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Earth system impacts of the European arrival and Great Dying in the Americas after 1492

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ABSTRACT

Human impacts prior to the Industrial Revolution are not well constrained. We investigate whether the decline in global atmospheric CO_2 concentration by 7–10 ppm in the late 1500s and early 1600s which globally lowered surface air temperatures by 0.15 °C, were generated by natural forcing or were a result of the large-scale depopulation of the Americas after European arrival, subsequent land use change and secondary succession. We quantitatively review the evidence for (i) the pre-Columbian population size, (ii) their per capita land use, (iii) the post-1492 population loss, (iv) the resulting carbon uptake of the abandoned anthropogenic landscapes, and then compare these to potential natural drivers of global carbon declines of 7–10 ppm. From 119 published regional population estimates we calculate a pre-1492 CE population of 60.5 million (interquartile range, IQR 44.8–78.2 million), utilizing 1.04 ha land per capita (IQR 0.98–1.11). European epidemics removed 90% (IQR 87–92%) of the indigenous population over the next century. This resulted in secondary succession of 55.8 Mha (IQR 39.0–78.4 Mha) of abandoned land, sequestering 7.4 Pg C (IQR 4.9–10.8 Pg C), equivalent to a decline in atmospheric CO_2 of 3.5 ppm (IQR 2.3–5.1 ppm CO_2). Accounting for carbon cycle feedbacks plus LUC outside the Americas gives a total 5 ppm CO_2 additional uptake into the land surface in the 1500s compared to the 1400s, 47–67% of the atmospheric CO_2 decline. Furthermore, we show that the global carbon budget of the 1500s cannot be balanced until large-scale vegetation regeneration in the Americas is included. The Great Dying of the Indigenous Peoples of the Americas resulted in a human-driven global impact on the Earth System in the two centuries prior to the Industrial Revolution.

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1. Introduction

The arrival of Europeans in the Americas in 1492 CE marks the onset of disease epidemics resulting in the loss of the majority of indigenous people living in the Americas over the subsequent century (Berlinguer, 1993; Cook, 1998; Crosby, 1972, 1976; Nunn and Qian, 2010). Indigenous land use was widespread before European arrival, particularly in Mexico, Central America, Bolivia and the Andes where terraced fields and irrigated agriculture was practised (e.g. Abrams and Nowacki, 2008; Chepstow-Lusty and Jonsson, 2000; Heckenberger et al., 2003; Hunter and Sluyter, 2015; Whitmore and Turner, 1992), and across Amazonia where diverse pre-Columbian land uses left its traces in the composition of contemporary Amazon forests (Clement et al., 2015; Levis et al., 2017; Maezumi et al., 2018a; Watling et al., 2018). Thus the Great Dying of the Indigenous Peoples of the Americas (Wolf, 1982) after 1492 CE likely led to a reduction in land use. Fields and fallow areas then underwent secondary succession and in many cases increased carbon stocks as they reverted towards similar prior states – with local, regional and potentially global consequences for the Earth System.

The uptake of carbon on the abandoned anthropogenic lands after European contact may have been large enough to impact the atmospheric CO_2 record (Dull et al., 2010; Faust et al., 2006; Lewis and Maslin, 2015; Nevle and Bird, 2008; Nevle et al., 2011; Ruddiman, 2005). Furthermore, at the same time high-resolution Antarctic ice-core records of atmospheric CO_2 concentration show an anomalously large decline of ~7–10 ppm (Ahn et al., 2012; MacFarling Meure et al., 2006) beginning in the 1500s with a minimum in the early 1600s (Fig. 1). Isotope analysis shows that the anomaly was driven by an increase in the terrestrial carbon sink (Fig. 1B, Bauska et al., 2015; Francey et al., 1999; Trudinger et al.,

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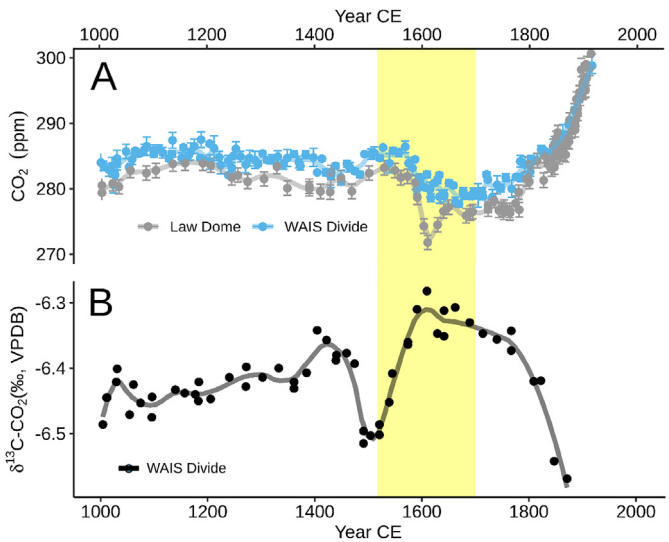

Fig. 1. Global atmospheric CO_2 time series. (A) The CO_2 concentrations recorded in two Antarctic ice cores: Law Dome (grey, MacFarling Meure et al., 2006) and West Antarctic Ice Sheet (WAIS) Divide (blue, Ahn et al., 2012). (B) Carbon isotopic ratios recorded in CO_2 from the WAIS Divide ice core (black, Bauska et al., 2015) showing an increased terrestrial carbon uptake over the 16th century (B). Yellow box is the span of the major indigenous depopulation event (1520–1700 CE). Loess smoothed lines for visual aid. Error bars are the 1-σ standard deviation. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

1999). Hence, the carbon uptake that is thought to have occurred following the arrival of epidemics in the Americas may have reduced atmospheric CO_2 levels and led to a decline in radiative forcing that may then have contributed to the coldest part of the Little Ice Age (Faust et al., 2006; Neukom et al., 2014).

However, modelling efforts attempting to reproduce the CO_2 decline from land use change (LUC) have so far been inconclusive, some showing an impact (Kaplan et al., 2011), while others do not (Pongratz et al., 2011). An alternative approach, using a forcing-fingerprint analysis, rules out internal variability of the Earth System, changes in the total solar irradiance (TSI), and volcanic forcing, as drivers of the change (Schurer et al., 2013). This study finds that the decline in atmospheric CO_2 contributed to the observed cooling, which is consistent with uptake following secondary succession in the Americas.

We therefore test the hypothesis that human actions impacted CO_2 levels and global surface air temperatures in the 16th and 17th centuries, just before the Industrial Revolution, by examining the evidence at each stage of its primary assumptions. First, the existence of a sufficiently large indigenous population in the Americas before 1492 CE. Second, the impact of anthropogenic land use on the environment. Third, the population decline estimates following the arrival and spread of European diseases. Fourth, the magnitude, extent and timing of the subsequent successional regrowth of vegetation and resulting carbon sequestration. We therefore compile all existing estimates from a comprehensive literature survey. These records are then cross-combined and sampled using two different statistical methods (Fast Fourier and Monte Carlo approaches) to obtain revised estimates of the 1492 CE population, per capita land use, mortality from European-contact diseases, and the subsequent uptake of carbon on the abandoned lands. For each term we also compute uncertainty estimates. We then combine these estimates to show the most likely impact of the Great Dying of the Indigenous Peoples of the Americas on atmospheric CO_2 levels. Finally, we place these new estimates of carbon uptake in the context of other changes to the 16th century carbon cycle.

2. The population of the Americas in 1492

The first population groups to arrive in North America between 20,000 and 15,000 years ago were of east Asian- and north Eurasian ancestry (e.g. Amick, 2017; Moreno-Mayar et al., 2018; Pedersen et al., 2016). The adoption of a sedentary, agricultural way of life in the Americas began 10,000–8000 BP (Piperno and Dillehay, 2008; Piperno et al., 2009). Large, complex civilizations emerged in North, Central and South America, further increasing population density, with abundant evidence for a large population living in the Americas prior to European arrival (e.g. Bolt and van Zanden, 2014; Canuto et al., 2018; Clement et al., 2015; Cook, 1998; Denevan, 1992a). However, as the epidemics spread, often ahead of the European explorers, pre-European population estimates were never formally documented in colonial censuses (Diamond, 1997; Dobyns, 1993). Hence, Native American populations were only documented in the decades after European contact, necessitating the use of indirect methods to estimate the pre-1492 population of the Americas. Here, we summarize all existing methodologies applied to reconstruct pre-contract indigenous population, and extract published regional estimates to calculate a revised hemispheric population estimate with uncertainty ranges.

2.1. Approaches to estimating the indigenous population at European arrival

Historical anthropologists and archaeologists estimate indigenous population numbers at contact by utilizing a range of documentary evidence, including sizes of armies, number of adult males, census data, tribute records, numbers of buildings, depopulation ratios, and historic clerical chronicles such as the number of baptisms and number of deaths in a community (Borah and Cook, 1960, 1969; Dobyns, 1966, 1983). The conversion from such evidence into population estimates has several limitations. Records of the sizes of armies and the sizes of settlements from just after Spanish arrival may be prone to miscounting and exaggeration (Denevan, 1992a) while the conversion from tributes to population numbers requires contentious assumptions to be made (Henige, 1998; Zambardino, 1980). These include the proportion of a population excluded from tributes, average tribute paid per house, number of people per house, conversion from goods into monetary value, spatial homogeneity of population structure and analogies to present day population structures (Borah and Cook, 1960; Sanders, 1976; Sanders et al., 1979).

Colonial census estimates are generally considered more reliable (Denevan, 1992a), but do not capture population levels before European contact (Borah and Cook, 1960). Accepting such censuses as representative of pre-contact populations led to studies from the early and mid-20th century giving very low 1492 CE population estimates (e.g. Kroeber, 1939; Rosenblat, 1954). Some estimate of the population loss on contact is necessary to provide more robust population numbers.

Archaeological data can also be used to estimate pre-contact population size, but again involves several assumptions, such as the number of houses in a settlement that are occupied at one time (Schacht, 1984). But in contrast to historical documents, new archaeological sites are regularly discovered and new and innovative multidisciplinary approaches are being applied to the data, adding new constraints on regional pre-contact population sizes (e.g. Canuto et al., 2018; Goldberg et al., 2016; Liebmann et al., 2016; Storey, 2012). Population densities can be inferred from the number of archaeological sites (Heckenberger et al., 2003), the number of archaeological features such as pottery, charcoal and fertile anthropogenic soils known as Amazonian Dark Earth (ADEs Heckenberger et al., 1999; Meggers, 2001). Expanding on this, the

"habitat density method" projects well-studied local population densities to other regions with similar environmental characteristics to calculate the total population under the assumption that population densities in different locations with the same habitat are similar (e.g. Denevan, 1970, 2003; Newson, 1996). Thus, all 1492 CE population estimates require data to be combined with assumptions to arrive at estimates.

2.2. New pre-Columbian population estimates

We summarize the existing evidence for pre-Columbian populations using seven geographical regions: the Caribbean, Mexico, Central America, the Inca Territory, Amazonia and contiguous forested area, North America and the Rest of the Americas. The Inca Territory at contact encompassed Peru, Bolivia, Ecuador, Colombia, Chile and parts of north-western Argentina; the Rest of Americas is composed of Venezuela, Uruguay, Paraguay and the rest of Argentina. We complied 129 estimates from 82 studies (Caribbean, n = 18; Mexico, n = 17; Central America, n = 23; Inca Territory, n = 26; Amazonia, n = 20; North America, n = 9; Rest of Americas, n = 6; total hemisphere, n = 10; Table 1). Below we discuss the range of estimates for each region and use them to calculate a total population estimate of the Americas in 1492 CE based on all existing data available at the time of this review.

Caribbean. The first contact between Europeans and Amerindians occurred when Columbus arrived in 1492 CE on the Caribbean island of Hispaniola (what is now Haiti and the Dominican Republic). The primary source for most modern estimates of the contact population is a contemporary eyewitness report by the Dominican friar Bartolomé de las Casas who reported a Hispaniola population of 4 million at the time of contact (Denevan, 1992a). However, studies based on this same report range from 60,000 that neglects contemporaneous reports of post-contact deaths (Verlinden, 1973, in Henige, 1978), to acknowledging some degree of depopulation with initial populations estimated at between 100,000 (Amiama, 1959; Rosenblat, 1976) and 8 million (Cook and Borah, 1971, Table S1). The 8 million estimate has drawn criticism for the worker-to-population ratio used, the assumption of a logarithmic population decline during 1492–1496 CE, and the inclusion of a controversial tribute count from 1496 CE (Henige, 1978). Most estimates are between 300,000 and 500,000 people in the Caribbean before European contact (Córdova, 1968; Dobyns, 1966; Morison, 1948; Moya Pons, 1979; Williams, 1970).

Mexico. Europeans arrived in what is now Mexico in 1519 CE. Yet, the first comprehensive census only took place in 1568 CE, and tribute records are only available as documentary evidence from the late 1540s (Cook and Borah, 1960; Whitmore, 1991). For central Mexico (the most populous region in Mexico) a population of 25.3 million in 1519 CE has been estimated from tribute records (Borah and Cook, 1969), which would make it one of the most populous regions in the world at the time. Zambardino (1980) highlights the uncertainties in Borah and Cook's approach and arrived at a population between 2.2 and 28 million. Dobyns (1966, 1983) suggests the highest numbers, up to 52 million for central Mexico, based on an extrapolation of depopulation ratios from the Valley of Mexico. These values are higher than some estimates for all of Mexico. For the other region with a substantial pre-Columbian population, the Yucatan peninsula, estimates range between 2.3 million (historic documents, Lange, 1971) and 13 million (extrapolation from number of houses, Morley, 1968). Considering all of Mexico, the lowest estimates, which either outright reject (Rosenblat, 1954) or question the accuracy (Sanders, 1972) of the early tribute records, are between 4.5 and 6 million. Intermediate estimates are ~16 million, based on a linear extrapolation from results of a modelling study incorporating a combination of population, agricultural and epidemiological models for the Valley of Mexico (Fig. 2, near Valle de Mezquital, Whitmore, 1991) and 17.2 million as a best-estimate based on a synthesis of previous estimates by (Denevan, 1992a). Pre-contact population estimates for central Mexico and Yucatan combined, which is considered representative for all of Mexico, range from less than 3 million to over 52 million with many at around 20 million (Table S1).

Central America. Population numbers for Central America (Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama) are based on sums of regional population estimates (Lovell and Swezey, 1982), reports on indigenous army sizes, tributes and carrying capacities (Fowler, 1988) as well as depopulation ratios (Dobyns, 1966). Estimates range from 0.8 million, based on the extrapolation of census data, omitting any significant population changes prior to the census date (Rosenblat, 1954) to 10.8–13.5 million based on depopulation ratios from better-documented Mexico (Dobyns, 1966), similar to a recent 7–11 million estimate for the Late Classic Maya period (650–800 CE, Canuto et al., 2018). Most estimates range between 4.75 million and 6 million (Sapper, 1924; Denevan, 1992a; Lovell and Lutz, 1995, Table S1).

