



Long-term ecological legacies in western Amazonia

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Abstract

1. Modifications of Amazonian forests by pre-Columbian peoples are thought to have left ecological legacies that have persisted to the modern day. Most Amazonian palaeoecological records do not, however, provide the required temporal resolution to document the nuanced changes of pre-Columbian disturbance or post-disturbance succession and recovery, making it difficult to detect any direct, or indirect, ecological legacies on tree species.
2. Here, we investigate the fossil pollen, phytolith and charcoal history of Lake Kumpak^a, Ecuador, during the last 2,415 years in c. 3–50 year time intervals to assess ecological legacies resulting from pre-Columbian forest modification, disturbance, cultivation and fire usage.
3. Two cycles of pre-Columbian cultivation (one including slash-and-burn cultivation, the other including slash-and-mulch cultivation) were documented in the record around 2150–1430 cal. year BP and 1250–680 cal. year BP, with following post-disturbance succession dynamics. Modern disturbance was documented after c. 10 cal. year BP. The modern disturbance produced a plant composition unlike those of the two past disturbances, as fire frequencies reached their peak in the 2,415-year record. The disturbance periods varied in intensity and duration, while the overturn of taxa following a disturbance lasted for hundreds of years. The recovery periods following pre-Columbian disturbance shared some similar patterns of early succession, but the longer-term recovery patterns differed.
4. *Synthesis.* The trajectories of change after a cessation of cultivation can be anticipated to differ depending on the intensity, scale, duration and manner of the past disturbance. In the Kumpak^a record, no evidence of persistent enrichment or depletion of intentionally altered taxa (i.e. direct legacy effects) was found but indirect legacy effects, however, were documented and have persisted to the modern day. These findings highlight the strengths of using empirical data to reconstruct past change rather than relying solely on modern plant populations to infer past human management and ecological legacies, and challenge some of the current hypotheses involving the persistence of pre-Columbian legacies on modern plant populations.

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KEYWORDS

cultivation, disturbance, fire, maize, palms, phytoliths, pollen, succession

1 | INTRODUCTION

Amazonia is one of the most biodiverse regions on Earth (Olson et al., 2001). This biodiversity has been shaped by an array of processes operating on a large range of temporal and spatial scales, including long-term tectonism (Hoorn et al., 2010), climate change (Liu & Colinvaux, 1985), riverine dynamics (Pupim et al., 2019), stochastic processes (Hubbell, 2001), biotic interactions (Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009) and canopy-gap dynamics (Mittelbach et al., 2007). Humans have also been implicated in shaping the species richness and relative abundances of species in Amazonia. In particular, it has been suggested that pre-Columbian peoples, or the indigenous inhabitants of the forest prior to European arrival, modified forest composition and left ecological legacies that persist at least until the modern day (Balée, 1989; Denevan, 2006; Erickson, 2006; Levis et al., 2017; Maezumi et al., 2018). People have lived within Amazonia for at least 13,000 years (Roosevelt, 2013), and modified their environment through hunting (Antunes et al., 2016; Redford, 1992), the use of fire (Barlow & Peres, 2006; Bush et al., 2015), deforestation (Laurance, Albernaz, Fearnside, Vasconcelos, & Ferreira, 2004), cultivation (Brugger et al., 2016; Bush, Piperno, & Colinvaux, 1989), soil modification (Glaser & Birk, 2012; Neves, Petersen, Bartone, & Heckenberger, 2004), enrichment of forest with useful species (Balée, 1989; Balée & Erickson, 2006; Levis et al., 2017) and the construction of earthworks (Pärssinen, Schaan, & Ranzi, 2009; Roosevelt, 1991; Watling et al., 2017).

Considerable disagreement exists regarding the scale of these transformations both in space and time (Bush et al., 2015; Clement et al., 2015; Ferreira, Levis, Iriarte, & Clement, 2019; Levis et al., 2017; Maezumi et al., 2018; McMichael & Bush, 2019; McMichael, Feeley, Dick, Piperno, & Bush, 2017; Piperno, McMichael, & Bush, 2019; Stahl, 2015). But regardless of the spatial and temporal scale of these modifications, the arrival of Europeans brought enslavement, maltreatment and novel diseases to a susceptible population. This arrival is suggested to have caused premature mortality of 90%–95% of the indigenous population in the 1600s (Black, 1992; Dobyns, 1983), with a concomitant abandonment of occupied lands (Smith, 1999). This rapid shift in land use is suggested to have caused a surge in carbon uptake (Dull et al., 2010; Koch, Brierley, Maslin, & Lewis, 2019; Nevle, Bird, Ruddiman, & Dull, 2011) and to have contributed to the hyperdominance of some plant species (Levis et al., 2012; ter Steege et al., 2013).

The ecological legacies left by pre-modern human activities can either be direct, that is, the intended product of manipulation of the environment, or indirect, that is, the unintended product of manipulation (Figure 1). Direct legacies would include the intentional enrichment of preferred species, or the intentional removal of non-preferred species (Clement et al., 2015). The direct enrichments or depletions caused by past human activities can affect the successional trajectory, or ecological legacy, in two ways. One possibility is

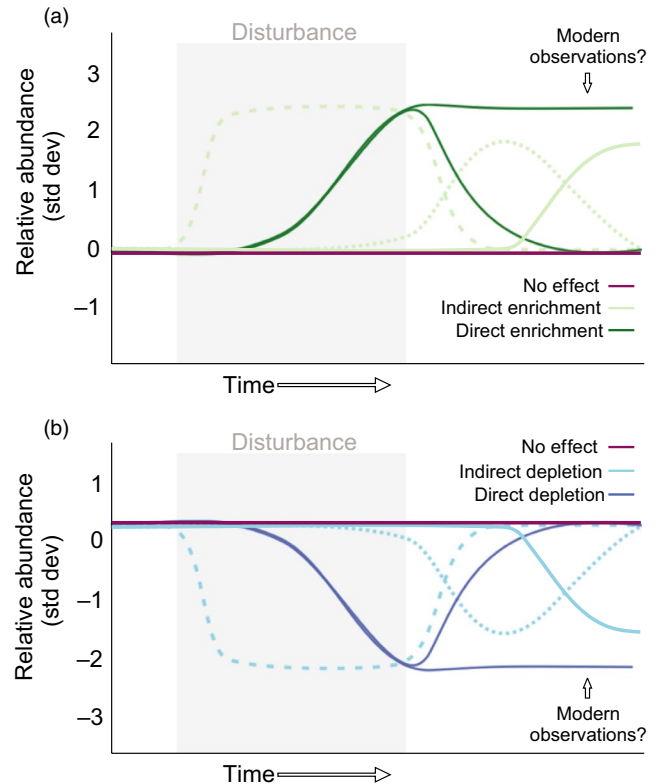


FIGURE 1 Schematic diagram showing the rise and fall of species through time in response to an episode of sustained disturbance (shaded grey). Panel (a) direct enrichment of preferred species (dark green line) which either maintain/increase population levels, or quickly rebound to pre-disturbance abundances after the disturbance ends. Indirect enrichment of species (light green line) that increase during or after disturbance, but which are not intentionally enriched or altered. Species that show no population change during disturbance are no effect species (purple line). Panel (b) direct depletion of non-preferred species (dark blue line) which either maintain/decrease population levels, or quickly rebound to pre-disturbance abundances after the disturbance ends. Indirect depletion of species (light blue line) that decrease during or after disturbance, but which are not intentionally depleted or altered. Species that show no population change during disturbance are no effect species (purple line)

that the populations that were enriched or depleted quickly rebound to pre-disturbance abundances (non-persistent enrichment/depletion, Figure 1). The other possibility is that enriched or depleted abundances of species persist through time, where enriched species establish reproductive populations that continue to the present day and depleted species do not recover to pre-disturbance abundances (Figure 1a). For example, palms with fruits eaten by people, such as peach palm *Bactris gasipaes* (Clement, 1988; Clement, Rival, & Cole, 2009; Hernández-Ugalde, Mora-Urpí, & Rocha, 2011), and Moriche *Mauritia flexuosa* (Rull & Montoya, 2014), along with Brazil nut *Bertholettia excelsa* (Levis et al., 2012; Scoles & Gribel, 2011;

Shepard & Ramirez, 2011), are cited as evidence of persistent forest enrichment legacies.

