocupação Polícroma no Baixo e Médio Rio Solimões, Estado do Amazonas*. Master’s Thesis, PPGA-MAE-USP, São Paulo.

Tang, Y., Horikoshi, M. and Li, W. (2016). ggfortify: Unified interface to visualize statistical results of popular R Packages. *The R Journal* 8, 478-489.

Teixeira S. G., and Maia M. A. M. (2009). “Análise da dinâmica das margens do Rio Madeira (AM) no período de 1987 à 2007 a partir de imagens de sensores remotos ópticos,” in *Anais do XIV Simp. Bras. Sens. Rem.* (São José dos Campos: INPE), 1559-1566.

ter Steege, H., Pitman, N. C., Phillips, O. L., Chave, J., Sabatier, D., Duque, A., et al. (2006). Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* 443, 444-447.

ter Steege, H., Pitman, N. C. A., Sabatier, D., Baraloto, C., Salomão, R. P., Guevara, J. E., et al. (2013). Hyperdominance in the Amazonian tree flora. *Science* 342, 1243092.

ter Steege, H., Pitman, N. C., Killeen, T. J., Laurance, W. F., Peres, C. A., Guevara, J. E., et al. (2015). Estimating the global conservation status of more than 15,000 Amazonian tree species. *Sci. Adv.* 1, e1500936.

Terborgh, J. (2012). Enemies maintain hyperdiverse tropical forests. *Am. Nat.* 179, 303-314.

Terrell, J. E., Hart, J. P., Barut, S., Cellinese, N., Curet, A., Denham, T., et al. (2003). Domesticated landscapes: The subsistence ecology of plant and animal domestication. *JAMT* 10, 323-368.

Thomas, E., van Zonneveld, M., Loo, J., Hodgkin, T., Galluzzi, G., and van Etten, J. (2012). Present spatial diversity patterns of Theobroma cacao L. in the neotropics reflect genetic differentiation in Pleistocene refugia followed by human-influenced dispersal. *PLoS One* 7, e47676.

Thomas, E., Alcázar Caicedo, C., McMichael, C. H., Corvera, R., and Loo, J. (2015). Uncovering spatial patterns in the natural and human history of Brazil nut (Bertholletia excelsa) across the Amazon Basin. *J. Biogeog.* 42, 1367-1382.

Toledo, M., Peña-Claros, M., Bongers, F., Alarcón, A., Balcázar, J., Chuviña, J., et al. (2012). Distribution patterns of tropical woody species in response to climatic and edaphic gradients. *J. Ecol.* 100, 253-263.

Valencia, R., Foster, R. B., Villa, G., Condit, R., Svenning, J.-C., Hernández, C., et al. (2004). Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. *J. Ecol.* 92, 214–229.

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

Vos, V. A., Vaca, O., and Cruz, A. (2015). *Sistemas Agroforestales en la Amazonía Boliviana*. La Paz: Centro de Investigación y Promoción del Campesinado.

Walker, R. S., and Ribeiro, L. A. (2015). Bayesian phylogeography of the Arawak expansion in lowland South America. *Proc. R. Soc. Lond., B, Biol. Sci.* 278, 2562-2567.

Waters, C. N., Zalasiewicz, J., Summerhayes, C., Barnosky, A. D., Poirier, C., Gałuszka, A., et al. (2016). The Anthropocene is functionally and stratigraphically distinct from the Holocene. *Science* 351, aad2622.

Watling, J., Iriarte, J., Mayle, F. E., Schaan, D., Pessenda, L. C. R., Loader, N. J., et al. (2017a). Impact of pre-Columbian “geoglyph” builders on Amazonian forests. *Proc. Natl. Acad. Sci. U.S.A.* 114, 1868–1873.

Watling, J., Iriarte, J., Maylec, F. E., Schaand, D., Pessendae, L. C. R., Loaderf, N. J., et al. (2017b). Reply to Piperno et al.: It is too soon to argue for localized, short-term human impacts in interfluvial Amazonia. *Proc. Natl. Acad. Sci. U.S.A.* 114, 201705697.

West, P., Igoe, J., and Brockington, D. (2006). Parks and peoples: the social impact of protected areas. *Annu. Rev. Anthropol.* 35, 251-277.

Wiersum, K. F. (1997a). Indigenous exploitation and management of tropical forest resources: an evolutionary continuum in forest-people interactions. *Agric. Ecosyst. Environ.* 63, 1–16.

