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A história humana através dos padrões de recrutamento e trajetórias de crescimento de *Bertholletia excelsa* em um castanhal na Amazônia Central

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Sinopse:

Esta dissertação de mestrado trata-se de um estudo sobre a relação entre fatores históricos e os distúrbios florestais em um castanhal da Amazônia central ao longo dos últimos três séculos. Através de análises dos anéis de crescimento, reconstruiu-se o recrutamento de cada castanheira no castanhal e sua trajetória individual de crescimento. Paralelamente, reconstruiu-se através de pesquisa bibliográfica o histórico da ocupação territorial e suas diferenças ao longo do tempo. Os resultados deste trabalho sugerem processos pelos quais humanos favoreceram o crescimento e estabelecimento de castanheiras e contribuíram para a atual estrutura do castanhal estudado. Além disso, alude a perda do conhecimento ancestral do manejo florestal realizado pelas antigas populações amazônicas.

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Resumo

Desde o momento em que os seres humanos chegaram à região amazônica, pelo menos a 12 mil anos, começaram a manejar a floresta, em um processo de domesticação de longo prazo. Mas com o colapso demográfico indígena após 1492, essa antiga relação entre humanos e florestas pode ter sido parcialmente perdida. *Bertholletia excelsa* Bonpl. (Lecythidaceae) é uma árvore icônica que domina vastas áreas da floresta amazônica e conhecida por ser usada, manejada e domesticada por humanos desde antes da chegada europeia na Amazônia. Considerando a íntima relação histórica entre os seres humanos e a castanha da Amazônia, ainda não está claro se a dinâmica das populações a longo prazo dessa espécie dentro da floresta foi conduzida por práticas de manejo e se essa interação mudou após o colapso das sociedades pré-coloniais. Aqui, reconstruímos mais de 300 anos da dinâmica populacional de um castanhal na Amazônia Central e relacionamos com a história humana nessa região. Para isso, combinamos as análises de anéis de crescimento que podem revelar o modo como as taxas de recrutamento e crescimento das árvores mudaram ao longo do tempo, com informações históricas sobre os principais fatos políticos e econômicos que podem ter impactado a vida de indígenas e colonos. Nossos resultados revelam que a intensificação do domínio político sobre a colônia em torno de 1800 coincidiu com fortes reduções de recrutamento e taxas de crescimento de B. excelsa, sugerindo o abandono das práticas de manejo indígena. Um pulso de recrutamento mais recente no século 20, associado a ciclos sem precedentes de liberação e supressão de crescimento, sugerem uma nova fase de gerenciamento envolvendo práticas não-indígenas. Nossas descobertas sugerem que os seres humanos têm historicamente dado forma a dinâmica da população de castanheiras, e aludem à perda do antigo conhecimento de manejo florestal com o colapso das sociedades pré-colombianas.

Abstract

From the moment Humans arrived in the Amazonian region, at least 12 ky ago, they started managing the forest, in a long term domestication process, yet with the indigenous demographic collapse after 1492, this ancient human-forest relationship may have been partially lost. *Bertholletia excelsa* Bonpl. (Lecythidaceae) is an iconic nut tree that dominates vast swaths of the Amazon forest, and known for being used, managed and domesticated by humans since before the European arrival. Considering the intimate historical relationship between humans and the Amazon nut tree, it remains unclear if the long term population dynamics of this species within the forest has been driven by management practices, and if this interaction changed following the collapse of pre-colonial societies. Here we reconstruct over 300 years of population dynamics for a living Amazon nut tree stand in Central Amazonia, and relate this dynamics with human history in that region. For this we combine the analyses of tree-rings that may reveal how tree recruitment and growth rates changed through time, with historical information on the main political and economical facts that may have impacted the lives of indigenous and colonists. Our results reveal that the intensification of political dominance over the colony around 1800 coincided with sharp reductions of recruitment and growth rates of *B. excelsa*, suggesting the abandonment of indigenous management practices. A more recent recruitment pulse in the 20th century, associated with unprecedented cycles of growth release and suppression, suggest a new management phase involving non-indigenous practices. Our findings suggest that humans have historically shaped nut tree population dynamics across the Amazon, and allude to the loss of ancient management knowledge with the collapse of pre-Columbian societies.

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Sumário

1. Introdução

A *Bertholletia excelsa* Bonpl. (Lecythidaceae) é uma árvore emergente da Amazônia, encontrada nas florestas de terra firme (Sousa *et al.*, 2014). É uma espécie de grande porte, que pode alcançar 60 metros de altura e mais de 3 metros de diâmetro (Salomão, 1991, 2009). A castanheira é uma espécie hiperdominante na floresta (ter Steege *et al.*, 2013), e a terceira que mais contribui com o estoque de carbono da Amazônia (Fauset *et al.*, 2015). Na floresta, a *B. excelsa* é uma espécie com tendência a formar adensamentos (castanhais), intercalados por áreas de baixa densidade de indivíduos (Mori & Prance, 1990; Scoles & Gribel, 2011; Scoles *et al.*, 2014). Shepard & Ramirez (2011) reuniram diversos estudos que associam atividades antrópicas de uso do solo do período pré-colombiano com a ocorrência de castanhais, corroborando as observações de Dubois (1992), que associa a dispersão e o desenvolvimento de castanheiras silvestres à influência indígena, sem descartar outros fatores ecológicos.

Outros estudos, no entanto, criticam a noção de que a dispersão dos castanhais seja oriunda de impacto fortemente antrópico (Peres e Baider, 1997), lançando a hipótese que a formação local de castanhais é dada quase exclusivamente pela dispersão de cutias (*Dasyprocta* sp., Rodentia), principal dispersora natural da espécie (Haugaasen *et al.*, 2012). A *B. excelsa* é uma espécie heliófita (Scoles 2010; Scoles *et al.*, 2014) e depende de clareiras para o seu crescimento, bem como para a sobrevivência das plântulas e indivíduos jovens (Mori & Prance 1990; Scoles *et al.* 2014; Sousa *et al.*, 2014).