Inca Territory. At its height, just before conquest in 1533 CE, the Inca Empire encompassed Peru, Bolivia, Ecuador, southern Colombia, Chile and parts of north-western Argentina (Fig. 2). The lowest estimate for the pre-Columbian Inca empire population is two million, based on a reconstructing depopulation rates from tribute records (Shea, 1976). The most comprehensive study on population dynamics of the Inca heartlands of Peru and Bolivia (Cook, 1981), is 9 million (3.3–14.2 million range) at the time of contact, derived from carrying capacity calculations, mortality figures and rates of change between colonial censuses throughout time. Subsequent studies tend to favour the higher end of these estimates (9–11.7 million, Montenegro et al., 1990; Denevan, 1992a). For the other regions of the Inca realm populations are suggested to be relatively small, between 300,000 and 1.5 million in each of Bolivia, Ecuador, Chile and Argentina, plus ~3 million in Colombia (Denevan, 1992a; Etter, 2000; Ocampo, 1997; Villamarín and Villamarín, 2000), with a range of 850,000 (Rosenblat, 1954)

Table 1
Population and land use at 1500 CE and 1600 CE in P08 (Pongratz et al., 2008a), HYDE 3.1 (Klein Goldewijk et al., 2010), KK10 (Kaplan et al., 2011), and this study. Also shown are their implied net global carbon uptakes as published in Pongratz et al. (2011) (for P08) and Kaplan et al. (2011) (for KK10 and HYDE 3.1) and the calculated net global carbon uptake from this study.

	P08	HYDE 3.1	KK10	This study (IQR)
Population at 1500 CE (million)	41.1	41.2	60	60.5 (44.8–78.2)
Land use per capita (ha per capita)	0.18	0.67	6.25	1.04 (0.98–1.11)
Land use area at 1500 CE (million ha)	7.5	27.7	372	61.9 (43.3–87.1)
Depopulation (%)	65%	76%	90%	90%
Population at 1600 CE (million)	14.2	9.7	6	6.1 (4.5–7.8)
Land use area at 1600 CE (million ha)	4.9	8.7	123	6.1 (4.8–7.4)
Land use change 1500–1600 CE	4	−6.9	−249.9	−55.8 (−38.5–79.7)
Net global carbon uptake (Pg C)	0.009	<0.1	40	7.4 (4.9–10.8)

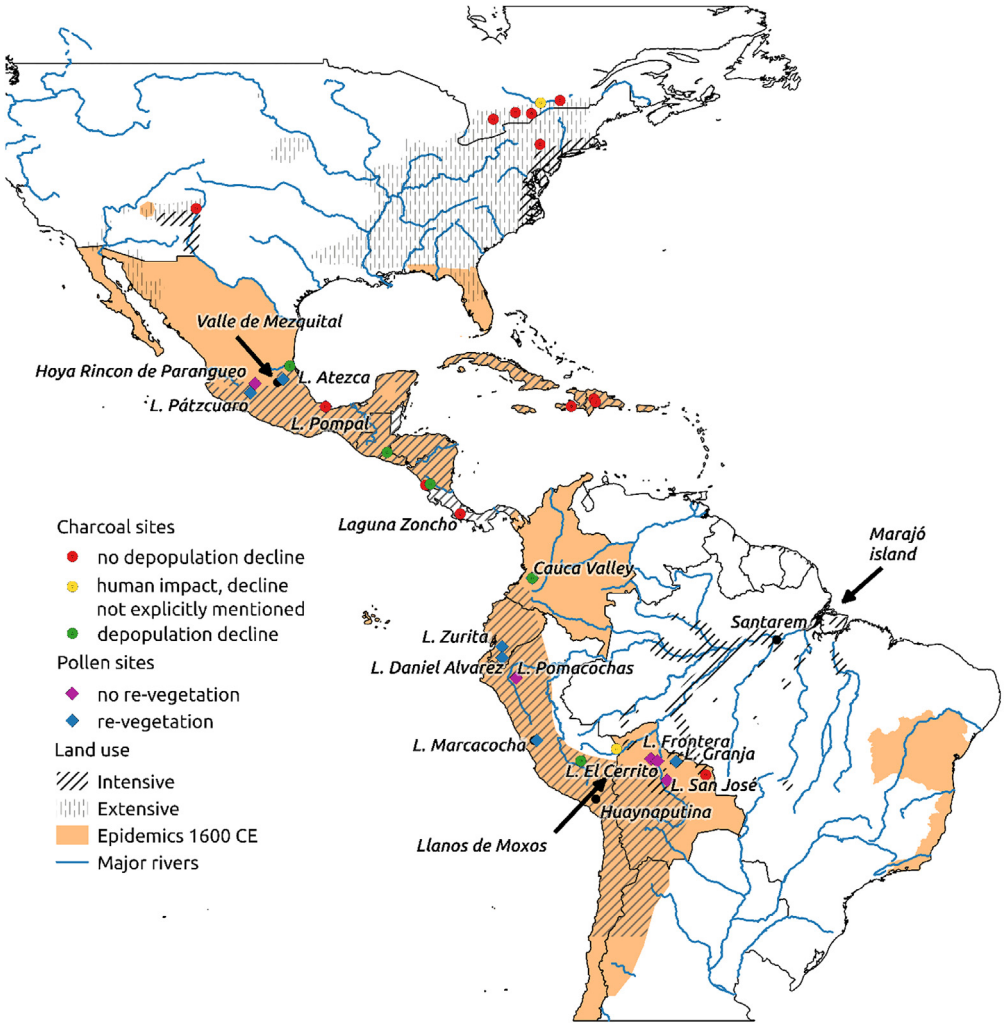

Fig. 2. Regions known to have been affected by disease outbreaks by 1600 CE and pre-Columbian land use. Disease outbreak data derives from Dobyns (1993) and Cook (1998). Land use extent is based on high densities of archaeological sites, earthworks and Amazonian Dark Earths occurrence (Clement et al., 2015; De Souza et al., 2018; McMichael et al., 2014; Whitmore and Turner, 1992). The locations of sites and records referred to in the text and later figures are also shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

to 5 million (Colmenares, 2007). Overall Inca Territory estimates range from 4.1 million to 43.8 million with a likely population of around 20 million, based on the sum of the most widely accepted figures for each of the regions (Table S1).

Amazonia. The vast drainage basin of the Amazon and contiguous forested areas are assumed to be regions of relatively low population density (Denevan, 1992a). Based on archaeological excavations, as historical documents are sparse, larger populations are assumed to have primarily settled in the lowland and lower upland drainage area of the Amazon and its tributaries (Clement et al., 2015; Denevan, 1992a; Roosevelt et al., 1991) as well as at the edges of savannas in Bolivia and Brazil (Erickson, 2000; Heckenberger et al., 2003) and along the northeastern coastline of South America (Rostain, 2008; Schaan, 2008, see Fig. 2). Population studies give a range between 1 million (Rosenblat, 1954) and 20 million (Oyuela-Caycedo in Denevan, 2012) living in Amazonia. Estimates include 1.5–2 million based on an average of present-day densities (Meggers, 1992), 3.2 million based on tribe-by-tribe counts (Hemming, 1995), 5.5 million extrapolated from eastern Ecuador (Newson, 1996), and from 5.1 to 20 million based on the extrapolation of studied population densities along floodplains and known regions of ADEs scaled to an estimated total extent of ADEs (Clement et al., 2015; Denevan, 1970, 1992b, 2012, 2014; Smith, 1999; Woods et al., 2013, see Fig. 2). The large range of the last approach is due to (i) uncertainty in the extent of ADEs; (ii) the proportion occupied at contact, and (iii) settlement size uncertainty (Woods et al., 2013). Recent findings, such as the early domestication of Amazon rice ~4000 BP (Hilbert et al., 2017; Watling et al., 2018), indicate larger populations, with most recent estimates ranging between 8 and 20 million people before Europeans arrived (Table S1).

North America. Europeans began to colonize North America (defined here as the United States of America and Canada) after Central and South America, thus regional and continent wide estimates are largely based on archaeological evidence, tribe-by-tribe counts and environmental carrying capacities (Milner and Chaplin, 2010, see Table S1). The lower range of population estimates for North America lies between 900,000 and 2.4 million, based on tribe-by-tribe counts for the period 1600 CE to mid-1800 CE (Kroeber, 1939; Ubelaker, 1976, 2006). The highest estimate of 18 million, established from analysing environmental carrying capacities (Dobyns, 1983), has been criticized for its assumptions on food acquisition strategies (Milner and Chaplin, 2010). More recent estimates derived from geospatial interpolation of archaeological

sites range between 2.8 million and 5.7 million (Milner and Chaplin, 2010). These intermediate figures are supported by a recent comprehensive regional-scale archaeological study (Liebmann et al., 2016).

Rest of the Americas. Not included in the other regions are estimates for Venezuela with 600,000–1.5 million, Uruguay and Paraguay, estimated together as 285,000–1.1 million, and Argentina with 300,000–500,000 people (Denevan, 1992a; Pyle, 1976; Rosenblat, 1954). All low estimates are based on census data (Rosenblat, 1954) while the higher bounds are based on pre-census eye-witness accounts for Argentina (Pyle, 1976) and a synthesis of previous estimates for Venezuela, Uruguay and Paraguay (Denevan, 1992a). The total estimate for the remainder of the Americas is between 1.2 and 3.1 million.

We then synthesize the 119 published population estimates, including the minimum and maximum estimate when given (Caribbean, n = 18; Mexico, n = 17; Central America, n = 23; Inca Territory, n = 26; Amazonia, n = 20; North America, n = 9; Rest of Americas, n = 6; Table 1) into a revised estimate. We included all the prior studies and did not make any judgement on their relative quality. To obtain regional population estimates, we first calculated estimates by country. For sub-national population data, we cross-combine each sub-national estimate from one part of a country with each sub-national estimate from another part of the country and calculate their sums to obtain national estimates (e.g. each estimate for Yucatan is paired with each estimate for Central Mexico, the sum of those forms estimates for Mexico). These estimates are then added to the existing estimates for their country (e.g. Mexico). National estimates within a region are cross-combined and their sums form a regional estimate for each of the seven regions: Caribbean, Mexico, Central America, Inca Territory, Amazonia and North America, and the Rest of the Americas (Table S1). Next, cross-combining and taking the sums of these regional estimates (2×10^{28} combinations) gives a hemisphere-wide population frequency distribution, with the higher occurrence rate of similar results reflecting higher frequencies in the distribution (Fig. 3A). Our estimate of the number of people living in the Americas in 1492 CE is 60.5 million, with an interquartile range (IQR) of 44.8–78.2 million, using the FFT approach (Fig. 4A). An alternate Monte-Carlo approach to combining the data results in a similar best estimate of 64.1 million (IQR 48.4–82.3 million; Table S2). When sufficient data is available we adopt the cross-combination approach for the rest of the variables we estimate later in the paper. The programming code for both approaches in available in the supplement.

These results are significantly higher than the often-quoted hemisphere 1492 CE population of around 40–41 million, based on Clark's 1967 literature review (Biraben, 1979; Durand, 1977; Henige, 1998; Klein Goldewijk et al., 2010, 2011; Pongratz et al., 2008b), but lower than the Dobyns (1966, 1983) estimate of 112 million. Our results are more similar to Denevan (1992a) 54 million, incorporating another 25 years of research findings after Clark's 1967 review, and the 60 million estimate used in the LUC dataset KK10 (Kaplan et al., 2011; Krumhardt, 2010, Table 1). For comparison, 60.5 million people living in the Americas in 1492 is lower than the population of Europe at the beginning of the 16th century, at 70–88 million (Durand, 1977) and that of China (including Mongolia) at about 100 million (Krumhardt, 2010), both larger populations in a smaller area (Europe 10 million km^2, China and Mongolia 11 million km^2, Central and South America, 18 million km^2). Thus, population density was lower in the Americas than in Asia or Europe at the time of European contact.

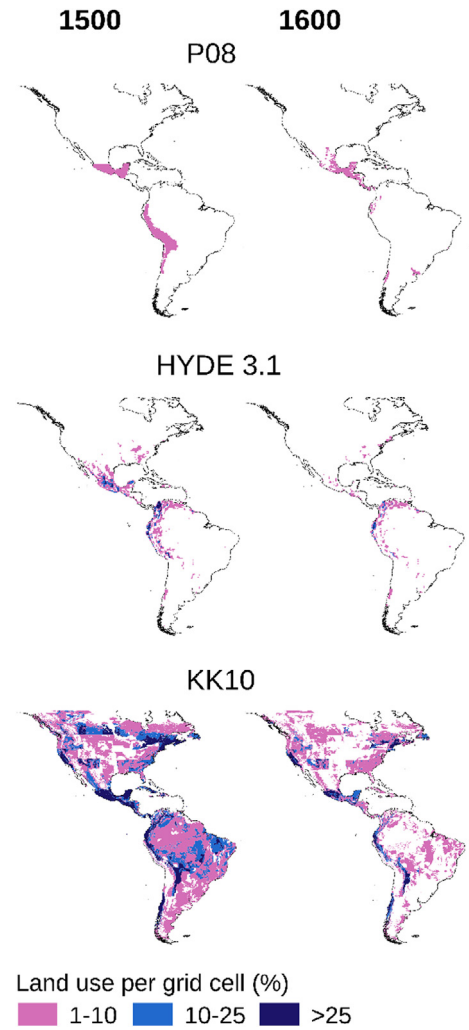

Fig. 3. Reconstructed spatial extent of anthropogenic land use at 1500 CE and 1600 CE in P08 (Pongratz et al., 2008a), HYDE 3.1 (Klein Goldewijk et al., 2011) and KK10 (Kaplan et al., 2011). The datasets vary in their underlying assumptions about land use (see text for details), leading to visibly different extents (Table 1).

3. Extent of anthropogenic land use in 1492

It is widely accepted that the indigenous population of the Americas in 1492 CE did not live in a pristine landscape (e.g. Barlow et al., 2012; Denevan, 2001; Heckenberger et al., 2003; Levis et al., 2017; Whitmore and Turner, 1992). The extent and complexity of pre-Columbian agricultural systems is well-constrained on a local scale for many areas based on a variety of evidence including historical documents, aerial photography and newer remote sensing techniques as well as field based archaeological studies (Canuto et al., 2018; De Souza et al., 2018; Denevan, 2001; Hunter and Sluyter, 2015; Liebmann et al., 2016; Loughlin et al., 2018; Maezumi et al., 2018a; Palace et al., 2017; Whitmore and Turner, 1992). Given the diversity of pre-Columbian land-use practices in the Americas, we first discuss the common land-use practices within our seven regions, then synthesize published land use per capita estimates for the regions, and the extent of pre-Columbian land use in each region to calculate a best estimate of anthropogenic land use in 1492 CE in the Americas.