Wiersum, K. F. (1997b). From natural forest to tree crops, co-domestication of forests and tree species, an overview. *NJAS* 45, 425-438.

Willis, K. J., Gillson, L., and Brncic, T. M. (2004). How“ virgin” is virgin rainforest? *Science* 304, 402–403.

WinklerPrins, A. M. G. A. , and Aldrich, S. P. (2010). Locating Amazonian Dark Earths: Creating an interactive GIS of known locations. *J. Lat. Am. Geogr.* 9, 33-50.

Wirth C., Messier C., Bergeron Y., Frank D., and Fankhänel A. (2009). “Old-growth forest definitions: a pragmatic view,” in *Old-growth forests: Function, fate and value*, eds C. Wirth, G. Gleixner, and M. Heimann (New York, Berlin, Heidelberg: Springer).

Woods, W. I., and McCann, J. M. (1999). The anthropogenic origin and persistence of Amazonian Dark Earths. *Yearb Conf. Lat. Am. Geogr*. 25, 7-14.

Woods, W. I., Denevan, W. M., and Rebellato, L. (2013). “How many years do you get for couterfeitting a paradise?,” in *Soils, Climate and Society Archaeological Investigations in Ancient America*, eds S. E. Hayes and J. D. Wingard (Denver: University Press of Colorado), 1–20.

Zeder, M. A. (2006). Central questions in the domestication of plants and animals. *Evol. Anthr.* 15, 105–117.

Zent, E. L., and Zent, S. (2004). “Amazonian Indians as Ecological Disturbance Agents: The Hotï of the Sierra de Maigualida, Venezuelan Guayana,” in *Etnobotany and Conservation of Biocultural Diversity*, eds T. S. Carlson and L. Maffi (Bronx, NY: NYBG Press), 79–112.

Zent, S., and Zent, E. (2012). Jodï horticultural belief, knowledge and practice: incipient or integral cultivation? *Bol. Mus. Para. Emílio Goeldi. Cienc. Hum.* 7, 293–338.

Zobel, M. (1997). The relative of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends Ecol. Evol.* 12, 266–269.

Zohary, D. (2004). Unconscious selection and the evolution of domesticated plants. *Econ. Bot.* 58, 5-10.

Zurita-Benavides, M. G., Jarrín–V, P., and Rios, M. (2016). Oral History Reveals Landscape Ecology in Ecuadorian Amazonia: Time Categories and Ethnobotany among Waorani People. *Econ. Bot.* 70, 1-14.

SUMMARY

The idea that Amazonian forests have been largely untouched by humans has fascinated naturalists, policy makers, the media, and natural and social scientists worldwide. For many decades, ecological studies overlooked the influence of past peoples in modern forests. However, humans arrived in the Amazon basin at least 13,000 years Before Present (BP) and populations expanded strongly around 2,500 years BP. Evidence of past human activities has been found in extensive areas previously considered pristine. Anthropogenic soils (Amazonian Dark Earths - ADE) and human-made earthworks found across the basin are examples of the landscapes domesticated by pre-Columbian peoples and evidence of large societies with considerable capacity for modifying the environment. Cultivation and management of Amazonian flora by past societies may have significantly contributed to the ecological patterns we see today.

These findings stimulated an academic debate about the pristineness versus domestication of Amazonian forests. Although most scientists agree that human impacts were spatially heterogeneous across the basin, the scale of past human influences in Amazonian forests remains controversial. A more realistic and broad-scale view is required (**Chapter 1**). In my thesis, I integrated data from different disciplines in the social and natural sciences to generate the first broad-scale assessment of the effects of long-term human influences in modern Amazonian forests and how these legacies are maintained by local management practices. I studied the Amazon forest as a mosaic of patches domesticated to different degrees by human-nature interactions.

To estimate the influence of past people on modern forests, I first compared the density of sedentary pre-Columbian occupation sites with ADE along some stretches of major white-water rivers and their black or clear-water tributaries that have been sampled by archaeologists. I counted the number of archaeological sites along 12-km sections for both river orders (major and tributary) and found the same density of sites along both orders, showing that archaeological sites are widespread across tributary rivers of the Central Amazon basin (**Chapter 2**). This result suggests that the influence of past societies in Amazonian landscapes is more extensive than previously imagined and deserves further investigation.