Indirect legacies include the responses of weedy or successional species that were not intentionally altered (Figure 1). Some populations can exhibit a short-term increase or decrease associated with disturbance that we term non-persistent, for example, *Ambrosia* or *Cecropia* would often be examples of non-persistent enrichments during disturbances (Figure 1).

Pre-Columbian people in Amazonia may have also depleted the relative abundances of some species (Clark, Clark, Sandoval, & Castro, 1995; Ferreira et al., 2019; Figure 1b). The depletions are likely to be among species that were cut to provide timber for construction or where consumption was a one-time disturbance, for example, harvesting for heart of palm (Haynes & McLaughlin, 2000). In Costa Rica, the absence of *Iriartea deltoidea* from forests near rivers in La Selva Biological Reserve was identified as a legacy effect of colonial era logging (Clark et al., 1995). In Amazonia, pollen percentages of *I. deltoidea* and phytolith percentages of taxa including *Iriartea* were lower when direct indicators of human activity (i.e. charcoal or crop pollen) were at their highest (Bush & McMichael, 2016; Heijink et al., 2020). Depletions, like enrichments, can be persistent, non-persistent or indirect (Figure 1b).

The intensity, manner, scale and duration of past disturbance all influence post-abandonment successional trajectories (Bodin, Molino, Odonne, & Bremond, 2020). In some areas, the land use was a polyculture featuring mixed crop field systems and orchards (Denevan, 2001). If abandoned, succession would have quickly displaced crop plants and disturbed-ground weeds with fast growing, light-loving trees, as a stage before a dense forest established (Bush & Colinvaux, 1988, 1994; Uhl, Clark, Clark, & Maquirino, 1982). Dwelling sites would have been surrounded by useful species (sensu Clement et al., 2015) ranging from dye plants to food plants. As many of these useful species would have been trees of mature forest, the successional trajectory would have followed a different path compared with the open ground. Consequently, the modern forest, perhaps no more than 400 years old, could still bear different ecological legacies, especially in non-natural enrichments of large long-lived trees (Bodin et al., 2020; Figure 1a).

Past human occupation of Amazonian forest systems is readily identified in palaeoecological records by an increase in the pollen and phytolith abundances of grasses, crops and taxa indicative of forest openings (gaps), or the presence of charcoal (Bush, 2002; McMichael Correa-Metrio & Bush, 2012; McMichael, Piperno, et al., 2012; Whitney et al., 2019). Addressing questions of past forest disturbance and recovery is best accomplished through a multiproxy approach that capitalises on the different strengths of the evidentiary lines. For example, though phytoliths cannot distinguish many of the tree taxa that can be identified with pollen, pairing the two proxies: (a) increases certainty in identifying cultivation and forest opening and (b) provides a more comprehensive view of the change in taxa associated with disturbance and recovery processes. Unlike pollen, phytoliths can also distinguish grasses to sub-family or sometimes even genera, making them particularly useful for disentangling

grasses typical of disturbed or open settings, grasses that grow under the forest canopy, and aquatic grasses (Morcote-Rios, Bernal, & Raz, 2016; Piperno, 2006b). Palms are also abundant producers of phytoliths and many phytolith morphotypes can be identified to genus (Piperno, 2006b).

The study of past disturbance in lowland rainforests also has to be conducted at an appropriate temporal scale. Most palaeoecological records are temporally coarse-grained, generally offering centennial resolution, and cannot assess the nuanced changes of pre-Columbian disturbance, post-disturbance recovery and various types of ecological legacies of tree species. Here, we provide an almost unprecedented temporal resolution for a multiproxy Amazonian palaeoecological record. Using fossil pollen, phytolith, and charcoal from the 2,415-year Lake Kumpak^a record, Ecuador, at 3–50 year time intervals, we assess the types, duration and variation of ecological legacies resulting from pre-Columbian fire, agriculture and forest disturbance.

2 | STUDY AREA

Lake Kumpak^a (2°50'11"S, 77°57'41"W; 333 m elevation) is located in lowland Amazonia, Ecuador (Figure 2a). The lake has a diameter of 420 m, a maximum water depth of 19.5 m and is thought to be volcanic in origin (Colinvaux, Millerf, & Liu, 1985; Figure 2b). Lake Kumpak^a is permanent and has no riverine influence, making it a rarity in Amazonian systems. The region receives approximately 2,000–3,000 mm of precipitation per year and lacks a defined dry season (<https://www.climate-data.org>; Liu & Colinvaux, 1988). Mean annual temperature is 24°C. Small streams deliver sediment-rich water to all sides of the mesotrophic lake (Figure 2b). A lack of outlets suggests that water level changes in response to precipitation. We found the lake to be anoxic below 2 m water depth (measured in 2014).

The lake was first cored in 1983 by Paul Colinvaux's team and a low-resolution 5,860-year history of its pollen and sediment stratigraphy was published (Liu & Colinvaux, 1988; Figure 2c,d). That study revealed a largely stable rainforest system, with more apparent ecological changes in the last 1,500 years than in the earlier portion of the record. The possibility that there was a human history was largely ignored in this initial study.

Following establishment of a Salesian mission station in the 1960s, most of the modern landscape surrounding Lake Kumpak^a has been modified for small-scale agriculture and grazing. Today, a small community of the Shuar nation inhabits the areas around the lake. In 2014, patches of secondary forest and pastures formed a fragmented landscape around the lake where pastures were dominated by introduced grasses, especially the African grass species *Brachiaria* (Figure 2e,f). Common secondary forest taxa were *Didymopanax*, *Piptocoma*, *Cordia*, *Terminalia*, *Caryodendron*, *Croton* and *Inga*. A range of crop taxa were farmed in the area, including *B. gasipaes* (peach palm), *Carludovica palmata* (native Panama-hat plant), *Manihot esculenta* (native Amazonian manioc), *Deguelia utilis* (barbasco plant), *Musa x paradisiaca* (banana), *M. sapientum* (plantain), *Ananas comosus*