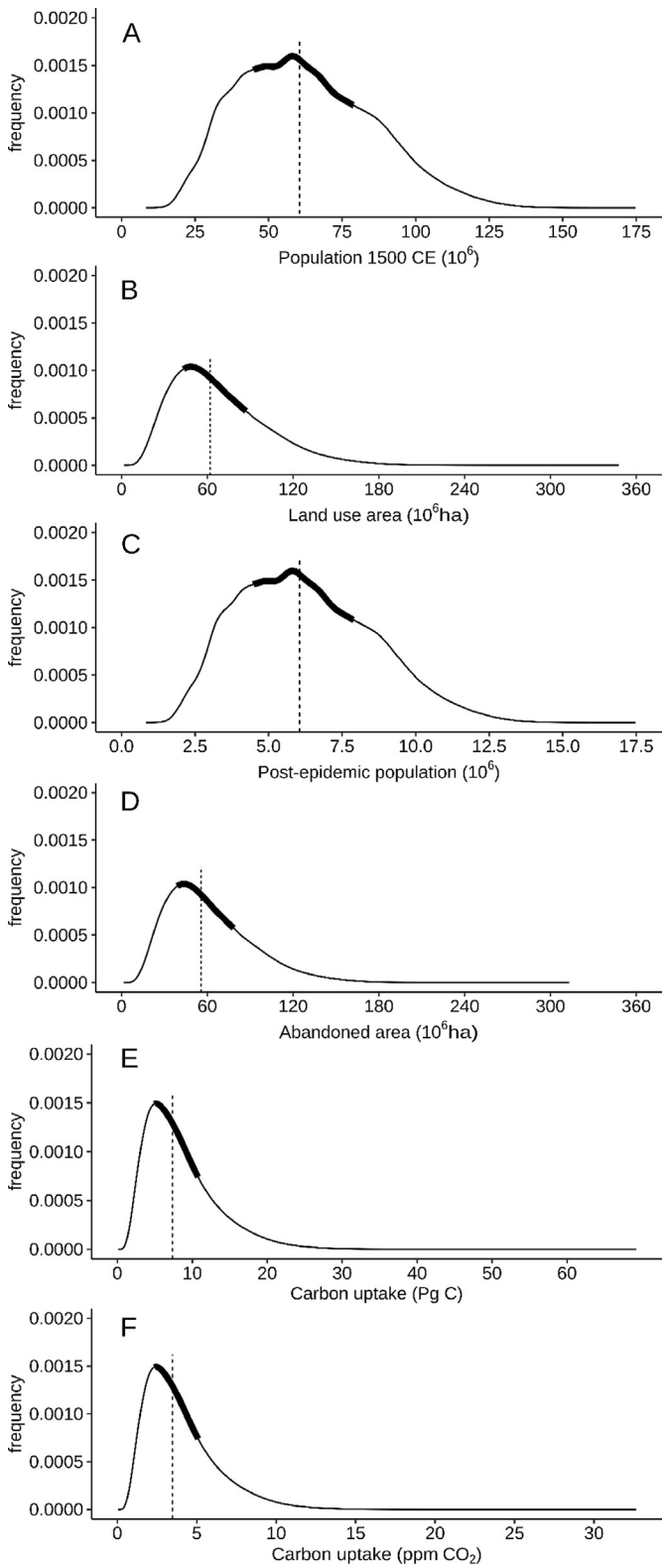

Fig. 4. Probability Density Functions showing frequencies of the indigenous population, in millions, of the Americas in 1500 CE (A); anthropogenic land use area in ha for 1500 CE (B); indigenous population after the Great Dying, in 1600–1650 CE (C); area of anthropogenic land abandoned due to the Great Dying, in Mha (D); carbon uptake in vegetation and soils over 100 years following anthropogenic land abandonment after the Great Dying, in Pg C (E); reduction in atmospheric carbon dioxide over 100 years following anthropogenic land abandonment after the Great Dying, in ppm (F); each derived from combining published regional estimates (see text for method). Bold lines indicate 25–75% interquartile range (IQR), narrow, dashed perpendicular line indicates the median, i.e. where cumulative frequencies pass 50%.

3.1. Land use practices in the pre-Columbian Americas

Caribbean. On most islands, semi-permanent or permanent anthropogenic land use was widespread by the time Europeans arrived (Ortiz Aguilu et al., 1991). Farming consisted mainly of mixed sweet potato (*Ipomoea batatas*), cassava (*Manihot esculenta*) and maize (*Zea mays*) as staple crops eaten together with protein sourced from fishing (Mickleburgh and Pagán-Jiménez, 2012). Stone-built terraces with drainage systems on the hillsides of Puerto Rico (Ortiz Aguilu et al., 1991), raised fields (Castilla-Beltrán et al., 2018) and semi-permanent agriculture on Hispaniola (Richards, 2006) suggest that Caribbean land use was comparable to that in Central America and populous regions of Amazonia. Fire was periodically used for slash and burn systems and small clearings that increased after European settlement (Castilla-Beltrán et al., 2018; Hooghiemstra et al., 2018).

Mexico. Large areas of land were under cultivation of maize fields, cacao and fruit orchards and house gardens (Whitmore and Turner, 1992). The remains of elaborate canal systems have been found in the wetlands of the Gulf Coast and the Basin of Mexico (Whitmore and Turner, 1992). The 700 km^2 Valle del Mezquital in central Mexico (Fig. 2) was extensively managed with fields, some with trees as agroforestry-type systems, irrigated through complex systems of dams and weirs connecting waterbodies in the basin and terraces along the hillsides (Hunter and Sluyter, 2015; Whitmore and Turner, 1992). A distinctive form of Mayan slash and burn agriculture, milpa, is still practiced in Yucatan. It is a combination of clearing, burning, planting, cropping and short fallow cycles (~4 years) with small plots of about 4 ha per family (Turner and Brush, 1987).

Central America. Along with Mexico, Central America was one of the most intensely used landscapes in the western Hemisphere with agricultural systems similar to central Mexico (Whitmore and Turner, 1992). In Costa Rica, pollen records from Lake Zoncho (Fig. 2) indicate that the local population moved from slash and burn agriculture towards permanent agriculture in the later stages of the Mayan Postclassic period (1000–1539 CE) most likely to avoid laborious repetitive clearing of land, due to the epidemics-driven decline in workforce (Clement and Horn, 2001). The abundant occurrence of charcoal in records suggests that fire was widely used as agricultural tool in Central America (Dull et al., 2010).

Inca Territory. Andean landscapes have been modified for over 8000 years (Dillehay et al., 2007), with evidence for the terracing of steep slopes to grow maize, quinoa (*Chenopodium quinoa*) and other staples appearing between 550 CE and 1000 CE (Kendall, 2013). While the actual extent of terracing fields in the Andean highlands is unknown, it was extensive, spanning steep and gentle slopes, and included elaborate canal systems for irrigation and runoff control (Denevan, 2001). Another indicator that the Inca significantly shaped their environment is evidence of managed afforestation to stabilize slopes (Chepstow-Lusty and Jonsson, 2000; Denevan, 2001). The use of fire for anthropogenic land use was widespread (Chepstow-Lusty et al., 1996).

Amazonia. A large body of research shows that locally intense landscape modifications occurred before Europeans arrived (e.g. Carson et al., 2014; Denevan, 2001; Erickson, 2010; Heckenberger et al., 2003; Mann, 2005; McMichael et al., 2012; Piperno et al., 2015). The alteration of forest by pre-Columbian groups in Amazonia ranged from the removal of non-useful plants and the protection of useful plants over simple seed dispersal and the relocation of seedlings to active fire management, the construction of earthen structures such as raised fields, ADE soils, homegardens and polyculture agroforestry (Heckenberger et al., 2003; Heckenberger and Neves, 2009; Levis et al., 2017, 2018; Maezumi et al., 2018a; Stahl, 2015; Woods et al., 2009). Modern forest

composition in southwestern and eastern Amazonia (Levis et al., 2017; Ter Steege et al., 2013) and along floodplain habitats (De Souza et al., 2018; McMichael et al., 2017) are thought to be strongly influenced by pre-Columbian plant cultivation as well as incipient tree domestication, alongside crop domestication, including rice (*Oryza* sp.), cassava, peanut (*Arachis hypogaea*) and chili pepper (*Capsicum* sp.) (Hilbert et al., 2017; Watling et al., 2018).

Anthropogenic structures such as ADEs, earthen mounds (raised fields) and large (5 km) ring ditches, roads (Heckenberger et al., 2003) and fish weirs (Blatrix et al., 2018; Erickson, 2000) point to large (>1000 people) pre-Columbian settlements all over Amazonia including coastal French Guiana, the seasonal dry eastern Amazonia (Marajó Island and Santarem Region), central Amazonia's Acre province, the upper Xingu river in Brazil, the Llanos de Moxos, and the Beni Province of Bolivia (Carson et al., 2015; De Souza et al., 2018; Heckenberger et al., 2003; Piperno et al., 2015; Roosevelt et al., 1991; Stenborg et al., 2018; Whitney et al., 2014, Fig. 2). The dominant construction period for raised fields and ring ditches was between 500 CE and 1450 CE (Roosevelt, 2013). The continuity of the population history of these sites and their population density however remain uncertain and vary between sites (Denevan, 2014; Meggers, 2001). The workforce required to construct these structures remains debated as the method of construction is uncertain, ranging from frequent large scale burning (Carson et al., 2015; Whitney et al., 2014) to episodically clearing with stone axes and low severity burning for agroforestry-type systems (Clement et al., 2015; Erickson, 2010; Stahl, 2015). Alternatively, it has been suggested that a small workforce may has gradually constructed them very slowly over several thousand years on the margins of forest clearings (Watling et al., 2017).

North America. Pre-Columbian land use in the US and Canada varied from largely nomadic hunter-gatherers in the north towards semi-permanent and permanent agriculture further south (Abrams and Nowacki, 2008; Stinchcomb et al., 2011). Mississippian people grew maize, squash (*Cucurbita pepo*) and beans in alluvial areas and constructed large earthen mounds (Delcourt and Delcourt, 2004). Pre-Columbian societies in the southwestern North America built terraces and practised floodwater farming (Doolittle, 1992). In eastern North America people practised rainfed agriculture with sunflower (*Helianthus annuus*) and squash as staple crops (Smith, 2006), whilst altered forest composition through selective planting. Fire management was practised from the Midwest to the east coast (Abrams and Nowacki, 2008).

This gives an overview on how and to what degree indigenous people in the Americas used land, but it should be emphasized that not all sites with recorded human impact were populated at the time Europeans arrived. For example, in Mexico and Central America some parts of previously used cities and land were abandoned, or used at lower intensity, following widespread societal transformation in the Maya civilization (Beach et al., 2015; Guderjan et al., 2009; Tainter, 1988). Furthermore, sampling bias may be important particularly for Amazonia as ease of access to sites limits the sampling distribution across the region (McMichael et al., 2017).

3.2. New pre-Columbian per capita land use estimate

To calculate the area of pre-Columbian land use we need to know the typical land area used to provide sustenance for a person living in the Americas prior to 1492 CE, the per capita land use. Here we review per capita land use estimates for each of our seven regions (Table 2).

Caribbean. No direct per capita land use estimates are available for the Caribbean. Considering the similarity in agricultural systems, a similar per capita land use can be assumed to Mexico and Central America. The spatially explicit LUC dataset from Kaplan et al. (2011), KK10, applies a land use area per capita estimate of ~1.5 ha to Mexico, Central America and the Caribbean. The HYDE 3.1 LUC dataset instead provides a spatially explicit population dataset (Klein Goldewijk et al., 2011), and by dividing the land use area by the population, per capita land use was 1.2 ha in this region in 1492 CE. The third dataset, P08 (Pongratz et al., 2008a), assumes zero land use per capita in the Caribbean.

Mexico. The most common land use form at the time, the milpa system with its four-year cropping cycle, translates into 0.57–1 ha per capita (Borah and Cook, 1963; Bullock et al., 2013; Morfín and Storey, 2016; Turner and Brush, 1987). Estimates however vary substantially between sites, likely due to differing environmental conditions and family sizes (e.g. 1.5 ha per capita, Drucker and Heizer, 1960). KK10 assumes a land use per capita of ~1.5 ha per capita, about three times larger than that of HYDE 3.1, at 0.39 ha per capita. Unlike the other two LUC datasets P08 separates land use into lowland and highland land use. It applies a cropland per capita for highlands of 0.2 ha, based on Collins (1983), and for lowland land use just 0.05 ha per capita, which is one-tenth of the lowest milpa estimate.

Central America. Pre-Columbian land use systems in Central America are very similar to Mexico (Whitmore and Turner, 1992) and many studies do not distinguish between the two regions. For KK10 this region is assumed to have the same per capita land use as Mexico, 1.5 ha per capita, while HYDE 3.1 is slightly higher than for Mexico, at 0.43 ha per capita, while P08 assumes zero pre-Columbian land use anywhere in Central America (Fig. 3).

Inca Territory. Observations of the Aymara people have shown that contemporaneous indigenous cultivation in the Andes requires 0.2 ha per capita (Collins, 1983), although this is likely influenced by colonial and modern day practices and thus has probably a higher productivity than its pre-Columbian form (Boserup, 1965; Ruddiman and Ellis, 2009). Again, HYDE 3.1 has larger values, 1.4 ha per capita. KK10 has not published an estimate for this region nor provides a spatially explicit population dataset to establish a land use per capita estimate. P08 has low values, at 0.05 ha per capita in the lowlands (the same as P08 in Mexico) and every more efficient agriculture, at 0.2 ha per capita, in the highlands. The Inca Territory is the only region in the Americas where P08 assigns a third value, for pasture, at 0.57 ha per capita (for llamas and alpacas, the only domesticated grazers). The other two LUC datasets do not assign pasture to the pre-Columbian Americas, assuming no widespread use of domesticated grazers.

Amazonia. Highly productive ADEs, as found along riverine settings, make intensive semi-/permanent cultivation possible, with 0.2–0.3 ha per capita used (Woods et al., 2009), but such soils cover only ~3% of lowland Amazonia (McMichael et al., 2014). The larger part consists of less productive soils where extensive cultivation with long fallow (~15 years average, up to 30 years) was mostly employed to farm cassava. These long fallow systems require between 1.25 ha per capita (Clark and Uhl, 1987) and 2.2 ha per capita (Dull et al., 2010). Where shorter fallows are possible (e.g. Guiana, 4–6 years) estimates are lower: 1–1.3 ha per capita (McKey et al., 2010). Dull et al. (2010) report an average 1.2 ha per capita for lowland tropical forest regions of the Americas. Surprisingly, HYDE 3.1 gives a calculated rate of 0.9 ha per capita for Amazonia, a lower value than seen in either the Inca Territory or Mexico. Per capita values for KK10 are not derivable for Amazonia, while P08 give zero anthropogenic land use anywhere in Amazonia or its contiguous forested area before 1492 CE.

