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Effects of Holocene climate change, volcanism and mass migration on the ecosystem of a small, dry island (Brava, Cabo Verde)

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Abstract

Aim: Palaeoecological data provide an essential long-term perspective of ecological change and its drivers in oceanic islands. However, analysing the effects of multi-scalar and potentially co-occurring disturbances is particularly challenging in dry islands. Here, we aim to identify the ecological consequences of the integrated impacts of a regional drying trend, volcanic eruptions and human mass migrations in a spatially constrained environment—a small, dry oceanic island in Macaronesia.

Location: Brava Island, Republic of Cabo Verde.

Taxa: Terrestrial vegetation and fungi.

Methods: We use palaeoecological analyses applied to a caldera soil profile that dates back to 9700 cal yr BP (calibrated years before the present). Analyses include pollen (vegetation history), non-pollen palynomorphs (changes in fern and fungal communities), grain-size distribution, loss-on-ignition and geochemistry (sedimentology and erosion regimes), microscopic tephra shards (volcanic ash deposition) and charcoal (fire regime).

Results: A regional drying trend after c. 4000 cal yr BP caused increased erosion but had limited immediate impacts on highland grassland vegetation. The expansion of fern-rich woody scrubland was contemporaneous with significant deposition of volcanic ash and erosion between 1800 and 650 cal yr BP. About 300 cal yr BP, exogenous plants expanded, grazing and fires increased, and there was a decrease of native vegetation cover.

Main conclusions: Throughout the Holocene, highland vegetation in Brava was characterized by the presence of open landscapes dominated by herbaceous species (e.g. Poaceae, *Forsskaolea*), with some presence of woody native taxa (e.g. *Ficus*, *Dodonaea*). A regional drying trend was a driver of erosion since the Mid Holocene but did not have an immediate influence on highland vegetation. Tephra deposition is a possible driver of vegetation change. Inter-island mass migration after volcanic events in Fogo

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Island c. 1680 CE potentially triggered land use change and intensification, causing a reduction of native vegetation in Brava.

KEYWORDS

African Humid Period, Anthropocene, Cape Verde, ecological change, environmental disturbances, Macaronesia, natural hazards, palaeoecology, tropical islands

1 | INTRODUCTION

Oceanic islands worldwide have been identified as frontline sites of major socio-ecological challenges (Baldacchino & Niles, 2011). It is known that they are epicenters of species extinctions and have generally experienced serious loss and fragmentation of habitats since human settlement, providing model systems for understanding human–environment interactions (Whittaker et al., 2017). Dry (climatically arid) island environments can be highly sensitive to disturbances such as an increase in extreme weather events or long periods of drought (Holmgren et al., 2006), and these natural factors can interact with and aggravate human impacts (Lindskog & Delaite, 1996). A comparison of disturbance dynamics before and after human arrival can increase our understanding of how human impacts overprint –or interact with– naturally occurring features of the island environment (Dearing et al., 2006; Paine et al., 1998). It is particularly challenging to develop records of long-term environmental change in dry regions due to poor microfossil preservation and a scarcity of undisturbed sediment archives (Brunelle et al., 2018). Nevertheless, palaeoecological research carried out in dry-land soil stratigraphic sequences can provide an essential historical perspective on ecological change in dry islands (e.g. van Leeuwen et al., 2008).

Cabo Verde is a tropical archipelago in the eastern Atlantic Ocean that has received increasing attention from ecologists and biogeographers in the last decade. Studies in this archipelago are yielding new insights on the diversification and evolutionary mechanisms of Macaronesian fauna and vascular flora (e.g. Romeiras et al., 2019; Vasconcelos et al., 2010) and of the challenges of conserving biodiversity in oceanic islands (e.g. Romeiras et al., 2016). Cabo Verde stands at a crossroads between sub-tropical Macaronesia and the dry Sahel region in terms of biogeography and ecology; species from the arid lowlands show similarities with mainland Africa, while mountainous vegetation show close relationships with the Canary Islands (Beyhl et al., 1990). To further our understanding of Cabo Verde's biodiversity and biogeography, it is vital to assess the composition and natural variability of its ecosystems through time, and the impacts that human settlement brought to different islands. For instance, it is thought that centuries of colonial land mismanagement in Cabo Verde, have led to habitat fragmentation and the soil depletion (Lindskog & Delaite, 1996; Norder et al., 2020). However, the role of volcanic hazards and climate fluctuations in long-term ecological changes and their interplay with anthropic pressures remain to be assessed. Volcanic eruptions can impact human societies

