REPORT

PALEOECOLOGY

Widespread reforestation before European influence on Amazonia

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An estimated 90 to 95% of Indigenous people in Amazonia died after European contact. This population collapse is postulated to have caused decreases in atmospheric carbon dioxide concentrations at around 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 substantially increased terrestrial carbon sequestration. On the basis of 39 Amazonian fossil pollen records, we show that there was no synchronous reforestation event associated with such an atmospheric carbon dioxide response after European arrival in Amazonia. Instead, we find that, at most sites, land abandonment and forest regrowth began about 300 to 600 years before European arrival. Pre-European pandemics, social strife, or environmental change may have contributed to these early site abandonments and ecological shifts.

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 around 1200 CE (hereafter, if not specified, years are of the Common Era) (*2*), perhaps nearing a carrying capacity. After 1492, an estimated 90 to 95% of the Indigenous population was lost to waves of disease—including smallpox, influenza, measles, and the common cold—sweeping through "virgin soil" communities or to warfare and slavery (*3*). This catastrophic loss of life resulting from European colonization has been called 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 to 10 parts per million (ppm) drop in atmospheric CO_2 concentrations known as the Orbis spike, which began around 1610 and presaged relatively low concentrations until around 1750 (Fig. 1) (*4*)—a decline that deepened the cooling of the Little Ice Age (1400 to 1800) (*5*). Whether the scale of CO_2 variation forming the Orbis spike was truly an unusual event has been questioned (*6*), as has 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 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 (*10*), Acuña (*11*), and La Condamine (*12*). Lured by rumors of gold, the first large Spanish expedition entered lowland Amazonia in 1541 (*10*). Friar Carvajal, the diarist of Orellana's expedition, reported large, healthy populations along many portions of the river, with no suggestion of mass disease (*10*). 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 (*12*). In contrast, a French surveyor, La Condamine, traveled down the Amazon River

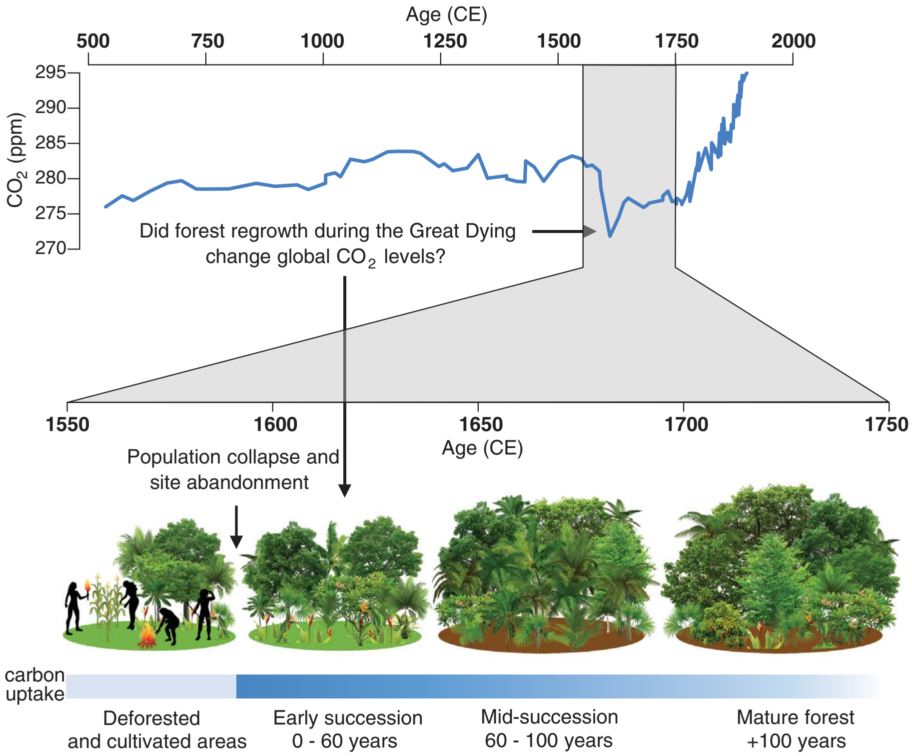

Fig. 1. How reforestation could relate to atmospheric carbon concentrations. Atmospheric CO_2 concentrations (blue line) (*5*) showing the 7 to 10 ppm decline at 1610 are attributed to the Great Dying. Expected carbon uptake patterns associated with occupation, abandonment, and forest recovery are shown for 1550 to 1750, assuming that the most intense sequestration takes place in the first century of succession (*41*).

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in 1743 but did not record the same high density of people on the riverbanks, suggesting a partially depopulated landscape (*12*). Although it seems most probable that any vegetation change associated with the Great Dying took place in Amazonia after 1639 (the year of Acuña's trip), we investigate the possibility that it occurred between 1550 and 1750, concurrent with low CO_2 levels (*8*, *9*).

