Ecological legacies of past fire and human activity in a Panamanian forest


DOI
10.1002/ppp3.10344

Publication date
2023

Document Version
Final published version

Published in
Plants, People, Planet

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Societal Impact Statement
Tropical forests provide global ecosystem services and harbor much of Earth’s terrestrial biodiversity, but the mechanisms driving the patterns of biodiversity remain uncertain. Palms are one of the most abundant and most widely used plant groups, particularly in the Neotropics. Our data highlight how both direct and indirect human influence that occurred decades to hundreds of years ago can affect the abundances of palm species in modern tropical forests. Our results highlight that biodiversity is dynamic, and changes through time, and that human activities can affect species composition for centuries in tropical forests.

Summary
- Human activities over the past decades and centuries, including fire, cultivation, and forest opening, may have left ecological legacies that persist in modern tropical forests, particularly among palms. We investigated whether past human activities affected modern palm abundances in a well-studied plot located in a tropical semievergreen forest of Panama.
- We analyzed soil cores for charcoal to reconstruct past fire events and phytoliths to reconstruct past vegetation changes. We dated as many charcoal fragments as possible to place a temporal framework on past fire events.
- Our analysis documented widespread fires that occurred 600–900 years ago across the plot. Oenocarpus mapora increased in abundance as a result of these fires, though other palms did not. A subsequent increase in O. mapora occurred later in the relative absence of fire and was likely due to game hunting during the construction of the Panama Canal.
- Our results showed that the enrichment of O. mapora was determined by disturbance characteristics (e.g., timing, type, and intensity), but the persistence of increased abundances was likely determined by traits (life history characteristics). These data highlight the complexity of human–environment interactions and how they can persist for centuries in settings with long-lived trees such as tropical forests. These data highlight the importance of adding a historical context to further understand modern ecological patterns and processes.
1 | INTRODUCTION

Disturbance regimes play a role in structuring ecosystems, often leaving biological or ecological legacies that can persist for decades to centuries (Franklin et al., 2000; Johnstone et al., 2016; Turner, 2010). In Neotropical systems, it has been suggested that disturbances in the form of past human activity, particularly during the pre-Columbian era (i.e., before European arrival to the Americas in AD 1492), may have altered species abundances and left ecological legacies on modern forest composition (Clement et al., 2015; Levis et al., 2017; Ross & Rangel, 2011). Fire rarely ignites and spreads without human intervention in the Neotropics because of high precipitation and humidity, which has been used to clear forests for millennia (Bush et al., 2008). Fire transforms tropical ecosystems, as most plants are not evolutionarily adapted to be fire tolerant (Uhl & Kauffman, 1990). A single burn can cause significant species turnover, and multiple burns can create a total shift in species (Barlow & Peres, 2008).

People were living in Neotropical forests and using fire for at least the last 13,000 years (Gosling et al., 2021; Lombardo et al., 2020; Piperno et al., 1990; Roosevelt et al., 1996). Hunting likely contributed to the extinction of Pleistocene megafauna ca. 13,000 years ago in Central America and the Peruvian Andes (Rozas-Davila et al., 2021, 2016). Plant cultivation in the Neotropics began in the early Holocene: people were cultivating a variety of domesticated seeds and crops by 7000 years ago (Piperno, 1998, 2011; Piperno et al., 1985, 1991; Piperno & Flannery, 2001; Piperno & Holst, 1998; Piperno & Jones, 2003). Locations where early cultivation and domestication were occurring were likely heavily deforested between 7000 and 5000 cal BP (Piperno et al., 1991). Human populations likely grew and expanded from then until reaching its peak over the last 1000–2000 years (Goldberg et al., 2016; McMichael & Bush, 2019; Piperno, 2011).

Diseases and warfare brought on by European arrival ca. 500 years ago significantly reduced indigenous populations across the Neotropics by up to 95% (Dobyns, 1966). When the occupied or managed lands were then abandoned, forests began a period of regrowth. Human impacts and activities, however, continued in many regions where Europeans colonized. As tropical trees can live for hundreds of years (Chambers et al., 1998), forest succession can take millennia. Thus, forests that were abandoned and began the process of recovery at the time of European arrival may still be in a mid-successional state.