by triggering migrations and land use shifts, as well as producing chemical, biological and even climatic alterations (Payne & Egan, 2019). Studying these multi-scalar and potentially co-occurring disturbances and their socio-ecological effects may provide a much-needed historical perspective on landscape degradation and ecosystem variability. This is pivotal to: (i) understanding the effects of regional to local scale environmental change in a spatially constrained ecological/socio-ecological system; (ii) improving biodiversity conservation guidance (Nogué et al., 2017); and (iii) planning responses to future environmental crises.

Cabo Verde comprises 10 volcanic islands and three islets in the African-Sahelian climatic region (Duarte & Romeiras, 2009). Within islands of steep topography (Santo Antão, São Nicolau, Santiago, Fogo and Brava), elevation has a strong influence on temperature (mean annual temperatures vary between 23 and 26°C at sea level and 17–20°C in the highlands) and moisture (Duarte et al., 2008; Rivas-Martinez et al., 2017). Over centuries and millennia, regional climatic fluctuations driven by the oscillations of the West African Monsoon are thought to have shaped natural vegetation composition and distribution (Neto et al., 2020). During the last African Humid Period (AHP: 12,000–5000 yr BP), the African monsoon migrated to the north, leading to higher precipitation in the Saharan region. After this phase, regional conditions became drier, leading to the present extensive Sahara Desert (Pausata et al., 2020). Near-shore marine records offshore from Senegal reveal sharp decreases in precipitation after 4000 cal yr BP as well as increases in the deposition of Saharan dust after 3500 and after 200 cal yr BP (Mulitza, Heslop, Pittauerova, Fischer, Meyer, Stuut, & Kuhnert, 2010; Tierney et al., 2017). After Portuguese settlement (1460 CE), ecosystems in the northern islands of Cabo Verde were transformed by direct and indirect anthropogenic disturbances (Castilla-Beltrán et al., 2019, 2020). In recorded history, episodes of socio-ecological distress in Cabo Verde were caused by volcanic eruptions, hurricanes and multi-annual droughts, which are thought to have destabilized colonial socio-ecological systems (Garfield, 2015; Green, 2012; Heckman, 1985; Lindskog & Delaite, 1996; Patterson, 1988). Over the last two decades, Cabo Verde vascular plants have become increasingly threatened, mostly as a consequence of the increase in exotic species, habitat degradation and human disturbance (Romeiras et al., 2016).

Brava (Portuguese for 'wild') is a small island (64 km²) with a maximum elevation of 976 m asl. It is regarded as one of the most fertile in Cabo Verde, earning it the title of the 'Garden Island'. It is one of the youngest of the islands, having formed c. 3.0 Ma, and it shares its



volcanic base with Fogo Island (Madeira et al., 2010). Brava harbours some of the most diverse vegetation of Cabo Verde and the highest total plant species richness, with 239 species, and second-highest endemic floral species richness, with 25 taxa (Duarte et al., 2008), but due to its small size it has received little attention regarding conservation initiatives. Brava's north-facing highlands (700–960 m) are well-placed for the capture of cloud moisture and favoured by humid local climates (Correia, 1996). Currently, it is estimated that 13% of Brava's land area is wooded, much of it comprising introduced taxa such as *Prosopis juliflora*, *Grevillea robusta*, and *Cupressus lusitanica*. Native vegetation is under pressure due to the grazing of cows, donkeys and goats (GEF/UNEP, 2015). Brava's neighbouring islands, Santiago and Fogo, were the first to be significantly settled by Europeans (c. 1460 and 1470 CE, respectively), but it is estimated that Brava remained only marginally inhabited until c. 1680 CE, when 'many families' from Fogo fled to take refuge in Brava after an earthquake and a major volcanic eruption (Correia, 2000; Mitchell-Thomè, 1981; Ribeiro, 1960) (Table S1). Here, we present multiple palaeoecological analyses to show how ecosystems and soils in Brava changed over the last 9700 yr in response to global-to-local and potentially co-occurring environmental changes, including regional drying, within-archipelago volcanism and inter-island human migration.