To unravel the effects of long-term human actions at the basin-wide scale, we investigated the relationship between the richness and abundance of 85 domesticated plant species found in Amazonian forests and the distribution of known archaeological sites (**Chapter 3**). We focused on domesticated species because they are known to have been propagated and selected by peoples in Amazonia and elsewhere in the Americas for food or other uses for a long time. I correlated data from more than 1,000 floristic inventories of the Amazon Tree Diversity Network (ATDN) with a map of more than 3,000 archaeological sites across different Amazonian geological regions compiled by the AmazonArch Network. Our analysis also incorporated environmental data to distinguish the relative importance of environmental conditions from past human factors on modern plant communities. We found that domesticated species were five times more likely to be common in floristic inventories than non-domesticated species and sometimes more abundant far from the places where they were domesticated, suggesting past human dispersal. The richness and abundance of these domesticated species increase with the proximity to archaeological sites and in areas with poorly drained soils and higher rainfall seasonality. Our results show that plant communities in Amazonia are structured by both natural and cultural processes, and refute the idea that these forests are largely untouched by humans.

To understand the relative contribution of past and recent human activities in shaping these current floristic patterns, we expanded our previous analyses to incorporate the influence of current activities (**Chapter 4**). We found that old-growth forests were transformed by both past and current peoples, but we showed that the effects of recent activities have a smaller role when compared to the persistent effects of pre-Columbian activities on forest composition. Overall, these new analyses strengthened the importance of ancient peoples in explaining the richness and abundance of domesticated species across Amazonia.

In **Chapter 5**, we investigated how Amazonian people enriched plant communities with useful and domesticated species. To answer this question, we collected extensive information from the literature and data in the field about how Amazonian peoples manage forest resources. With this information, we developed a conceptual model that showed eight key categories of forest management practices that alter natural ecological processes and transform pristine into domesticated forests. Our model allows inferences about how human societies developed ways to interfere with natural ecological processes through time, which created more productive and useful forests across the basin. This long-term process resulted in numerous and diverse patches of useful trees and palms around archaeological sites where humans have lived for centuries or millennia. Thus, a diverse assemblage of useful plant species persists in Amazonian forests due to long-term management practices (**Chapters 3-5**).

In **Chapter 6**, we compared the effect of ancient and recent management practices on Amazonian forest soils and vegetation at different distances from pre-Columbian and contemporary villages settled in protected areas. We found that soil nutrients of old-growth forests increased with the proximity to ancient villages, but did not increase with the intensity of recent management activities. By enriching

soil nutrients in and around their villages, past societies provided the conditions for forests enriched with species of great interest to modern Amazonian societies. Overall, our results support the hypothesis that ancient management practices have a stronger influence in soils of old-growth forests than recent management practices.

This thesis reveals the persistence of a cultural heritage in modern Amazonian forests, which was created by ancient societies and maintained by present-day peoples. During the millennia that humans have lived in Amazonia, they interacted with nature, modifying landscapes around their villages into forest mosaics formed by patches rich in fertile anthropogenic soils and forest resources, such as foods, medicines and construction materials. To conclude, Amazonian forests hold legacies of past human activities that can only be fully understood by interdisciplinary studies and that require local management practices to be maintained through time.

RESUMO

A ideia de que as florestas amazônicas foram praticamente intocadas por humanos tem fascinado naturalistas, tomadores de decisão, a mídia e cientistas naturais e sociais em todo o mundo. Por muitas décadas, os estudos ecológicos negligenciaram a influência dos povos do passado nas florestas modernas. No entanto, os seres humanos chegaram à bacia amazônica há pelo menos 13.000 anos Antes do Presente (AP) e as populações expandiram-se dramaticamente em torno de 2.500 anos AP. Evidências de atividades humanas passadas foram encontradas em extensas áreas anteriormente consideradas intocadas. Solos antropogênicos (Terras Pretas de Índio – TPI, também chamadas de Amazonian Dark Earth – ADE) e estruturas de terra feitas pelo homem (obras de terra) encontrados em toda a bacia são exemplos de paisagens domesticadas por povos pré-colombianos e sinais de grandes sociedades com considerável capacidade de modificar o meio ambiente. O cultivo e o manejo da flora amazônica por sociedades do passado podem ter contribuído significativamente para os padrões ecológicos que vemos hoje.