O fruto da *B. excelsa* é um pixídio lenhoso extremamente duro, que contêm castanhas em seu interior, que possuem grande utilidade e valor econômico, servindo para fins alimentícios (Mori & Prance, 1990). A castanheira é de grande importância histórica e cultural para as populações tradicionais da Amazônia, e seus produtos são utilizados há gerações como fonte de alimentação e renda (Menezes *et al.*, 2005). A primeira evidência de uso humano de sementes de castanha-do-brasil remonta a mais de 11.000 anos (Roosevelt *et al*., 1996). Florestas com alta densidade de castanheiras estão localizadas na proximidade de sítios arqueológicos ocupados por sociedades sedentárias pré-colombianas na Amazônia (Thomas *et al*., 2015). Além disso, populações domesticadas de castanha-do-brasil, com grandes sementes, foram encontradas em florestas da Amazônia Central (Clement *et al*., 2010). De forma geral, a magnitude da influência que as populações Amazônicas pré-colombianas exerceram na biodiversidade continua sendo debatido na atualidade (Levis *et al*., 2017; McMichael *et al*., 2017). De um lado, questiona-se de forma geral, o grau de antropização da Amazônia (Piperno *et al*., 2015; McMichael *et al*., 2017), enquanto, por outro lado, propõe-se uma Amazônia antropizada (Clement *et al*., 2015; Lins *et al*., 2015; Levis *et al*., 2017). A origem do padrão de ocorrência, assim como a distribuição da castanha-do-brasil na bacia amazônica, são questões que integram o debate sobre a domesticação da espécie e da paisagem amazônica (Thomas *et al*., 2014; Thomas *et al*. 2015).

Neste trabalho, reconstruímos o histórico de distúrbios florestais em um castanhal por meio da análise de anéis de crescimento. Embora existam estudos que reconstroem o histórico da dinâmica de clareiras e distúrbios florestais (Baker *et al*., 2005; Baker & Bunyavejchewin, 2006; Rozendaal *et al*., 2010), pouca atenção tem sido dada à origem desses distúrbios (Baker *et al*., 2005), muitas vezes atribuindo-os a fatores naturais temporais e espacialmente aleatórios (Hubbell *et al*., 1999). Baker *et al*. (2005) enfatizam a importância dos distúrbios florestais para a estrutura e funcionamento dos ecossistemas. Os distúrbios afetam diretamente a dinâmica da comunidade, alterando a disponibilidade de recursos (Denslow *et al*., 1998). São importantes na manutenção da diversidade, proporcionando ocasionais períodos favoráveis para o recrutamento de espécies arbóreas (Warner & Chesson, 1985).

A regeneração da castanha-do-brasil é influenciada principalmente pela disponibilidade luz no sub-bosque (Scoles *et al*., 2011; Scoles & Gribel, 2011; Sousa *et al*., 2014). Castanhais que estão atualmente sob influência humana têm taxas de regeneração e crescimento mais altas do que as populações nativas com menor grau de antropização (Paiva *et al*., 2011; Scoles & Gribel, 2011; Ribeiro *et al*., 2014; Scoles *et al*., 2014 Scoles & Gribel, 2015; Scoles & Gribel, 2012). As taxas de incremento anual em diâmetro desta espécie em plantações manejadas, com alta incidência de luz, chegam a ser três vezes maiores do que na floresta (Schöngart *et al*., 2015). Estas informações nos motivaram a reconstruir temporalmente as perturbações ambientais que criaram condições favoráveis para o estabelecimento e crescimento de árvores de *B. excelsa*.

Por meio da análise retrospectiva de anéis anuais de crescimento é possível obter dados de longos períodos de variações de crescimento de árvores (Brienen *et al*., 2006), que são fundamentais para o entendimento da dinâmica da floresta (Worbes, 2002). Existem estudos que reconstroem a trajetória de crescimento da *B. excelsa* para detectar eventos de liberação e supressão de crescimento, dando evidências sobre a dinâmica florestal e o regime de perturbações (Brienen & Zuidema, 2005; Schöngart *et al*., 2015). A anuidade dos anéis de crescimento de *B. excelsa*, formados pelo padrão anatômico alternado de fibras e parênquima, foi confirmada por Brienen & Zuidema (2005) e Schöngart *et al.* (2015) comparando com plantio de idade conhecida e com dados climáticos de precipitação. Estudos que estimam a idade de castanheiras sugerem em geral idades máximas entre 400-500 anos (Camargo *et al.*, 1994; Brienen & Zuidema 2006; Schöngart *et al.*, 2015).

Existe certa dificuldade em separar as influências humanas de outras variáveis ambientais quando analisamos distúrbios florestais formadores de clareiras no passado. Aqui, reconstruímos a história dos distúrbios florestais ocorridos em uma paisagem com um castanhal próximo a Manaus, na Amazônia Central, por meio do crescimento de castanheiras e o castanhal. Paralelamente, consultamos diversas fontes históricas, político-econômicas, e demográficas da região desde o começo da ocupação pelos colonizadores, a mais ou menos quatro séculos. Assim, consideramos o panorama histórico de ocupação humana como fator de perturbação florestal. Apresentamos aqui evidências de que as práticas, tanto dos indígenas do período pré-colombiano como das populações tradicionais que ocuparam o território mais recentemente, favoreceram o desenvolvimento do castanhal.

2. Objetivos

2.1. Objetivo geral

Associar a reconstrução de padrões de estabelecimento e crescimento diamétrico de uma população de *Bertholletia excelsa* (Lecythidaceae) na Amazônia Central (Lago Purupuru) por meio de analises de anéis de crescimento com o panorama histórico da ocupação humana da região de estudo considerando informações sobre a historia, demografia e ocupação, política e socioeconômica durante os últimos séculos.

2.2. Objetivos específicos

1. Estimar a idade de indivíduos de uma população de *B. excelsa* de diferentes classes diamétricas e o seu período de estabelecimento por meio de analises de anéis anuais de crescimento;

2. Construir trajetórias de crescimento individuais e detectar eventos de liberação e supressão;

3. Reconstruir o crescimento em diâmetro da população de *B. excelsa*.

4. Coletar informações sobre o panorama histórico da região do sítio de estudo dos últimos quatro séculos abordando a ocupação, demografia e socioeconômia.

5. Associar a reconstrução do crescimento diamétrico e estabelecimento da população de castanheiras com o contexto do panorama histórico da região.

HUMAN HISTORY THROUGH THE RINGS OF AMAZON NUT TREES.

Andrade, V.L.C., Flores, B.M., Levis, C., Clement, C.R. and Schöngart, J.

Human history through the rings of Amazon nut trees

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Abstract

From the moment Humans arrived in the Amazonian region, at least 12 ky ago, they started managing the forest, in a long term domestication process. *Bertholletia excelsa* is an iconic nut tree that dominates vast swaths of the Amazon forest, known for being used by humans since before the European arrival. Considering the intimate historical relationship between humans and the Amazon nut tree, it remains unclear if the long term population dynamics of this species has been driven by management practices, and if this interaction changed following the collapse of pre-colonial societies. Here we reconstruct over 300 years of population dynamics for a living Amazon nut tree stand in Central Amazonia, and relate this dynamics with human history in that region. For this we combine the analyses of tree-rings that may reveal how tree recruitment and growth rates changed through time, with historical information on the main political and economical facts that may have impacted the lives of indigenous and colonists. Our results reveal that the intensification of political dominance over the colony around 1800 coincided with sharp reductions of recruitment and growth rates of *B. excelsa*, suggesting the abandonment of indigenous management practices. A more recent recruitment pulse in the 20th century, associated with unprecedented cycles of growth release and suppression, suggest a new management phase involving non-indigenous practices. Our findings suggest that humans have historically shaped nut tree population dynamics across the Amazon, and allude to the loss of ancient management knowledge with the collapse of pre-Columbian societies.

