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Title: **Widespread reforestation before European influence on Amazonia**

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Abstract:

An estimated 90-95% of indigenous people in Amazonia died following European Contact. This population collapse is postulated to have caused decreases in atmospheric CO_2 concentrations at c. 1610 CE, as a result of a wave of land abandonment in the wake of disease, slavery and warfare, whereby the attendant reversion to forest significantly increased terrestrial carbon sequestration. Based on 39 Amazonian fossil pollen records, we show that there was no synchronous reforestation event associated with such an atmospheric CO_2 response following European arrival in Amazonia. Instead, we find that, at most sites, land abandonment and forest regrowth began c. 300 - 600 years before European arrival. Pre-European pandemics, social strife or environmental change may have contributed to these early site abandonments and ecological shifts.

One Sentence Summary: Pollen records show that site abandonment and forest regrowth in Amazonia began up to 600 years before European arrival.

5   **Main Text:** The scale and the spatial and temporal patterns of human population dynamics in Amazonia have long been controversial. Early models suggest an exponential increase that perhaps continued until European contact (*1*), but more recent assessments suggest that population growth was slowing by c. 1200 CE (hereafter all ages are expressed as CE) (*2*), perhaps nearing a carrying capacity. After 1492, an estimated 90-95% of the indigenous population was lost as waves of disease, including smallpox, influenza, measles, and the common cold, swept

10   through 'virgin soil' communities, as well as by warfare and slavery (*3*). This catastrophic loss of life resulting from European colonization has been termed the 'Great Dying of the Indigenous Peoples of the Americas' (*4*). The population collapse is commonly considered a turning point in human influence on Amazonian landscapes, as inhabited sites were abandoned and land used for crop cultivation became fallowed (Fig. 1). One suggested manifestation of the attendant surge in forest regrowth was a 7-10 ppm drop in atmospheric CO_2 concentrations,

15   known as the Orbis spike that began c. 1610 and presaged relatively low concentrations until c. 1750 (Fig. 1) (*4*); a decline that deepened the cooling of The Little Ice Age (1400-1800) (*5*). Whether the scale of CO_2 variation forming the Orbis spike was truly an unusual event has been questioned (*6*), as was the link to New World depopulation (*7*). Of all the Americas, the greatest potential carbon response to the Great Dying would have been manifested in the vast, high-biomass, forests of Amazonia (*8, 9*). If the decline in CO_2 concentrations was caused by the Great

20   Dying, the depopulation and reforestation must have been rapid and widespread (Fig. 1).

    Eyewitness accounts of the state of Amazonian populations in the first 200 years after European contact are sparse, but three accounts stand out, those of Carvajal (*11*), Acuña (*12*), and de la Condamine (*13*). Lured by rumors of gold, the first large Spanish expedition entered lowland Amazonia in 1541 (*11*). Friar Carvajal, the diarist

25   of Orellana's expedition reported large healthy populations along many portions of the river, with no suggestion of

mass disease (*11*). A similarly positive account of societies and living conditions is provided by Acuña, a Spanish priest who traveled from Quito to Belem in 1639. These two early accounts could have been flavored by a desire to present a land of opportunity to royal courts in Europe (*13*). In contrast, a French surveyor, de la Condamine, traveled down the Amazon River in 1743, but did not record the same high density of people on the riverbanks, suggesting a partially depopulated landscape (*13*). Although it seems most probable that any vegetation change associated with the Great Dying took place in Amazonia post-1639 (the date of Acuna's trip), we investigate the possibility that it occurred between 1550 and 1750 concurrent with low CO2 levels (*8, 9*).

Although it is challenging to estimate pre-collapse population size, assumptions of near-synchronous forest regrowth are readily testable using paleoecology. Fossil pollen recovered from lake sediments provide a metric for reconstructing local forest cover and land use (*14*). If the Great Dying induced the rapid, synchronous forest regrowth, then pollen contained in these fossil pollen records should show the strongest switch of the last 2000 years between open ground and weedy species (as signals of a deforested landscape) to dominance of forest taxa between 1550 and 1750 (Fig. 1). This signal should be particularly strong because lakes were preferred settlement sites for indigenous populations (*14*).