2 | MATERIALS AND METHODS

Our study of ecological change in the highlands of Brava consists of multiple analyses of palaeoenvironmental information contained in a 220-cm soil profile excavated in a volcanic caldera (810 m asl). We recorded the changes in the plant, fern and fungal communities using fossil pollen grains, and fern and fungal spores (non-pollen palynomorphs; NPPs). For changes in organic matter content we carried out Loss on Ignition analysis (LOI), for identifying the occurrence of fire we quantified charcoal particles, for shifts in sedimentology we used X-ray fluorescence (XRF) and grain size distribution (GSD) analysis, and to assess the occurrence of significant episodes of deposition of volcanic ash we studied the abundance of microscopic tephra shards.

2.1 | Fieldwork and sample collection

In May 2019, we visited Brava Island and carried out excavations and soil-profile sampling in two highland calderas: Cova Galinha (CG, 810 m asl) and Fundo Mato (FM, 750 m asl). We selected the Cova Galinha caldera (14°51'26.2"N, 24°42'09.5"W) for this study based on its superior micro-fossil preservation, that could be linked to finer sediment grain sizes and the absence of gravel-dominated soil horizons. Cova Galinha caldera is currently used for low-intensity agriculture, mostly maize (*Zea mays*) cultivation and cattle grazing. We opened a 2.0 × 1.0-m trench in the centre of the caldera and collected a set of samples of about 30 g of sediment every 5 cm (sample

set A, taken across horizontally at c. 2 cm thickness), and a set of contiguous 2-cm³ block samples (sample set B) (Figure 1). We placed the samples in sealed plastic bags. The samples were transported to the University of Southampton and stored in a cold room at +4°C within the School of Geography and Environmental Science.

2.2 | Dating methods

To develop a chronological model of the Cova Galinha site we obtained 10 radiocarbon (RC) dates: nine from bulk sediment samples and one AMS RC date from a macrofossil sample via the Belfast and SUERC Radiocarbon laboratories (Table 1). We also carried out Pb-210 and Cs-137 analysis on the top meter of the core using sample set A, to achieve precise chronological control of sediment deposits in the last 120–150 years. These analyses were undertaken in the GAU-Radioanalytical Laboratories at the National Oceanography Centre (Southampton), using gamma spectrometric-analysis in HPGe well-type detectors (Cundy et al., 2006). We used Bacon in R (Blaauw & Christen, 2013) to calculate the age-depth model based on all dates and defined level 20 cm as the level representing post-CE 1950, based on a sharp increase in Cs-137 and two 'post-bomb' RC dates (Figure S1).

2.3 | Granulometry, elemental composition and Loss on Ignition analyses

For Grain size distribution (GSD), we used sample set A and sample set B for the section 80–40 cm. We used a Mastersizer Hydro (Malvern), programmed to measure soil properties through measurement of non-spherical soil grains. We carried out a minimum of five 20-second measurements per sample. Results were averaged once the standard deviation score of the three size fractions Dx10, Dx50 and Dx90 was equal to or below 0.5, 0.3 and 0.5, respectively.

For elemental composition analysis, we used set A (5 cm intervals). We used a hand-held X-ray Fluorescence (XRF) device (de Lima et al., 2019), model Niton XL3T GOLDD, using a test-stand. In measurements of 160-seconds per sample, we obtained proportion values (%) of elements above a detection limit of 0.001%.

For Loss on Ignition analysis, (LOI) we used sample set B (contiguous 2 cm samples). We used a high-precision scale, and followed the Heiri et al. (2001) protocol, ashing dry samples for 4 h at 550°C. LOI was calculated using the weight value of the dry sample and the ashed sample and used as a proxy for sample organic content.