Historical Ecology / Pre-Columbian Amazon / Disturbance history / Bertholletia excelsa

The long term human influence on domesticated plants across the Amazon has recently been revealed to be much broader than most ecologists imagined (1). While most ecologists tend to see the Amazon as a pristine forest, most archaeologists, anthropologists and etno-botanists argue that the forest has been deeply transformed by humans (2). An iconic example of a plant deeply connected to the lives of Amazonian peoples, which also has a major ecological role in the functioning of Amazonian forests is the large, dominant and widespread Amazon nut tree. This massive tree has been used by humans for more than 11,000 years (3), and represents a cornerstone of Amazonian conservation (4). The Amazon nut is one of the main non-timber Amazonian forest products, and its seeds are sold worldwide through a process ranging from collectors in the forest to processing and sale (4). In addition, it is a hyper-dominant species in forests, both in number of individuals (5) and in biomass (6), which indicates its extreme importance in forest structure, carbon stock and biogeochemical cycles. Nevertheless, the factors that explain their current distribution across the Amazon basin remain unknown (7-8). Forests with high Amazon nut tree density, locally called *castanhais*, are often in the vicinity of archaeological sites, where sedentary pre-Columbian societies lived (9), which could be the result of long term forest management, favoring nut tree populations.

Amazon nut trees are long-living and light-demanding pioneers (10, 11), and the survival and development of the seedlings depends of favorable light conditions in gaps or below canopy disturbances in the forest (11, 12). Natural disturbance events, such as tree-fall gaps, extreme droughts/floods and blowdowns, may influence the Amazon nut growth and recruitment, as well as influence the structure and dynamics of many forest ecosystems (13). But these natural events are often attributed to a stochastic nature (14). Still, humans are also considered agents of forest disturbance since the end of the Pleistocene in Neotropical forests (15). Human management practices performed by indigenous and rural Amazonian populations, such as removing non-useful plants by weeding the understory in forest trails, managing fire, forest cleaning and cultivating useful individuals (Levis et al., in prep) increase light entrance in the understory, and are a well know to facilitate the recruitment and growth of Amazon nut trees (12, 16, 17). Because of this ancient interaction between humans and the Amazon nut tree, studying the long term dynamics of populations may reveal when the forest was more intensely managed by humans.

One way to assess how tree populations responded through time to environmental conditions, such as light availability, is by analyzing annual tree growth rings (18-23). Although several studies have used tree rings to reconstruct disturbance history (such as gap dynamics over time) in tropical forests (18, 19, 21), little attention has been given to the origin of these disturbances (18). Studies with Amazon nut trees have reconstructed the growth trajectory of individuals to detect changes in growth dynamics in relation to disturbances and recourse availability along time (20, 23). For instance, releases and suppressions in tree growth, which are abrupt changes in the individual's growth trajectory, may give insights on disturbance regimes and stochastic episodes (24). The nature of the disturbances that formed gaps in castanhais has been receiving increasing attention (12, 16, 17). Nevertheless, reconstruction of disturbance history based on tree ring data associated with human history data is still practically non-existent for the Amazon nut tree, probably due to the difficulty in separating human and natural disturbances.

In this study, we analyze the tree-ring data in the light of historical political-economic and demographic changes that happened in the last three centuries at the Central Amazon region, to understand how indigenous and colonial histories influenced the dynamics of the Amazon nut population. The central question is whether human occupation represented a source of disturbances (through management) that altered the establishment, clustering and growth of *B. excelsa* trees, and if these disturbances changed during the transition from the indigenous to the colonial periods.

Significance Statement

Amazon nut is a conerstone tree from the Amazon forest. Understand the relationship between the Amazon nut populations called *castanhais* and long-term human history remains a challenge. If population dynamics of this species within the forest has been driven by human management practices, this interaction could have changed following the collapse of pre-colonial societies. We reconstruct the growth dynamics history of an ancient *castanhal* in Central Amazonia by using tree ring analyses, and relates it to the regional occupation by indigenous and colonists over the lasts three centuries. Our findings suggest that *castanhais* had historically shaped by humans across the Amazon, and the management knowledge of these ancient human populations probably was lost with the collapse of pre-columbian societies.

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Results

The colonial history of Central Amazonia

Regional occupation before the European arrival

Before the European conquest, Central Amazonia was densely occupied by indigenous people that left significant signatures in the soil and in the forest (7). Archaeological evidence found in the *castanhal* area, include the presence of charcoal in the soil and many domesticated tree species such as *Hevea brasiliensis* (Euphorbiaceae) and *Elaeis oleifera* (Arecaceae), indicate that humans managed these forests in different historical moments (25, 26). Also, archaeological sites with anthropogenic soils were found less than 5 kilometers from the *castanhal* area. There is lack of historical information from the period previous to the first European travelers, but it is well known that the Mura Indians occupied the territory by the time of Portuguese arrival (27, 28). These Indians were know for using the Amazon nut as food resource (29), and historical artifacts from the colonial period were found in Mura indigenous communities that are still settled in the region (26).

Arrival of colonizers at the mouth of the Rio Negro

In 1657 ocurred the first Portuguese expedition to the Rio Negro (27). With the construction of fort *São José do Rio Negro* about a decade later, the territory where today is located the city of Manaus began to be colonized (27). This settlement soon became a point of indigenous slave' trading and a source of "Indian manpower" for the Portuguese crown (27). Mura Indians had a great war experience and knew ambush tactics (28, 30-33), bravely attacking their enemies to resist colonization (28, 30-33). Mura opposition was so strong that the firsts Portuguese settlers avoided crossing the Amazon river or leaving the limits of their settlements (27).