While there is not a 1:1 relationship between pollen percentages and forest cover percentages, records from dense rainforest settings do provide a sensitive index of even small-scale disturbances (*15, 16*). Consistently, within the forested portion of Amazonia, relatively undisturbed forest produces 95-100% forest pollen *(12)*. Where human disturbance occurs, forest pollen percentages decrease while percentages of open ground and shrubby taxa increase Fossil pollen of weeds, grasses, and crops are usually accompanied by charcoal, which is a direct indicator of anthropogenic forest burning, as natural fires (lightning-induced) occur rarely in Amazonian forests (*17*). An important taxon in assessing forest disturbance and early stages of recovery is *Cecropia,* a short-lived, fast-growing, shade-intolerant pioneer tree that produces abundant and easily identifiable pollen (*18*). *Cecropia* occurs naturally as a canopy gap-colonist within forests, and hence is part of our forest pollen component, but it is favored by anthropogenic disturbance and commonly forms a dominant stage in forest succession on abandoned land (*19*). Abandonment of fields in much of Amazonia would be expected to pass through a *Cecropia*-rich early successional stage. As the forest matures, *Cecropia* would be competitively excluded from all but forest gaps, and so a peak of *Cecropia* pollen in fossil pollen records should be a sensitive marker of the onset of the Great Dying.

To determine whether reforestation between 1550 and 1750 was associated with changes in global CO_2 levels, we assess changes in land use, forest cover, and *Cecropia* abundances for the last 2000 years based on fossil pollen and charcoal data derived from 39 lake sites across Amazonia (*20*).

5   About 80% of the 39 sites contained signals of forest opening, burning, or cultivation consistent with pre-European occupation (Fig. 2A, database S1). A spatially and temporally heterogeneous pattern of deforestation, reforestation and, by inference, carbon uptake was evident in the pollen data across the 39 sites (Figs. 2, S1-S2). To assess even minor changes in forest cover, the proportion of sites showing a 5 or 10% increase or decrease in forest pollen were assessed. Sites exhibiting evidence of deforestation at values > 5% peaked between 350 and

10   750, while the proportion of sites showing evidence of reforestation was greatest between 750 and 1550 (Figs. 2c, S1-S2). During the Great Dying period, the number of sites where forest pollen was increasing roughly equalled those where it was falling in abundance (Fig. 2B,C, S1), effectively rejecting the hypothesis of widespread and synchronous reforestation sufficient to cause decreases in atmospheric CO_2 levels. Instead of a strong signal of reforestation during or following the Great Dying, our empirical data show that changes in Amazonian land use and

15   forest cover took place several centuries before European arrival (Fig. 2C).

        Nine sites out of 39 contain at least 10 pollen samples in the last 1000 years (Fig. S3), and provide centennial-scale temporal resolution (hereafter high-resolution sites). These sites offer the opportunity to investigate trajectories of site disturbance and forest recovery (Fig. 3, database S1). Eight of the nine high-resolution sites contain pollen and charcoal evidence of occupation in the pre-Columbian era and provide evidence

20   of changes in forest pollen percentages before, during or after the Great Dying (Fig. 3, database S1). Taken together, the nine sites do not show a pattern of synchronous or substantial reforestation during the Great Dying period (Fig. 3). Instead, these records contain a range of temporal patterns of pre-Columbian occupancy, i.e., long-term sustained use, intermittent use and non-use *(17-25).* An example of a site showing long-term use is Lake Caranã (Fig. 3), which provides evidence in its fossil pollen and charcoal record of a continuous history of

25   occupation with the frequent use of fire, maize (*Zea mays*) and squash (*Cucurbita* spp.) cultivation. Archaeological data at Caranã evidence the formation of Amazonian Dark Earth over the last 2000 years (*22*). Despite this intensity of use, no significant change in total forest pollen is associated with the Great Dying at Lake Caranã. Lakes

Rogaguado and Granja were the only pollen records to increase forest pollen abundance by > 10% between 1550

and 1750 (Fig. 3). Most of the increase at Rogaguado occurred from 1650-1750 CE. While Granja lies in riparian

forest today, it is within 1 km of flooded savanna. A modest increase in precipitation at this site could have caused

an increase in forest pollen representation, but that same increase would not affect other locations that were

5   already fully forested. Progressively wetter conditions at Granja over the last 2000 years should have led to

increased forest cover, but instead grassland was maintained by human activities until abandonment, ca. 1300-