Essas descobertas estimularam um debate acadêmico sobre a virgindade versus a domesticação das florestas amazônicas. Embora a maioria dos cientistas concorde que os impactos humanos eram espacialmente heterogêneos na bacia amazônica, a escala da influência humana passada nas florestas atuais permanece controversa. É necessária uma visão mais realista e em larga escala (**Capítulo 1**). Em minha tese, eu integrei dados e práticas de diferentes disciplinas das ciências sociais e naturais para gerar a primeira avaliação em larga escala dos efeitos das influências humanas de longo prazo nas florestas atuais da Amazônia e como esses legados são mantidos por práticas de manejo locais. Estudei a floresta amazônica como um mosaico de manchas domesticadas em diferentes graus pela interação homem-natureza.

Para estimar a influência dos povos do passado nas florestas atuais, comparei a densidade de sítios pré-colombianos de ocupação humana sedentária (TPI) ao longo de alguns trechos dos grandes rios de águas brancas e seus afluentes de águas negras ou claras que foram amostrados por arqueólogos. Eu contei o número de sítios arqueológicos para ambas as ordens fluviais (principais e tributárias) e encontrei a mesma densidade de sítios de terra preta por secções de 12 km ao longo de ambas as ordens, mostrando que os sítios arqueológicos também estão espalhados pelas margens dos rios tributários da Amazônica Central (**Capítulo 2**). Esse resultado sugere que a influência das sociedades do passado nas paisagens amazônicas é mais extensa do que se imaginava e merece uma investigação mais aprofundada.

Para desvendar os efeitos das ações humanas de longa duração na escala da bacia, investigamos a relação entre a riqueza e a abundância de 85 espécies de plantas domesticadas encontradas nas florestas amazônicas e a distribuição de sítios arqueológicos conhecidos (**Capítulo 3**). Nós focamos o estudo em espécies domesticadas porque elas são conhecidas por terem sido propagadas e selecionadas por povos na Amazônia e em outros lugares das Américas para alimentação ou outros usos por um longo período de tempo. Eu correlacionei dados de mais de 1.000 inventários florísticos da Rede de Diversidade de Árvores da Amazônia (ATDN) com um mapa de mais de 3.000 sítios arqueológicos mapeados em diferentes regiões geológicas e compilados pela Rede AmazonArch. Nossa análise também incorporou dados ambientais para distinguir a importância relativa das condições ambientais locais e dos fatores humanos passados nas comunidades vegetais do presente. Descobrimos que espécies domesticadas tinham cinco vezes mais probabilidade de serem comuns em inventários florísticos do que espécies não domesticadas e, às vezes, as domesticadas são mais abundantes longe dos locais onde elas foram domesticadas, sugerindo eventos de dispersão humana passada. A riqueza e a abundância dessas espécies domesticadas são maiores nas proximidades de sítios arqueológicos e em áreas com solos pouco drenados e com maior sazonalidade das chuvas. Nossos resultados mostram que as comunidades vegetais na Amazônia são estruturadas por processos naturais e culturais, e refutam a ideia de que essas florestas são praticamente intocadas pelos seres humanos.

Para entender a contribuição relativa de atividades humanas passadas e recentes na formação desses padrões florísticos, nós expandimos nossas análises anteriores ao incorporar a influência das atividades atuais (**Capítulo 4**). Descobrimos que as florestas maduras foram transformadas pelos povos do passado e do presente, mas mostramos que os efeitos das atividades recentes têm um papel menor quando comparados aos efeitos persistentes das atividades pré-colombianas na composição da floresta. De modo geral, essas novas análises reforçaram a importância das atividades dos povos antigos para explicar a riqueza e a abundância de espécies domesticadas na Amazônia como um todo.

No **Capítulo 5**, investigamos como os povos da Amazônia enriqueciam as comunidades de plantas com espécies úteis e domesticadas. Para responder a essa pergunta, coletamos extensivamente informações da literatura e dados de campo sobre como os povos amazônicos manejaram os recursos florestais. Com essas informações, desenvolvemos um modelo conceitual que demonstrou como oito categorias principais de práticas de manejo florestal alteram os processos ecológicos naturais e transformam florestas pristinas em florestas domesticadas. Nosso modelo permite inferências sobre como as sociedades humanas desenvolveram maneiras de interferir nos processos ecológicos naturais ao longo do tempo, o que criou florestas mais produtivas e úteis ao longo da bacia (**Capítulo 5**). Esse longo processo resultou em numerosas e diversas manchas de árvores e palmeiras úteis ao redor de sítios arqueológicos onde as pessoas viveram por séculos ou milênios. Assim, um conjunto diversificado de espécies de plantas úteis persiste nas florestas amazônicas devido às práticas de manejo por um longo período de tempo (**Capítulos 3-5**).