Colonial political periods

In 1695, the missionaries (Franciscans, Carmelitas, Jesuits) arrived at the São José do Rio Negro's Fort, and the settlement expanded, incorporating indigenous people of different ethnicities (27). During this period, colonizers (i.e., missionaries, soldiers, colonists) made constant incursions into the forest to search for slaves, forest products, territorial expansion and wealth (27, 34). During the Catholic colonization period (1688 - 1750), the Portuguese crown granted land and power to church entities (34, 35), while the Mura people remained in their forest territory, not appearing among pacified Indians (27). Attacks between settlers and Mura`s became frequent during thus period (30-33). In 1750, the Marquis of Pombal began a new developmental project for the Amazon region. His objective was to create an indigenous and colonists wage labor reserve (34). The crackdown on indigenous people who disobeyed the government rules was intensified by military forces. Over time, Mura Indians were attacked every year by government forces. Those found or captured in their villages were enslaved or killed (28). By 1774, colonists demanded indigenous extermination as the only means to avoid complete downfall of the Central Amazonia occupation project (28), with resulted in indigenous population colapse (36). The spatial context of this rowdy period is shown in Fig. 1*A*.

Rubber expansion and Amazon nut tree management

In early 19th century, the Brazilian Amazon was going through a period of low economy and smallpox outbreaks (34, 35). From the 1840's onwards, with the rubber market expansion, the Amazon has experienced an accelerated economic growth (27, 34). The commercial exploitation of Amazon nut seeds occurred in parallel with rubber extraction, and export flows were increasing for both products (37). In 1848 the Amazon nut began to appear in the records of exports (37). Efforts of the Brazilian government to meet the demand for labor in the Amazon, brought thousands of migrants, especially from the northeast region, and the forest began to be reoccupied (37-39). The neo-colonists that reoccupied the region brought beyond their own management knowledge, different tools that used by the indigenous that previously occupied the territory. Hundreds of rubber trees in our study area still have signs of extraction by tappers from this period (26).

Recent occupation

In the Manaus port, from 1941 to 1945 were registered the departure of 72.278 people from the urban center to the interior of the state (27). During World War II, the rubber economy had a strong increase in exports. During this period, the village that is currently based in the study area arrived with the rubber tappers (according to local informants). These people favored in their backyards the emergence of several nut trees that we call here *planted castanhal* just nearby the studied *castanhal*. Currently, Purupuru Lake has a large number of inhabitants on its banks, most involved in agriculture, Amazon nut extraction, hunting and exploitation of other forest products.

Brazil nut population dynamics

Nut-tree population structure

The *castanhal* was divided into two recruiting pulses (fig. 2*C*). The density of the *castanhal* is 3.2 trees ha^{-1}. DBH ranged from 9.9 to 192.6 cm and the Basal Area was 5,6 m^2 ha^{-1}, indicating that it is a dominant species in the area (17). The *planted castanhal* had a much higher density of 30,8 trees ha^{-1}, and a basal area of 7,2 m^2 ha^{-1}. The *planted castanhal* in the village, and trees from the 2nd recruitment pulse in the forest had more individuals of small sizes, indicating higher recruitment rates, whereas the 1st recruitment pulse had only large individuals (Fig. S1).

***Castanhal* growth dynamics**

The estimated mean age of individuals from the 1st recruitment pulse was 303 years, whereas trees from the 2nd pulse were substantially younger, with a mean age of only 119 years (Table S1). The final phase of the 1st pulse (early 19th century) had an extremely low recruitment rate, 0.025 trees yr^{-1}. Moreover, trees from the 1st pulse had significantly lower diameter growth rates than those from the 2nd Pulse ($t = -3.121$, $p < 0.01$) as shows Fig. S2.

The analyses of individual tree growth revealed that forty trees underwent at least one release event during its growth trajectory, and seven trees went through at least one suppression event. The rest of the sampled individuals not presented significant changes in growth trajectories. These release/suppression events began to occur from 1886 (Fig. 2*D*). The maximum number of four trees simultaneous experiencing a release events peaked around 1950 and 1998, and suppression events at 1985.

Analysis of the median growth change percentage (%GC) showed periods of accelerated growth in the decades 1780, 1790, 1830, 1840, 1920, 1940, 1970, and 1990 (Fig. 2*E*). Long periods of accelerated population growth and release/suppression events indicate phases of higher disturbance frequency (18). The longest period of fast growth (%GC > 0) was of 18 consecutive years, during the 1830-40's, and the longest period of slow growth (%GC < 0) was of 17 consecutive years, during the 1810-20's. The growth-releasing events in the last century were consistent with to periods of rapid growth (Fig. 2 *D and E*), resulting in a positive relationship ($r^2 = 0.41$) between these two disturbance indicators.

Discussion

Based on the analyses of more than three centuries of Amazon nut tree population dynamics, our results confirmed the idea that this emblematic and highly useful tree species has been intimately connected with humans through their forest management practices. We observed abrupt reductions in tree growth and recruitment rates around 1800 (Fig. 2 *C and E*), reflecting the potential impact of political changes that led indigenous populations to abandon the forest and their management practices (Fig. 2 *A and B*). Following this hiatus in the local forest history, our findings indicate the start of a second growth and recruitment period with unprecedented patterns, likely associated with non-indigenous management during the rubber economic period.

Natural disturbances (i.e. blowdowns, fires and lightings) may also influence the growth, recruitment, and suppression and release events of Amazon nut (20, 23), since they cause changes in solar irradiation in the understory. These events have a random temporal nature (14) and can be a source of misunderstanding if it were not for the historical basis to help understand the observed temporal changes. In addition, growth change analysis (Fig. 2*E*) and the identification of Release and Suppression events (Fig. 2*D*) are subjected to a treatment that dilutes the strong intra-annual influences (19, 24) that can cause misunderstandings. The multiple relations between the Purupuru Lake *castanhal* and human activities during more than three centuries (Fig. 2) reveal that human presence is associated with disturbances that promote tree growth, as well as release and suppression events. The intensity of these disturbances is likely related to landscape management practices that possibly changed from the first period of human occupation to the second. We suggest that the higher intensity of these disturbances during the 2nd recruitment pulse than the 1st is related to the differences between the forest management by indigenous and colonists. Forest management intensified when people with technological capacity for landscape modification settled in the region. We present evidence that pre-colonial indigenous occupation favored the growth and establishment of Amazon nut trees, as did the more recent human population who re-occupied the area. The fundamental differences between these two periods of occupation were the instruments used for landscape management and mainly the increase in demand for nuts that grew along with local and global trade (37).

The Mura Indians who occupied the region extensively during the 17th and 18th centuries had great war knowledge and extremely high mobility in their territory (28). Forest management practices used by these indigenous populations were likely responsible for the dynamics observed in the 1st recruitment period, since they were still present in that time (Fig. 2*B*). The final phase of the first pulse coincides with the end of the war between Portuguese colonizers and Mura populations (Fig. 2*A*). During this period, human population density was low, disease outbreaks wasted the region (27), and the Purupuru lake site was a location vulnerable to attacks by both Indians and colonizers. As a consequence, forests in that region were abandoned. Without frequent disturbances associated with indigenous forest management, a well-established tree community with dense tree cover was probably formed. Because young Amazon nut trees require light penetration in the understory to grow and recruit the population (11), this explains why in the same period, recruitment rates collapsed, and the strongest drop in tree growth was recorded (Fig. 2*E*). This suggests that the abandonment of the area took place a few years before the period between pulses, approximately in the half 18th century, when the most Mura indians surrender for the government forces (30, 32).