1400 CE (*23*). After 1300 CE forest cover increased from 20% to >40% in about a century (Fig. 3). Thus, this was not

a site where there was a cycle of deforestation, use, and reforestation, as seen at all the other occupied sites;

rather human activity suppressed a natural, climatically-induced, trend of rainforest expansion. Among the other

10   sites containing pollen evidence of maize cultivation, fluctuations in forest pollen percentages, indicative of forest

clearance and recovery, varied in timing. Sauce (*24*) and Ayauch[i] (*25*) had records of long-term forest clearance,

whereas Lake Kumpak[a] (*26*) was used episodically. Quistococha (*27*), and the saline Limon (*28*) provided evidence

of human occupation (burning), but no crop pollen. None of the nine sites shows increases in forest pollen during

the Great Dying. Lake Pata lies on an inselberg above the Amazon plain, with very thin soils that preclude

15   cultivation (*29*). A high-resolution pollen analysis of Lake Pata revealed no evidence of human occupancy and

forest pollen percentages were >95% throughout the last 2000 years (Fig. 3) (*29*).

       When looking at deviations in forest pollen abundance from the 2000-yr mean pollen percentage of each

record, only Lake Rogaguado showed significant forest increases during the Great Dying period, particularly from

1650-1750 CE (Fig. 4A). Other lakes showed either no deviation throughout the record or forest percentages that

20   increased relative to mean values between 950-1350, i.e., 300-600 years prior to the Great Dying event. The

largest increase in the mean value of all forest pollen deviations occurred from c. 1250-1350, with no significant

increase during the Great Dying period (Fig. 4A, black line). Between 950 and 1350, *Cecropia* pollen percentages

showed the largest increases (ca. 5%) from mean values, whereas during the Great Dying values were ca. 5% lower

than the long-term mean (Fig. 4B). These data are inconsistent with a postulated peak in post-disturbance

25   succession and rapid carbon uptake following the Great Dying. The negative deviations from the mean *Cecropia*

values for each of the nine lakes correspond with charcoal declines. Such cessation of burning is strongly

associated with land abandonment (Fig. 4B,C). The discontinuous charcoal peaks at most sites suggest that forest

burning was intermittent, and where it occurred, it ceased before the Great Dying (Fig. 4C); a probable indicator of abandonment. The only site to show a decrease in burning between 1650-1750 was Lake Quistococha. Lake Quistococha is located near the city of Iquitos, Peru, in a region where the Jesuits established the Mainas Missions from 1638-1767 (*30*).

Our empirical observations are consistent with archaeologically-derived models (*2*) that suggest stable or falling populations for centuries before European arrival. The mechanisms driving the cultural change or site abandonment from c. 950-1350, however, have yet to be identified. We consider three possibilities that are not mutually exclusive: climate change, societal change, and disease. If climate were mainly responsible, lakes within close proximity to each other would be expected to contain synchronous changes in pollen and charcoal, and regional geographic trends associated with environmental gradients (e.g., Fig. 2A) should be evident in the dataset. They are not. Trends in forest pollen abundance do not seem to have a distinct geographic pattern (Figs. 2B, S1-S2), and neighboring sites often show non-synchronous peaks of fire and periods of fire absence (Fig. 4) (*31, 32*) suggesting that climate change is unlikely to be a complete explanation for the abandonment of sites between 950 and 1250. Our findings do not, however, discount the possibility that climate change could have contributed to a societal response of changing land use, and thus changing forest cover percentages (*23*). Isotopic data from regional speleothems and lake records both support a trend toward increasing climate variability between 800 and 1200 (*33, 34*). De Souza et al. (*35*) suggested that complex, hierarchical, societies relying on specialized food provisions were more susceptible to these climate variations than simpler, more egalitarian societies accessing a breadth of food resources. Many of the sites used in this study have no accompanying archaeological data to determine past human vulnerability to climate change. Nevertheless, even if human populations were resilient, some sites may simply have become too flood- or drought-prone to continue to be desirable, forcing migration to new locations.