North America. Published per capita land use estimates are not available for North America, but likely ranged from ~1 to 1.5 ha per capita for intensive slash and burn with short fallows (Doolittle, 1992) to several hectares per capita for large-scale fire-based

Table 2
Published land use per capita estimates (ha per capita) used for the different regions to calculate the pre-Columbian land use extent. Hemisphere is combined North and South America. Pongratz et al. (2008a) assumes different land uses for Highlands (^{H}), Lowlands (^{L}) and Pasture (^{P}).

Study	Published per capita land use (ha per capita)						
	Caribbean	Mexico	Central America	Inca	Amazonia	North America	Hemi-sphere
Lewis and Maslin (2015)	–	–	–	–	–	–	1.3
Kaplan et al. (2011)	–	~1.50	~1.50	–	–	–	6.25
Klein-Goldewijk et al. (2011)	0.26	0.43	0.36	1.65	0.53	0.54	0.67
Dull et al. (2010)	1.2	1.2	1.2	–	1.2	–	–
McKey et al. (2010)	–	–	–	–	1.28	–	–
Woods et al. (2009)	–	–	–	–	0.20–0.30	–	–
Ruddiman and Ellis (2009)	–	–	–	–	–	–	0.8
Nevle and Bird (2008)	–	1	1	1	–	–	1
Pongratz et al. (2008b)	–	0.2^{H} 0.05^{L}	0.2^{H} 0.05^{L} 0.57^{P}	–	–	–	0.18
Ruddiman (2007)	–	–	–	–	–	–	2
Denevan (2003)	–	–	–	–	1	–	–
Beckermann (1987)	–	–	–	–	2.2	–	–
Clark and Uhl (1987)	–	–	–	–	1.25	–	–
Turner and Brush (1987)	–	0.57–1.00	–	–	–	–	–
Collins (1983)	–	–	0.2	–	–	–	–
Drucker and Heizer (1960)	–	1.5	1.5	–	–	–	–
This study (median)	0.73	1.1	1	1.33	1.23	0.54	1.04 (0.98–1.11)

forest clearing to support indigenous hunting strategies (Abrams and Nowacki, 2008; Anderson, 2006), based on similar farming systems in other regions in the Americas. For HYDE 3.1, we calculate 0.5 ha per capita for the US and Canada, more efficient than anywhere in Central or South America. P08 assume zero land use across the US and Canada, and the land use per capita estimates for KK10 are not derivable.

Rest of Americas. There are no direct estimates of per capita land use from Venezuela, Uruguay, Paraguay and Argentina. For HYDE 3.1 we calculate 1.9 ha per capita for Venezuela as well as Uruguay, 0.2 ha per capita for Paraguay and 0.4 ha per capita for Argentina, while again, P08 assumes zero land use anywhere in these four countries and land use per capita estimates for KK10 are not derivable.

3.3. New pre-Columbian anthropogenic land use extent estimate

We group per capita estimates from 16 studies into the same regions as for the population estimate (section 2.2), with hemisphere estimates (Lewis and Maslin, 2015; Nevle and Bird, 2008; Ruddiman, 2007; Ruddiman and Ellis, 2009) applied to all regions (Table 2). This results in 63 regional estimates of per capita land use (Caribbean, n = 9; Mexico, n = 11; Central America, n = 9; Inca Territory, n = 9; Amazonia, n = 14; North America, n = 5; Rest of Americas, n = 6; Table 2), which we cross-multiply with the population estimates of the corresponding region to obtain every possible combination of pre-contact land use area estimates per region and sum them using the same methods described in section 2.2. Our median land use is 1.04 ha per capita (IQR 0.98–1.11 ha per capita), and the total extent of anthropogenic land use in 1492 CE is therefore 61.9 million ha (IQR 43.3–87.1 million ha; Table 1; Fig. 4B).

Our new per capita land use estimates are closest to Nevle and Bird (2008), 1 ha per capita, and the 1.3 ha estimated by Lewis and Maslin (2015). Our estimates are six times larger than the P08 value (0.18 ha per capita) and nearly double the HYDE 3.1 value (0.68 ha per capita). On the other extreme, Ruddiman's (2007) figure is twice what we find (2 ha per capita), and the KK10 value is six times as large as our estimate, at 6.25 ha per capita. Our total anthropogenic land use area of 61.9 million ha in 1492 CE is very different from all three of the land-use database values utilized in modelling studies, P08, HYDE 3.1, and KK10. It is nine times as large as P08 (7.5 million ha) and a little over double the HYDE 3.1 value (27.7 million ha), but is six times smaller than the KK10 of 375 million ha (Table 1). Note that none of these land cover product values fall within the IQR derived from the empirical data, and diverge from each other on per capita land use (which varies thirty-five-fold) more than on the 1492 population (which vary by 50%). Only KK10 has agricultural activity that spans the same region as the literature shows, but employs a too large per capita land use (Fig. 3). We highlight that per capita land use estimates vary substantially on a regional scale and are not well constrained compared to population estimates. For example, per capita land use estimates in Mexico vary more than threefold despite being a well-studied region. Our results show that pre-Columbian populations were large enough, and their per capita land use comparable to other regions of the world at that time (Europe, 0.5–1 ha per capita; China, ~0.5 ha per capita, Klein Goldewijk et al., 2017), to practice agriculture at a scale that transformed their environment to an extent that population changes after European arrival would have probably had a substantial impact on the environment.

4. The Great Dying

Accounts from contemporary eyewitnesses and documentary evidence from census data report a widespread collapse of the indigenous population over the decades after European contact (e.g. Cook, 1981, 1998; Diamond, 1997; Dobyns, 1993; Mann, 2005; Lewis and Maslin, 2015, 2018). Such a large population decline meant that the indigenous population would not have been able to manage their existing agricultural systems over such large areas. While other factors such as warfare, the enslavement of indigenous people, and hunger following social disintegration resulting from the loss of such a large fraction of societies meant even larger population losses (e.g. Cook, 1998; Mann, 2005; Dobyns, 1993; Lovell and Lutz, 1996), we focus on the epidemics as the main driver behind the majority of the deaths in the Great Dying.

4.1. Unprecedented mortality rates after European arrival

Existing evidence suggests that the indigenous population collapse was primarily caused by the introduction of pathogens

unknown to the American continent ("virgin soil epidemics") together with warfare and slavery (Black, 1992; Crosby, 1976; Dobyns, 1993; Joralemon, 1982; Mann, 2005; McNeill, 1977). Part of a wider Columbian Exchange of once-separate continental fauna and flora, these epidemics were introduced by European settlers and African slaves and were passed on to an indigenous population that had not been previously exposed to these pathogens and therefore did not initially possess suitable antibodies (Dobyns, 1993; Noymer, 2011; Walker et al., 2015). Such diseases included smallpox, measles, influenza, the bubonic plague, and later malaria, diphtheria, typhus and cholera. Most of these diseases originated from domesticated farm animals from Europe to which Native Americans had no prior exposure (Lewis and Maslin, 2018). The relative absence of American diseases arriving in Europe can therefore be explained by the low number of domesticated animals in the pre-contact Americas (Diamond, 1997; Lewis and Maslin, 2018; McNeill, 1977). Thus, influenza, smallpox, bubonic plague and other diseases ravaged the Americas, and not vice versa. Such diseases typically individually killed ~30% or more of the initial population. Hence a series of epidemics in rapid succession could have led to the loss of whole societies.

Overall, hemisphere wide post-epidemics population estimates range between 4.5 million and 14.4 million for 1600–1700 CE (Denevan, 1992a; Dobyns, 1966; McEvedy and Jones, 1977, Table 3). These studies are less clear on their assumptions than their reports of pre-contact population estimates. Furthermore, the rate of loss is strongly influenced by the chosen dates used to calculate it (Dobyns, 1966). Loss rates ranging from 40% (McEvedy and Jones, 1977) to 95% (Dobyns, 1966), with Denevan's (1992a,b) more recent update producing a robust initial population estimate of 54 million (similar to our 60.5 million) that results in a 90% decline to 5.6 million in 1600 CE.

We review the published regional depopulation percentages and post-epidemics population estimates for each of our seven regions. Fig. 2 illustrates the spread of these diseases based the documented locations of disease outbreaks during the first century after European arrival.

Caribbean. Following the first disease outbreak in 1497 CE on the island of Hispaniola, the first census for the whole island was established in 1508 CE and arrived at 60,000 indigenous people (Moya Pons, 1992), a reduction of 85% within 16 years if Bartholomew Las Casas' initial 4 million estimate was to be correct. A review of nadir populations, the estimated low point of a population, gives a population of 22,000 for the whole of the Caribbean by 1570 CE, corresponding to a 99% reduction from the 4 million estimate (Dobyns, 1966).

Mexcio. The first documented old World pathogens first reached the continent in southern Mexico (Cook, 1998). Here the most devastating outbreak occurred in 1520 CE when a single smallpox epidemic killed an estimated 30–50% of the indigenous population of Mexico (Cook and Borah, 1960; Dobyns, 1993; McCaa, 1995). Following the first comprehensive census in 1568 CE the population of central Mexico had already declined to 2.7 million (Sanders et al., 1979), which corresponds to a maximum decline of 87% within the first 50 years of European arrival when using a pre-contact population of 20 million (Whitmore and Turner, 1992). The nadir population of 1.5 million, equalling a total population decline of 93%, is reached in 1650 CE (Dobyns, 1966). Thus, a rapid population collapse of up 90% is plausible for the most populous parts of the country.

Central America. Combining the initial population estimates (315,000 to 2 million) and the 1550 CE population of 121,000–430,000, results in a 62–79% loss of Mayan population in Guatemala within 30 years of contact (Lovell and Lutz, 1995; Zamora, 1983). For all of Central America, Dobyns (1966) review on nadir populations gives a low point of 540,000 by 1650 CE, which corresponds to a depopulation of 90% based on pre-contact population of 6 million (Denevan, 1992a).

Inca Territory. Between 30% and 50% of indigenous populations in the Inca Territory reportedly died in the late 1520s as smallpox epidemics spread into the Inca kingdom (Cook, 1998). Some regions such as coastal Peru experienced only little initial decline (~10%, Shea, 1976), which supports the idea of waves of localized epidemics rather than subcontinent wide pandemics (Storey, 2012). By 1620 CE about 670,000 indigenous people remained in the Inca heartland, which is equivalent to a depopulation of 93% based on an initial population of 9 million (Cook, 1981).

Amazonia. Robust post-epidemics population estimates and depopulation percentages are sparse, with most studies applying a 90% population decline over a poorly defined post-contact period (Dobyns, 1966; Dull et al., 2010). A review on Amazonian archaeology concludes that in the Upper Xingu region, Brazil, an indigenous group (Xinguano) that occupied thousands of towns had been reduced to around 500 people by the time of the first comprehensive survey in the 1950s, corroborating a high depopulation rate estimate (Heckenberger and Neves, 2009).

North America. The first documented contact between indigenous groups and Europeans took place at the North American east coast in the 1530s when explorers reported dense Iroquois settlements. These settlements disappeared by the end of the 1600s (Sauer, 1980), 20 years before the first recorded smallpox epidemic that would kill 90% of the native population of New England (Davies, II, 2012). In the Jemez province, southwestern United States, an archaeological study found that a depopulation of 87%

Table 3
Calculated depopulation percentages from published hemisphere-wide pre-contact population estimates and their corresponding posts-epidemics population estimates (2nd column) as well as relative to a standardized median 1600 CE population of 6 million people (3rd column).

Study	Published Depopulation Rate (%)	Standardized Depopulation Rate (%)
Klein-Goldewijk et al. (2010)	76	85
Krumhardt (2010)	90	90
Pongratz (2008a,b)	65	85
Maddison (2001)	31	70
Henige (1998)	–	85
Denevan (1992a)	90 (87–91)	89
Dobyns (1966, 1983)	96	94
Biraben (1979)	71	85
McEvedy and Jones (1977)	40	58
Durand (1977)	65	85
Clark (1967)	68	85
Rosenblat (1954)	–	55
Kroeber (1939)	–	29
This study (median)	–	90

occurred within 100 years after contact (1541–1640 CE, Liebmann et al., 2016). By 1800 CE an estimated one million indigenous people were left in North America (Denevan, 1992a). Dobyns (1966) suggests the low point of 490,000 was reached in the 1930s, although it can be assumed that the initial waves of epidemics during the 1600s and 1700s were responsible for most of the depopulation.

Rest of the Americas. We found no depopulation estimates for Venezuela, Argentina, Uruguay and Paraguay.

Only seven regional post-epidemic population estimates, or mortality rate estimates, have been published for 1600–1650 CE (Caribbean, n = 1; Mexico, n = 1; Central America, n = 1; Inca Territory, n = 2; Amazonia, n = 0; North America, n = 2; remainder, n = 0). It is therefore not possible to apply the same approach to estimating the population reduction as we used to calculate the pre-contact population and land use. Instead, we use the median of the estimates for the population of the Americas at 1600 CE, six million people (Denevan, 1992a; Dobyns, 1966; McEvedy and Jones, 1977; Klein Goldewijk et al., 2010; Krumhardt, 2010), and our calculated pre-contact population of 60.5 million (IQR 44.8–78.2 million) to estimate mortality. Based on these estimates 54.5 million people died (IQR 39.0–72.4 million; Fig. 4C), or 90% of the pre-contact population (IQR 87–92%). This is at the higher end of estimated losses (Table \tab:depopulationrate), but is consistent with those regions that are better studied (e.g. Central Mexico, Inca Territory) and when multiple waves of epidemics affecting the indigenous population, as well as warfare, slavery, and famine, are taken into account.

A mortality of up to 95% is higher than other virgin soil epidemics throughout history (Table 4, Crosby, 1972). While most of the other epidemics in history however were confined to a single pathogen and typically lasted for less than a decade, the Americas differed in that multiple pathogens caused multiple waves of virgin soil epidemics over more than a century. Those who survived influenza, may later have succumbed to smallpox, while those who survived both, may then have caught a later wave of measles. Hence, there were documented disease outbreaks in the Americas that killed 30% of the remaining indigenous population over 50 years after initial contact, i.e. between 1568 CE and 1605 CE (Black, 1992; Thornton, 1987). Indeed, high mortality rates from non-endemic diseases within indigenous communities were still common in the mid-1800s (Boyd, 1992). With at least eight major diseases documented (smallpox, influenza, measles, typhus, pneumonia, scarlet fever, malaria and yellow fever), a 30% mortality per new arrival – not uncommon for virgin soil epidemics – would result in a depopulation of 95% (Table 4). The depopulation is therefore much higher than might initially be expected from comparison with for example, the Black Death epidemic in Europe in the fourteenth century which was caused by a single pathogen (see Table 4).