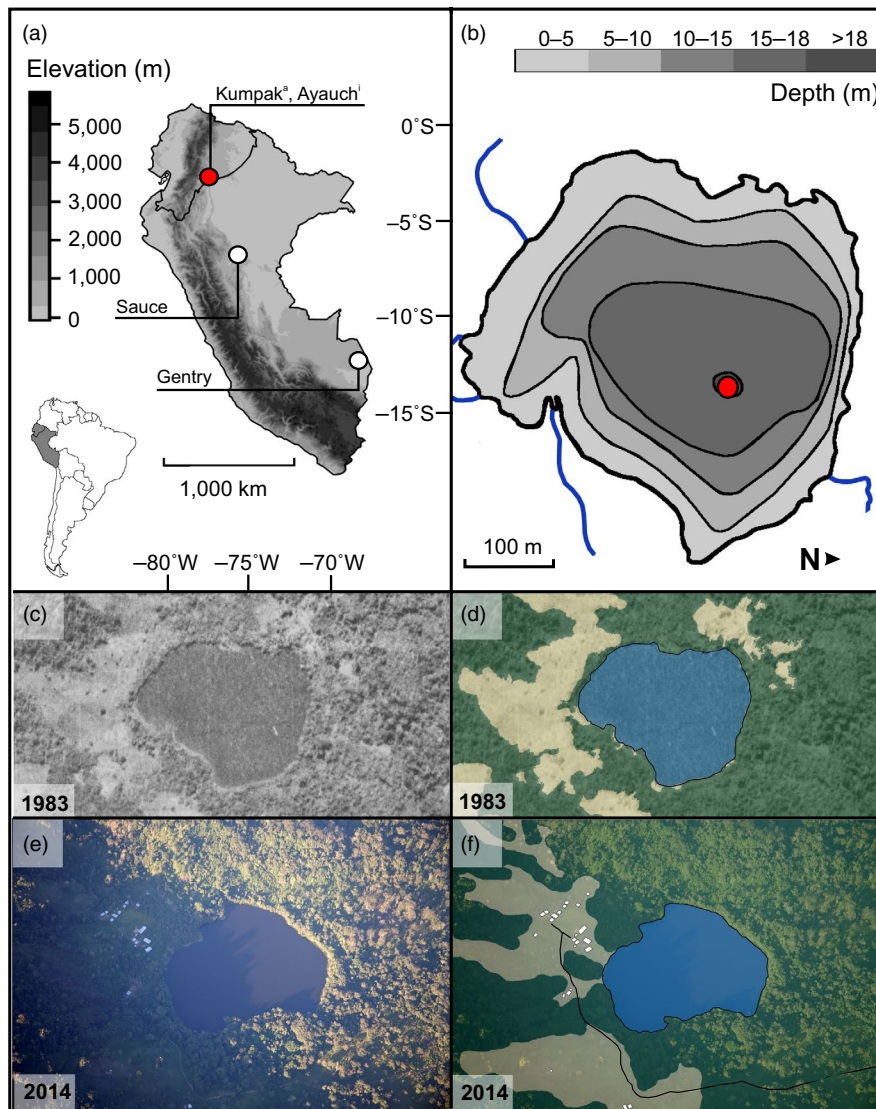


FIGURE 2 Map of the study area of Lake Kumpak^a, Ecuador. (a) Map of South America with a focus on Ecuador and Peru showing study site Lake Kumpak^a and sites Lake Ayauchⁱ (Bush & Colinvaux, 1988), Lake Sauce (Bush et al., 2016) and Lake Gentry (Bush et al., 2007). (b) Bathymetry map of Lake Kumpak^a showing coring location (red circle) and inlet streams (blue lines; modified from Liu & Colinvaux, 1988). (c) Aerial photography of Lake Kumpak^a from 1983 (De Oliveira, Steinitz-Kannan, Miller, & Colinvaux, 1986). (d) Land cover types present in 1983, including forested areas (green) and open areas (yellow). (e) Aerial photography of Lake Kumpak^a from 2014 (photo: Luke Parsons, 2014). (f) Land cover types present in 2014, including forested areas (green), open areas (yellow) and buildings (white)

(pineapple), *Carica papaya* (papaya) and *Zea mays* (maize). The vegetation closest to the lake shore was dominated by remnant forest taxa with a closed canopy, including *Mauritia*, *Wettinia*, *Symphonia*, *Sapium*, *Deguelia*, *Erythrina*, *Ficus*, *Virola*, *Hieronyma*, *Triplaris* and *Homalium*. Undisturbed primary forest existed on slopes and ridges further north and west of the basin. Aerial photography from the early 1980s (Liu & Colinvaux, 1988) compared with 2014 show similar trends in openness, suggesting that the area has been consistently kept open for almost 30 years (Figure 2c–f), but this does not imply no change in the tree composition within the forest.

3 | MATERIALS AND METHODS

In July 2014, an 18.0-m sediment core was retrieved from 19.5 m water depth. The core was wrapped in the field in sections of 1 m, transported to Florida Institute of Technology and stored at 4°C. The sediment core represents the limit of coring ability as bedrock was not reached. Terrestrial macrofossil remains ($n = 15$) were isolated and radiocarbon dated to establish the Kumpak^a chronology

(Supporting Information: Methods; Blaauw & Christen, 2011; R Development Core Team, 2019; Reimer et al., 2013).

Subsamples were taken for pollen and phytoliths at every 5 cm from 0 to 530 cm core depth and at every 10–20 cm for the intervals from 530 to 760 cm. Charcoal was subsampled at 1–5 cm resolution throughout the 760 cm section. Pollen samples ($n = 126$) were treated according to standard methodology (Supporting Information: Methods; Fægri, Kaland, & Krzywinski, 1989; Stockmarr, 1971) and a minimum of 300 pollen grains was counted in each sample. Identification of pollen grains was made using appropriate keys (Colinvaux, De Oliveira, & Moreno, 1999; Roubik & Moreno, 1991), the Neotropical Pollen Database (Bush & Weng, 2007) and the reference collection at Florida Institute of Technology. Extended maize counts were performed on all subsamples. Phytolith samples ($n = 131$) were prepared according to standard methodology (Piperno, 2006b) and a minimum of 200 phytoliths were counted in each sample (Piperno, 2006b; Supporting Information: Methods). Phytolith keys (Morcote-Ríos et al., 2016; Pearsall, 1978; Piperno, 2006b) and the reference collection at University of Amsterdam were used for identification. Pollen and phytolith samples were analysed using Zeiss

Axioskop photomicroscopes with magnifications of 400 \times , 630 \times and 1,000 \times . Pollen and phytolith types were grouped into ecological assemblages to aid interpretation (Tables S1 and S2; Gentry, 1996). Each identified pollen or phytolith was assigned to one of four vegetation types: (a) grasses, (b) herbs, (c) arboreal and (d) palms.

Charcoal samples ($n = 515$) were prepared according to standard methodology (McMichael, Correa-Metrio, et al., 2012; McMichael, Piperno, et al., 2012; Whitlock & Larsen, 2001; Supporting Information: Methods) and examined under an Olympus stereoscope at 7–70 \times magnification. ImageJ software (Rasband, 1997–2018) was used to calculate the volume (mm^3/cm^3 ; Weng, 2005) of all charcoal particles within each sample. Fossil percentage diagrams were constructed using C2 (Juggins, 2007).

Detrended correspondence analysis (DCA) was performed using R (R Development Core Team, 2019) and the *VEGAN* package (Oksanen et al., 2013) on the pollen and phytolith data, separately, to quantify trends in (dis)similarity between samples (slices of time within the stratigraphic sequence), and to determine which taxa within pollen or phytolith assemblages were most responsible for driving those differences (also see Supporting Information: Methods). We also used the DCA results to determine whether successional trajectories or ecological legacies could be seen in the data.

4 | RESULTS

The 18.0-m core spans the last 5,400 years, and all 15 radiocarbon ages were accepted to provide the chronology (Table S3; Figure S1). This paper focused on the last 2,415 years (760 cm), where sediment accumulation rate averaged 3.24 years per centimetre and remained consistent almost throughout the entire core (Figure S1). This 760 cm of sediment was dominated by alternating pale and dark organic clay laminations of very thin thickness (<1 mm) interspersed with medium (2–5 mm) to very thick (>10 mm) laminations (Supporting Information: Results; Figure S2).

The temporal resolution of sampling provides a c. 3- to 15-year resolution for charcoal occurrence and a c. 15- to 50-year periodicity for pollen and phytolith data. Old-growth arboreal pollen and phytoliths were prominent features throughout the Kumpak^a record, Ecuador, with values fluctuating between 30% and 90% for pollen and 35%–95% for phytoliths (Figure 3). In the pollen record, decreases in old-growth arboreal forest and palm elements (e.g. Moraceae, Urticaceae, *Iriartea*, *Alchornea*, *Didymopanax*, *Celtis*, *Mimosa* and *Mauritia-Mauritiella*) were due to a replacement in the assemblage by grasses (Poaceae and *Z. mays*), herbs (e.g. *Acalypha*, Piperaceae and Asteraceae) and arboreal secondary forest elements (e.g. *Cecropia*; Figure 3a). The phytolith record followed similar trends as the pollen record (Figure 3b). Rugose spheres, which are mainly produced by arboreal old-growth forest taxa (e.g. Piperno, 2006b), are present in high percentages throughout most of the record (Figure 3b). Oblong echinate and globular echinate phytoliths, which represent palm genera such as *Euterpe*, *Hyospathe* and *Attalea* (Huisman, Raczka, & McMichael, 2018; Morcote-Ríos et al., 2016),

and conical palm phytoliths representing taxa such as *Bactris*, *Iriartea*, *Wettinia*, *Aiphanes* and *Socratea* (Huisman et al., 2018; Morcote-Ríos et al., 2016), all increased at the expense of the rugose spheres. The increased abundances of palm phytoliths did not occur, however, in samples with the highest abundances of weedy taxa, grasses, *Heliconia* phytoliths or maize phytoliths (Figures 3b and 4).