When it comes to light demanding tree species, such as the Amazon nut tree, periods of increased tree growth are often indications of gap formation (18, 21). Our tree ring analyses revealed periods of accelerated population growth in the second half of the 18th century, and from the mid-20th onwards (Fig. 2*E*). The main difference between these two growth periods is the absence of release and suppression events in the first period (before the 20th century). Although a smaller number of trees with such an old growth record (Fig. S3), this contrast suggests that in the last century, the nature of disturbances changed in the forest, becoming strong enough to cause up to four synchronous releases and suppressions (Fig. 2*D*). Absence of release and suppression events in the past does not mean absence of forest disturbance, but suggest that disturbances were more subtle and homogeneous across the area.

Moments when the *castanhal* presented growth rates above the median (Fig. 2*E*) indicate the increase of solar radiation in the understory (11). A moment of fast growth between 1835 and 1862 coincides with the arrival of a large number of migrants coming from the Brazilian northeast, mainly from Ceará, to work on rubber extraction (39). Amazon nut production and rubber extraction occurred naturally, since these two tree species are colected in different seasons (37), allowing continuous productivity throughout the year. Moreover, the exploitation of the *castanhais* in the Amazon grew together with rubber extraction, and even more with the rubber downfall (37). The 2nd pulse of nut tree recruitment, started around 1840, and the trees grew on average faster rhythm than those of the 1st pulse (Fig. S2). The first growth release event occurred in the late 19th century, during the first rubber boom (Fig. 2 *A and D*). Exactly in the decade when this first event happened, hundreds of families were registered in the municipality of Careiro da Várzea, corresponding to a few thousand immigrants (38). Thereafter, the demographic density of the region increased exponentially, along with disturbance indicators in the *castanhal* and also the emergence of the *planted castanhal*.

By associating a dendroecological approach to this human historical context, we evaluated temporal influences of past and contemporary human management pratices (Levis et a., *in prep*) in the same *castanhal*. Our findings are similar to other studies in Amazonian terra firme forests using tree-ring analyses (20, 23), repeated diameter measurements (10), dendrometer bands (40) and radiocarbon-dating (41), which indicate maximum tree ages of 400-500 years with mean diameter increment rates of 3.2-5.3 mm year^{-1} (20). Only the ^{14}C-dating analysis of three individuals of Amazon nut trees indicated much higher tree ages (668-996) and diameter increment rates in the range of 0.6-1.9 mm year^{-1} (42). In terms of growth release and suppression events, we found percentages similar to Schöngart et al. (2015), who analyzed 20 Amazon nut trees in the Purus River region and 21 trees in the Trombetas River region. These similar trends suggest that other *castanhais* have probably been affected by long-term human history.

Other observed response patterns in tree growth relative to human disturbances are worth highlighting, such as the accelerated growth of the whole nut tree population peaking during the 1940's and 1950's, along with increased release events, both during World War II when the rubber revival occurred (Fig. 2*A*). Furthermore, in the 1970s and 1990s accelerated population growth associated with release events indicate favorable tree growth conditions, linked to nut tree management by migrants. Interestingly, there is a declining trend in recruitment after 1850 (Fig. 2*C*), which may be related to the intensification of commercial nut extraction (8). Nut collection for commercial purposes, without proper forest management to promote tree recruitment, may be responsible for the decrease in recruitment (8), as observed from the rubber boom. Perhaps motivated by an intense commercial pressure, local inhabitants planted another Amazon nut stand in their village in the last seventy years. If we consider the *planted castanhal* as part of the population in a modern kind landscape, that trees are a counterpoint to the decline in recruitment.

According to the age reported by local informants, and DBH measures, the oldest trees in the *planted castanhal* had 72 years, and mean diameter of 92cm, which means a growth of 7,83mm.yr^{-1}. These younger nut trees planted in the village grew faster than all nut trees we studied in the forest stand (Fig. 1*B*). These sixty seven trees were not included in the analysis because they grew under different resource conditions, and were managed by a modern human population belonging to a contrasting socio-economic and cultural context, with different technological capacity to modify landscapes than the completely lost technologies of pre-colonial populations. With this new approach we relate the pattern changes in tree growth with the anthropogenic influence. Furthermore, we believe that it is possible to extend the understanding of these relationships to other *castanhais* and even other managed species that present annual growth rings on tropical forests.

Conclusion

Human management actions enriched Amazonian forest landscapes with useful species over the last millennia (1, 6), including the Amazon nut tree. Our findings strongly suggest that the forest we studied was also part of this process, and allude to the loss of indigenous forest management knowledge with the collapse of pre-Columbian societies. Moreover, our study shows that tree ring analysis may contribute to historical ecology research by revealing the frequency and intensity of local disturbances in a high temporal resolution. Over time, changes in territorial occupation and socioeconomic aspects are closely linked to tree growth dynamics. If we extend this understanding to a larger scale, we are possibly dealing with human actions that, through the management of this emblematic species, have contributed to their hyperdominance in richness (5) and biomass productivity (6) in the Amazon rforest.

Our approach provided insights about the domestication of Amazonian forests by showing the potential for detecting the impact of ancient and recent human management in forested landscapes. This interaction has clearly changed over the last few centuries. Indigenous forms of management, like silvicultural techniques and itinerant farming (43), following the modern tools used by colonists have involved different ways of environment modifying. Our results support the idea that humans have had great influence on the Amazon Forest since pre-colonial times (1, 7). Patterns we revealed also suggest that the collapse of indigenous societies implied in the permanent loss of complex ecological knowledge, and in the widespread regrowth of abandoned managed forests across the Amazon basin. Broadening our understanding of the outcome of long-term interaction between humans and forests enriched with Amazon nuts, we encourage community management to ensure the preservation of the forest in a socially sustainable way.

Materials and Methods

Brief historical background

Following Portuguese arrival in 1657, historical sources described that the territory (SI Methods) as always associated with Mura Indians occupation (28, 30). The late 17th and entire 18th centuries were periods marked by the demographic growth of Manaus city and the collapse of Mura populations (27, 30), mainly associated with political periods of intense conflicts between indigenous populations and colonizers (34, 35). The 19th and 20th centuries were periods marked by immigration fluxes associated with critical economic phases, for instance the Rubber Booms (27, 38), and with the most recent human occupation.