One of the likely ecological legacies of past human activities includes altering the abundances of palms, one of the most common and widely used plant groups in the tropics (Bernal et al., 2011; McMichael, 2021; Muscarella et al., 2020). The canopy palm, *Iriartea deltoidea*, provides an example of the potential ecological legacies on modern abundances. *I. deltoidea* is the most common tree in much of western Amazonia (Pitman et al., 2001) and is found all the way up to the lowland forests of Costa Rica (Clark et al., 1995). *I. deltoidea*, however, is virtually absent from lowland Panama (Condit et al., 2002). It is a widely used tree in settings where it is found (Bernal et al., 2011; Henderson et al., 1997). In the forests of Costa Rica, past human harvesting and removal may have led to the absence of *I. deltoidea* in all size classes greater than 1 m in height in the modern landscape (Clark et al., 1995). It remains unknown, however, as to whether the harvesting was during the pre-Columbian period or more recently during the postcolonial period, or both (Clark et al., 1995). It is also unknown whether its absence from Panama is the result of past human depletion. That the loss of *I. deltoidea* in Costa Rica may be comparatively recent is mirrored by studies in the western Amazon. Human activities were correlated with decreased abundances of *I. deltoidea*, but the population recovered about 150–200 years after abandonment (Åkesson et al., 2021; Bush & McMichael, 2016).

This example highlights the complexity in predicting ecological legacies on modern palm abundances. While the type of disturbance (e.g., enrichment/depletion, fire, deforestation, and cultivation) affects the long-term changes in vegetation, so does the frequency and intensity of past disturbances and the timing of the most recent disturbance (Åkesson et al., 2021; McMichael, 2021). Hunting may also leave ecological legacies by altering the abundance of seed dispersers or seed predators, particularly if it occurs for sustained periods (Bush et al., 2015).

The attributes that confer usefulness among tropical species are often its provision of fruit, construction timber, thatch, or medicinal properties; each of these uses corresponds with ecological traits. For example, palms with larger size and higher trunk densities are more commonly used for construction, fruit size is a strong predictor of desirability to humans, and only the largest and strongest leaves are used for thatch (Bernal et al., 2011; Guimarães et al., 2008). It is possible that plants harvested extensively for one-time uses, such as construction or for heart of palm, are likely to have been made rarer by indigenous use (depleted), whereas those used iteratively to provide fruit and thatch would have become more common (enriched) (McMichael, 2021). Traits may also relate to persistence (or lack thereof) of an ecological legacy, especially those related to post-disturbance success.

Phytoliths provide a way to assess ecological legacies and the extent to which past human activities determine modern patterns of palm abundances. Phytoliths are silica-based microfossils that are becoming increasingly used to reconstruct past vegetation change in settings where pollen typically oxidizes and degrades, such as in many terrestrial soils (Piperno, 2006). Phytoliths are particularly sensitive to detecting old growth forests, forest openings, cultivation, and changes in palm abundances, and recent work has improved the capabilities of distinguishing various palm genera and species (Huisman et al., 2018; Witteveen et al., 2022). These characteristics make charcoal and...
phytolith analysis collected from soils underlying modern forest plots a useful approach to determining past changes in palm abundances and whether the changes reflect past human activities (e.g., Heijink et al., 2020; Piperno et al., 2021). Here, we ask whether the occurrence or timing of past fire, cultivation, or forest openings (here considered disturbances) correspond with signals of enrichment or depletion of palm species from a well-studied forest plot in Panama. We also assess long-term changes in palm abundances and discuss the role of plant traits (life history characteristics) in structuring the persistence of ecological legacies.

2 | METHODS

2.1 | Site description and field sampling

The Gigante Peninsula (Figure 1a) is a semievergreen tropical forest system with high precipitation levels (average 2600 mm per year) (Condit et al., 1996, 2000; Windsor, 1990). Ninety percent of annual rainfall occurs during the wet season between April and mid-December. Humidity ranges from 62% to 95% in dry and wet seasons, and temperatures range between 22 and 35°C (Windsor, 1990). The soils of the Gigante Peninsula are considered relatively fertile for lowland tropical forests, and the area is densely forested (Wright et al., 2011).