The changes in abundances of conical palm phytoliths, which represent genera such as *Iriartea*, *Wettinia* and *Bactris*, were similar, but not exact, to those seen in the *Iriartea* pollen record (Figure 3). Botanical inventory surveys conducted by David Neill in 2014 observed *Wettinia*, a genus common to the ever-wet forests of the Andean piedmont (Kahn & De Granville, 2012), in abundance around the lake edge of Kumpak^a. Small stands of peach palm *B. gasipaes* were also observed in the adjacent farmlands, but no individuals of *Iriartea* were observed in the vicinity of the lake, supporting the modern decline of *Iriartea* observed in the pollen record (Figure 3). As conical phytoliths were present in the modern phytolith assemblages, and were common around the lake edge, we interpret changes in conical phytoliths as representing changes in *Wettinia* and *Iriartea* populations through time. *Wettinia* has most likely always been present to some degree around the lake, and when the populations of *Iriartea* declined over the last 150 years, *Wettinia* populations have persisted (Figure 3).

The globular echinate phytoliths, which represent genera such as *Mauritia*, *Euterpe*, *Attalea* and *Hyospathe* (Huisman et al., 2018; Morcote-Ríos et al., 2016), varied primarily between 1% and 10%, with occasional samples containing up to 20% (Figure 3). Abundant adult *M. flexuosa* individuals were observed around the lake edges during the vegetation surveys. The persistence of *Mauritia* pollen and the globular echinate phytoliths through time revealed that these stands have been present in similar abundances for most of the last 2,400 years (Figure 3).

These changes in forest and palm composition happened primarily in the absence of fire. Despite searching for charcoal in over 500 samples, fire was only detected in 13 samples, and only in extremely low quantities until the modern clearing of the landscape that occurred in the AD 1960s (Figure 3). The presence of charcoal and maize pollen or phytoliths provided the temporal brackets of human disturbance periods, which allowed us to assess trajectories of ecological change in the subsequent recovery periods.

4.1 | Disturbance and recovery at Lake Kumpak^a

An increase in secondary forest elements at c. 2250 cal. year BP occurs before the onset of a disturbance phase, lasting from c. 2150 to 1430 cal. year BP (Figures 3 and 4; Figure S3). During the disturbance, a few pinhead-sized charcoal fragments (c. 0.06 mm^3/cm^3) were found at c. 2120 cal. year BP and 1770 cal. year BP. Maize pollen and/or phytoliths, however, were found in 12 of 17 samples (71%), with the highest frequency of maize findings between c. 1820 and 1450 cal. year BP (Figure 3). Grass pollen increased to 5% and grass phytoliths reached values up to 18% (Figure 3). Herbs also increased during the disturbance, including Piperaceae (15%),