The timing of observed reforestation in the lowlands coincides with the relocation of an estimated 25% of the indigenous population from the Andes into the coastal lowlands between c. 1000 and 1200 (*36*). This migration is associated with the collapse of the Tiwanaku and Wari cultures, rapid climate change, and evidence of increased warfare evidenced by cranial trauma (*37, 38*). In the Amazon lowlands, increased hostility is inferred from archaeological contexts amid a cultural expansion reflected in the spread of the polychrome tradition of decorated

pottery (*39*). To find abandonment of apparently unrelated lowland settings at the same time as that of the

highlands raises the possibility of a common cause. Climate change, conflict, and disease could underly both

patterns of behavior. Disease outbreaks have yet to be documented in the lowlands, but skeletal remains provide

evidence of the Andean expansion of tuberculosis between 1000 and 1300 (*40*). Trading between lowland and

5   highland communities, which is known for this period (*41*), could have easily spread disease and created pre-

European pandemics across the region. Thus, the interaction of climate change, social tensions and possibly even

the emergence of novel non-European diseases could have caused the observed destabilization of Amazonian

populations centuries before the Great Dying period. Populations in some areas of Amazonia may already have

been declining when Europeans arrived, a decline that was accelerated by the impacts of disease following

10   European contact. Furthermore, our data suggest that the timing of reforestation was heterogenous with many

sites showing an increase in forest cover as much as 600 years before the Great Dying. We find no evidence that

human-induced vegetation change in Amazonia influenced global CO_2 concentrations either during the early

reforestation event documented here or during the Great Dying.

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SYM, FEM. Those contributing to figures and analyses: MNN, SYM. Those also contributing to writing: WC, FEM, TK.

List of supplementary materials:

Supplementary materials

Materials and Methods

Figs. S1-S3

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Database S1 (separate file)

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Figure legends

Fig. 1: How reforestation could relate to atmospheric carbon concentrations. Atmospheric CO_2 concentrations (blue line) (*5*) showing the 7-10 ppm decline at 1610 are attributed to the Great Dying. Expected carbon uptake patterns associated with occupation, abandonment, and forest recovery are shown for 1550-1750, following the observation that the most intense sequestration takes place in the first century of succession (*10*).

Fig. 2: Sites used in the analysis. A) Distribution of 39 lake sediment records shown in the context of precipitation of the driest quarter (i.e. the 3 consecutive months per year with the lowest precipitation values) (*21*) with larger symbols representing the high-resolution sites (Figs. 3, 4A-C). Color-coding indicates whether evidence of past human occupation was present in the record. B) Forest change during the Great Dying period. Color coding indicates whether pollen percentages at each site had increased (green) or decreased (purple) at least 5% during the Great Dying period, compared with samples in the previous time window. C) The proportion of sites that were losing or gaining either 5% or 10% of forest pollen (compared with samples in the previous time window) over the last 2000 years, using 200-year time bins (-50 to 1950). Dark gray vertical bar indicates the Great Dying period.

Fig 3: Variability in pollen percentages of forest taxa over the last 2000 years documented at the nine high-resolution lake sites. Sites are color-coded by the percentage of samples in the record containing the presence of maize pollen, a direct indicator of cultivation (External database S4-12). Vertical grey bar indicates the Great Dying period (1550-1750 CE).

Fig. 4: Changes in forest pollen abundance and forest burning. Percentage differences from the site mean (0-2000 CE) for A) forest pollen and B) *Cecropia*, for the nine high-resolution sites. Data are interpolated to 100-year time slices. C) The Charcoal Index values represent the charcoal abundance data for each lake, scaled and standardized to values between 0 (absence of fire) and 100 (maximum charcoal abundance given that all samples contain charcoal). The standardization allows comparisons across sites