Although it is challenging to estimate precollapse population size, assumptions of near-synchronous forest regrowth are readily testable using paleoecology. Fossil pollen recovered from lake sediments provides a metric for reconstructing local forest cover and land use (*13*). 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 past 2000 years between open ground and weedy species (signaling 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 (*13*).

Although 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 (*14*, *15*). Consistently, within the forested portion of Amazonia, relatively undisturbed forest produces 95 to 100% forest pollen (*14*). Where human disturbance occurs, forest pollen percentages decrease, while percentages of open ground and shrubby taxa increase. Fossil pollen of weeds, grasses, and crops is usually accompanied by charcoal, which is a direct indicator of anthropogenic forest burning, as natural (lightning-induced) fires rarely occur in Amazonian forests (*16*). 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 (*17*). *Cecropia* occurs naturally as a canopy gap–colonist in 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 (*18*). Abandoned 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 past 2000 years using fossil pollen and charcoal data derived from 39 lake sites across Amazonia (*19*).

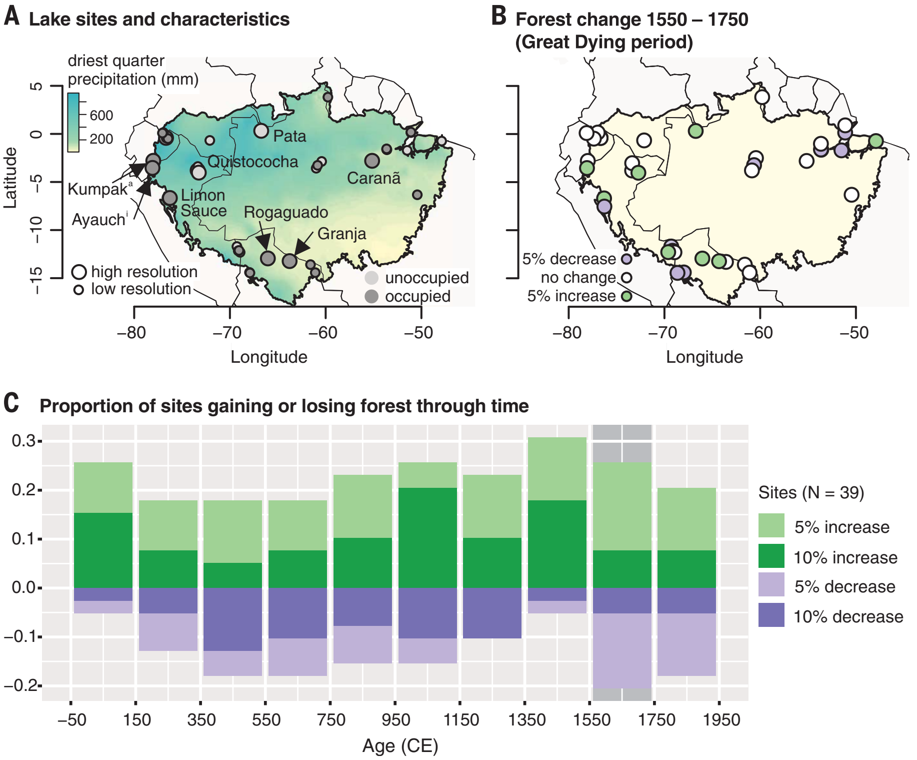

Fig. 2. Sites used in the analysis. (**A**) Distribution of 39 lake sediment records shown in the context of precipitation of the driest quarter (i.e., the three consecutive months per year with the lowest precipitation values) (*20*), with larger symbols representing the high-resolution sites (Figs. 3 and 4). 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 past 2000 years, using 200-year time bins (50 BCE to 1950 CE). Dark gray shading indicates the Great Dying period.

About 80% of the 39 sites contained signals of forest opening, burning, or cultivation consistent with pre-European occupation (Fig. 2A and data 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 (Fig. 2 and figs. S1 and S2). To assess even minor changes in forest cover, the proportion of sites showing a 5 or 10% increase or decrease in forest pollen was assessed. Sites exhibiting evidence of deforestation at values >5% peaked between 350 and 750 CE, whereas the proportion of sites showing evidence of reforestation was greatest between 750 and 1550 CE (Fig. 2C and figs. S1 and S2). During the Great Dying period, the number of sites where forest pollen was increasing roughly equaled those where it was falling in abundance (Fig. 2, B and C, and fig. 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 after the Great Dying, our empirical data show that changes in Amazonian land use and forest cover took place several centuries before European arrival (Fig. 2C).