2.4 | Pollen and non-pollen palynomorph analyses

To determine vegetation, fern and fungal community changes, and assess the presence of herbivores, we processed 44 2-cm³ samples from set A for pollen and NPP analyses following standard procedure that included sieving with 10 µm mesh, processing with hydrofluoric

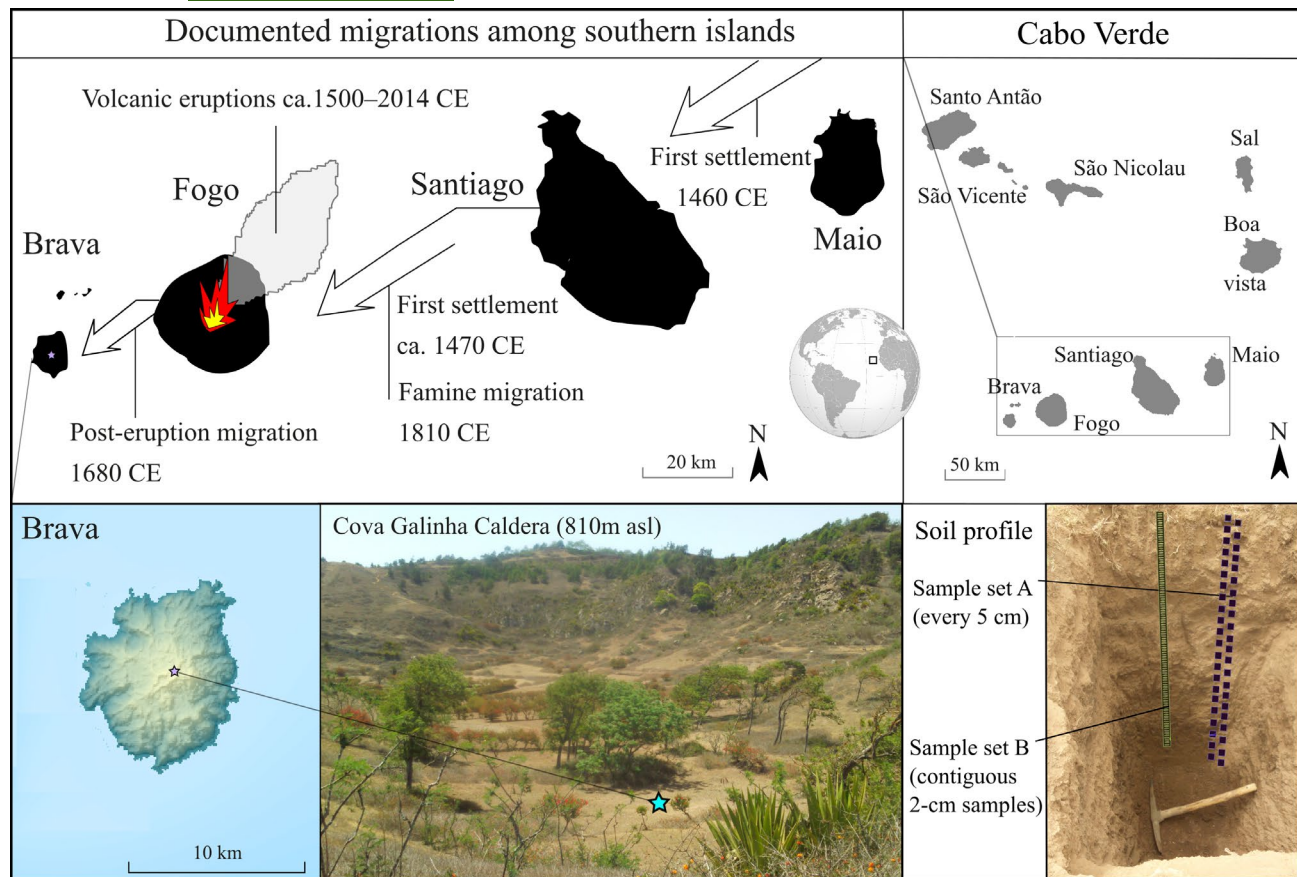


FIGURE 1 Maps of Cabo Verde with information of documented migrations between southern islands. Topographical map of Brava modified after Danielson and Gesch (2011). Pictures of Cova Galinha caldera and the studied soil profile (modified to show sampling strategy) taken by the authors.

TABLE 1 Radiocarbon dates of the Cova Galinha site, Brava Island, Cabo Verde, and their calibration. ^{14}C enrichment value is reported in ages between 1950 CE and the present.