(16). Mean values (black line) for panels A-C indicate the average value across all sites
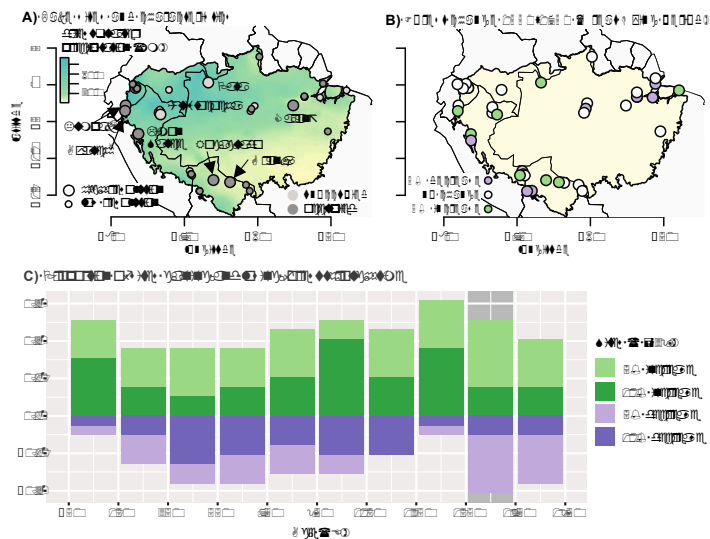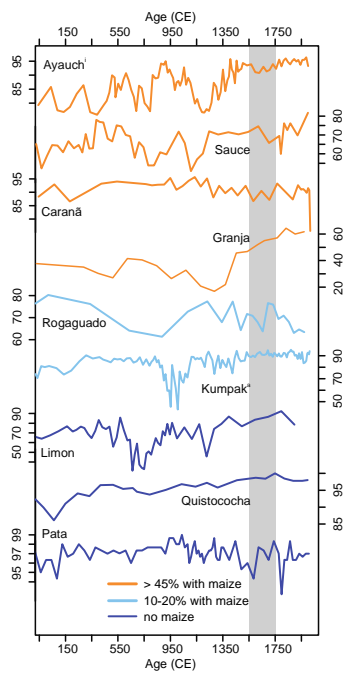
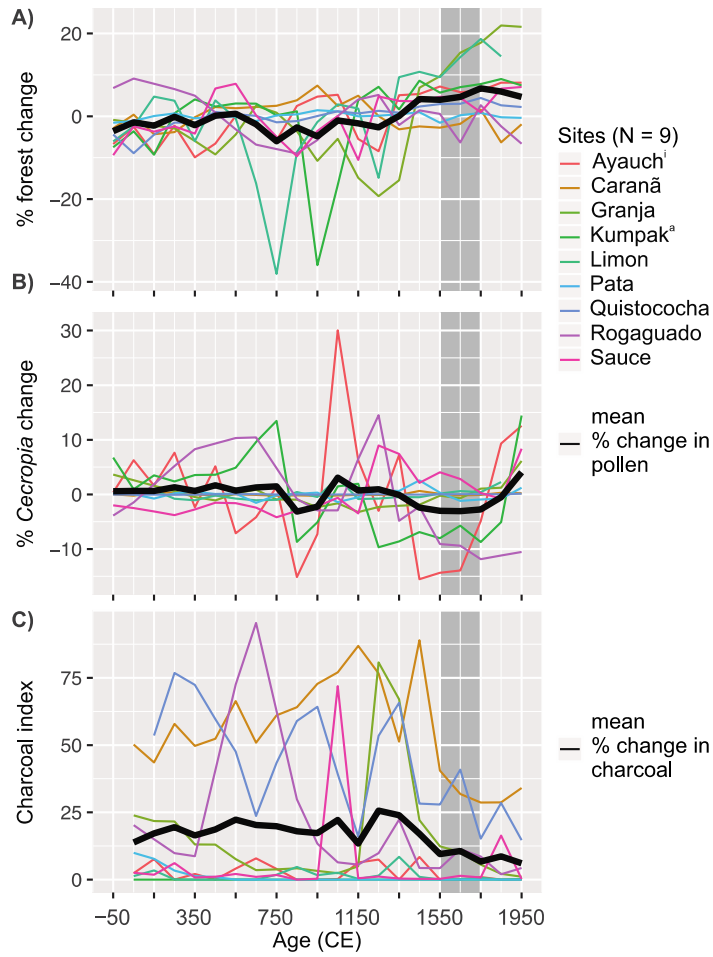for each 100-year time window.