In 1997, a 38.4-ha forest dynamics plot was established on the Gigante Peninsula (−79.85342, 9.102242; Figure 1b) by the Smithsonian Tropical Research Institute. The plot is located approximately 5 km south of the 50-ha forest dynamics plot on Barro Colorado Island (BCI) (Figure 1a). At the Gigante plot, every freestanding tree of more than 20 cm diameter at breast height (DBH) has been recorded, with recurring censuses in 1998, 1999, 2000, 2001, 2003, 2008, 2013, and 2018. All trees ≥10 cm diameter at breast height (DBH) have been mapped and identified in 36 40 m² subplots (totaling 26.6 ha) within the forest dynamics plot. The subplots have all trees measured >1 cm DBH and have also been used for a long-term fertilization experiment (Wright et al., 2011; Yao et al., 2018). No fires have occurred at the Gigante or BCI forest plots since monitoring began. The elevation of the Gigante forest plot ranges between 50 and 90 m above sea level (m.a.s.l). Prior to construction of the Panama Canal from 1881 to 1914, Gigante and BCI were hilltops connected via marshy lowlands; the flooding of Lake Gatun to form the canal in 1913 isolated the hilltops.

Within the Gigante forest plot, 42 soil cores were collected at either 5 or 10 cm depth intervals up to a total of 80 cm, or as far as the water ground level allowed (Figure 1b and Dataset S1). All samples from the 42 cores were analyzed for charcoal to obtain fire history (N = 361; Figure 1b). Samples from eight of the cores (Figure 1b, red circles) were also analyzed for phytoliths to obtain vegetation history (N = 75). Within a 5-m radius of each core site, we also collected 7–10 pinch samples from the soil surface. The pinch samples were combined into one surface sample per core site (N = 8) and used to represent the modern vegetation. One of the cores used for phytolith analyses (G40) fell into a fertilization experiment subplot.

2.2 | Laboratory analysis

Charcoal analysis was performed on 4–19 cm³ of soil that was volumetrically measured from each of the core samples and from surface samples. Each sample was boiled for 15 min in 3% hydrogen peroxide (H₂O₂) and sieved at 500 μm. Charcoal was identified from the remaining material using an Axioshot stereoscope, and all fragments recovered were photographed. We used ImageJ software (Rasband, 2005) to calculate the surface area (mm²) of each charcoal fragment. The surface area was then converted to volume (mm³) (Weng, 2005), and
measurements were standardized between samples by dividing the charcoal volume by the volume of the initial soil sample (mm³/cm³).

For phytolith analysis, H₂O₂, HCl, and KMnO₄ were used to remove organic material, carbonates, and humic acids, respectively. Bromoform (CH₂Br₃) with a specific gravity of 2.3 g/cm³ was added to the remaining soils to separate the phytoliths and microspheres from the remaining soil material. The extracts were mounted in Naphrax, and phytoliths were identified using a Zeiss Axio Scope.A1 microscope with differential interference contrast (DIC) at 630–1000× magnification. Phytoliths were identified using published reference material (Huisman et al., 2018; Morcote-Ríos et al., 2016; Piperno, 2006; Piperno & McMichael, 2020) and reference material in the University of Amsterdam Palaeoecology Laboratory. At least 250 phytoliths were counted for each sample.

2.3 | Data analysis

We submitted charcoal fragments (>1 mg) to DirectAMS (Seattle, Washington, USA) for ¹⁴C AMS radiocarbon dating (N = 14). The “Bchron” package (Parnell, 2016) for R (R Development Core Team, 2013) was used to calibrate the radiocarbon dates and to generate cumulative probabilities of fire events within the plot. All dates were calibrated using the IntCal20 calibration curve (Reimer et al., 2020) and reported at the 2-sigma confidence level. The ages of modern dates were calculated using the percent modern carbon amounts in the “IntCal” package for R (Blaauw, 2021). Using the charcoal abundance data, we calculated (i) the total charcoal volume (mm³/cm³) of each sample, (ii) the summed charcoal volume of all samples (depth intervals) within each core, and (iii) the total charcoal volume per depth interval summed across all cores.