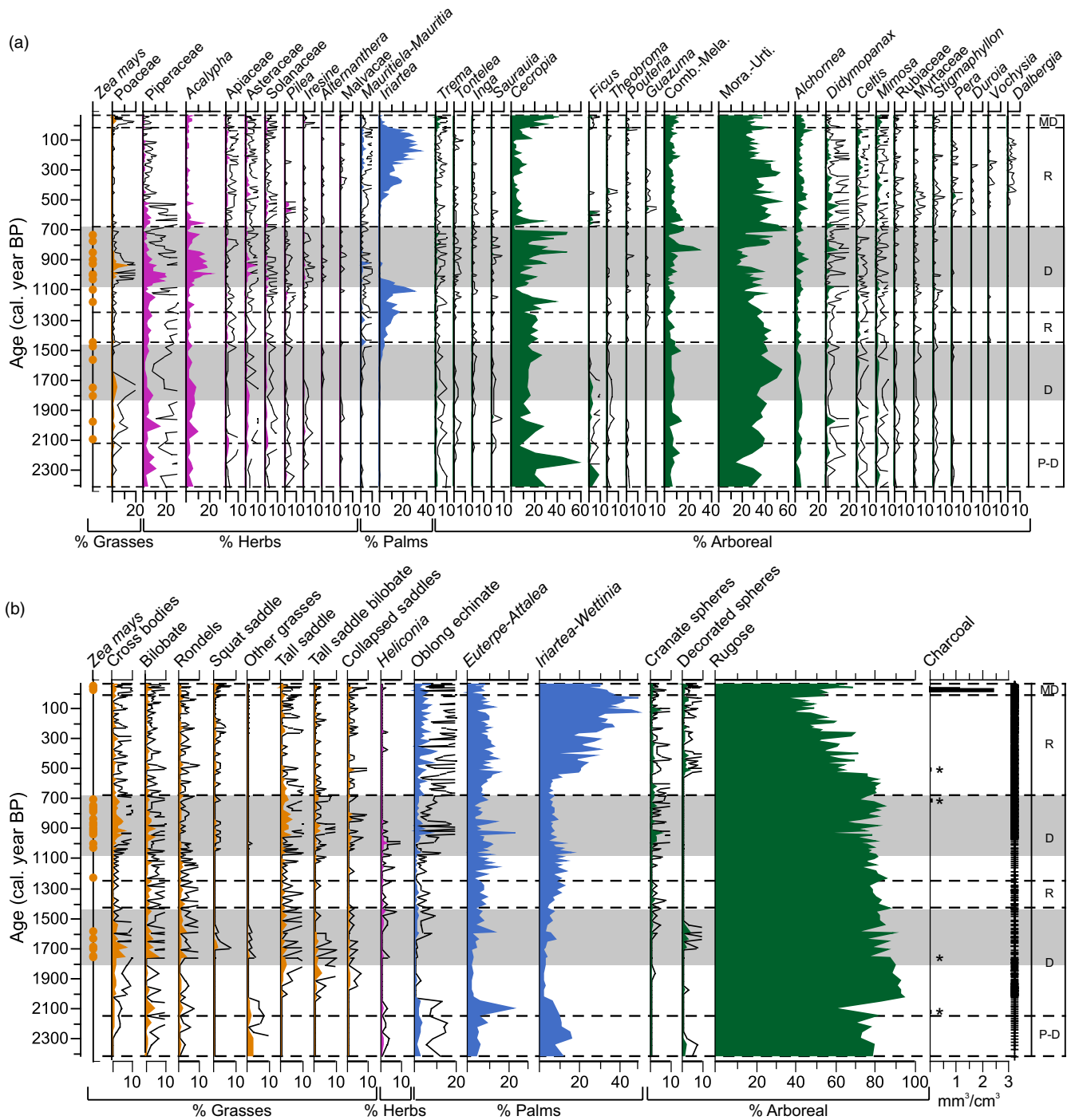


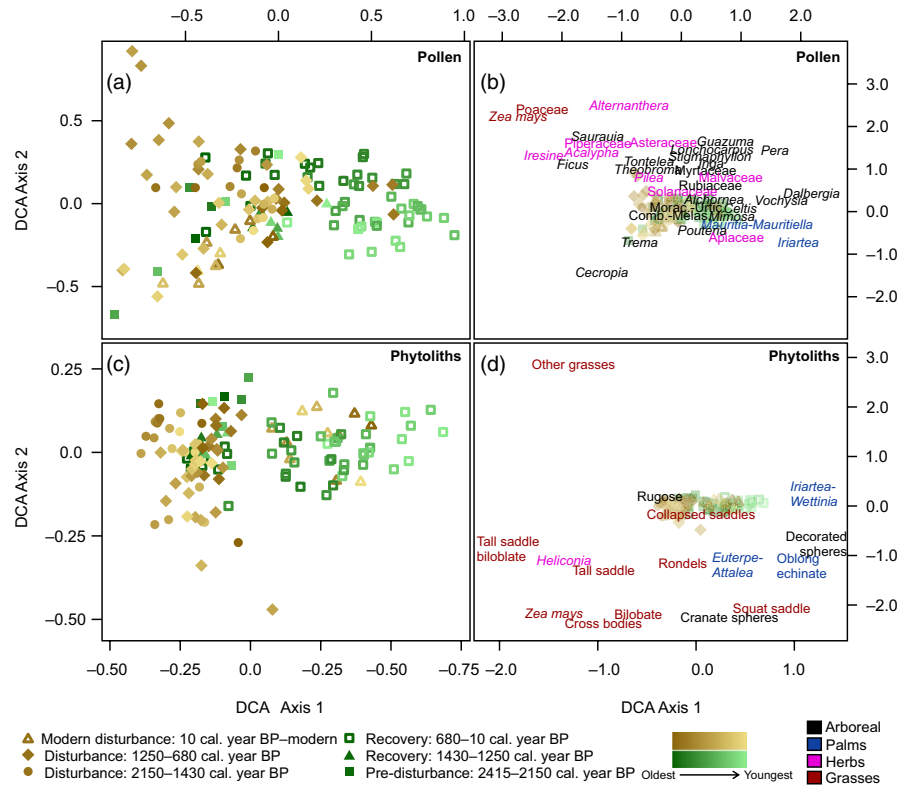
FIGURE 3 Percentage diagrams for (a) fossil pollen and (b) phytoliths and charcoal (mm^3/cm^3) plotted against time (cal. year BP) showing the most abundant taxa from Lake Kumpak^a, Ecuador. Maize pollen and phytoliths are shown as presence (orange circles) and grey bars indicate times of most intense disturbance during the two pre-modern disturbance phases. Asterisks indicate minute quantities of charcoal and plus signs indicate charcoal sample effort. Comb. indicates the family Combretaceae, Mela. indicates the family Melastomataceae, Mora. indicates the family Moraceae and Urti. indicates the family Urticaceae. P-D = pre-disturbance, R = recovery, D = disturbance and MD = modern disturbance. Colour available in online version

Acalypha (11%), Asteraceae (3.5%) and Solanaceae (2.5%). After c. 1600 cal. year BP, grasses and herbs started to decline due to increased abundances of arboreal secondary forest and palm taxa including *Cecropia*, Combretaceae, Melastomataceae, *Iriartea* and other palms with oblong echinate phytoliths such as *Euterpe* and

Attalea (Figure 3). Arboreal pollen and phytoliths continued to have high values over the next c. 350 years (maxima of 80% and 90%, respectively), with, that is, *Iriartea* pollen reaching values up to 20%.

Renewed disturbance and maize cultivation re-appeared in the record after c. 1250 cal. year BP until c. 680 cal. year BP (Figure 3),

FIGURE 4 Detrended Correspondence Analyses biplots of fossil pollen data (a and b), eigenvalues 0.2008 and 0.07919 on axes 1 and 2, and phytolith data (c and d), eigenvalues 0.1422 and 0.02908 on axes 1 and 2, from Lake Kumpak^a, Ecuador, showing sample and species scores separated in six categories: pre-disturbance (2415–2150 cal. year BP; green squares), disturbance (2150–1430 cal. year BP; yellow circles), recovery (1430–1250 cal. year BP; green triangles), disturbance (1250–680 cal. year BP; yellow diamonds), recovery (680–10 cal. year BP; green open squares) and modern disturbance (10 cal. year BP to modern; yellow open triangles). A colour gradient of the oldest to youngest sample (dark to light) is also shown. Species are categorised in four vegetational groups: grasses (red), herbs (pink), palms (blue) and arboreal (black)



coinciding with decreased abundances of arboreal types (including *Iriartea*, Moraceae, Urticaceae, conical palm phytoliths, *Didymopanax*, *Stigmaphyllon*, Myrtaceae and *Mimosa*). Grasses and herbs increased, with grass pollen (12%) and grass phytoliths (14.5%) reaching maxima between c. 1070 and 680 cal. year BP (Figures 3 and 4). Compared with the previous disturbance, this phase appears to have been more intense and longer lasting, with maize pollen and/or phytoliths found in 19 of 37 samples (51%). Increases in herbs such as *Acalypha* (22.5%), Asteraceae (8%), *Iresine* (2%), Piperaceae (20%) and Solanaceae (2.5%) were evident as *Cecropia* pollen fluctuated (c. 3%–50%). Fire was very rare during this disturbance period (Figure 3).

With the decline of grasses and herbs after c. 680 cal. year BP, arboreal secondary taxa (*Cecropia*, *Ficus* and *Guazuma*) increased slightly for c. 50–300 years while other arboreal old-growth forest pollen and phytolith types increased steadily up to c. 80% and 80%, respectively (Figure 3). The highest increases in *Iriartea* pollen (35%) have occurred over the last 600 years, though populations have declined over last 100 years. *Iriartea* had near absence values (<1%) after c. 10 cal. year BP, coinciding with modern-day disturbance (Figure 3) when grass pollen and phytoliths increased in abundances to 4% and 5%, respectively, and maize phytoliths were found in 5 of 11 samples. Arboreal old-growth forest pollen and phytoliths declined (both with 50%) and *Cecropia* reached values above 40%. A small fire event is suggested by the presence of charcoal fragments at c. 480 cal. year BP (Figure 3).

The highest fire frequency in the Lake Kumpak^a record occurred in the modern era. Fire frequency was higher during the last 80 years compared with any other portion of the record, with charcoal fragments identified between c. –15 cal. year BP and –30 cal. year BP (Figure 3). Two of the seven samples containing charcoal in the modern

disturbance period also contained evidence of maize cultivation. Even with the fires during this period at Lake Kumpak^a, the vegetation was less impacted than in the past. Percentages of modern maize and grasses were lower in the modern disturbance period than those found at c. 2150–1430 cal. year BP and c. 1250–680 cal. year BP (Figure 3).

The Detrended Correspondence Analyses (DCA) for pollen and phytoliths highlighted the successional trajectories following disturbance (Figure 4). The modern samples in the pollen spectra lay towards the negative ends of Axes 1 and 2, whereas the modern phytoliths were positioned in the middle of the plot. Samples from the most intense disturbance and subsequent recovery period (1250–680 cal. year BP) had values at the extreme ends of DCA Axis 1 (Figure 4a,c). Samples containing crop pollen and phytoliths were on the negative end of DCA Axis 1, and the herb elements in the recovery periods of both the pollen and phytolith data can then be seen to move towards 0 on DCA Axis 1 (Figure 4b,d). The arboreal mid- to late successional taxa found in the recovery periods are located on the positive end of DCA Axis 1 of both the pollen and phytolith data. The disturbance and succession trajectories seen in the DCA are all in the context of the arboreal old-growth forest taxa located in the middle of the biplot (Figure 4b,d).

5 | DISCUSSION

The Lake Kumpak^a record is a rarity in Amazonian systems as it comes from a permanent lake without riverine influence, offering the potential for an unusually detailed sedimentology. The high deposition rate allowed us to reconstruct charcoal at an almost

continuous resolution of 3.24 years, confirming the true rarity of fire in this system, and pollen and phytoliths at a c. 15- to 50-year resolution. The laminated sediments and ^{14}C ages provided reassurance that there has been little post-depositional disturbance, allowing an almost linear age model to be constructed (Figure S1). Our study broadly supported the original pollen reconstruction from Lake Kumpak^a, which had samples every 100–300 years, but had no corresponding charcoal or phytolith analysis (Liu & Colinvaux, 1988). Our study, however, documented the ability of multi-proxy palaeo-ecological datasets analysed on decadal time scales to address questions regarding the long-term disturbance and recovery patterns of Amazonian forests.