Nine sites out of 39 contain at least 10 pollen samples from the past 1000 years (fig. S3) and provide centennial-scale temporal resolution (hereafter referred to as high-resolution sites). These sites offer the opportunity to investigate trajectories of site disturbance and forest recovery (Fig. 3 and data S1). Eight of the nine high-resolution sites contain pollen and charcoal evidence of occupation in the pre-Columbian era and provide evidence of changes in forest pollen percentages before, during, or after the Great Dying (Fig. 3 and data S1). 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 nonuse (*16*–*24*). 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 occupation, with the frequent use of fire and maize (*Zea mays*) and squash (*Cucurbita* spp.)

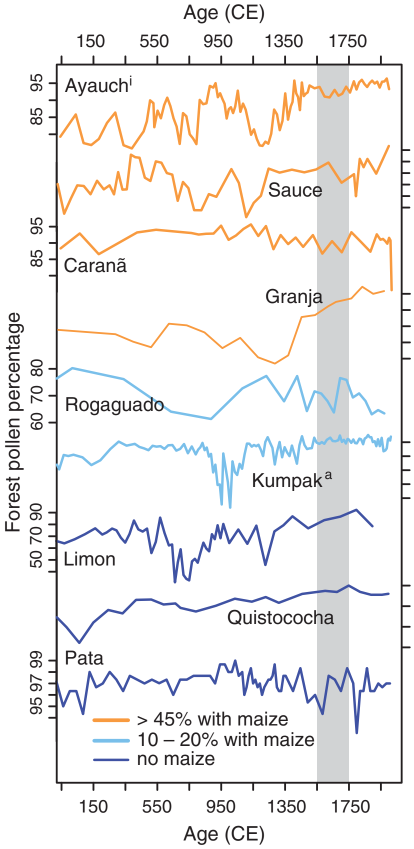

Fig. 3. Variability in pollen percentages of forest taxa over the past 2000 years, documented at the nine high-resolution lake sites. Sites are color coded by the percentage of samples in the record containing the presence of maize pollen, a direct indicator of cultivation (see tables S4 to S12 in data S1). Dark gray shading indicates the Great Dying period (1550 to 1750 CE).

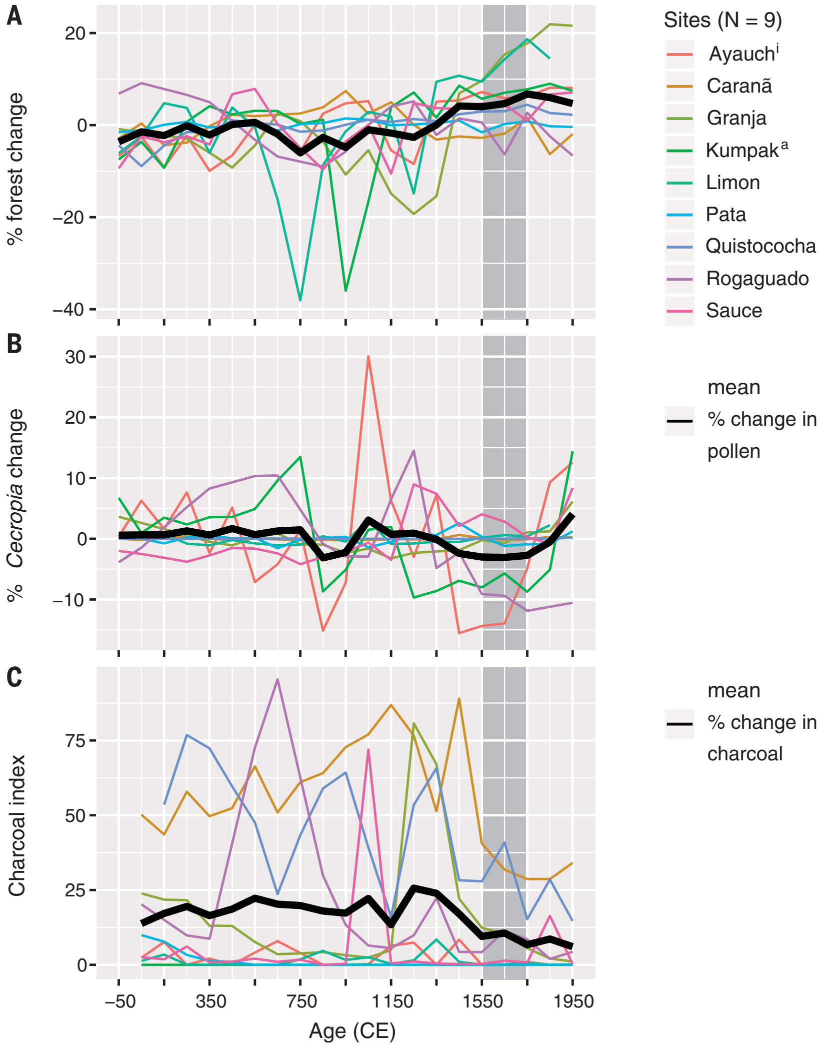

Fig. 4. Changes in forest pollen abundance and forest burning. Percentage differences from the site mean (0 to 2000 CE) for (**A**) forest pollen and (**B**) *Cecropia*, for the nine high-resolution sites. Data are interpolated to 100-year time bins. (**C**) The charcoal index values represent the charcoal 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 (*15*). Mean values (black line) for (A) to (C) indicate the average value across all sites for each 100-year time window.