For the phytolith analysis, we calculated the relative percentage of all morphotypes counted within each sample (silt fractions with unfractonated sand) (Piperno, 2006). We also assessed the phytolith morphotypes produced by each of the palm species occurring in the modern botanical surveys at the Gigante forest plot to aid in the interpretation of changes in palm abundances through time. We performed detrended correspondence analysis (DCA) on the phytolith percentage data to look for patterns of vegetation (dis)similarity within and between depth intervals and cores. We also calculated the trends of change (% in surface sample – % in basal sample; TOC) and magnitude of change (maximum % – minimum %; MOC) of phytolith types within each core (McMichael et al., 2015). Basal samples were between 70 and 80 cm depth.

3 | RESULTS

3.1 | Fire history

We retrieved 14 charcoal fragments from the soils collected at the Gigante forest plot that were large enough for ¹⁴C AMS dating (Table S1 and Figure 2). The dated charcoal fragments indicated that fires occurred across multiple areas of the plot from 1300 to 650 calibrated years before present (hereafter cal yr BP), which is the equivalent of AD 650–1300. Older fires also occurred in local areas in the northernmost and southernmost areas of the plot around 2300, 2800, and 9000 cal yr BP (Table S1 and Figure 2). One date close to the center of the plot (core G44) was modern in age, and based on the percent modern carbon values, likely occurred around AD 1976 (Table S1 and Figure 2). Abundances of charcoal within the samples ranged from 0 to 13 mm³/cm³, though reached 31 mm³/cm³ in the surface sample of core G44 (Figures 2 and S1a). Charcoal was most abundant in the

![FIGURE 2](image-url) Charcoal data from the forest plot in Gigante, Panama: charcoal abundances and the most probable ¹⁴C AMS (accelerator mass spectrometry) age of charcoal fragments for (a) surface samples, (b) soil core samples from 0 to 30 cm depth, and (c) soil core samples from 30 to 80 cm depth. Maps are shown in Universal Transverse Mercator (UTM) projected coordinate system for Zone 17 using NAD27 datum (x axis = easting, y axis = northing). A Shuttle Radar Topography Mission (SRTM)-derived digital elevation model (DEM) is displayed over the extent of the study site, with elevations ranging between 50 and 90 m above sea level.
upper 10 cm of soil, and abundances decreased below 30 cm
(Figure S1b). Charcoal abundances were highest in the central regions
of the plot where the recurrent fire ages of 650–950 cal yr BP were
documented (Figures 2 and S1a).

3.2 | Vegetation change at Gigante

We identified 44 total phytolith morphotypes within the eight soil
cores, including three arboreal, 13 palm, and 26 grass morphotypes
(Dataset S1). Silt size rugose and decorated spheroid (both produced
by arboreal taxa) and palm phytoliths dominated the assemblages
(Figure 3). Grass phytoliths (Poaceae) were present in 80 out of 83
samples (Figure 3). The total grass percentages (Figure 3) were com-
posed of disturbance grasses (e.g., Panicoideae) and understory
grasses (e.g., Bambusoideae) (Figure S2). Heliconia phytoliths, which
indicate forest openings, were found in 29 out of 83 samples
(Figure 3). The percentages of total grass phytoliths typically ranged
from 0% to 10%, but cores G1, G6, G15, G23, and G40 contained
>10% between 20 and 60 cm depth (Figure 3). Trend-of-change met-
rics for grass phytoliths were less than 5% in five of eight cores,
though when it exceeded 5%, it was always in the negative direction
(Figure 4). There were no phytoliths from cultivars (e.g., maize, squash,
and manioc) identified in any of the samples. Charcoal was present in
all the cores analyzed for phytoliths except core G4 (Figure 3).