For indigenous people that survived, immunity to most of the European diseases would be acquired during childhood of future generations (Black, 1992; Crosby, 1976; Dobyns, 1993; Jones, 2003; Noymer, 2011). Two main hypothesis, not mutually exclusive, have been proposed to explain why the depopulation continued until centuries after initial contact. The first is that the low genetic diversity between the indigenous hosts has facilitated the spread of potent pathogens (Black, 1992, 1994; Lewis, 2010; Lindenau et al., 2013; Salzano and Callegari-Jacques, 1988; Wang et al., 2007). The ancestors of the modern Native Americans migrated most likely from East Asia into North America (Goebel et al., 2008; Moreno-Mayar et al., 2018; Raghavan et al., 2015). Due to their small initial group size, the newly established population of the Americas had a lower level of genetic diversity compared to the original Asian population ("founder effect") which would have lowered resistance against diseases from certain pathogens (Black, 1994; Lindenau et al., 2013). However, despite this there is no evidence for a causal relationship between genetic differences and the increased severity of the impacts of diseases (Walker et al., 2015).

A second "environmental hypothesis" (Walker et al., 2015) suggests that the effects of the European conquest and the consequences of the epidemics amplified the already devastating deadliness of the diseases (Crosby, 1976). Direct effects of the European conquest included warfare and the exploitation of indigenous populations (Livi-Bacci, 2008), including their forced relocation of people and slavery (Nevle and Bird, 2008). The consequences of famine from crop failure due to epidemic-driven labor shortages (Jones, 2003; Marr and Kiracofe, 2000) and lack of nursing care (Joralemon, 1982) led to a decline in birthrates following social stress and subsequently further population decline (Cook, 1998). Additionally, cultural factors such as no prior knowledge of quarantine procedures (Jones, 2003) and people moving along major trade routes and to areas more remote from direct European contact are likely to have contributed to the spread of epidemics. Thus, societal breakdown following ongoing war, slavery and famine due to shortage of healthy labor force likely increased the potency of epidemics in the Americas (Jones, 2003) with 90% of the population lost by 1600 CE (IQR 87–92%).

5. Extent of land use cessation and secondary vegetation succession

The decimation of Indigenous American populations by re-occurring waves of epidemics combined with societal disruption likely drove large reductions in agricultural activity. The absence of anthropogenic land use would mean that these areas would have undergone secondary succession. Using indigenous population decline estimates and their per capita land use we can estimate the extent to which vegetation succession in the Americas occurred following the Great Dying in the first century after European arrival, and how this may have impacted resulting carbon sequestration.

5.1. Secondary succession dynamics

The pathways of secondary succession will differ depending on the vegetation at abandonment, the proximity of sources of seeds,

Table 4
Single virgin soil epidemics through history and their mortality.

Region	Year	Mortality	Epidemic	Study
Athens	430 BCE	25%	smallpox	Littman (2009)
Japan	735 CE	30%	smallpox	Hays (2005)
Europe	1347–1351 CE	30–50%	bubonic plague	Benedictow (2004)
Mexico	1520 CE	30–50%	smallpox	McCaa (1995)
Mexico	1545–1548 CE	80%	cocolitzli	Cook and Simpson (1948)
Inca empire	1585–1591 CE	30–60%	Smallpox & measles	Cook (1981)
Iceland	1707–1709 CE	20–25%	smallpox	Hays (2005)
NW U.S.	1830–1840 CE	87%	malaria	Boyd (1992)

type of past anthropogenic land use, the soil, the climate, and exogenous disturbances such as fires (e.g. Chazdon et al., 2016; Griscom et al., 2017; Marín-Spiotta and Sharma, 2013; Poorter et al., 2016). However, in almost all cases an increase in plant biomass occurs over time, increasing the carbon stored on the land. For example, in an area where previously tropical forest has been cleared to plant annual crops microclimatic conditions are usually hotter and drier than suitable for most tropical forest species. When anthropogenic land use ceases, light-demanding, "pioneer" tree species that are more heat and moisture tolerant establish first, changing the microclimate and facilitating growth of typical tropical forest species (Guariguata and Ostertag, 2001; Rozendaal et al., 2017). Light availability in the understorey decreases as succession progresses, allowing the establishment of trees that will replace the pioneers, further increasing carbon stocks. However, in wetter forests, with their denser canopy than in drier forests, the transition from light-demanding pioneer species to later-successional forest species occurs at a faster rate compared to dry forests. Thus, while vegetation success increases carbon stocks and typically increases plant species diversity, rates depend on several factors, but typically, carbon stocks rise rapidly over the initial decades and then the rates of sequestration slows, with forest structure typically becoming similar to mature undisturbed systems within about 100 years (Martin et al., 2013), as does plant biodiversity (Chepstow-Lusty et al., 2009; Platt Bradbury, 2000). However, structure and composition may never return to the prior vegetation state, only something somewhat structurally and functionally similar. One method of investigating successional changes following the Great Dying is to assess the paleo-ecological evidence.

5.2. Paleo-ecological evidence for widespread vegetation change

The widespread cessation of indigenous land use implies extensive secondary successional vegetation regrowth. This rapid change of land use is expected to cause fire use as a land management tool to decline, seen in sediment records as a reduction in charcoal. Secondary succession and implied increasing carbon stocks would be reflected in pollen records. We review the evidence for both in turn.

Charcoal. The use of fire as an agricultural tool for land clearance before the arrival of Europeans is well documented (Bush et al., 2008; Mayle and Power, 2008; Nevle et al., 2011), although there are exceptions such as fire-free agriculture documented French Guiana (Iriarte et al., 2012). Given the near-ubiquity of fire for agricultural production, any collapse in agricultural land use could be expected to be mirrored by a decreasing abundance of macro-charcoal in sediment cores near agricultural areas, record resolution permitting (Clark, 1988; Dull et al., 2010; Nevle and Bird, 2008; Nevle et al., 2011). Although it is possible that the prior land use could lead to forests with a differing structure and species composition from the pre-anthropogenic land use, meaning the new forests may have a differing natural fire regime than that prior to human impacts (e.g. Bush et al., 2007; Maezumi et al., 2018b). Furthermore, climatic changes associated with the drop in atmospheric CO_2 and air temperatures may also affect rainfall and hence the probability of fires. Paleo-ecological reconstructions of biomass burning indicate a period of reduced fire activity in the Americas during the 1500s, although different studies attribute the reduction to different causes (Dull et al., 2010; Marlon et al., 2008, 2013; Nevle and Bird, 2008; Nevle et al., 2011, Fig. S1).

One group of studies (Dull et al., 2010; Nevle and Bird, 2008), examining charcoal records from sites across tropical Meso- and South America, attribute the decline in biomass burning to the indigenous population collapse. Another group of studies (Marlon et al., 2008, 2013; Power et al., 2013) argue that the driver was a change in the climate. The latter group suggest biomass burning was already in decline on a hemisphere-wide scale before Europeans arrived, following a shift towards wetter conditions that suppressed biomass burning globally. Of course, these two hypotheses are not mutually exclusive, the decline in charcoal deposits and biomass burning may be due to both climate and the human depopulation. Hence, it is possible that regional climate is driving a decline in biomass burning in the 1500s, but at a subset of sites where the human population also collapsed, this decline in biomass burning is being misattributed solely to climate. Alternatively, locations with an apparent loss of human population and concomitant decline in charcoal may be being solely attributed to people, rather than a mixture of direct human and climate forcing impacts. This attempt at defining one of two causal mechanisms is further complicated by the non-random location of study sites and that a decline in anthropogenic burning and increased carbon uptake from regrowing vegetation may amplify any climate-driven decline in burning via a feedback effect. The decline in biomass burning in the Americas is broadly consistent with the abandonment of agriculture following the Great Dying, although how much of this reduction is directly attributable the human population reduction is debated.

To analyse local fire histories to assess whether climate or humans are the cause for changes in the charcoal record we use our seven regions and select all records from the Global Charcoal Database that cover the period 1500–1600 CE at a resolution of <50 years, which is sufficient to capture potential population changes following the European contact epidemics (version 4.0.3, paleofire R-package, Blarquez et al., 2014). The sample sizes are: Mexico, n = 2; Central America, n = 4; Caribbean, n = 4; the Inca Territory, n = 4; Amazonia, n = 2; North America, n = 8 (Fig. 2). To compare the records we first normalize the biomass burning reconstruction to z-scores via Box-Cox transformation, where $z_i = (x_i - \underline{x}_{0-1750})/s_{\underline{x}(0-1750)}$, with $\underline{x}_{0-1750}$ being the charcoal value over the base period from year 0 until 1750 (i.e. pre-industrial) and $s_{x(0-1750)}$ the standard deviation over this period (Power et al., 2013). Of the selected 24 records, half (12) exhibit a persistent decline or low point in biomass burning during the 1500s (dating uncertainty 35–60 years), with most (10) located in Meso- and South America, and two in North America (see Fig. S1). Of the 12 records, biomass burning declines have been attributed to the population collapse following European epidemics in three case studies representing five records (Berrío et al., 2002; Chepstow-Lusty et al., 1998; Dull et al., 2010), one study notes that the record has an anthropogenic fire signature but does not attribute the decline in biomass burning to a cause (Bush et al., 2007), one study attributes changes in two records (of the same location) to climatic fluctuations (Kennedy et al., 2006), while for the other four no explanation on the cause of the decline was given (Carcaillet et al., 2006; Higuera-Gundy et al., 1999; Muller et al., 2003). All six records with attributed anthropogenic fire signatures are in regions with high pre-Columbian populations: Mexico (Dull et al., 2010), Central America, specifically Nicaragua (Dull et al., 2010); and the Andean highlands in Colombia (Berrío et al., 2002) and Peru (Bush et al., 2007; Chepstow-Lusty et al., 1998). Absence of human activity in two records from Hispaniola (Dominican Republic) led the authors conclude that climatic changes as the likely cause for the observed changes (Kennedy et al., 2006). The studies with records showing a decrease or low point in biomass burning during the 1500s tend to focus on the more distant past (Caribbean, North America, Higuera-Gundy et al., 1999; Muller et al., 2003) or on a different aspect of fire and landscape (North America, Carcaillet et al., 2006). Overall, at a series of sites with large pre-Contact populations charcoal records show a decline in biomass burning that authors attribute to rapid population declines after European contact. Our analysis shows

that declining biomass burning in six locations throughout the Americas – 25% of records – was caused by the indigenous population decline, while at a further 25% of records showed a decline in burning not attributed to a local population decline (climate or unknown) with the remaining 50% of records show no discernible trend.

Pollen. From sedimentary pollen records, used to reconstruct the composition of local plant communities, it is possible to infer nearby land use and settlement history. For example, a change from presence to absence of maize or other cultivated plants, followed by an increase in successional plant species could indicate LUC due to the site being abandoned, either because of deaths or movement of the local population. A recent compilation of pollen records classifies 14 sites in Meso- and South America as influenced by human activity that cover the period 1500–1700 CE (Flantua et al., 2016, for locations of sites, see Fig. 2; for corresponding studies, see Table S4). At seven of these sites vegetation changes are attributed to depopulation following European contact, at four sites land use increased after European contact (Brugger et al., 2016; Bush et al., 2015; Goman and Byrne, 1998; Park et al., 2010), while at three sites abandonment occurred before 1492 CE (Whitney et al., 2013, 2014). In Central America, at Laguna Atezca site abandonment coincides with European arrival in 1519 CE (Conserva and Byrne, 2002), while in Pátzcuaro basin the record indicates widespread deforestation until the Spanish arrived at 1541 CE (Platt Bradbury, 2000). In the Inca territory, a site in the southern Cauca Valley in Colombia shows reforestation occurred at around 1500 CE (± 25 years), which the authors link to depopulation at the time of Spanish arrival (Berrío et al., 2002). Further south near the city of Loja, land use ceased at two sites between 1600 CE (± 43 years) and 1660 CE (Niemann and Behling, 2010; Niemann et al., 2013). Near Cusco, in the Inca heartland, the important and widely planted tree Alnus, declined after 1500 CE (± 40 years) while successional species increase. After European arrival around 1530 CE these land cover changes became even more pronounced, with rapidly colonizing herbs and shrubs taking over previously maintained pastures, likely due to a reduction in anthropogenic land use (Chepstow-Lusty et al., 1998, 2009). At this site charcoal concentrations do not decline, possibly implying that the remaining population attempted to clear overgrown land for cultivation, but largely failing to keep the successional species at bay (Chepstow-Lusty et al., 2003). In northeast Bolivia, climate-driven expansion of dense canopy forest (1556 CE ±36 years) follows a period of extensive ring-ditch construction that previously kept the forest from encroaching into the savanna (Carson et al., 2014). Overall, 50% of sites (7 of 14) showed a change in vegetation that was attributed by the authors of the studies to a decline in land use following European contact after 1500 CE, while three sites (20%) show a decline in anthropogenic land use before 1492 CE and four sites (30%) show an increase in anthropogenic land use after European arrival. Thus, the pollen data tends to agree with the independent historical evidence that population declines led to vegetation succession at several locations throughout the Americas.

5.3. New estimate for the extent of abandoned agricultural area after the Great Dying

By multiplying the population that died in each region (regional population × depopulation rate), cross-multiplied with the corresponding regional estimates of per capita land use we estimate 54.5 million people died, and a median area of 55.8 million ha of anthropogenic land use was abandoned and recovered to forest or another natural vegetation (IQR 39.0–78.4 million ha; Fig. 4D). This represents about 1% of the total landmass of the Americas being abandoned following European arrive and the spread of waves of pandemic diseases.

Our best estimate is closest to that of Lewis and Maslin (2015) at 65 million ha recovering and Nevle and Bird (2008) at 35–90 million ha. All other estimates lie outside our calculated interquartile range. Well above our estimated range is KK10 that gives a 250 million ha recovering, while Ruddiman (2007) and Faust et al. (2006) suggest 110 and 100 million ha respectively. Below our IQR are the other two LUC datasets: HYDE 3.1, assumes only 7 million ha recovering; while P08 reports the opposite pattern, with an increase in anthropogenic land use after European arrival, of 4 million ha (Table 1). The wide differences in published overall values are explained by the choice of low or high initial hemisphere population estimates combined with low or high mortality rates and low or high per capita land area requirements. At the low extreme, the P08 anthropogenic land area in 1600 CE is positive because an increase in pasture offsets the small recovery from a decline in cropland. In turn the cropland area decline is small because P08 assume a small initial indigenous population that is combined with a very low mortality rate and extremely low per capita land area estimates (Table 1). Indeed, in this model, there is an expansion in land use in northern Mexico, Central America and the southeastern coast of Brazil; Fig. 3). Similarly, HYDE 3.1 assumes a small initial population, a population decline smaller than historic documents suggest, and a relatively low per capita land use. At the high extreme, KK10 is driven by an extremely large per capita land use, some six times our central estimate, but is combined with initial population estimates and mortality rates that are similar to our central estimate. The strength of our approach is the absence of such covariance as all available combinations are evaluated, and suggests substantial LUC – the recovery of 56 million ha of land – followed the arrival of the Europeans in the Americas after 1492 CE.