5.1 | The intensity of past disturbances at Lake Kumpak^a

Based on our aerial imagery, the modern landscape around Lake Kumpak^a, consisting of a village of around 60–100 people and of a mosaic of farmland and regrowth, appears to have been more or less stable for the last 30 years (Figure 2c–f). Though all the forest around the lake is disturbed, there is about 80% forest cover. The corresponding pollen assemblages during this recent period of 80% forest cover contain about 93% forest pollen, of which <5% were from palms (Figures 3 and 5). The arboreal elements found in the pollen assemblages included: Moraceae, Urticaceae, Combretaceae,

Melastomataceae, *Alchornea*, *Didymopanax*, *Celtis* and *Cecropia* (Figure 3).

In the modern botanical inventory surveys, species of *Didymopanax*, Moraceae, Combretaceae and Melastomataceae were observed in remnant forest around the lake, providing a confirmation between the modern vegetation and corresponding pollen assemblages. Phytolith assemblages during the last 30 years included c. 60% forest taxa, 35% palm taxa and 5% grass taxa (Figures 3 and 5). Clearly, the common palms around the lake today, primarily *Wettinia*, *Mauritia* and *Bactris*, were more strongly represented in phytolith than pollen sequences. Maize was also being grown around the lake when it was cored in 2014, which was detected in the phytolith samples (Figure 3). These values of forest cover, grass and maize derived from the pollen and phytolith samples, combined with the areal imagery and field surveys (Figure 2), provide a benchmark with which past clearance and disturbance can be compared.

Driven by increased abundances of grasses, herbs and the arboreal secondary taxa *Cecropia*, the modern pollen samples plot near the negative extremes of Axes 1 and 2. The DCA suggest that the modern pollen samples reflect substantial disturbance, though not as extreme as some samples from either of the two earlier periods of cultivation (c. 2150–1430 cal. year BP and 1070–680 cal. year BP; Figure 4a,b). The phytoliths clearly show the modern disturbance to be quite different to that of earlier episodes as modern samples cluster with those from the earlier recovery periods (Figure 4c). DCA Axis 1 of the phytolith record was largely driven by the increased

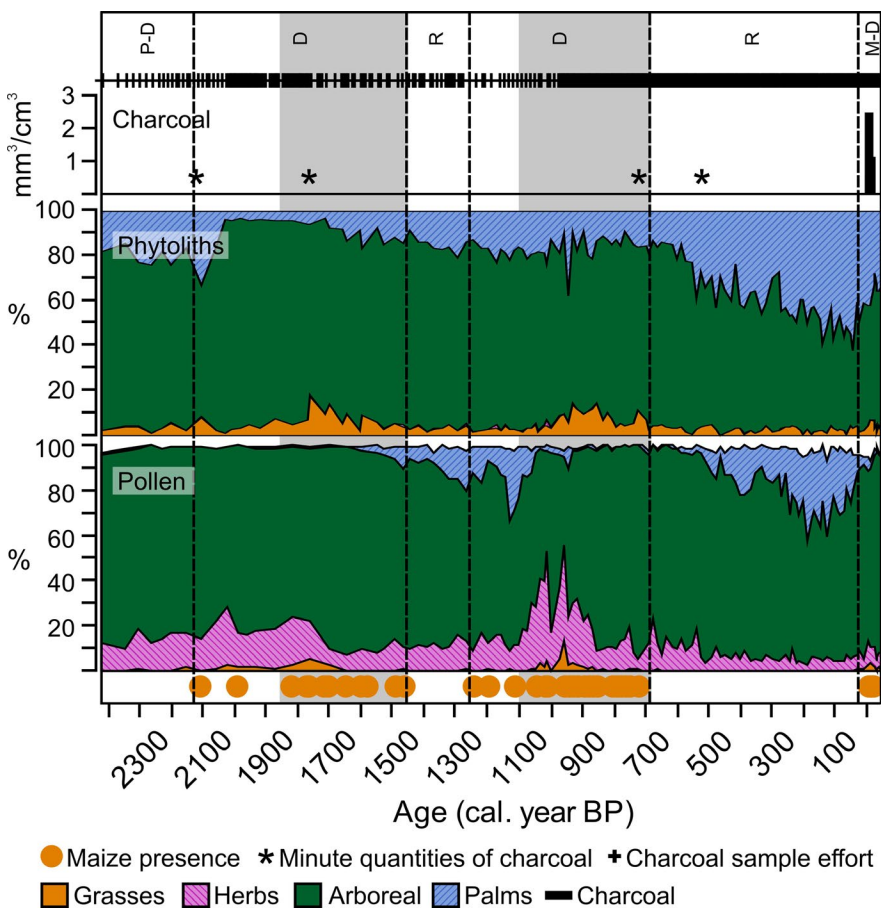


FIGURE 5 Fossil percentage summary diagrams for pollen and phytoliths plotted against time (cal. year BP) from Lake Kumpak^a, Ecuador, showing taxa separated in four vegetation groups, including grasses (orange), herbs (pink), arboreal (green) and palms (blue). Maize pollen and phytolith presence (orange circles) and the charcoal volume (mm^3/cm^3) are shown. Black asterisks for charcoal indicate minute quantities and plus signs indicate charcoal sample effort. Dashed lines show the delineation of disturbance and recovery periods, and grey bars denote the times of most intense disturbance during the two pre-modern disturbance phases. Colour is available in the online version

abundances of palm phytoliths over the period of 550 cal. BP to the modern period (Figure 4d). Phytoliths are not as sensitive as pollen to the changes in the non-palm arboreal vegetation and the placement of the modern disturbance samples is driven by the palm phytolith type *Iriarteia-Wettinia*. *Iriarteia* and *Wettinia* are currently indistinguishable, but the differing patterns of change in the pollen and phytoliths can be used to differentiate these taxa. *Iriarteia* pollen declines sharply in the modern disturbance, but the *Iriarteia-Wettinia* phytoliths do not. *Iriarteia* was not recorded in the modern flora at the lake, but *Wettinia* was observed on the shoreline. As a result, the modern phytolith samples were statistically similar to those of the forest regrowth periods in the DCA, even though ecologically they were not.

The period from c. 1070 to 680 cal. year BP was probably the most intensely disturbed of the entire record (Figures 3–5), based on the amounts of *Cecropia*, Poaceae, *Z. mays*, and herb taxa in the pollen and phytolith data. In disturbed Amazonian forests, as much as 50% of the pollen signal comes from *Cecropia*, a pioneer secondary forest species that produces enormous quantities of pollen (Bush & Rivera, 1998). Percentages of *Cecropia* are similar between the modern system and the period from c. 1070 to 680 cal. year BP, though the amount of landscape opening may have varied. Palm abundances in both the pollen and phytolith record are low during this period compared with recovery periods and the modern period (Figures 3–5). The decline in arboreal elements was also significantly larger from 1070 to 680 cal. year BP than during the modern disturbance period (Figures 3–5). The reduction in forest pollen percentage is probably not linearly related to the area of forest clearing (Whitney et al., 2019), but it may provide a guide to estimating the extent of disturbance. Arboreal elements comprise 90% of the modern pollen assemblages of the last 30 years, where land clearance is known to affect 20% of the landscape (Figure 2c–f). When arboreal percentages decrease to 75% of the pollen assemblage, it suggests land clearance may have increased a similar amount, or up to 35% of the area around the lake. While this is a very speculative number, it is safe to say that the combined pollen and phytolith data suggest that the peak of clearance at c. 950 cal. year BP was substantially larger than that of today, and palms were likely disproportionately removed (Figures 3 and 5).