cultivation. Archaeological data at Carañ evidence the formation of Amazonian Dark Earth over the past 2000 years (*21*). Despite this intensity of use, no notable change in total forest pollen is associated with the Great Dying at Lake Carañ. Lakes Rogaguado and Granja were the only pollen records that showed an increase in forest pollen abundance by >10% between 1550 and 1750 (Fig. 3). Most of the increase at Rogaguado occurred between 1650 and 1750 CE. Although 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 already fully forested. Progressively wetter conditions at Granja over the past 2000 years should have led to increased forest cover, but instead, grassland was maintained by human activities until abandonment, at around 1300 to 1400 CE (*22*). After 1300 CE, forest cover increased from 20 to >40% in about a century (Fig. 3). Thus, Granja 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 sites containing pollen evidence of maize cultivation, fluctuations in forest pollen percentages, indicative of forest clearance and recovery, varied in timing. Sauce (*23*) and Ayauchi (*24*) had records of long-term forest clearance, whereas Lake Kumpaka (*25*) was used episodically. Quistococha (*26*) and the saline Lake Limon (*27*) provided evidence of human occupation (burning) but no crop pollen. None of the nine sites showed increases in forest pollen during the Great Dying. Lake Pata lies on an inselberg above the Amazon plain, with very thin soils that preclude cultivation (*28*). A high-resolution pollen analysis of Lake Pata revealed no evidence of human occupancy and forest pollen percentages that were >95% throughout the past 2000 years (Fig. 3) (*28*).

When looking at deviations in forest pollen abundance from the 2000-year mean pollen percentage of each record, only Lake Rogaguado showed notable forest increases during the Great Dying period, particularly from 1650 to 1750 CE (Fig. 4A). Other lakes showed either no deviation throughout the record or forest percentages that increased relative to mean values between 950 and 1350, i.e., 300 to 600 years before the Great Dying event. The largest increase in the mean value of all forest pollen deviations occurred from about 1250 to 1350, with no substantial increase during the Great Dying period (Fig. 4A, black line). Between 950 and 1350, *Cecropia* pollen percentages showed the largest increases (~5%) from mean values, whereas during the Great Dying, values were ~5% lower than the long-term mean (Fig. 4B). These data are inconsistent with a postulated peak in post-disturbance succession and rapid carbon uptake after 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. 4, B and 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 and 1750 was Lake Quistococha, which is located near the city of Iquitos, Peru, in a region where the Jesuits established the Mainas missions from 1638 to 1767 (*29*).

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 around 950 to 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. But they are not. Trends in forest pollen abundance do not seem to have a distinct geographic pattern (Fig. 2B and figs. S1 and S2), and neighboring sites often show nonsynchronous peaks of fire and periods of fire absence (Fig. 4) (*30*, *31*), suggesting that climate change is unlikely to be the sole 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 (*32*, *33*). De Souza *et al.* (*34*) 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 about 1000 and 1200 CE (*35*). This migration is associated with the collapse of the Tiwanaku and Wari cultures, rapid climate change, and—as evidenced by cranial trauma—increased warfare (*36*, *37*). 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 (*38*). 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 underlie 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 (*39*). Trading between lowland and highland communities, which this period is known for (*40*), 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 after European contact. Furthermore, our data suggest that the timing of reforestation was heterogeneous, with many sites showing an increase in forest cover as many 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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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S3
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Data S1

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Science

Widespread reforestation before European influence on Amazonia

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Pre-Columbian reforestation in Amazonia

An early 17th-century temporary reduction in global atmospheric carbon dioxide (CO_2) levels was previously attributed to reforestation in Amazonia after the catastrophic loss of life of the indigenous population caused by diseases brought by European invaders. Using fossil pollen data from Amazonian lake sediments with temporal resolution over the past millennium, Bush *et al.* found that forest recovery began 300 to 600 years before the population crash. The more recent nadir in atmospheric CO_2 was not associated with rapid reforestation at that time. The vegetation changes appear to be the result of changing patterns of land use in the centuries preceding the European arrival and the resulting devastation, whereas the cause of the CO_2 decline remains enigmatic.

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