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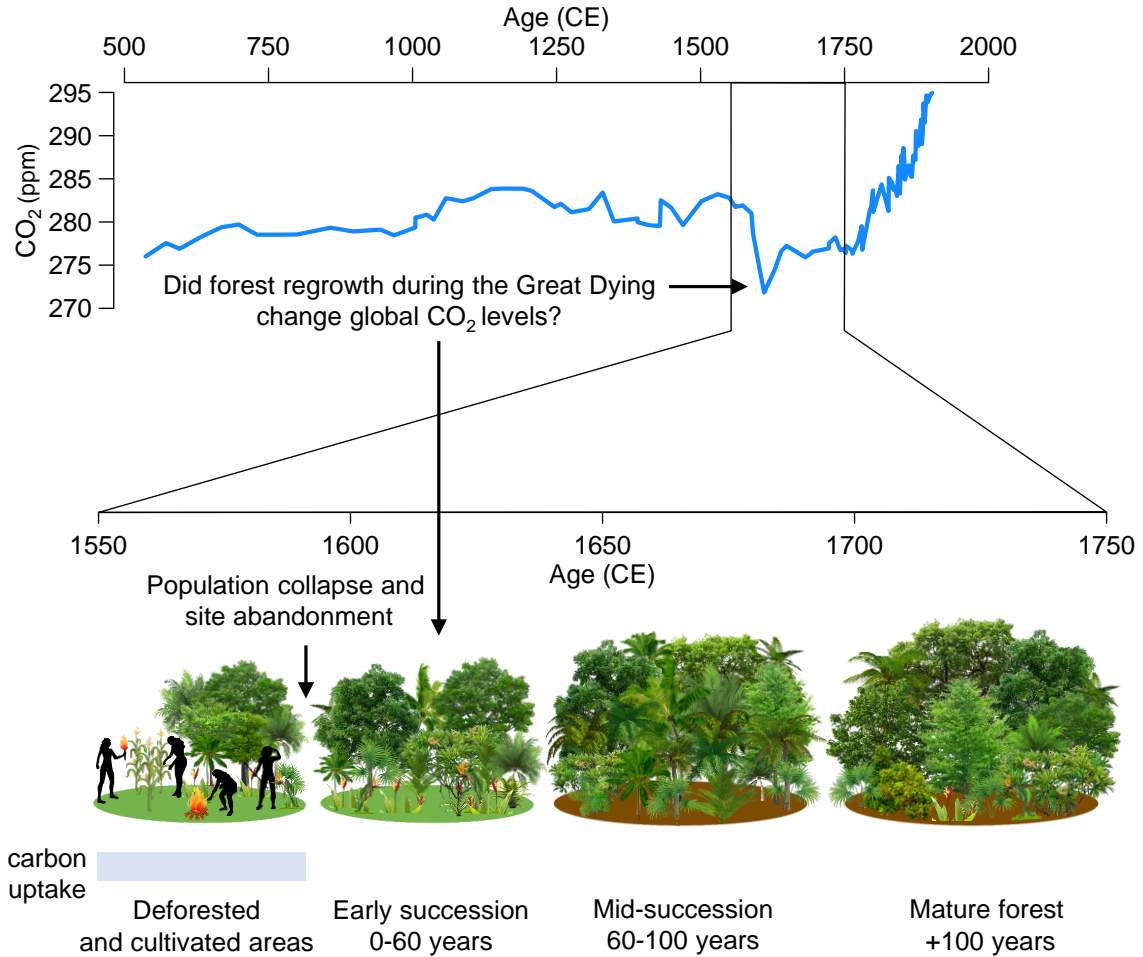
Fig. 1

Fig. 2

Fig. 3

Fig. 4

Supplementary Materials for

Widespread reforestation before European influence on Amazonia

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This PDF file includes:

Materials and Methods
Supplementary Text
Figs. S1 to S3
Captions for databases S1

Other Supplementary Materials for this manuscript includes the following:

Materials and Methods

Analysis of lake sediments

We compiled fossil pollen and charcoal data from 39 lake-sediment records (database S1) in Amazonia *sensu stricto* (*42*). We did not include pollen or charcoal reconstructions from peatland or palm swamp settings. To be included, all sites had to have a minimum of six fossil pollen samples within the last 2000 years and appear to be continuous records. The categorization of 'occupied sites' for the 39 lake sediments was based on the presence of cultigen pollen (predominantly *Zea mays*), increases in the pollen of grasses and weeds, or the presence of charcoal.

For each site (N = 39), we calculated the total forest percentage of all tree and shrub taxa contained in the pollen record (including *Cecropia*) (database S1). *Cecropia* pollen percentages are also shown separately, as this tree is an indicator of site abandonment and early successional forest regrowth (*43*). Raw pollen counts were not available for all lakes, but for those reported, pollen counts are generally > 300 grains per sample (database S1). At Lake Caranã, *Mauritia* pollen was so abundant that it represented > 84% of the total pollen sum (*22*). As *Mauritia* is an obligate wetland palm, this local pollen representation could mask changes in forest cover in the adjacent uplands. Consequently, *Mauritia* was excluded from the pollen sum for Lake Caranã, and forest pollen percentages were recalculated. Prior work in modern Amazonian settings has shown that forest disturbance by humans (*15, 16*) is revealed by a reduction in the proportion of forest pollen by 5-10%. Based on prior assays of the sensitivity of forest pollen representation to human disturbance we tabulated the proportion of sites that in contiguous samples lost or gained at least 5% or 10% of total forest pollen for each 200-year time window from -50 to 1950 (databases S1, Fig. S1).