No **Capítulo 6**, comparamos os efeitos das práticas de manejo antigas e recentes nos solos e na vegetação da floresta amazônica a diferentes distâncias de vilas pré-colombianas e contemporâneas presentes em áreas protegidas. Descobrimos que os nutrientes do solo das florestas maduras aumentaram com a proximidade de aldeias antigas, mas não aumentaram com a intensidade das atividades recentes de manejo. Ao enriquecer os nutrientes do solo ao redor de suas aldeias, as sociedades do passado forneceram as condições para as florestas enriquecerem com espécies de grande interesse das sociedades modernas da Amazônia. Em geral, nossos resultados apoiam a hipótese de que práticas antigas de manejo têm uma influência mais forte nos solos das florestas maduras do que as práticas de manejo recentes.

Esta tese revela a persistência de um patrimônio cultural nas florestas amazônicas atuais, criado por sociedades antigas e mantido pelos povos atuais. Ao longo de milhares de anos de ocupação humana na Amazônia, as pessoas interagiram com a natureza, modificando paisagens em torno de suas aldeias em mosaicos florestais formados por manchas ricas em solos antropogênicos férteis e recursos florestais, como alimentos, remédios e materiais de construção. Para concluir, as florestas de hoje mantêm legados de atividades humanas passadas que só podem ser plenamente compreendidos por estudos interdisciplinares e que requerem práticas de manejo locais para serem mantidos ao longo do tempo.

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Terra Preta (Rio Madeira)

Bernardo Flores, Carolina Levis e Ricardo Braga-Neto

Bm Em F#7
Da lixeira surgiu a fertilidade
onde antes era aldeia, hoje é comunidade

Bm G F#7 Bm
Partimos de Manaus em busca de história
do povo dessa terra, guardada na memória

Bm A7
Uma história que não é... ensinada na escola

Bm G F#7
é contada oralmente ou cantada na viola

REFRÃO
Em A7 Bm
É a terra preta,
onde tudo o que se planta dá
não sabemos a receita,
Bm G F#7
mas o caboclo a sabe usar
--

Bm G F#7
A pobreza natural do solo que aqui existe
transformada intencional pelo índio que persiste

Bm A7
E a mata do entorno, traz a sombra e a vida
Bm G F#7
foi cuidada e enriquecida, hoje alimenta a quem precisa

Em A7 Bm
Tem caiaué, tucumã, teperebá
balde de cuia leva a peia quem quebrar
A7 Bm
se cavou, pote de índio encontrou
G F#7
o biribá, o povo selecionou

Music written during fieldwork of this thesis

A História dos Tapajó

Bernardo Flores e Carolina Levis

Bm Em G F7
O Frei Carvajal contou
o que viu quando ali passou
em longas canoas
milhares de índios guerreiros

Depois a coroa chegou
era pombalina que se iniciou
fazendo-os abandonar
todos seus terreiros
--

Bm A G F7
Esta guardada na terra
a sua cronologia
revelando a historia
dessa linda nação

Sempre presente
pois hiato não havia
por mais de três mil anos
ate a chegada de uma missão

REFRÃO
Os Tapajó
que cantavam noite e dia
Os Tapajó
viviam só na alegria
--

Um ribeirinho me disse
se na serra eu subisse
encontraria sinais
dos seus ancestrais

Onde a samauma sagrada
trazida de longe e plantada
cercada de piquiás
taberebazeiros e uxizais

A mata por eles moldada
tem tanta serventia
o leite do amapá
que alimenta e da energia

o piquia tem o seu sabor
mas alivia inchaço e a dor
uxi mata a fome na mata
e chama a caça para o caçador

Ao baixar o Rio Negro (chocalho)
da Cabeça do Cachorro (chocalho)
vai encontrar conhecimento (chocalho)
do índio e do caboblo (chocalho)

Bm Em F#7 A
Quando eu cheguei um velho Macu
Nukak ou Hupda eu não sei....
Usava ipadu, cachaça lhe neguei
ao horizonte a mata, eu pensei....