Data analysis

We use the TSAP-Win program to visually cross-dated all the sampled individual (SI Methods) tree-ring series (20). Compared to other tree-ring studies with *B. excelsa* using entire stem discs (20, 23), this study is based on non-destructive sampling of cores, which partially limits the capacity to extract entire cores from the largest trees. Cores obtained from large trees also often have the problem of missing pith in the samples, which limits the age estimate. Frequently occurring tree-ring anomalies, such as wedging, double, false and discontinuous growth rings, are more difficult to detect on cores compared to stem discs and can result in inconsistent ring-width patterns among individuals, leading to dating errors. By combining tree-ring series into a mean curve, we minimize dating errors, which we estimate to be lower than 2 %.

We transformed radial increment to diameter increments by multiplying by a factor of two and adjusted the sum of diameter increments to the DBH of the tree measured in the field (23). For each tree, we established age-diameter relationships for its entire lifetime. We sampled eleven trees with entire cores and forty eight with missing piece at the center. In the absence of rings in the center of a tree, we estimated the distance to the pith and used the individual mean growth to age estimation (44). We adjusted all individual series by an age-diameter regression model to estimate the age of the un-sampled trees.

The individual diameter increment curves were then transformed into relative growth rates to estimate the year-by-year growth change percentage (%GC), as suggested by Nowacki & Abrams (1997):

$\%GC_i = [(M_2 - M_1)/M_1] \times 100$

where $\%GC_i$ is the percentage of growth change for year i, M_1 indicates the preceding 10-yr mean diameter growth (including year i) and M_2 is the subsequent 10-yr mean diameter growth. This method expresses the growth change as a percentage of the previous growth period. The comparison of sequential 10-year ring-width means were used to detect sustained growth increases or decreases that indicate changes in resource availability, often related to canopy disturbance, while discounting strong inter-annual influences caused by climate fluctuations (19, 24). The first and last ten years of the individual tree-ring series are excluded from the analysis. Growth releases were defined by values above 100 %GC and growth suppressions by values below -50 %CG, both during at least five consecutive years (20). We also analyzed the year by year median value of %GC among all sampled trees to reconstruct the *castanhal* population growth rate over time. We started this analysis from 1768, when the sample depth was at least of three individual trees (Fig. S3).

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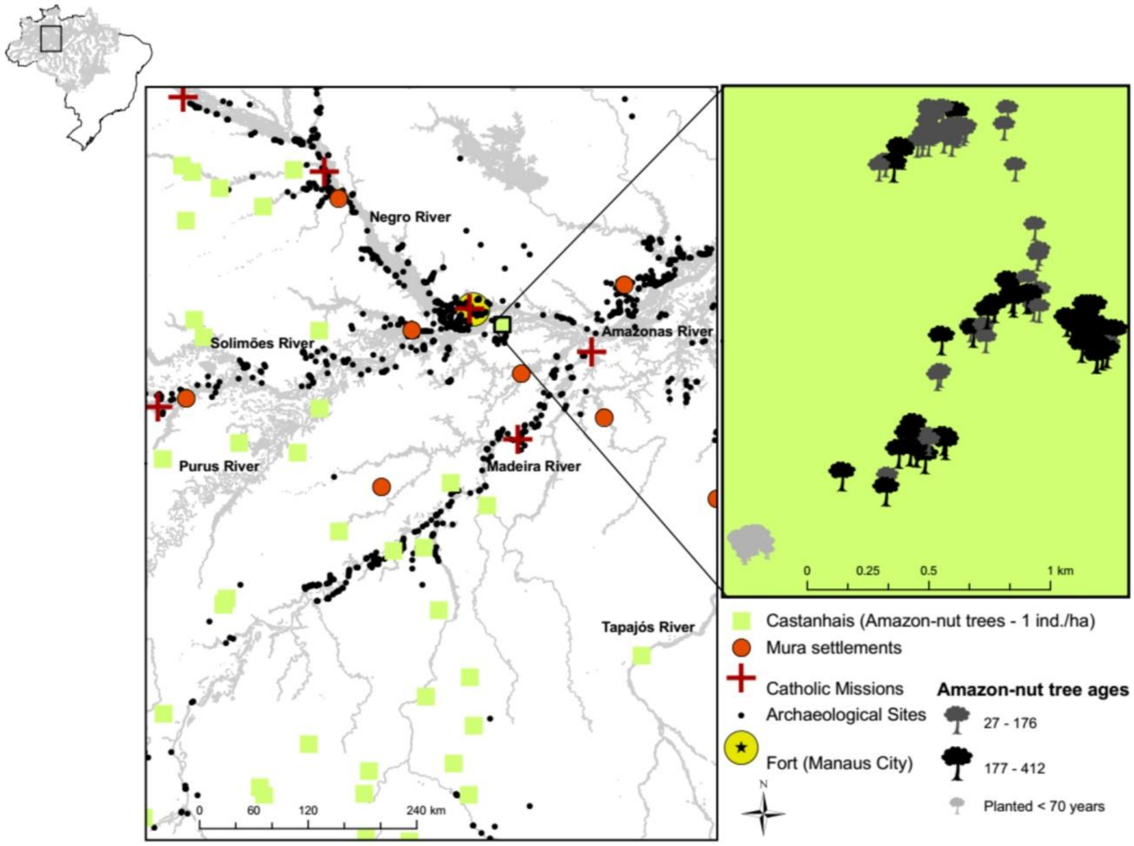

Fig. 1. A - Panorama of territorial occupation during the 18th century. Orange circles represent major Mura settlements (28), red crosses represent Catholic mission settlements, yellow circle indicates a major Portuguese military base (now, Manaus city), green squares represent *castanhais*, and black dots represent archaeological sites of currently undefined ethnic relationship. B - Spatial distribution of Amazon nut trees in the *castanhal* analyzed here. Black trees were established on the first recruiting pulse and the gray trees are from the second recruiting pulse.