Herbaceous and grasses in the pollen and phytolith record suggest the landscape around Lake Kumpak^a in the earlier period of disturbance from 2150 to 1430 cal. year BP was slightly more open than it was today (c. 20%–30% openness), though not as open as it was between 1070 and 680 cal. year BP (Figures 3 and 5). Maize cultivation was found in both the pollen and phytolith records, indicating local cultivation (Jarosz et al., 2003; Piperno, 2006a; Raynor, Ogden, & Hayes, 1972), and palms were significantly less abundant than in today's landscape, suggesting the indigenous inhabitants exploited them.

At Kumpak^a, despite the evidence of multiple centuries of maize cultivation, remarkably little charcoal was recovered from the sediment (Figures 3 and 5). Between 1070 and 680 cal. year BP charcoal fragments were only found in one sample, occurring at the very end of the disturbance period. Fire was also rare in the earlier period of disturbance, from 2150 to 1430 cal. year BP, with similar amounts

of forest taxa as the modern forests (Figure 5). Charcoal abundances at Lake Kumpak^a were orders of magnitude less than in other Amazonian lakes containing similar evidence of maize cultivation, for example, Lakes Ayauchⁱ, Sauce and Gentry (Supporting Information: Discussion; Bush et al., 2016; Bush, Silman, & Listopad, 2007; McMichael, Bush, et al., 2012; McMichael, Correa-Metrio, et al., 2012). Lake Ayauchⁱ, just 25 km away from Kumpak^a, was occupied for over 6,000 years with maize cultivation and long-term fire use, suggesting that slash-and-burn agriculture was used to manage the landscape (Bush & Colinvaux, 1988; McMichael, Bush, et al., 2012; McMichael, Correa-Metrio, et al., 2012; Piperno, 1990). Natural fires are almost non-existent in western Amazonia, as the wet conditions of the forests limit the spread of fire, and findings of charcoal fragments in palaeoecological records have repeatedly been linked with human land use (Aragao et al., 2008; Bush et al., 2007, 2016; Cochrane, 2009; Cochrane & Schulze, 1999; Kelly et al., 2018; McMichael, Correa-Metrio, et al., 2012; Nepstad et al., 2004; Urrego et al., 2013).

Fire may not have been an important management tool at Lake Kumpak^a. Charcoal was almost uniquely associated with maize (Figures 3 and 5), but the paucity of samples containing charcoal, and the low amounts of charcoal found in those samples, suggest that the cultivation around Lake Kumpak^a was not reliant on fire. One possibility was that rather than using slash-and-burn cultivation, the inhabitants of Kumpak^a may have been using slash-and-mulch (Joslin et al., 2011). This technique helps to retain nutrients volatilised during burning, and limits soil compaction, which reduces erosion from a denuded forest surface (Hölscher, Möller, Denich, & Fölster, 1996; Jordan, 1985). Mulching reduces weed growth while providing a slower, more sustained nutrient release than burning, and runs less risk of carbon ignition and soil degradation than slash-and-burn (Arroyo-Kalin, 2012; Joslin et al., 2011; van Vliet, Adams, Vieira, & Mertz, 2013). The fertility of the soils around the lake is not known, but if the origin of the lake is a volcanic maar, the soils may be more fertile than typical of Amazonia (Rostain, 2012). The Lake Kumpak^a data appear to be the first empirical evidence for the pre-Hispanic use of slash and mulch in western Amazonia.

5.2 | Disturbance and recovery

The composition of pollen from the modern disturbance period falls within the variability of past disturbances, and shares characteristics with both the disturbance ending at 1430 cal. year BP and 680 cal. year BP (Figure 5). Our pollen and phytolith data, however, suggest that modern human disturbance between 10 and –10 cal. year BP (AD 1940–1960), and the subsequent modern occupation, created ecologically different conditions from those that occurred in the past (Figures 4 and 5). As with past cultivation periods, *Iriarteia* and most other arboreal forest elements decline abruptly while disturbance taxa such as *Cecropia*, *Trema*, Solanaceae and Poaceae increase in abundance. During the modern disturbance, however, none of the herb taxa (e.g. Asteraceae, Piperaceae and *Acalypha*) increased in

percentages as they did during and after past disturbances. The differences between the modern disturbance period and past disturbances are probably caused by the increased reliance on fire in modern times compared with the past (Figures 3 and 4), and are consistent with expectations of slash-and-burn agriculture (Arroyo-Kalin, 2012; van Vliet et al., 2013).

Though some of the patterns of early succession are similar between the two past disturbance events, there are differences in the longer-term recovery patterns. For example, within 100 years of the cessation of maize cultivation, *Ficus*, a longer-lived pioneer genus, increased in abundance following the more intense disturbance ending at 680 cal. year BP, but not the one ending at 1430 cal. year BP (Figure 3; Figure S4). Myrtaceae increase within 100 years after the cessation of both disturbances, but the increase was much larger in the more intense disturbance period. Within 200 years following the more intense disturbance ending at 680 cal. year BP, taxa representative of mid-successional forests, such as *Dalbergia*, *Pera* and *Vochysia* became more abundant in the landscape (Figure 3). These increases did not occur in the less intense disturbance ending at 1430 cal. year BP. Part of the succession differences between these two disturbance events is likely related to the differing disturbance intensities. The total duration of the recovery period is much shorter with the disturbance ending at 1430 cal. year BP compared with the disturbance ending at 680 cal. year BP (Figures 3, 5 and 6).

5.3 | Ecological legacies

The predominant idea among archaeologists regarding ecological legacies is that useful species were deliberately enriched or depleted

in the pre-Columbian era, and that those altered abundances have persisted until the modern era (Ferreira et al., 2019; Levis et al., 2012, 2017; Figure 1). Under this scenario, useful or domesticated species in the Lake Kumpak³ sediment record should have flourished during the peak of maize cultivation and show persistently elevated abundances even after the cessation of cultivation (direct and persistent enrichment; Figure 1a). Our record does not support this contention as no useful taxa (i.e. Lecythidaceae, *Theobroma*, *Mauritia*, etc.) showed such a permanent pattern of enrichment. We also saw no evidence of persistent depletion, as the taxa with depleted populations, that is, *Iriartea*, recovered (Figure 6). Instead, our data show that while pre-Columbian activities can alter recovery trajectories for hundreds of years following the cessation of a disturbance, the trajectories do not include evidence of persistent enrichment or depletion (Figure 6).

Though many taxa are either too rare for a pattern to be reliably detected or simply show no significant response to land use change (e.g. *Mauritia*), we identify 14 taxa as showing a positive population response to the phases of disturbance and recovery. Taxa with the highest abundances during maize cultivation were as follows: *Acalypha*, Asteraceae, *Cecropia*, Combretaceae, *Iresine*, *Lonchocarpus*, Malvaceae, Piperaceae, Poaceae, *Saurauia*, Solanaceae, *Tontelea*, *Trema* and *Z. mays* (see Figure 6 for representative responses of *Acalypha* and *Cecropia*). Among these taxa Malvaceae, *Tontelea* and *Zea* (Clement et al., 2015) could be useful species and therefore the product of direct enrichment, whereas the others are most likely to have been indirect enrichments. Some of these are known to be early successional taxa (e.g. *Cecropia*, *Trema*, *Acalypha*, Asteraceae, Piperaceae) that are non-persistent and decrease shortly after cultivation ends (Figures 3 and 6). *Ficus* and some mid-successional