A7 Bm
Por que viver assim, onde o branco é tão ruim
sem dinheiro pra comprar,

G7 F#7 Bm
o que de graça a natureza pode dar

Bm Em F#7
Da mata à mandioca
uma floresta à maniva da lugar
o caranã cobre a maloca
como é bom o vinho do patauá

REFRÃO
Bm Em F#7 Bm
Kuekaturetê
puranga ara, um bejú para você
B7 Em G F#7 Bm
Se me agradecer, com prazer
vou dizer, tymaresê
\---

Bm Em F#7
Pimenta e peixe faz kinhapira
do igapó vai parar no cacurí
se tem respeito ao Curupira
sempre haverá para os que estão por vir

REFRÃO
Bm Em F#7
Dona Guria abre a clareira
queima carvão para plantar bananeira
em sua roça põe semente de umari
para depois ir colher na capoeira

A7 Bm
Yandé ruca iwi-pixuna (minha casa a terra preta)
Yasu re kaá keté iwi eté (vou pra mata lugar onde moro)
Yawareté puranga pituna (olha a onça, boa noite)

G7 F#7 Bm
Até amuramé (até qualquer outro dia)
A7 G7 F#7 Bm

Até qualquer outro dia (Rio Negro)

Bernardo Flores e Carolina Levis

Music written during fieldwork of this thesis

SHORT BIOGRAPHY

Carolina Levis was born on the 28th of April 1987 in Rio de Janeiro (Brazil). Carolina first studied in the Sá Pereira primary school (1991-1997) and graduated from the *Colégio São Vicente de Paulo* (1998-2004), both in Rio de Janeiro. Her family had a small ranch in the mountains of Rio de Janeiro, where she spent most school holidays during childhood and discovered her passion for all life forms. During high school, Carolina was a volunteer teacher assistant in the program of "youth and adult education" (EJA in Portuguese) at the *Colégio São Vicente de Paulo*, as well as with socio-educational activities with vulnerable kids of the "*Obra do Berço*" project. She also spent four months studying in the Morgantown High School (West Virginia, United States) while her aunt was doing a PhD and this was her first opportunity to experience the university environment.

In 2005, Carolina started a bachelor's degree in Geography at the Pontifical Catholic University (PUC-RIO), but her dream to become a biologist and study in a public university in Brazil, which led her to study Biological Sciences at the Federal University of Rio de Janeiro (UFRJ), where she graduated in 2010. During her undergraduate studies, she did an internship at the Institute for Research of the Rio de Janeiro Botanic Garden – IP/JBRJ, working with experiments in forest restoration in the Atlantic Forest Program. She was also involved in environmental education and agroecology in two UFRJ extension projects "*ÉA Vila*" and "*Capim Limão*", coordinating and carrying out activities in public schools.

Pursuing another dream, Carolina moved to Manaus (Amazonas, Brazil) to do her master's degree and discover the Amazonian forests, peoples and histories, where she met very special people that inspired her in life and science. She did her MSc studies at the National Institute of Amazonian Research (INPA, Brazil) evaluating the influences of past human activities in Central Amazonian forests, under the supervision of Dr. Flavia R. C. Costa and Dr. Charles R. Clement, with whom Carolina has been working for eight years.

Since her master's degree, she has been part of two Brazilian research groups at INPA, "*Terra Preta Nova*" and "*Conservação e Manejo da Biota Amazônica*", and three international networks, the Amazon Tree Diversity Network (ATDN), the Amazon Forest Inventory Network (RAINFOR) and the Amazonian Archaeological Sites Network – AmazonArch. In September of 2012, Carolina had the opportunity to work as a visiting researcher at the Forest Ecology and Management Group of Wageningen University & Research (WUR) and met Dr. Marielos Peña-Claros and Prof. Dr. Frans Bongers, who inspired her to do a PhD, expanding her previous study and approaches to the whole Amazon basin.

In 2014, she started a joint PhD (double degree) in Ecology at INPA (Brazil) and in Production Ecology and Resource Conservation at WUR (The Netherlands). During her PhD, she discovered science as a vocation and had the opportunity to collaborate with Prof. Dr. Hans ter Steege (Naturalis Biodiversity Center) and more than 160 researchers of at least 15 nationalities and numerous scientific disciplines. She has learned the importance of publishing in high impact journals and understood how large-scale studies depend on a collaborative effort in data collection and analysis, and writing scientific articles. During her PhD studies, Carolina received three research awards.

For her career, she wants to use her creativity in connecting people and ideas to produce innovative and interdisciplinary studies that can meet local human needs and contribute to biodiversity conservation. Carolina seeks to make a difference in building knowledge for a society that needs to reunify nature and culture.