Sample depths	Lab code	Material	RC Age (cal yr BP)	^{14}C Enrichment (% Modern $\pm 1\sigma$)	Calibrated age (95% confidence interval)
20–18 cm	SUERC-92980	Macrofossils		127.40 ± 0.58	Post-1950 CE
20–18 cm	SUERC-92979	Bulk		105.30 ± 0.48	Post-1950 CE
52–50 cm	SUERC-92978	Bulk	772 ± 37		760–663 cal yr BP
72–70 cm	SUERC-92977	Bulk	2314 ± 37		2433–2161 cal yr BP
120 cm	UBA-42113	Bulk	4057 ± 29		4785–4435 cal yr BP
140 cm	SUERC-92976	Bulk	6500 ± 38		7481–7321 cal yr BP
155 cm	UBA-42112	Bulk	7273 ± 34		8169–8014 cal yr BP
170 cm	SUERC-92975	Bulk	6341 ± 40		7414–7170 cal yr BP
195 cm	UBA-42111	Bulk	5484 ± 29		6390–6210 cal yr BP
220 cm	UBA-41128	Bulk	8665 ± 45		9736–9536 cal yr BP

acid (HF) to eliminate excess silica, acetolysis (Erdtman, 2013) and adding one tablet of *Lycopodium* exotic spores for calculating concentrations (batch nr 140119321, avg 19,855 spores per tablet). We used a high-power microscope to identify palynomorphs at $\times 400$ and $\times 1000$ magnification and consulted African pollen atlases (e.g. Gosling et al., 2013) and our Cabo Verde and Canary Islands

reference collections stored at the University of Southampton and the University of La Laguna to identify pollen grains. NPP literature was used to identify fungal and fern spores (van Geel et al., 2003; Gelorini et al., 2011). All pollen grains were included in the calculation of the total pollen sum and categorized as local (endemic and native taxa to Cabo Verde), introduced, derived from long-distance



transport, or unidentifiable (mostly too damaged to identify). The latter was included in the sum to account for unidentified components of the vegetation. We counted a maximum of four microscope slides per level, reaching a minimum of 250 pollen grains in samples with abundant pollen (55–0 cm), a minimum of 100 grains in much of the rest of the record, but we included counts over 50 pollen grains in the section with scarcer pollen abundance (115–195 cm). The pollen and NPP (ferns and fungal spores) data are presented as percentages over the pollen sum.

2.5 | Macro- and micro-charcoal

For macro-charcoal quantification we used 44 2-cm² samples from sample set A (taken every 5 cm) and sieved the material through a 180-μm sieve. We used a low-power microscope to count charcoal fragments directly after sieving. We performed micro-charcoal quantification in pollen-slides by counting angular opaque particles between 10 and 180 μm alongside exotic *Lycopodium*, until reaching

a sum over 200 items and then calculating micro-charcoal concentrations (Finsinger & Tinner, 2005).

2.6 | Silica structures: phytoliths and tephra

For phytolith and tephra analyses, we used a dry ashing sample preparation (Parr et al., 2001) on sample set B. We sieved the samples through 10 and 180-μm sieves. We tested density separation using sodium polytungstate at density 2.5 sg in 10 samples, which resulted in the flotation of more than 50% of the material. As a cost-effective alternative, we followed recommendations of Lentfer and Boyd (1998) for sandy sediments, directly mounting microscope slides using Canada balsam, a method we previously used for diatom and phytolith analysis in Cabo Verde (Castilla-Beltrán et al., 2019). We used phytolith literature (e.g. Piperno, 2006) for phytolith identification. We spiked the samples with a known quantity of exotic *Lycopodium* spores (batch nr 140119321, avg 19,855 spores per tablet) to calculate the concentration of phytoliths and tephra shards