The increase in the relative abundance of palm phytoliths from the
bottom (deeper levels) to the top (upper levels) was the predominant sig-
nal of vegetation change (Figure 3). The DCA, which assesses (dis)similar-
ity of phytolith assemblages between all samples, showed the
abundances of globular echinate (GE) phytoliths was the major driver of
variation among samples (DCA Axis 1; Figure S2). GE phytoliths were
the most abundant palm morphotype in the surface samples and depths
from 0 to 20 cm in the cores (Figure 4), which are produced by Attalea,
Elaeis, Synechanthus, and Oenocarpus mapora in the Gigante forest plot
(Table 1). O. mapora was the most common palm found in the plot
(Table 1). Samples containing increased abundances of GE phytoliths also
contained increased abundances of open-forest and disturbance indica-
tors, such as Heliconia phytoliths or grasses from the Panicoideae

FIGURE 3  Stratigraphic diagram of phytolith and charcoal abundances found in the eight soil cores analyzed from the Gigante forest plot in
Panama. Morphotypes shown in green represent arboreal phytoliths, purple represents palm phytoliths, and orange represents the total grass
phytoliths. The presence of Heliconia phytoliths (an open forest indicator) and charcoal (mm$^3$/cm$^3$) are also shown. GE = globular echinate
phytolith morphotypes. Conical V1 = conical variant 1 phytoliths as defined by Huisman et al. [2018].
subfamily (bilobates, rondels, crosses) (Figures 3 and S2, Dataset S1). The trend of change values (surface % – basal %) for GE phytoliths ranged from 20% to 61%, and the magnitude of change values (maximum % – minimum %) within the cores ranged from 21% to 61% (Figure 4).

Conical variant 1 (C1) morphotypes, which are produced by Bactris, Astrocaryum, and Socratea exorrhiza (Table 1), were also abundant in the soil cores (Figure 3). The conical morphotypes were less abundant in the surface samples compared with core samples with depths from 0 to 20 cm (Figure 3). The DCA also indicated that samples with increased percentages of conical palm phytoliths were associated primarily with closed forest phytolith types and lacked open forest (pannicoid) grasses and Heliconia, but commonly contained saddle, rectangular, or trapezoidal phytoliths primarily produced by closed forest (understory) grasses (Figure S2 and Dataset S1) (Morcote-Ríos et al., 2015; Piperno, 2006). Trends of change of C1 phytoliths ranged from –3% to 6%, and the magnitude of change values ranged from 2% to 9% (Figure 4).

The increases in GE phytoliths from the bottom to the top of the core were accompanied by large decreases in the percentages of rugose sphere phytoliths (Figures 3 and 4). On Gigante, rugose spheres are produced by a number of arboreal genera including Acalypha, Aspidosperma, Hirtella, Licania, Protium, Pseudobombax, and Sorocea (Piperno, 2006; Piperno & McMichael, 2020). Decorated spheres, produced by genera such as Aspidosperma, Protium, Pseudobombax, and Sorocea on Gigante, had magnitude of change values >10% in most cores (Figure 4). The variability of change of the decorated spheres, however, had no consistent direction. Their trend of change was less than 5% (in either the positive or the negative direction) for five of the eight cores (Figure 4). When the trend of change values exceeded 5%, it was always in the positive direction.

4 | DISCUSSION

4.1 | The human history

The oldest charcoal recovered from the Gigante forest plot dated to ca. 9000 years ago (Figure 2 and Table S1), which was a time when Panama was wetter than modern (Bush et al., 1992), and is likely to represent human-ignited fire. Evidence of early Holocene human activity is found in Panama at a number of sites (Dickau et al., 2007; Ranere & Cooke, 2021). Sites with ceramics and evidence of slash and burn cultivation dating to ca. 5000 yr BP have been discovered in the Chagres region (Griggs, 2005; Iizuka, 2017; Piperno & McMichael, 1985), only 11 km from the Gigante forest plot. The hilltop of what is now BCI, where the Smithsonian Tropical Research Institute has a 50-ha forest plot was established (Figure 1a), is shown to have been occupied between 1700 and 400 years ago (Piperno, in press). Charcoal and phytolith studies of terrestrial soils across the BCI forest plot show that although charcoal was uncommon, prehistoric inhabitants cleared

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<tr>
<th>Genus</th>
<th>N</th>
<th>GE var. 1</th>
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<th>GE var. 4</th>
<th>GEE var. 1</th>
<th>GEE var. 2</th>
<th>RE var. 1</th>
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<td>Attalea**</td>
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Notes: The number of species occurring in the plot is listed below each genus name, and the number of individuals of all species within the genus is listed under column N. Phytolith classifications denoted with * are from Runge 1999, and with ** are from phytolith descriptions and images of the same subfamily as the genus listed in the PhytCoreDB (http://www.phytcore.org/phytolith/). Non-starred genera were compared with reference material based at the University of Amsterdam. The variant numbers for each morphotype correspond with those published in (Huisman et al., 2018) and (Witteveen et al., 2022).