LIST OF PUBLICATIONS

International scientific journals

Gomes, V. H., IJff, S. D., Raes, N., Amaral, I. L., Salomão, R. P., Coelho, L. S., ... **Levis, C.**, … et al. (2018). Species Distribution Modelling: Contrasting presence-only models with plot abundance data. *Scientific reports* 8, 1003.

Levis, C., Flores, B. M., Moreira, P. A., Luize, B. G., Alves, R. P., Franco-Moraes, J., et al. (2018). How people domesticated Amazonian forests. *Frontiers in Ecology and Evolution* 5, 171.

Levis, C., Costa, F. R. C., Bongers, F., Peña-Claros, M., Clement, C. R., Junqueira, A. B., et al. (2017). Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science* 355, 925–931.

Levis, C., Clement, C. R., Ter Steege, H., Bongers, F., Junqueira, A. B., Pitman, N., et al. (2017). Forest conservation: humans' handprints. *Science* 355, 466–467.

Junqueira, A. B., **Levis, C.**, Bongers, F., Peña-Claros, M., Clement, C. R., Costa, F., and ter Steege, H. (2017). Response to Comment on "Persistent effects of pre-Columbian plant domestication on Amazonian forest composition". *Science* 358, eaan8837.

Goulart, A. C., Macario, K. D., Scheel-Ybert, R., Alves, E. Q., Bachelet, C., Pereira, B. B., … **Levis, C.**, … et al. (2017). Charcoal chronology of the Amazon forest: A record of biodiversity preserved by ancient fires. *Quaternary Geochronology* 41, 180-186.

Alves, R. P., **Levis, C.**, and Clement, C. R. (2016). Use and Management of Piquiá Suggest in situ Domestication along the Lower Tapajós River, Brazilian Amazonia. *Economic Botany* 70, 198-202.

Schietti, J., Martins, D., Emilio, T., Souza, P. F., **Levis, C.**, Baccaro, F. B., et al. (2016). Forest structure along a 600 km transect of natural disturbances and seasonality gradients in central-southern Amazonia. *Journal of Ecology* 104, 1335-1346.

Fauset, S., Johnson, M. O., Gloor, M., Baker, T. R., Monteagudo, A., Brienen, R. J., … **Levis, C.**, … et al. (2015). Hyperdominance in Amazonian forest carbon cycling. *Nature Communications* 6, 6857.

Poorter, L., Sande, M. V. D., Thompson, J., Arets, E. J. M. M., Alarcón, A., Álvarez-Sánchez, J., … **Levis, C.**, … et al. (2015). Diversity enhances carbon storage in tropical forests. *Global Ecology and Biogeography* 24, 1314-1328.

ter Steege, H., Pitman, N. C., Killeen, T. J., Laurance, W. F., Peres, C. A., Guevara, J. E., … **Levis, C.**, … et al. (2015). Estimating the global conservation status of more than 15,000 Amazonian tree species. *Science Advances* 1, e1500936.

Mitchard, E. T., Feldpausch, T. R., Brienen, R. J., Lopez-Gonzalez, G., Monteagudo, A., Baker, T. R., … **Levis, C.**, … et al. (2014). Markedly divergent estimates of Amazon forest carbon density from ground plots and satellites. *Global Ecology and Biogeography* 23, 935-946.

ter Steege, H., Pitman, N. C. A., Sabatier, D., Baraloto, C., Salomão, R. P., Guevara, J. E., … **Levis, C.**, … et al. (2013). Hyperdominance in the Amazonian Tree Flora. *Science* 342, 1243092.

Cintra, B. B. L., Schietti, J., Emillio, T., Martins, D., Moulatlet, G., Souza, P., … **Levis, C.**, … et al. (2013). Soil physical restrictions and hydrology regulate stand age and wood biomass turnover rates of Purus-Madeira interfluvial wetlands in Amazonia. *Biogeosciences* 10, 7759-7774.

Levis, C., de Souza, P. F., Schietti, J., Emilio, T., da Veiga Pinto, J. L. P., Clement, C. R., and Costa, F. R. C. (2012). Historical human footprint on modern tree species composition in the Purus-Madeira interfluve, central Amazonia. *PLoS One* 7:e48559.