Nine of the 39 lake sedimentary records (referred to as high-resolution sites) contain at least two dates over the last 2000 years, and over 10 pollen and charcoal samples in the last 1000 years (database S1, Fig. S3). The high-resolution sites are used to provide temporally detailed changes in the amount of forest pollen abundances before, during, and after the Great Dying period (1550-1750). We show the changes in forest pollen percentages for all the high-resolution sites, and also the deviation from the mean forest percentage for each site in 100-year time bins. We also present the mean of those deviations across sites for the last 2000 years. We show the same for *Cecropia* pollen.

The charcoal samples reported here were collected by many investigators, and thus sample preparation and measurement methods did not follow a standardized protocol (Database S1, Table 1). Without such a protocol a standardization method is necessary to account for differences in laboratory procedure, catchment size, and sediment properties when comparing charcoal amounts across sites (*44*). We performed proportional relative scaling to standardize the charcoal abundance data from each lake record (*45*), and report it as the Charcoal Index Value.

$$Charcoal\ Index\ Value = \left(\frac{c_i}{c_{max}} * 100\right) * f/N$$

This approach scales each measurement (c_i) within each lake sediment record to a value ranging between 0 and 100, where 0 is the absence of charcoal and 100 is the maximum abundance measurement for that record (c_{max}). The scaled measurements are then multiplied by the proportion of samples within the record containing charcoal (f/N). Proportional relative scaling is particularly robust in assessing fire in systems where fire is infrequent or rare, because

0 is used as the true absence value, and samples containing small or infrequent amounts of charcoal are down-weighted (*45*). The scaled data are reported as the Charcoal Index value. We show the Charcoal Index values for each site, and the mean of the Charcoal Index values across all sites (N = 9) for 100-year time windows for the last 2000 years.

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Supplementary Text

References (see main text for full list of references)

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Fig. S1.

Summary of the change in forest per 200 years over the last 2000 years in the 39 study sites. The gray bar identifies the period of arrival of Europeans. See database S1, for references and site characteristics.
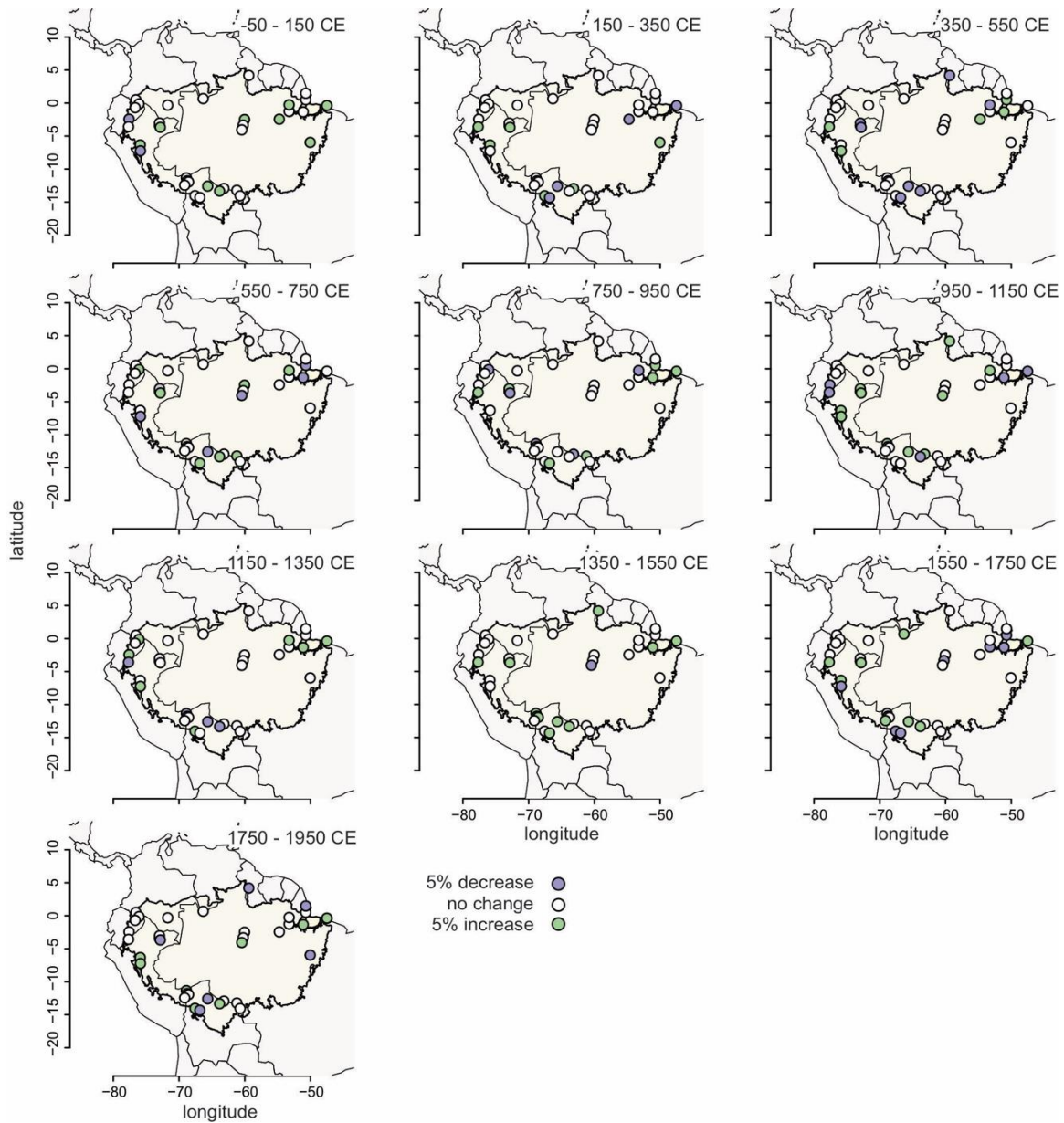
Fig. S2