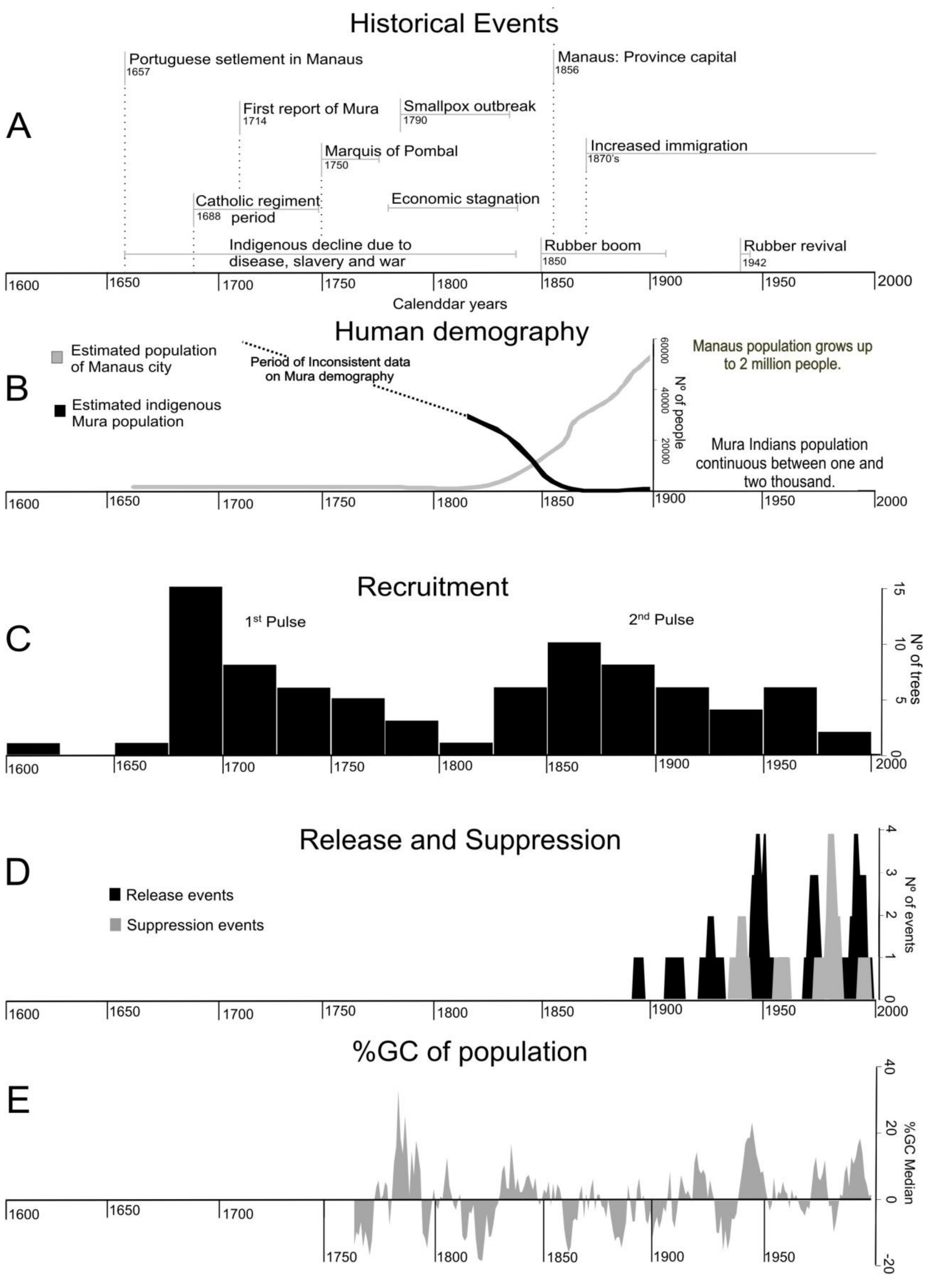

Fig. 2. historical timeline and tree dynamics comparison. A – Events of historical importance to understand the territorial dynamics of the region of this study in central Amazonia; B – estimated population for indigenous Mura and colonizers; C - Number of Amazon nut trees recruited over 25 year periods; D - Black bars indicate the number of trees passing through

release events, and gray bars indicate the number of trees passing through suppression events; E – Median relative diameter growth of Native Amazon nut Stand population.

Supporting Information

SI Methods

Study Area

We studied an old Brasil nut stand located in the municipality of Careiro da Várzea, 30 km south of Manaus (fig. 1*A*) near the Purupuru Lake, in a forested landscape in central Amazonia rich and abundant in useful tree species, and with high density of *Terra Preta* archaeological sites (1, 2). The area is a low altimetry plain, composed of small creeks (igarapés) and dikes connected to upland forests (*terra firme*) (2). The Amazon nut trees that form the stand are patched in the upland forest, but some trees are also found along trails used by the local extractive population.

Tree sampling

Within the area, each *Bertholletia excelsa* tree was georeferrenced and its diameter at breast height (DBH) was measured. Some of these trees were planted in a small densification by the present inhabitants of the region, we named these trees of *planted castanhal* (fig. 1*B*), corresponding to sixty-seven new trees planted over the last 70 years. We did not collect amples of trees within *planted castanhal* to tree ring analysis. The other trees within the native stand, was termed *castanhal*, which were the central theme of our study. To reconstruct the history of disturbances we randomly collected increment cores of 0,5 - 1,5 cm in diameter for tree-ring analyses from trees of different size within the *castanhal*. We collected two samples at DBH-height from 11 individuals with DBH < 40 cm, 12 trees between 40-80 cm, 20 trees between 80-120 cm, and 18 individuals with DBH > 120 cm. In total 59 trees were sampled, representing 70 % of the nut trees that occur in the *castanhal*. The bore holes were later capped with carnauba wax (*Copernicia prunifera* - Aracaceae) to avoid pathogen damage. Core surfaces were sanded with decreasing grain sizes (up to 600) to increase the distinctiveness of the growth rings, characterized by alternating fibrous zones and parenchyma tissue (3, 4). Tree rings were identified on all 118 cores (2 per tree), using a 40x magnification stereomicroscope. Ring width was measured along the radii to the nearest 0.01 mm using a digital measurement table (Lintab, Rinntech, Germany), simultaneously producing curves of current radial increment.

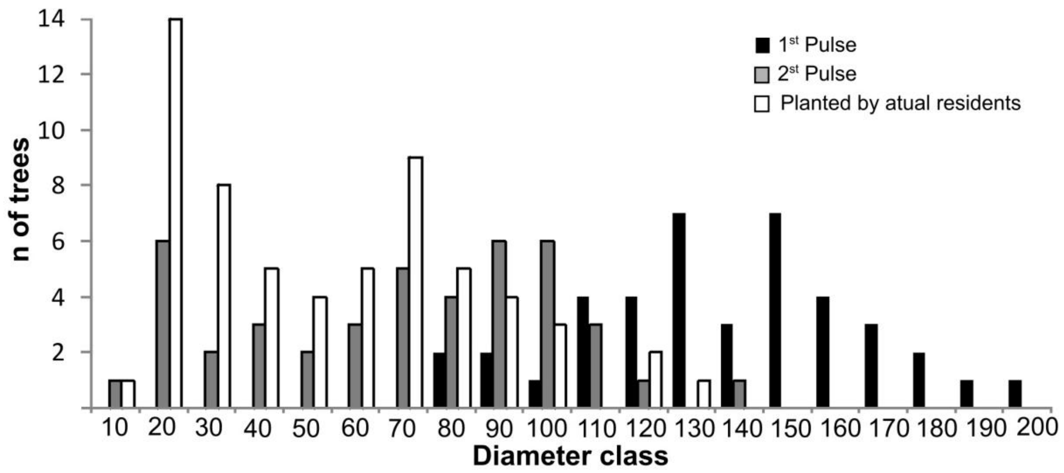

Fig. S1. Distribution of Amazon nut trees in 10 cm size class intervals at 1st recruitment pulse (black bars), 2nd recruitment pulse (grey bars) and planted castanhal (white bars).