Abbreviations: C, conical phytolith morphotypes; GE, globular echinate phytolith morphotypes; RE, reniform morphotypes.
forests in some areas during that time for their living spaces, while little-altering other areas (Piperno, in press).

Prior to the flooding of Lake Gatun and the construction of the Panama Canal (1913), the BCI and Gigante forest plots (Figure 1a) would have been in one contiguous landscape. Eight out of the 14 fire ages at Gigante occurred from 600 to 900 years ago, as did five out of seven obtained from the BCI forest plot, located ca. 5 km away (Figure 1a) (Piperno, 1990, in press). We dated all the individual charcoal fragments found in the soils that were large enough for $^{14}$C dating, but found only one fragment that was modern, and none between 600 cal yr BP and modern (Table S1). Given the absence of evidence, we consider it unlikely that widespread or recurrent fire occurred after 600 cal yr BP in the Gigante forest plot. Within the BCI 50-ha forest plot, archaeological surveys have uncovered pottery and debitage from stone tool manufacture, and paleoecological data have documented fire and forest clearing (Piperno, 1990). We did not find any direct evidence of cultivation or pottery, but our phytolith results show that forests were also being burned and opened at Gigante (Figure 3). The data from both locations suggest parts of the previously unified landscape of the Barro Colorado Nature Monument experienced significant disturbances during the pre-Columbian era, predominantly 900–600 years ago.

Hunting occurred across the Gigante Peninsula, likely in pre-Columbian times, but also in the historic era from at least the period of canal building (AD 1881–1914) until it became a protected area in AD 1979. As late as the 1970s, hunters commonly set campfires and smoked bush meat in the area (Wright, S.J., personal communication). No sign of recent fire was documented in the original botanical surveys at the Gigante forest plot in AD 1981 (Wright, S.J., personal communication). Thus, the charcoal fragment dated to the 1970s (core G44, Table S1), which was retrieved from a surface sample that contained extremely high charcoal abundances (Figure 3), likely resulted from campfires or a bushsmoke smoking site and did not reflect a larger fire event that caused significant ecological damage or turnover.

4.2 Changes in palm abundances through time

It cannot be assumed that the phytoliths are the same age as a dated charcoal fragment from the same sample (Piperno, 2006; e.g., Piperno & Becker, 1996; Piperno et al., 2021). We cannot be certain as to when the documented increases in GE phytoliths began without direct dates on phytolith assemblages. The charcoal and phytolith data from Gigante, however, showed patterns that were repeated across all soil cores. Fire events and forest openings were recurrent and widespread (Figures 2 and 3), and the increases in GE phytoliths also occurred consistently across the plot (Figures 3 and 4).

It is thus likely that the increases of GE phytoliths in the soil cores collected across the Gigante forest plot occurred at least partially because of the repeated and widespread forest burning ca 900–600 years ago.

Of the nine identified palm genera (composing 13 species) occurring within the Gigante forest plot, *Oenocarpus*, *Synechanthus*, *Elaeis*, and *Attalea* produce GE phytoliths (Table 1). There are relatively few individuals of *Synechanthus* (17), *Elaeis* (7), and *Attalea* (3) in the plot. The seven individuals of *Elaeis oleifera* (Kunth) Cortés, a swamp habitat specialist (Legendre & Condit, 2019), are all found in the low-lying southwest corner of the plot. The changes in GE phytoliths are thus unlikely to represent changes in this species. *O. mapora*, however, comprises 68% of the total palm individuals in the plot (Table 1), is common across the Barro Colorado Nature Monument (Figure 1a) (Denslow & Guzman, 2000), and is not highly correlated with microtopography or habitat type (Svenning et al., 2006). Accordingly, we interpret the changes in globular echinate palm phytoliths in our soil cores to mainly represent changes in the abundances of *O. mapora* (Figure 5a) through time.