Spatial and temporal pattern of sites showing increases or decreases in forest pollen of > 5%, using 200-year windows. Light yellow outline shows boundaries of Amazonia sensu stricto (38).
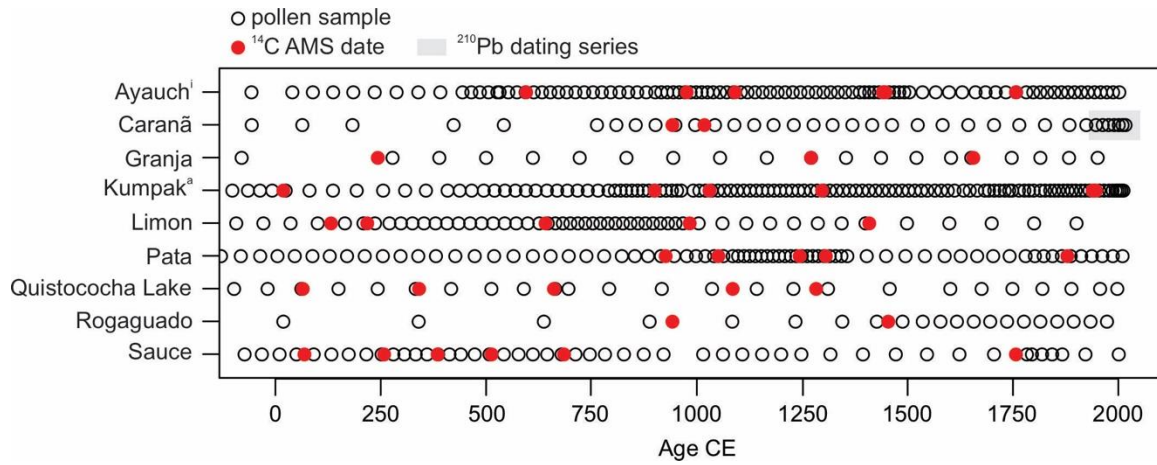
Fig. S3

Sampling resolution of the nine high-resolution sites used in the analyses. See database S1 for further site characteristics and data.

Additional Data table S1 (separate file)

Database S1 contains the data on the site characteristics, pollen, and charcoal data used in this analysis. Table 1 contains all of the metadata on the sites and references to original publications. Table 2-3 contains the percentages in forest pollen change compared with the previous samples (for 5% and 10%) thresholds. The remaining tables contain the charcoal and pollen data for the nine high-resolution sites used in the analysis.