Publications (Books, Annals of conferences and other articles)

Clement C. R., Junqueira, A. B., Moreira, P. A., Lins, J., **Levis, C.**, Cabral, T. S., and Lima, P. P. (2015). "Ecologia histórica e a criação da agrobiodiversidade na Amazônia: lições para a agroecologia" in *Agrobiodiversidade e Agroecologia* , eds. J. Santilli, P. Bustamante, R. L. Barbieri R. L. Coleção Transição Agroecológica – Associação Brasileira de Agroecologia (Brasília, DF: Embrapa), 27-50.

Levis, C., Silva, M. S., Silva, M. A., Moraes, C. P., Neves, E. G., Tamanaha, E. K., et al. (2014). "What do we know about the distribution of Amazonian Dark Earth along tributary rivers in Central Amazonia?," in: *Antes de Orellana - Actas del 3er Encuentro Internacional de Arqueología Amazónica*, ed. S. Rostain (Lima, Peru: Instituto Francés de Estudios Andinos), 305-311.

Levis, C. et al. (2013). *A disputa desigual entre peixes nativos e exóticos do semiárido*. (Natal, RN: EDUFRN), 76p.

Clement, C. R, Lins, J., Junqueira, A. B., Jakovac, A. C. C., Cabral, T. S., **Levis, C.**, et al. (2013). Uma Revolução Beckeriana para a biodiversidade brasileira. *Jornal da Ciência*, Rio de Janeiro; avaliable online at http://www.museu-goeldi.br/portal/node/986.

PE&RC Training and Education Statement

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

Review of literature (4.5 ECTS)

The legacy of landscape domestication by pre-Columbian peoples in the Amazon forest

Writing of project proposal (4.5 ECTS)

The legacy of landscape domestication by pre-Columbian peoples in the Amazon forest

Post-graduate courses (11.4 ECTS)

Spatial sampling for mapping; PE&RC and SENSE (2015)

FNP Summer School: governing landscape restoration;
Wageningen School of Social Science (2015)

Mixed linear models; PE&RC and SENSE (2015)

III Area seminar; Graduate Program in Ecology, INPA, Brazil (2016)

Ethnobiology; Graduate Program in Ecology, INPA, Brazil (2016)

Origin and domestication of cultivated plants;
Graduate School in Plant Genetics Resources, UFSC, Brazil (2017)

Species distribution modelling; Graduate Program in Ecology, INPA, Brazil (2017)

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

Journal of Biogeography: historical ecology (2015)

Economic Botany: ethnobotany (2016)

Competence strengthening / skills courses (1.5 ECTS)

Workshop gender and diversity; WUR (2015)

PhD Workshop carousel; WGS (2015)

Competence assessment; WGS (2015)

Field: in the frontiers of climate change: the forest as the city; National Forest of Tapajós,
Archaeology in Amazonia (2016)

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

PE&RC Day (2014)

PE&RC Symposium vegetation: soil interactions: from rhizosphere to ecosystem (2014)

PE&RC First years weekend (2015)

Discussion groups / local seminars / other scientific meetings (8.1 ECTS)

FEM Journal club; WUR, the Netherlands (2015)

Terra Preta symposium; WUR, the Netherlands (2015)

1st Workshop on the upper Madeira River project; Newton Fund, INPA, Brazil (2015)

2nd TPI Workshop; Porto Velho, Brazil (2016)

Discussion group meeting Ecological Theory and Application; WUR, the Netherlands (2016)

Seminars of Plant Ecology; INPA, Brazil (2017)

Seminars of indigenous studies of NEAI; UFAM, Brazil (2017)

Seminars of science; INPA, Brazil (2017)

2nd Landcover6K workshop; Trinidad, Bolivia (2017)

International symposia, workshops and conferences (10.3 ECTS)

Annual Conference of the Society for Tropical Ecology (GTÖ); oral and poster (2015)

Annual Meeting of the Association of Tropical Biology and Conservation (ATBC); oral presentation (2016)

Annual Meeting of the Association of Tropical Biology and Conservation (ATBC); oral presentation
and co-organizer of symposium (2017)

IV Encuentro Internacional de Arqueología Amazónica (IV EIAA); oral presentation and discussion panel (2017)

Lecturing / supervision of practicals / tutorials (0.3 ECTS)

Trends in forest and nature conservation course, reconsidering pristine nature: what do we aim to conserve?” (2015)

Co-supervision of BSc students

Ethnobotany and domestication of the Amazon (Evelien Konings)

Uses, management and domestication of Amazonian tree and palm species,
an ethnobotanical analysis (Robin Bredero)

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