Disturbance regimes affect the distributions and abundances of *O. mapora*. Drought events have been shown to induce high rates of mortality of *O. mapora* on BCI (De Steven, 1989). Following the drought and mortality events, however, *O. mapora* exploited the canopy openings, and recruitment was more successful in disturbed forests than in non-disturbed old-growth forests (De Steven, 1989). Our DCA also showed that the samples containing elevated abundances in *O. mapora* phytoliths (GE phytoliths) also had elevated abundances of phytoliths indicative of open forests (e.g., panicoid and chloridoid grasses and *Heliconia*) compared with other samples (Figure S2). The documented post-disturbance recruitment success of *O. mapora* combined with its co-occurrence with other phytoliths indicative of canopy openings provides further evidence that the increases in their abundances occurred because of the widespread and recurrent fires ca. 600–900 years ago. *O. mapora* is also widely used by indigenous people in Panama (e.g., Balick, 1986; Dalle & Potvin, 2004; Henderson et al., 1997) and may have also been intentionally enriched (promoted) in the pre-Columbian era.

The soil surface samples contained much higher abundances of *Oenocarpus* (GE) phytoliths than even the samples found in the uppermost depths of the cores (Figures 3 and S2). This finding suggests that there is an additional and more recent driver of increases in *O. mapora* abundances that is not related to the fire-driven changes 600 or more years ago that are seen deeper in the cores. Hunting reduces seed predators and changes the seed dispersal patterns of many plant species, including palms (Galetti et al., 2013; Markl et al., 2012; Wright et al., 2000; Wyatt & Silman, 2004). Hunting and defaunation had a significant effect on *O. mapora* seed success in Central Panama, where hunting resulted in a 59% decrease of seed predation on the ground (Beckman & Muller-Landau, 2007). Hunting and other activities such as cutting trails or building camps during construction of the Panama Canal also created disturbance and mortality events among the trees, giving *Oenocarpus* additional possibilities to recruit and increase in abundance. These activities also occurred in the Gigante region after canal construction and until it became protected in AD 1979.

*Oenocarpus* individuals can potentially live for centuries (Richard Condit, personal communication), and it may take 50–100 years for
seedlings to reach adult status (>8 m in height) (De Steven, 1989). Given this, the adult O. mapora trees (>8 m height) in the Gigante forest plot are likely >100 years old and successfully recruited during the disturbances that occurred during and following canal building (Figure 5b). Following canal building, hunting pressure may have decreased and less individuals of O. mapora survived (Figure 5b). O. mapora recruitment has likely slowed significantly since protection in AD 1979 due to an increased number of seed predators coming back into the system (Figure 5b).

Besides O. mapora, S. exorrhiza is the second most abundant palm species at Gigante (Table 1). S. exorrhiza produces conical variant 1 (C1) phytoliths (Huisman et al., 2018; Witteveen et al., 2022). At Gigante, C1 phytoliths range from 3% to 10% in the surface samples (Figure 3) and likely represent S. exorrhiza abundances because of its relatively high abundance in the modern landscape. I. deltoidea, which also produces primarily C1 phytoliths (Huisman et al., 2018), is remarkably rare in lowland Panamanian forests (Condit et al., 1996) and absent in the modern Gigante plot. These data further suggest that the changes in C1 phytoliths through time represent changes in S. exorrhiza. The soil records indicate that S. exorrhiza abundances have generally increased through time, though with more spatial variability and lesser magnitude than O. mapora (Figure 4). It is possible, however, that the changes in C1 phytoliths occurred from fluctuating abundances of Socratea, Astrocaryum, and Bactris. The observed decline of C1 type within the top 20 cm of soil profiles could also reflect a decline in Iriartea due to direct depletion by people over the last decades to centuries, as Clark et al. (1995) have proposed in Costa Rican forests. The percentages of C1 phytoliths, however, were never as abundant at Gigante compared with locations where Iriartea is a dominant member of the modern vegetation assemblage (Heijink et al., 2020).