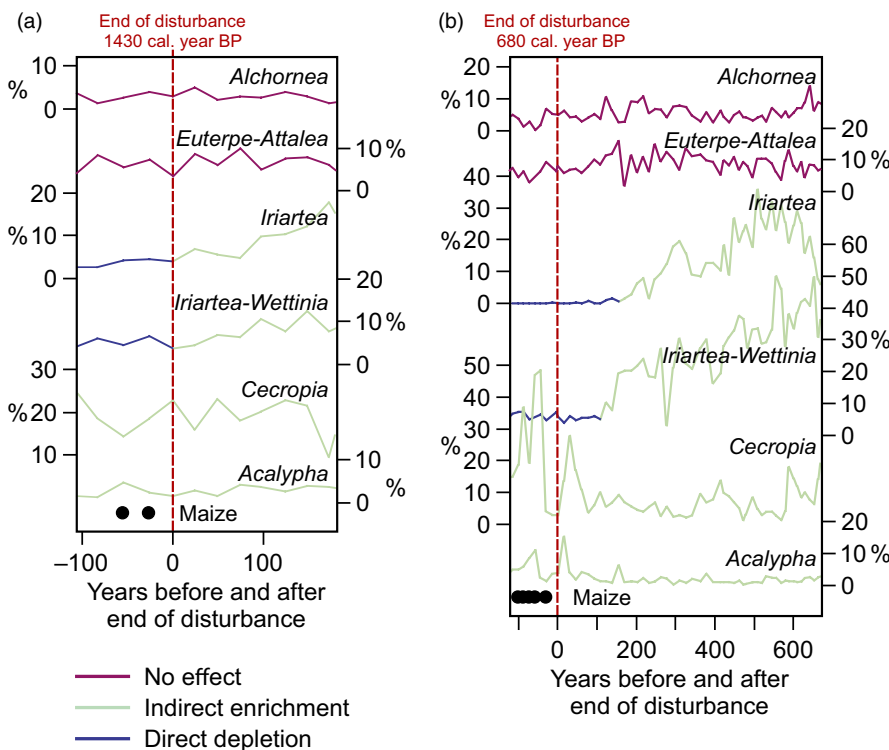


FIGURE 6 Detailed views of the last 100 years of disturbance and post-disturbance successional trajectories (recovery periods) of representative taxa at Lake Kumpak³, Ecuador (Figure S4). Panel (a) the disturbance event that ended at 1430 cal. year BP; panel (b) the disturbance event that ended at 680 cal. year BP

taxa showed post-occupation increases, followed by declines about 100 years into the succession (Figures 3 and 6; Figure S4). Here, we classify these as indirect, non-persistent ecological legacies (Figures 1a and 6; Figure S4).

Iriartea deltoidea is one of the commonest trees of western Amazonia (ter Steege et al., 2013, 2020), and has consistently shown a negative response to human activity in palaeoecological records (Figure 4; Bush & McMichael, 2016; Heijink et al., 2020). At Lake Kumpak^a, the periods of maize cultivation coincided with the loss of *Iriartea*, which is to be expected, as it would have been harvested for timber (Supporting Information: Discussion; Bernal et al., 2011; Clark et al., 1995; Zambrana et al., 2007). A century or more after the depletions of *Iriartea* populations ended, they recovered at Lake Kumpak^a. The populations also recovered to levels that exceeded those in the pre-cultivation period (Figures 3 and 6) and its abundance prior of the last 5,200 years (Liu & Colinvaux, 1988). We classify this population expansion as an indirect persistent enrichment that terminates with another direct depletion in near-modern times.

Our observations fit with the known autecology of *Iriartea* in that it is known to be a mid-successional species that can grow at high stem densities in floodplain forests subject to long-term disturbance by rivers (Balslev, Luteyn, Ollgaard, & Holm-Nielsen, 1987; Pitman et al., 2001). It seems unlikely that the increases seen in the Lake Kumpak^a record resulted from *Iriartea* being cultivated for remote usage, as transporting trunks the 3 km to the nearest river would have been problematic. Far more likely is that *Iriartea* regrew naturally as an early-mid successional species, and that its surge in abundance c. 200 years after cultivation ended was the synergistic effect of regional increased precipitation levels (van Breukelen, Vonhof, Hellstrom, Wester, & Kroon, 2008) and the release from human exploitation. These surges in abundance may have also been facilitated by changes in the soil, drainage or soil erosion caused by occasional fire and cultivation. *Iriartea* maintained high populations for >500 years after abandonment, that is, several tree generations (Pinard, 1993).

It is evident that generational time, individual longevity and tree size must be taken into account in estimating direct and indirect legacy effects. For example, a large, long-lived, tree such as *Bertholletia excelsior* (Brazil nut) or a clonal individual such as *B. gasipaes* (peach palm) could exhibit direct legacy effects, as it could be the same individual that was tended prior to European arrival. Conversely, short-lived species such as *Theobroma cacao* (cocoa), *Tontelea* (edible fruits) or *Inga edulis* (ice-cream bean) will re-sort their abundances through multiple generations, and without human intervention are likely to revert to lower abundances (Figures 4–6; Whitney et al., 2014). Consequently, short-lived species or earlier successional species are far less likely to show a direct linkage to pre-Columbian forest than late succession, long-lived species, and any apparent enrichment in those taxa is more likely to reflect subsequent disturbances, such as those that occurred during the Amazonian rubber boom of c. 1850–1920 (McMichael, Feeley, et al., 2017; McMichael, Matthews-Bird, Farfan-Rios, & Feeley, 2017).

The successional dynamics and lack of persistent ecological legacies at Lake Kumpak^a show that modern abundances of useful species should not be used to infer past human activity. High abundances of useful species are found in forests that contain no evidence of past human impact (Bodin et al., 2020). Natural floodplain and gap succession are all that are required to account for the great majority of *Iriartea* occurrences (Pitman et al., 2001). The ability of seeds to disperse also plays a large role in the relative abundances of many tropical forest plants. For example, local palm abundances may decrease if seed dispersers are lost, but increase if, despite poor seed dispersal, seed predators are also lost (Wright et al., 2000). Hunting and deforestation that occurred from the time of the early Jesuit missions in the 1600s, through the Amazonian rubber boom of AD 1850–1920, to the modern era, are all likely to have shaped the relative abundances of many Amazonian plants. Indeed, these more recent activities are more likely to have legacy effects on the forest than those occurring before European arrival.

6 | CONCLUSIONS

We were able to document successional dynamics and potential for ecological legacies for hundreds of years following the cessation of a disturbance from Lake Kumpak^a in lowland Amazonian Ecuador, at time intervals of 5–50 years. Our data contained three different disturbance periods over the last 2,415 years, including the period of modern disturbance (Figure 1c–f). The disturbances all varied in intensities and durations. The modern disturbance period, which contained the highest fire frequency, was compositionally different from the two past disturbance periods, which contained little to no fire. The Lake Kumpak^a record suggests that the intensity of disturbance, the duration of the disturbance and the presence or absence of fire in the disturbance regime affect the subsequent successional trajectories and potential ecological legacies.

We found evidence of non-persistent enrichment and depletions of taxa, but those legacies were not present in the modern-day forest. It takes hundreds of years for a complex tropical forest to regain its pre-disturbance composition, in which time early and mid-successional species become rarer. Many taxa considered to be useful species are best suited to early successional settings and would be outcompeted during succession. We found no evidence of persistent enrichment or depletion of taxa (i.e. direct legacy effects) in a setting that contained pre-Columbian cultivation until c. 680 cal. BP. These findings underscore the inaccuracy and uncertainty of using modern plant population densities to infer past human management and ecological legacies without corresponding direct empirical data. Our data also reinforce the potential power of drawing upon highly resolved multiproxy data palaeoecological datasets to address important questions in neoecology.

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AUTHORS' CONTRIBUTIONS

C.M.Å., M.F.R., S.N.H., M.P., Jo.V., D.N. and Ja.V. performed the research; C.M.Å., C.N.H.M. and M.B.B. analysed the data; C.M.Å., C.N.H.M. and M.B.B. wrote the paper, with input from all authors; M.B.B. and C.N.H.M. designed the research project; C.M.Å., C.N.H.M., D.N. and M.B.B. conducted the field work.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13501>.

DATA AVAILABILITY STATEMENT

The datasets generated from this study are available through the Dryad Digital Repository <https://doi.org/10.5061/dryad.xksn02vd8> (Åkesson et al., 2020) and through the NEOTOMA Paleocological Database (<https://neotomadb.org/>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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