6. Post-epidemic carbon uptake from secondary vegetation succession

The abandonment of 56 million ha of land in the 1500s following the deaths of 55 million people would have resulted in widespread vegetation succession coupled with a decrease in human driven fire activity. The new vegetation is likely to store substantially more carbon (thereby removing it from the atmosphere) over a relatively short timescale. For example, the above ground biomass (AGB) of tropical forest in Amazonia is 161 Mg C ha^{-1}, fourteen times greater than maize cropland at 11 Mg C ha^{-1} (Malhi et al., 2006; Yan et al., 2017). The recovery time of above and below ground biomass and carbon stocks is fast, typically 55–95 years depending on the system (Hughes et al., 1999; Martin et al., 2013; Poorter et al., 2016; Read and Lawrence, 2003).

6.1. Secondary vegetation succession carbon dynamics

While moisture, temperature, soil and disturbance events influence the rate of biomass accumulation, increases are typically rapid in the first two decades after abandonment and slowing thereafter. Rates are typically lower in drier forests compared to wetter forests (Rozendaal et al., 2017), meaning mature tropical dry forests generally have a lower biomass than tropical wet forests (Poorter et al., 2016). Thus, continental-scale average biomass recovery rates may be improved by using biome or region-specific estimates.

A recent synthesis of Neotropical biomass data from forest inventory plots in secondary growth forests shows that fast AGB recovery is due to a high average net carbon uptake into live biomass, of 3.1 Mg C ha^{-1} yr^{-1}, with 75% of the expected final biomass accumulated in the first 20 years after abandonment, and a 90% recovery within 40–100 years (Poorter et al., 2016). Similarly, a

synthesis of Mexican secondary tropical forest data finds that AGB carbon accumulates fastest during the first 25 years after abandonment (4.7±0.5 Mg C ha^{-1} yr^{-1}) and slows down thereafter (to 3.0±0.7 Mg C ha^{-1} yr^{-1}, Orihuela-Belmonte et al., 2013). In dry forests carbon accumulation rates are around four times lower compared to wet forests (Poorter et al., 2016). Accumulation rates of lowland and montane tropical forests have been found to be similar (Fehse et al., 2002; Spracklen and Righelato, 2016). Recovering forests outside the tropics sequester substantially less carbon, just 0.7 Mg C ha^{-1} yr^{-1} for the U.S. (Williams et al., 2012). Differences in the rate of AGB accumulation appear to be mainly influenced by differing environmental conditions rather than the specific type of previous land use (Orihuela-Belmonte et al., 2013; Poorter et al., 2016).

Soil carbon changes follow a similar pattern: carbon stocks increase at a rate of 1.0 ±0.1 Mg C ha^{-1} yr^{-1} over the first 20–30 years before slowing down (Don et al., 2011; Marín-Spiotta and Sharma, 2013), although some studies report substantial increases in soil carbon until 70 years after abandonment (Pregitzer and Euskirchen, 2004). A review of soil carbon stores for low-to mid-latitudes found that reverting to forest from cropland increases carbon in the upper 20 cm of soil by 0.5 Mg C ha^{-1} $year^{-1}$ (Shi et al., 2013). In areas where the natural vegetation is not forest, studies of the conversion of cropland to grassland provide a similar scenario to the abandonment of fields. In these studies, soil carbon increased by 1.2 Mg C ha^{-1} yr^{-1} (Don et al., 2011). Taken together, both vegetation recovery and soil carbon uptake following agricultural abandonment imply substantial carbon uptake in the 1500s across the estimated 56 million ha abandoned farmland.

6.2. New estimate of carbon uptake from vegetation succession

To calculate the total carbon uptake following anthropogenic land use abandonment and resulting natural vegetation re-establishment we multiplied the increase in carbon stocks (per unit area per unit time) and the regrowth area estimate. We first compiled above ground (n = 112) and soil carbon uptake (n = 38) rates following abandonment within each of our seven regions (Table 5). From these studies that predominantly report short-term (<20 years) uptake rates, we then assume that these apply for the first 20 years, and for longer-term uptake, we assume this is at 8% of the short-term value over the next 80 years, following Orihuela-Belmonte et al. (2013). The 100-year uptake rate is then calculated as $uptake\ rate \times 20\ years + uptake\ rate \times 80\ years \times 0.08$. We assign the carbon uptake rates to our seven regions and cross-sum the aboveground carbon uptake rates (Caribbean, n = 18; Mexico, n = 23; Central America, n = 23; Inca Territory, n = 6; Amazonia, n = 18; North America, n = 1, Remainder regions, n = 23) and soil carbon uptake rates (Caribbean, n = 6; Mexico, n = 7; Central America, n = 7; Inca Territory, n = 1; Amazonia, n = 6; North America, n = 4; remainder, n = 7; Table 5) to calculate all possible combinations of net total carbon uptake rates per region. We cross-multiply these with the previously calculated abandoned areas for each region to calculate a frequency distribution of the total carbon sink (Fig. 4E).

The median carbon uptake is 7.4 Pg C (IQR 4.9–10.8 Pg C, 1 Pg = 1×10^{15} g) from the abandonment of 55.8 million ha of land in the Americas over the 100 years after 1517 CE (date of first documented mainland epidemic). A major source of uncertainty is the land that would have been under various stages of fallow states meaning their continued succession may have led to a more modest uptake of carbon than we estimate here. Furthermore, the large uncertainty in the per capita land use estimates also means that relatively small changes in this parameter result in substantial changes in abandoned land area and terrestrial carbon uptake. Our new estimate is in the lower end of the range of published estimates using area and median carbon uptake values, which range from 7 Pg C to over 20 Pg C a century after the arrival of Europeans and their diseases in the Americas (Table 6). Despite this, our estimate confirms other studies suggesting a globally significant uptake of carbon into the land surface at this time (Faust et al., 2006; Lewis and Maslin, 2015; Nevle and Bird, 2008; Ruddiman, 2007). Our results are most closely in line with two published studies: Nevle and Bird (2008) and Lewis and Maslin (2015), whose range both include 7.4 Pg C uptake (Table 6).

By contrast, the modelling results based on KK10, HYDE 3.1 and P08 land use change estimates are all outside the IQR uptake we estimate (4.9–10.8 Pg C). KK10 reports carbon uptake of 40 Pg C, well above our value, while both HYDE 3.1 and P08, give near zero uptake, and so are well below our central estimate and the lower limit of our IQR (Table 6). This is because only in KK10 is LUC of large enough magnitude, 248 million ha, due to the large land use per capita values (Kaplan et al., 2011, Table 1). Using HYDE 3.1 with the same model, Kaplan et al. (2011) did not find an observable perturbation of carbon stock due to the small area of abandoned land, at 6.9 million ha, ultimately due to a much lower depopulation estimate and lower per capita land-use rates than we find (Table 1). The zero carbon uptake in vegetation in Pongratz et al. (2011) is substantially smaller than our estimate. This is firstly because the low depopulation estimate and very small per capita land use combine to result in only to a small abandoned area of cropland. The carbon uptake from the LUC is then almost completely offset by an assumed legacy carbon emissions from the soil. This modelled result is the opposite of that found in meta-analyses of field studies, which report an increase in soil carbon almost immediately after agricultural abandonment in tropical forest regions (Don et al., 2011; Marín-Spiotta and Sharma, 2013), and is not seen in other model studies (Kaplan et al., 2011). Furthermore, if soil carbon release were to fully offset carbon stocks, forest reforestation would not work as a climate mitigation strategy. Measurements, monitoring and modelling shows that it does (e.g. Arora and Montenegro, 2011; Griscom et al., 2017; Smith et al., 2014).

While we show that there is substantial carbon uptake following the abandonment of agriculture in the Americas following European arrival, some 7.4 Pg C over the 100 years from 1517 CE, the two modelling studies covering this period do not replicate the results we find from our data synthesis. This is due to combinations of three different primary reasons (the size of the population loss, per capita land use, and legacy soil carbon fluxes), although KK10, if it were parametrized with lower per capita land use assumptions, would likely to be the closest to our assessment of the published literature.

7. Post-epidemic land use change impacts and the 16th century carbon cycle

Our estimate of a 7.4 Pg C increase in the carbon stored on land following the Great Dying, i.e. in the 100 years after 1517 CE, corresponds to a decline in atmospheric CO_2 of approximately 3.5 ppm (Fig. 4E; IQR 2.3–5.1), where 2.12 Pg C equals 1 ppm CO_2 over decadal timescales (Trudinger et al., 2002). The magnitude and timing of this increase in carbon stocks on the land surface is consistent with an abrupt 7–10 ppm decrease in atmospheric CO_2 (14.8–21.2 Pg C) beginning in the 1500s and ending in the early 1600s, shown in two high resolution ice cores from Antarctica, the Law Dome and the West Antarctic Ice Sheet (WAIS) ice cores (Fig. 1, Ahn et al., 2012; MacFarling Meure et al., 2006). Thus a simple calculation implies that 35–50% of the 14.8–21.2 Pg C reduction can be attributed to the Great Dying, if all other radiative forcing agents

Table 5
Published above ground (A) and soil carbon (B) uptake rates for the different regions in our analysis and their means.

Study	Caribbean	Mexico	Central America	Inca	Amazonia	North America
	A) Above ground carbon uptake rate (Mg C ha^{-1} yr^{-1})					
Brown and Lugo (1992)	–	–	–	–	1.5–5.5	–
Hughes et al. (1999)	2.3–4.5	2.3–4.5	–	–	2.3–4.5	–
Woomer et al. (1999)	–	–	–	–	4.9–7.5	–
Silver et al. (2000)	6.2	6.2	–	–	6.2	–
Watson et al. (2000)	–	–	–	–	3.1–4.6	–
Nepstad et al. (2001)	–	–	–	–	2.5–5	–
Fehse et al. (2002)	5.9–6.9	5.9–6.9	5.9–6.9	5.9–6.9	–	–
Schroth et al. (2002),[a]	–	–	–	–	4	–
Read and Lawrence (2003)	2.3–3.4	2.3–3.4	–	–	2.3–3.4	–
Urquiza-Haas et al. (2007)	2.6–3.0	2.6–3.0	–	–	2.6–3.0	–
Williams et al. (2012)	–	–	–	–	–	0.7
Orihuela-Belmonte et al. (2013)	4.2–5.2	4.2–5.2	–	–	4.2–5.2	–
Gilroy et al. (2014)	4.3	4.3	4.3	4.3	–	–
Poorter et al. (2016)	3.1	3.1	–	–	3.1	–
Spracklen and Righelato (2016),[b]	1.5–6.7	1.5–6.7	1.5–6.7	1.5–6.7	–	–
mean (this study)	4.1	4.1	5.1	5.1	4.0	0.7
	B) Soil carbon uptake rate (Mg C ha^{-1} yr^{-1})					
Rhoades et al. (2009)	1.9	1.9	1.9	1.9	–	–
Silver et al. (2000)	0.2–1	0.2–1	0.2–1	–	0.2–1	–
Follett et al. (2001)	–	–	–	–	–	0.04–0.21
Kimble et al. (2002)	–	–	–	–	–	0.1–0.4
Don et al. (2011)	0.6–1.8	0.6–1.8	0.6–1.8	–	0.6–1.8	–
Marín-Spiotta and Sharma (2013)	0.9–1.1	0.9–1.1	0.9–1.1	–	0.9–1.1	–
Shi et al. (2013)	0.5	0.5	0.5	–	0.5	–
Conant et al. (2017)	0.9	0.9	0.9	0.9	0.9	0.9
mean (this study)	0.9	0.9	0.9	1.4	0.9	0.2

[a] Both AGB and soil carbon.
[b] Combined average from 1.7 to 9.8 Mg C ha^{-1} yr^{-1} (<10 years after abandonment) and 1.3–4.1 Mg C ha^{-1} yr^{-1} (10–20 years after abandonment).

Table 6
Published estimates of carbon uptake following conquest driven reforestation, including estimates from this study with interquartile range (IQR).

Study	Carbon uptake from reversal to natural vegetation (Pg C)
Lewis and Maslin (2015)	7–14
Kaplan et al. (2011) - KK10	40
Kaplan et al. (2011) - HYDE 3.1	<0.1
Pongratz et al. (2011)	0.009
Dull et al. (2010),[a]	2–5
Nevle and Bird (2008)	7–18
Ruddiman (2007)	14
Faust et al. (2006)	17–20
This study	7.4 (IQR 4.9–10.8)

[a] Neotropical lowlands only.

and carbon sinks and sources are assumed to have remained constant.

However, without corroborating evidence such analyses could merely be quantifying an unusual coincidence. Furthermore, other radiative forcing agents may have changed over this time period, and carbon sinks and sources will not remain constant given the land-use change perturbation to the carbon cycle following the abandonment of 56 million ha of anthropogenic land. Ideally, fully coupled Earth System Model simulations that alter the known forcing agents in factorial-type experiments, including (i) the atmospheric CO_2 decline, (ii) changes in total solar irradiation, (ii) the impact of volcanic eruptions, and (iv) anthropogenic land use change, in the Americas and the rest of the world, are required to precisely attribute the changes to the Earth system and fully understand the anthropogenic and non-anthropogenic carbon cycle impacts over the 1500s. Such analyses are not available, therefore this section presents the available evidence, firstly to show that the observed atmospheric CO_2 decline is largely caused by a large terrestrial sink, coinciding with the enhanced carbon uptake from LUC in the Americas and secondly, to show that the increased terrestrial sink is not primarily caused by other changes at the time, including total solar irradiation (TSI) or volcanic eruptions. Finally, we estimate the major carbon fluxes in the 1500s to balance the global carbon budget at this time to the assess the impact of the Great Dying on the Earth system. Such an investigation has assumed more importance recently, with the impact of the Columbian Exchange, including the Great Dying impacts on atmospheric CO_2 concentrations, being proposed as the beginning of a new geological epoch dominated by human actions, termed the Anthropocene (Lewis and Maslin, 2015, 2018).

7.1. Land carbon uptake and the 1610 decline in atmospheric CO_2

The Law Dome record shows a steep decrease in atmospheric CO_2 of 10 ppm, beginning moderately at around 1530 CE, and intensifying from ~1570 CE with a clear low-point of 272 ppm at 1610 CE, followed by a small increase until 1650 CE, when consistently low levels are maintained until 1750 CE, the beginning of the

Industrial Revolution (MacFarling Meure et al., 2006). The WAIS record also shows a rapid decrease in CO_2 beginning around 1570 CE, followed after 1600 CE by a slower decrease to a minimum at 1650 CE, with low levels remaining until the beginning of the Industrial Revolution around 1750 CE (Ahn et al., 2012). While both show a similar 16th-century decline, more clearly seen when the records are plotted as anomalies, as in Fig. 5A, there are differences in magnitude of the two absolute minima, ~3 ppm, and the timing of that absolute minima, 1610 CE or 1650 CE. These differences are thought to be due to dating uncertainty, local CO_2 variation and imprecise experimental uncertainty estimation (Ahn et al., 2012). Both records show an unusual decline and the lowest CO_2 concentrations in the last two millennia (Ahn et al., 2012).