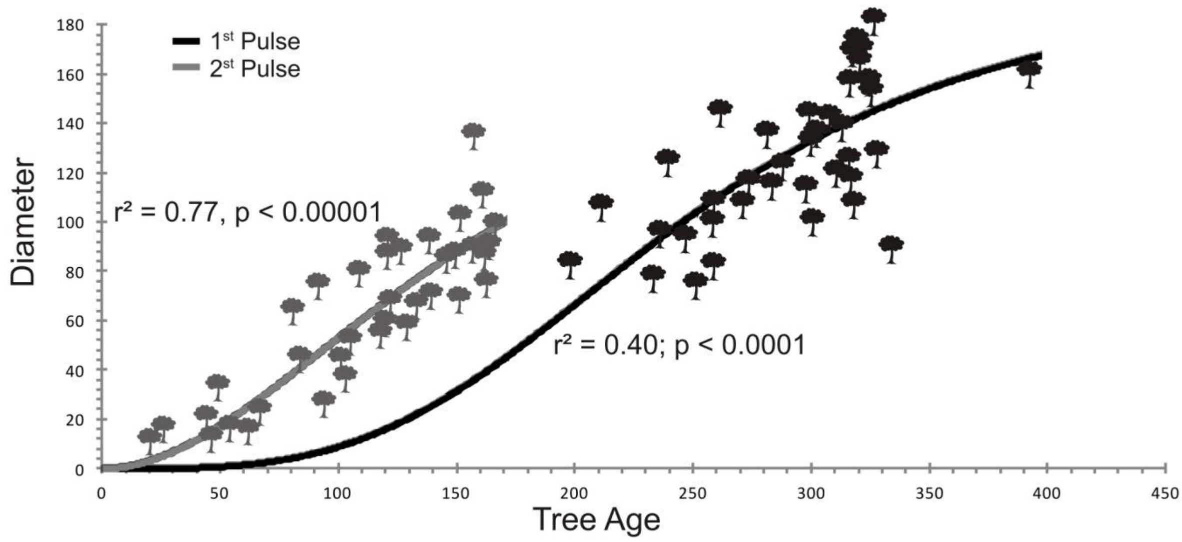

Fig. S2. Age-diameter relations for the two recruitment pulses of Amazon nut trees. The points are the treetops. Trees in black represent the individuals of the first pulse, and the trees in gray represent the individuals of the second pulse. Black and gray lines represent the sigmoidal regression of the first and second pulse, respectively. In the boxes, the years at which each recruitment pulse started.

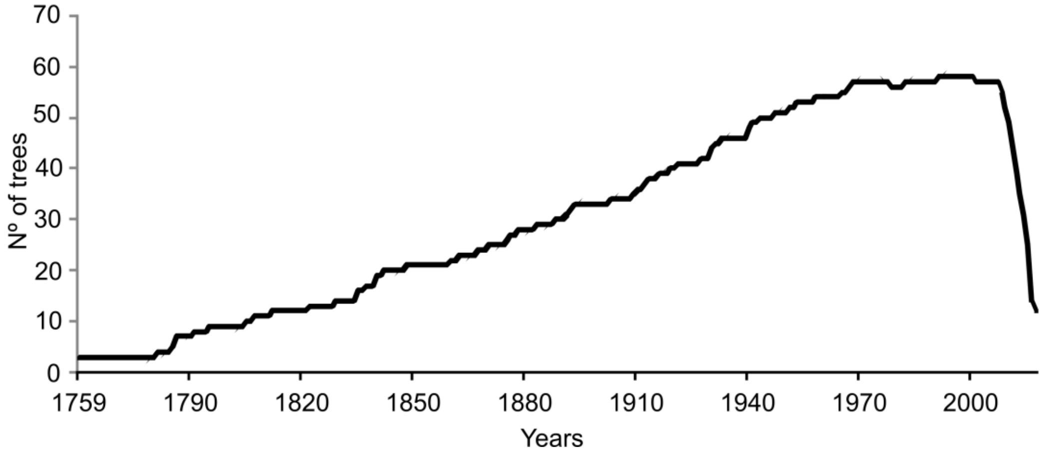

Fig. S3. Sample Depth. Number of trees with ring records over time.

Table S1. Number of Amazon nut individuals in each recruiting pulse and mean (minimum-maximum) of diameter, tree age, and mean diameter growth rates.

Recruitment Pulse	Period of establishment	Nº of individuals	Diameter (cm)	Age (yr)	Mean Diameter increment (mm.yr^{-1})
1º Pulse	1604 - 1818	41	132.7 (70.5 – 192.6)	303 (198 – 412)	4.38 (3.71 – 5.05)
2º Pulse	1840 - 1989	43	64.7 (10.0 – 113.3)	119 (27 – 176)	5.20 (3.61 – 7.79)
Total/Means	---	84	97.9	209	4.80

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3. Conclusão

Nosso estudo mostra que análises de anéis de crescimento podem contribuir com pesquisas de ecologia histórica, revelando a freqüência e a intensidade de distúrbios locais com alta resolução temporal. Nossa abordagem revelou o potencial de análises baseadas historicamente para detectar o manejo de antigas e recentes populaões humanas nas paisagens florestais amazônicas. Na Amazônia Central, o manejo florestal praticado por humanos mudou claramente ao longo dos últimos séculos, enquanto muitas terras de posse indígena foram dominadas por colonos envolvendo diferentes sócio-economias e tecnologias. Através desta nova forma para descobrir a influência humana a longo prazo em paisagens historicamente domesticadas, o castanhal que estudamos mostrou ser parte do amplo processo no qual os seres humanos enriqueceram a Floresta Amazônica com espécies úteis. Nossas descobertas sugerem que o colapso das sociedades indígenas em toda a Amazônia Central foi acompanhado pela perda permanente de conhecimentos ecológicos e pelo crescimento generalizado das florestas manejadas abandonadas.

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