FIGURE 5 (a) Illustration of Oenocarpus mapora highlighting the traits that allow it to successfully recruit and persist in the landscape following disturbances. All illustrations were created by N. Witteveen. (b) The potential effect of past disturbances on modern O. mapora distributions on the Gigante peninsula in Panama. Based on growth rates and estimated lifespan of O. mapora, we assigned general categories of time to the frequency histogram of the height measurements of individuals in the Gigante forest plot. The frequency of smaller individuals is low, suggesting that the period of protection (AD 1979 to present) where hunting and other disturbances are absent, results in low recruitment levels.

4.3 | Plant traits as drivers of ecological legacies

Plant traits or life history characteristics play a role in structuring successional changes (Lasky et al., 2014) and thus may also affect ecological legacies. O. mapora has several traits that give it an advantage for long-term persistence in the landscape (Figure 5a), but further statistical testing would be needed to confirm whether traits can explain why some species persist and others do not. O. mapora thrives in light conditions and quickly colonizes canopy gaps, making it a dominant competitor following mortality events or disturbances that open the forest (De Steven, 1989). This characteristic lends itself to competitive dominance under a wide array of disturbance types and intensities. It also has higher 30-year survival rates than even the most long-lived trees on BCI (Richard Condit, personal communication). These characteristics, along with its long lifespan, are likely at least partially responsible for the ability of O. mapora to persist in the landscape over at least centennial timescales.

Clonal reproductive strategies have often been linked with competitive dominance (Janzen, 1976). Where seedlings survive, O. mapora forms clonal clumps (De Steven, 1989) (Figure 5a). The clonal clumps of O. mapora result in high leaf litter concentrations and low light levels that can alter the local seed bank (Farris-Lopez et al., 2004). These changes can decrease the establishment of small-seeded and shade-intolerant species, allowing O. mapora to outcompete other species (De Steven, 1989; Farris-Lopez et al., 2004) (Figure 5a). These processes create positive feedbacks of favorability for O. mapora establishment and persistence. Similar positive feedbacks occur in southwestern Amazonia with Guadua, a genus of bamboo that prefers light, successfully colonizes disturbed areas, physically overloads other species, and is clonal (Griscem & Ashton, 2003). The bamboo dominance in these forests has likely persisted for at least thousands of years (McMichael et al., 2013).
The phytolith data (Figure 3 and 4) and height distributions of modern *O. mapora* individuals (Figure 5b) suggest that past human activities occurring both during the prehistoric and historic periods have led to multiple waves of increases in abundances that have persisted into the modern landscape. These waves may have resulted directly through enrichment or indirectly through fire, hunting, and creating forest openings (Figure 3). Our results highlight that it is more than just the disturbance characteristics that determine the ecological legacies of past human activities. Traits are often correlated with usefulness (e.g., many large-seeded species are useful) and life history characteristics may determine the probability of long-term persistence (or depletion). The relative roles of disturbance characteristics, traits, and life history characteristics in determining the persistence and strength of long-term ecological legacies remain to be determined. There are likely variations among species, but patterns may exist between traits or life history characteristics.

**ACKNOWLEDGEMENTS**

We would like to thank Annemarie Philip at the University of Amsterdam for preparing phytolith samples, Nicole Ward for assistance with charcoal analysis, Thya van den Berg and Mayke Nieuwkerk for preliminary phytolith analyses, and Joe Wright and Rick Condit for logistics of fieldwork and insightful discussions on the trees of Gigante. CNHM would like to thank Smithsonian Tropical Research Institute for a short-term fellowship in 2010. CNHM, BMH, and NHW are funded by European Research Council Starting Grant (ERC StG 853394).

**CONFLICT OF INTEREST**

All authors have no conflicts of interest to declare.

**AUTHOR CONTRIBUTIONS**

CNHM conceived the ideas, collected the samples, supervised data analysis, participated in data analysis and figure generation, and wrote the manuscript. VV performed the phytolith analysis. BMH assisted with phytolith and charcoal analysis, analyzed data, and generated figures. NHW assisted with phytolith and charcoal analysis, analyzed data, and generated figures. DRP assisted in interpreting data and editing the manuscript. WDG assisted in editing the manuscript. MBB assisted in interpreting the data and editing the manuscript. All authors contributed to manuscript revisions.

**DATA AVAILABILITY STATEMENT**

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information
Additional supporting information can be found online in the Supporting Information section at the end of this article.