The isotopic signature of the CO_2 in the ice cores shows this reduction was driven by an increase in terrestrial carbon uptake, indicated by a preferential uptake of ^{12}C over ^{13}C through photosynthesis, leading to ^{13}C atmospheric CO_2 enrichment (Bauska et al., 2015). Specifically, the increase in $\delta^{13}C$–CO_2, beginning after ~1520 CE, shows a near-constant rate of terrestrial carbon uptake until around 1610 CE and a cessation of the sink thereafter, most consistent with the pattern of CO_2 reduction seen in the Law Dome record (Fig. 1). Additionally, $\delta^{13}C$ data from tropical shallow water sclerosponges also indicates that the decline in atmospheric CO_2 is caused by an increase in the terrestrial carbon uptake (Böhm et al., 2002), as do changes in carbonyl sulfide (COS) captured in Antarctic ice cores that are directly related to changes in photosynthesis (Rubino et al., 2016). Furthermore, a series of modelling studies also point to a carbon uptake on land at this time (Bauska et al., 2015; Joos et al., 1999; Rubino et al., 2016; Stocker et al., 2011; Trudinger et al., 2002). The mean of these model studies is an terrestrial carbon uptake of 19.9 Pg C (Table S5) Thus, the overall temporal pattern and magnitude of both the decline in CO_2, changes in $\delta^{13}C$–CO_2, and data-driven models of the carbon cycle are consistent with uptake into terrestrial vegetation and soils. This unusual event of a rapid and large increase in terrestrial carbon stocks is consistent with a role for secondary succession following epidemics in the Americas after the arrival of Europeans, although there are other potential interpretations in the literature which we discuss in the next section.

7.2. Explaining the 1610 CE CO_2 decline and land carbon uptake

To more fully understand the changes to the Earth system in the 1500s and 1600s we compile data from 1000 CE to 1800 CE for (A) the atmospheric CO_2 concentration, (B) global surface air temperatures, and three potential drivers of these changes, (C) Total Solar Irradiation, (D) volcanic eruptions, and land carbon fluxes, as (E) the carbon flux to the land, (F) LUC in the Americas, and (G) LUC in the rest of the world (Fig. 5). Beyond visual comparisons that imply a strong role for LUC in the Americas, we can also assess the contribution of each of the potential drivers of changes in atmospheric CO_2 and global surface air temperature by calculating their radiative forcing impact on air temperatures.

The lower atmospheric CO_2 coincides with lower surface air temperatures (Fig. 5A). A global synthesis of over 500 paleoclimate records shows that 1577–1694 CE is the only period of significant global cooling within the past two millennia, and the only part of the Little Ice Age (LIA) that was global in extent (Fig. 5B from, Neukom et al., 2014). This analysis shows that the cooling over this period was 0.15°C. How does this compoare with the radiative forcing impact of the 3.5 ppm decline in atmospheric CO_2 at this time? This would be expected to reduce radiative forcing by 0.07 W m^{-2} (i.e. 5.35 W m^{-2}×ln(274.5 ppm CO/278 ppm CO_2); 5.35 W m^{-2} is the radiative forcing constant of CO_2, Myhre et al., 1998). Scaling this decline in radiative forcing by a climate sensitivity parameter of 0.3–1.2 K [W m^{-2}]$^{-1}$ (Myhre et al., 2013), suggests that LUC in the Americas over the 1500s and early 1600s is directly responsible for reducing global surface air temperature of 0.03–0.08°C. A second scaling approach gives a similar answer: using a fully coupled Earth System Model simulation reforesting the tropics in the 100 years after 2000 CE (Arora and Montenegro, 2011), but scaled linearly to our 56 million ha reforestation area, indicates a slightly greater reduction in temperature of 0.04–0.13°C. This suggest that 20–87%, with a mid-point of about 50%, of the 0.15°C reduction in temperatures can be attributed to the radiative forcing from the reduction in atmospheric CO_2 resulting from the Great Dying.

The changes in TSI, shown in Fig. 5C appear unlikely to be the key driver of the 1610 CE CO_2 decline and subsequent temperature reduction, despite such suggestions in the literature (Joos et al., 1999; Pongratz et al., 2008a; Trudinger et al., 2002). For TSI the Spörer Minimum (1416–1537 CE) and the Maunder Minimum (1645–1715 CE) are commonly suggested to explain the cool periods during LIA conditions seen in Europe, but these events leave a gap between the mid-1500s to mid-1600s, and so are not the cause of the increased land carbon stocks or the decline in temperature during this period (Schurer et al., 2013; Owens et al., 2017). Furthermore, TSI decreased substantially over the 1300s (Vieira et al., 2011), when no major change in land carbon uptake occurred (Bauska et al., 2015), suggesting there two variables are not well coupled (Fig. 5C *cf* 5E). While there was no long-term increase in TSI during the period of increasing terrestrial carbon stocks, interannual changes in TSI may have contributed to the CO_2 and temperature decline, which has the potential to impact photosynthesis and terrestrial carbon uptake. For the period 1580–1610 TSI was 0.11–0.31 W m^{-2} above the long-term 1000–1800 CE mean, thus of opposite sign to that necessary to explain lower temperatures, while at 1610 CE itself, TSI was 0.01–0.12 W m^{-2} below 1000–1800 CE mean, suggesting some contribution to decreased temperatures at this time. Overall, the documented changes in TSI cannot explain the anomalously low CO_2 levels over the late 1500s seen in the ice core records, nor lower global temperatures in the 1600s as seen in the paleoclimate temperature reconstructions, nor the larger increase in carbon stored on land (Schurer et al., 2013; Owens et al., 2017).

The impacts of aerosols from large volcanic eruptions, seen in Fig. 5D, can also be ruled out as the dominant cause of carbon uptake on land from 1520 CE to 1610 CE, despite such suggestions in the literature (Joos et al., 1999; Pongratz et al., 2011; Trudinger et al., 2002). Of the forty largest eruptions in the past 2500 years, only one occurred in the 1520–1610 CE period (Huaynaputina, Peru, in 1601 CE), whereas two occurred in the century prior (1453 CE, 1458 CE, both Kuwae, Vanuatu) and two in the century after it (1641 CE, Mt Parker, Philippines; 1695 CE, unknown location, Sigl et al., 2015). For documented tropical eruptions, which have the potential to impact the Earth system for longer, there were five during 1520–1610 CE compared to four during the following century; while only five extratropical eruptions occurred during 1520–1610 CE compared to 14 over the following century (Sigl et al., 2015). Probably the most similar 100 years in terms of total volcanic eruptions to 1510–1610 CE was 1610–1710 CE (Fig. 5D), which did not show a large increase terrestrial carbon uptake (Fig. 5E). Volcanic eruptions typically cause global temperatures to drop for a minimum of two to a maximum of ten years (Frölicher et al., 2011; Sigl et al., 2015). Such short-term change of the expected radiative forcing does not reflect the temporal pattern of land carbon stock increase inferred from the isotopic signature of Antarctic ice-core CO_2 records (Fig. 1) or double-deconvolution method (Fig. 5E). Overall, modelling studies investigating the impacts of volcanic eruptions suggest that they decreased surface air

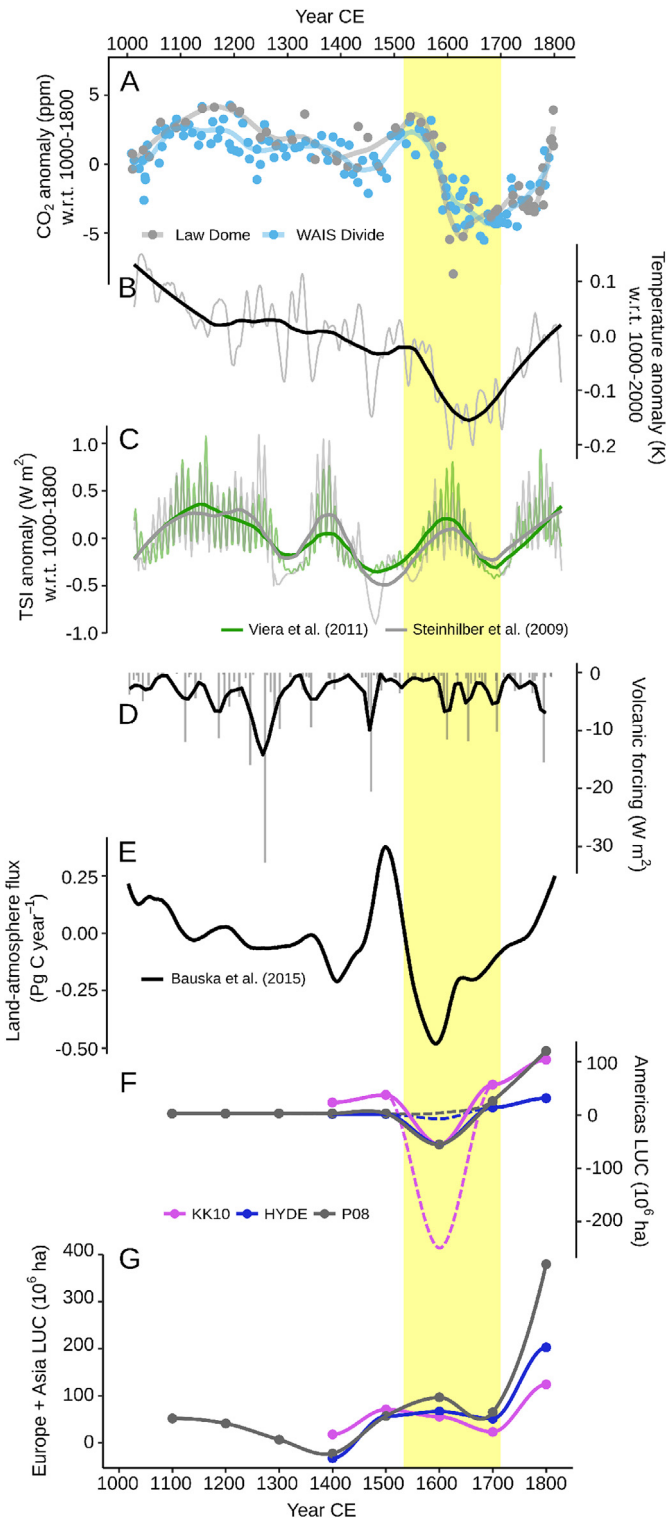

Fig. 5. Impact of changes in radiative forcing on atmospheric CO_2 and temperature 1000–1800 CE. A) CO_2 concentrations recorded in two Antarctic ice cores: Law Dome (grey, MacFarling Meure et al., 2006) and West Antarctic Ice Sheet (WAIS) Divide (blue, Ahn et al., 2012); B) Global mean temperature reconstruction from northern and southern hemisphere proxies, anomaly compared to the means from 1000 to 2000 CE (Neukom et al., 2014, grey, smoothed in black); C) Total Solar Irradiation anomaly compared to the means from 1000 to 2000 CE from Steinhilber et al. (2009, grey) and Vieira et al. (2011, green); D) volcanic, radiative forcing (grey, individual eruptions; black, smoothed, Sigl et al., 2015); E) Land-atmosphere flux based on double deconvolution of WAIS CO_2 data (Bauska et al., 2015); F) Land use change (LUC) in the Americas from the LUC reconstructions KK10 (purple, Kaplan et al., 2011), HYDE 3.1 (blue, Klein Goldewijk et al., 2011), and P08 (grey, Pongratz et al., 2008a). The 1600 CE value has been replaced with the LUC estimate from this review (solid lines) and the original LUC reconstruction is plotted for comparison (dashed lines); G) LUC in the two other regions with considerable agrarian societies at the time, Asia and Europe based on the three LUC reconstructions. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

temperatures modestly over the period of the long LIA that affected the northern hemisphere between 1440 CE and 1920 CE, but are unlikely to be the primary cause of the increase in land carbon uptake over the 1500s (Schurer et al., 2013; Owens et al., 2017).

While the case for the importance of LUC in the Americas is increasingly recognized there has been a suggestion that LUC outside of the Americas over 1500 CE to 1600 CE could mask the uptake of LUC in the Americas. This would lead to no detectable impact of LUC globally on the Earth System, and hence no impact on atmospheric CO_2 levels or surface air temperature (Pongratz et al., 2011). Such a scenario, while possible, would not be compatible with the diverse evidence that there was net terrestrial carbon uptake at that time somewhere on Earth.

LUC emissions in the rest of the world would, however, need to be lower than the LUC uptake in the Americas for there to be a net sink, assuming all other factors remain constant. Extracting the LUC in Europe and Asia (the most populous and well-studied regions) from the three global LUC datasets, HYDE 3.1, KK10 and P08, each show that LUC emissions continued after 1500 CE but were considerably smaller (1.6±1.7 Pg C) than the carbon uptake in the Americas (7.4 Pg C, Fig. 5G). This suggests an overall terrestrial carbon sink from 1500 CE to 1650 CE, consistent with the diverse evidence of a land sink at this time. Overall, of the potential drivers of the decline in atmospheric CO_2 in the 1500s and early 1600s, and the resulting decrease in global surface air temperature, the temporal pattern of LUC in the Americas fits best, rather than changes in the radiative forcing from TSI or volcanic eruptions, or the carbon cycle impact of LUC outside of the Americas (Fig. 5).

An alternative to assessing the radiative forcing impact of the LUC following the Great Dying, suggested in Ruddiman (2013), is to consider the surface air temperature decline over the 1500s and early 1600s, ~0.15°C and estimate the expected change in atmospheric CO_2 from such a temperature decline. Therefore, any additional CO_2 reduction that is not associated directly with the reduction in temperature, is assumed to be associated with LUC uptake of carbon. The coupled Climate-Carbon Cycle Model Intercomparison Project (C4MIP) models show that the temperature land surface feedback, termed γ_{TL}, is −40 to −70 Pg C K^{-1}, meaning as temperatures warm, carbon is released from the land to the atmosphere (Cox et al., 2013). Mechanistically, this is because both gross primary productivity (GPP), i.e. photosynthesis, and autotrophic (plant) respiration (R_a), tend to decrease in cooler conditions, as does a similar set of processes in soils. But the response of R_a to cooling is less relative to the response of GPP, meaning overall net primary productivity increases and thereby carbon stocks on land. Hence a 0.15 K reduction in temperature equals an increased terrestrial uptake of 8.3 (±2.3) Pg C (mean from -40×0.15 to -0.70×0.15), or ~4 ppm CO_2 over the 1500s and early 1600s. Thus, all else being equal, of the 7–10 ppm reduction in atmospheric CO_2 seen in the ice core records, we would expect that the vegetation regeneration following the Great Dying accounts for the remainder, some 3–6 ppm CO_2. This is consistent with the 3.5 ppm CO_2 uptake we find in this study.

However, temperature changes are not the only change at this time. In addition to γ_{TL} changes in atmospheric CO_2 also affect the carbon stored on land. The CO_2 land surface feedback, termed β_{TL}, is estimated to be 0.5–1 Pg C ppm^{-1} CO_2, meaning as CO_2 increases so does land carbon storage (Cox et al., 2013). Mechanistically, this is because CO_2 is a substrate for photosynthesis, thus lower CO_2

means less photosynthesis, lower NPP, and lower carbon storage on land. Thus, this feedback reduces land uptake over the 1500s by 3.5–10 Pg C.

Combining both feedbacks ($\gamma_{TL} + \beta_{TL}$) from the decrease in surface temperature and CO_2 over the 1500s, adds ~8.3 Pg C to the land due to lower surface temperatures, that is offset by ~6.4 Pg C (mean β_{TL} 0.75 Pg C ppm^{-1} × a mid-value of 8.5 ppm decline) due to lower CO_2, leaving a net uptake into the land surface of 1.9 Pg C or about 1 ppm CO_2 reduction solely from lower temperatures and CO_2 levels (Fig. 6). This level of terrestrial carbon uptake from the temperature and CO_2 changes accounts only for 9–13% of the 7–10 ppm reduction in atmospheric CO_2 and implies a dominant role for LUC in balancing the global carbon budget for the 1500s. Furthermore, by adding the net change of 1.9 Pg C from the temperature and CO_2 feedbacks to our new estimate of LUC carbon uptake in the Americas, 7.4 Pg C, gives a total of 9.3 Pg C additional uptake into land in the 1500s, or 4.4 ppm CO_2. Thus, using this method, some 45–65% of the 7–10 ppm decline in atmospheric CO_2 can be explained by LUC in the Americas, after accounting for the Earth system feedbacks from the change in temperature and CO_2 on the land surface at this time.

Through multiple routes we arrive at the conclusion that LUC in the Americas played an important role in driving lower atmospheric CO_2 in the late 1500s and early 1600s. This is counter to conclusions reached by previous modelling studies that have not highlighted LUC as a dominant driver of terrestrial carbon uptake in the 1500s. Some of these are older publications (Joos et al., 1999; Trudinger et al., 2002), that may have not highlighted this factor because depopulation of the Americas has only more recently become well-known and incorporated into LUC datasets (Kaplan et al., 2011; Klein Goldewijk et al., 2011; Pongratz et al., 2008a,b). Other more recent studies that include LUC after 1500 CE ague that it was not sufficient to drive changes in atmospheric CO_2 (Pongratz et al., 2011). This is partly a result of using old 1960s depopulation data combined with the assumption of extremely low per capita estimates of land use and partly due to legacy carbon fluxes that are not supported by observational studies (see section 6.2).

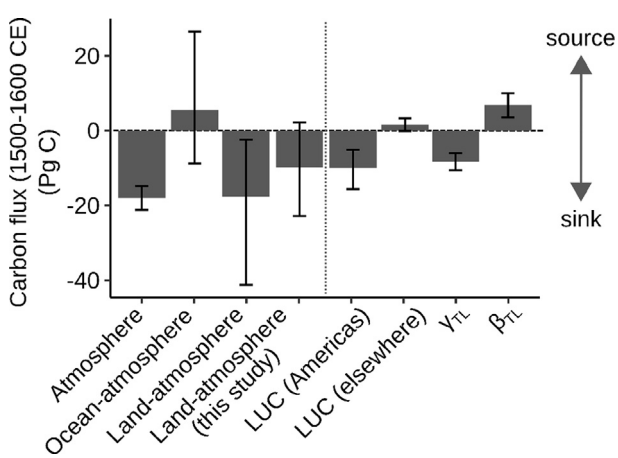

Fig. 6. Carbon fluxes from 1500 to 1600 CE relative to those from 1400 to 1500 CE. The first 3 bars, atmosphere, land-atmosphere and ocean-atmosphere fluxes are the mean from double deconvolution approaches (Bauska et al., 2015; Joos et al., 1999; Rubino et al., 2016; Trudinger et al., 2002) and a GCM (Pongratz et al., 2011), the fourth bar is the land-atmosphere flux estimated in this study, which is the sum of the four last bars, LUC (Americas), terrestrial carbon fluxes due to temperature (γ_{TL}), CO_2 feedbacks (β_{TL}), and LUC elsewhere. LUC (Americas) is calculated in this study; γ_{TL} and β_{TL} are based on feedback strength from C4MIP models reported in Cox et al. (2013); LUC (elsewhere) is the average of KK10 (Kaplan et al., 2011), HYDE 3.1 (Klein Goldewijk et al., 2011), and P08 (Pongratz et al., 2008a) datasets Europe and Asia, the most populous and well-studied regions outside the Americas. Error bars are the min-max.

Most recently, Rubino et al. (2016) argued that lower surface air temperatures drove terrestrial carbon uptake, rather than an increase in secondary forest succession. They analysed carbonyl sulfide (COS) concentrations from ice-cores, which track GPP, demonstrating that synchronous GPP and R_a decline lead to an increase in land carbon uptake between 1520 CE and 1610 CE. Despite their conclusion, this result corroborates with our interpretation of the temperature response of the global carbon cycle at this time. Indeed, Rubino et al. (2016) explicitly estimate the land surface temperature feedback, γTL, as between −10 and −90 Pg C K^{-1}, based on the decline in GPP, which is comparable to the C4MIP range used in this study (−40 to −70 Pg C K^{-1}).

However, Rubino et al. (2016) then conclude that vegetation recovery from LUC is incompatible with the declining GPP, and so cannot be the cause of the change in land carbon stocks. Yet observations of terrestrial carbon stocks do not support such conclusion. The carbon stored in vegetation is determined by both the carbon input into a system – the net primary productivity, NPP, i.e. GPP minus R_a – and how long a unit of fixed carbon stays in the system, the carbon residence time (CRT). It is the CRT that lengthens during vegetation succession, from just 1–6 years in agricultural crops to ~50 years in many forests (Galbraith et al., 2013). Critically, GPP and NPP do not change radically over time as vegetation regenerates following cropland abandonment, yet carbon stocks rapidly increase (Anderson-Teixeira et al., 2012). Small changes in CRT are well known to have large impacts on vegetation carbon stocks, despite not typically being included in models (Ahlström et al., 2015; Friend et al., 2014; Galbraith et al., 2013). Thus the assumption made by Rubino et al. (2016) that vegetation succession and declining GPP are incompatible is incorrect (succession continues even if temperature declines and GPP and NPP are lower). Furthermore, as COS has no known or theorized relationship to CRT, COS cannot be used in a straightforward manner to evaluate LUC impacts on land carbon stocks. Thus, lower GPP due to lower temperatures, and an increase in carbon stocks following LUC in the Americas, are not the mutually exclusive mechanisms described by Rubino et al. (2016).

Overall, the change in a forcing agent (a large abrupt LUC) driving a reduction of atmospheric CO_2 (widespread vegetation regrowth), its location (carbon uptake on land), its timing (1520–1610 CE), and its magnitude (7–10 ppm CO_2) each fit with the evidence for the impact of the arrival of Europeans in the Americas directly. By summing the impacts about half of the reduction in atmospheric CO_2 can be attributed to LUC following the Great Dying (4.4 ppm of 7–10 ppm CO_2 reduction).

7.3. The 16th century carbon budget

Given that the atmosphere, oceans and land surfaces are linked, a reconstruction of the global carbon budget of the century between 1510 CE and 1610 CE can provide a more comprehensive understanding of the role of LUC in the Americas on the Earth System at this time. Indeed, assessing the changes in atmospheric and oceanic carbon fluxes provides an independent assessment of the necessary uptake on land required to balance the global carbon budget. For the centuries prior to the 1500s, there was no change in atmospheric CO_2 concentration (Fig. 5A), thus the carbon released from global LUC was offset by enhanced carbon uptake somewhere else in the Earth system, most likely in peatlands (Bauska et al., 2015; Ruddiman, 2007; Stocker et al., 2017). We therefore need to assess the change in the global carbon budget in the 1500s compared to the 1400s, which is detailed in Fig. 6.

The decline in atmospheric carbon, 14.8–22.2 Pg C, is well known (Fig. 6). Whether the oceans acted as a source or sink of carbon to the atmosphere relative to the 1400s is less clear (see

Table S5). A number of double deconvolution studies and one GCM study have estimated the ocean response to the carbon uptake on land, giving a mean carbon source to the atmosphere of 5.5 Pg C relative to the 1400s (−8.8 to 26.5 Pg C range, Bauska et al., 2015; Joos et al., 1999; Pongratz et al., 2011; Rubino et al., 2016; Trudinger et al., 1999, 2002, Fig. 6). While it should be noted that the results range from a sink to a large source, a strong ocean carbon sink over that period is not supported by the increase in $\delta^{13}C-CO_2$ (see section 7.1), thus a carbon source from oceans to atmosphere appears much more likely (Fig. 6). Such a carbon source from ocean to atmosphere requires an even larger carbon uptake on land to balance the carbon budget than the atmospheric CO_2 decline alone suggests. Given the known decline in atmospheric carbon, 14.8–21.2 Pg C, and the addition of carbon from the oceans to the atmosphere (5.5 Pg C), the necessary mean land sink to balance the global carbon budget is approximately 23.5 Pg C over the 1500s (mid-range atmospheric carbon decline, 18 Pg C plus the ocean source).

A mean land sink of 23.5 Pg C being needed to balance the carbon budget of the 1500s is considerably larger than the carbon uptake from LUC in the Americas we compute above, at either 7.4 Pg C, or 9.3 Pg C uptake on land including the temperature and CO_2 feedbacks. However, these values are an underestimate. From the 1400s to the 1500s LUC in the Americas shifted from a source of 2.5 ± 2.3 Pg C (mean of mid-ranges of KK10, HYDE3.1, and P08 land use of 19.2nbsp;± 17.7 million ha in the 1400s, assuming the 0.13 Pg C per 1 million ha derived in this study), to a sink of 7.4 Pg C following the Great Dying. Hence, a net carbon uptake from LUC in the Americas of 9.9 (5.1–15.6) Pg C in the 1500s compared to the 1400s. However, carbon was also lost from LUC elsewhere in the world. This added a net 1.6 (±1.7) Pg C to the atmosphere from the 1400s to the 1500s (mid-range KK10, HYDE 3.1, and P08 LUC in the most populous and well-studied regions, Europe and Asia, an increase from 64nbsp;± 7.1 million ha anthropogenic land in the 1400s to 76.1nbsp;± 20.5 million ha in the 1500s, a difference of 12.1nbsp;± 13.4 million ha, assuming of the same 0.13 Pg C per 1 million ha).

Thus the total LUC carbon storage on land in the 1500s compared to the 1400s is (i) the net uptake from LUC in the Americas of 9.9 Pg C (IQR 5.1–15.6 Pg C), (ii) a net release from LUC from the rest of the world of 1.6nbsp;± 1.7 Pg C, (iii) the land temperature feedback response increasing carbon storage on land by 8.3nbsp;± 2.3 Pg C, (iv) the land CO_2 feedback leading to a release of 6.8nbsp;± 3.3 Pg C (Fig. 6). Combined, these fluxes lead to a net increase in carbon stocks on the land surface in the 1500s, relative to the 1400s, of 9.8 Pg C (ranging from a small source to large sink, −2.2 to 22.8 Pg C; Fig. 6). The lower error boundary, a terrestrial carbon source, is not supported from the $\delta^{13}C-CO_2$ evidence in ice cores and marine records (see section 7.1). Only those figures in the upper part of the range of estimates close the global carbon budget in the 1500s (requirement is a lower bound of 14.8 Pg C less atmospheric carbon plus the ocean source). This implies our estimate of the increase in carbon stocks following the Great Dying may be low.

Balancing the global carbon cycle in the 1500s implies substantial land sink, as even if the ocean was neutral and the atmospheric decline was at the lower boundary of 14.8 Pg C, the 9.8 Pg C land sink we calculate is smaller than the required land sink to close the carbon budget. At the other extreme, if the oceanic source was at the upper end of the range, 26.5 Pg C, and the atmospheric decline was also at the top of the range, 22.1 Pg C, then the land absorbed 48.6 Pg C in the 1500s. Of course, every term in the reconstructed 1500s carbon budget has a large uncertainty, as the land sink may be up to 22.8 Pg C, so it is possible to close the budget by combining the terms within these ranges. However, the likelihood, given an oceanic carbon source at this time, is that our central value for the land sink is underestimated. This may plausibly be because (i) the land temperature feedback is too weak, (ii) the CO_2 feedback is too strong, or (iii) the per capita land use used in the LUC in the Americas calculation is too small. The latter may be particularly important, as the much larger per capita land use employed in the KK10 dataset may be closer to reality, which would substantially increase carbon uptake on land in the Americas (Kaplan et al., 2011). Indeed, if per capita land use was double our median estimate, at 2.08 ha per person, still a modest value, total uptake would be 18.8 Pg C. By contrast, the temperature and CO_2 feedback parameters are unlikely to radically change with updated work. Overall, while the carbon budget in the 1500s is uncertain, it appears impossible to balance the global carbon cycle at this time without large terrestrial uptake including substantial land use change in the Americas as a result of the Great Dying.

8. Conclusion

We estimate that 55 million indigenous people died following the European conquest of the Americas beginning in 1492. This led to the abandonment and secondary succession of 56 million hectares of land. We calculate that this led to an additional 7.4 Pg C being removed from the atmosphere and stored on the land surface in the 1500s. This was a change from the 1400s of 9.9 Pg C (5 ppm CO_2). Including feedback processes this contributed between 47% and 67% of the 15–22 Pg C (7–10 ppm CO_2) decline in atmospheric CO_2 between 1520 CE and 1610 CE seen in Antarctic ice core records. These changes show that the Great Dying of the Indigenous Peoples of the Americas is necessary for a parsimonious explanation of the anomalous decrease in atmospheric CO_2 at that time and the resulting decline in global surface air temperatures. These changes show that human actions had global impacts on the Earth system in the centuries prior to the Industrial Revolution. Our results also show that this aspect of the Columbian Exchange – the globalisation of diseases – had global impacts on the Earth system, key evidence in the calls for the drop in atmospheric CO_2 at 1610 CE to mark the onset of the Anthropocene epoch (Lewis and Maslin, 2015, 2018). We conclude that the Great Dying of the Indigenous Peoples of the Americas led to the abandonment of enough cleared land in the Americas that the resulting terrestrial carbon uptake had a detectable impact on both atmospheric CO_2 and global surface air temperatures in the two centuries prior to the Industrial Revolution.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2018.12.004.

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