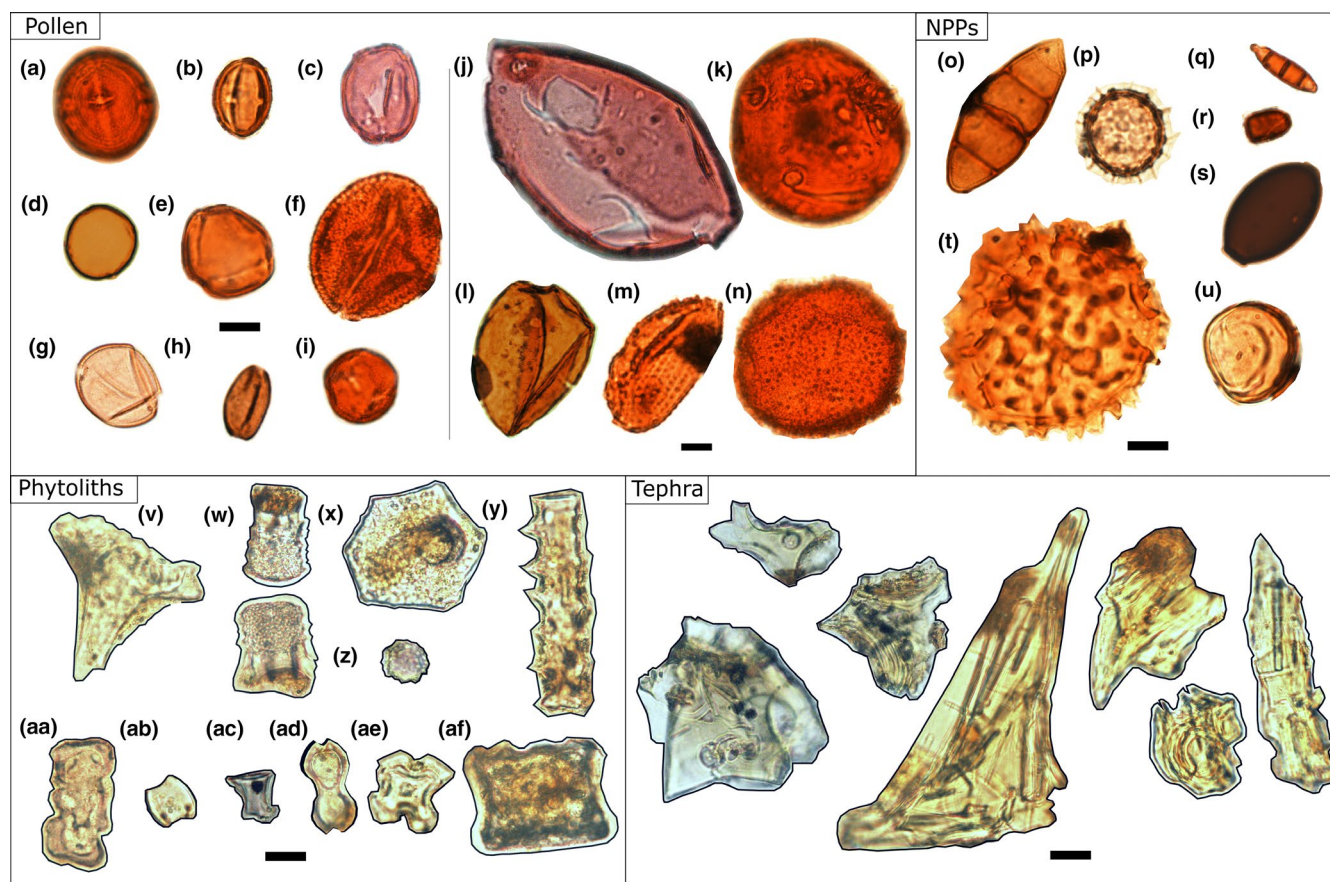


FIGURE 2 Selected microfossils documented in the Cova Galinha site, Brava Island, Cabo Verde. **Pollen:** (a) *Dodonaea viscosa*, (b) Primulaceae-type, (c) cf. *Dracaena*-type, (d) Urticaceae, (e) *Lavandula*, (f) *Euphorbia tuckeyana*, (g) *Ficus*-1, (h) *Ficus*-2 (CV-4), (i) *Portulaca*-1, (j) *Zea mays*, (k) *Ipomoea*, (l) *Cerealia*, (m) *Commelina benghalensis*, (n) *Portulaca*-2. **NPPs:** (o) *Alternaria*, (p) *Lycogala-Urocystis*, (q) *Fusarium*, (r) *Sporormiella*, (s) *Podospora*, (t) *Anthoceros*, (u) *Monoete psilate*-2. **Phytoliths:** (v) Hair-cell, (w) *Commelina benghalensis*, (x) Cyperaceae, (y) Elongated echinate, (z) Globular echinate (cf. *Phoenix*), (aa) Wavy trapezoid, (ab) Saddle, (ac) Rondel, (ad) Bilobate cf. Chloridoidea, (ae) Cross var. 1 (*Zea mays*), (af) Rondel crown-top (*Zea mays*). **Tephra:** Selected shards from core section 70–30 cm. All scale bars are 10 μm.

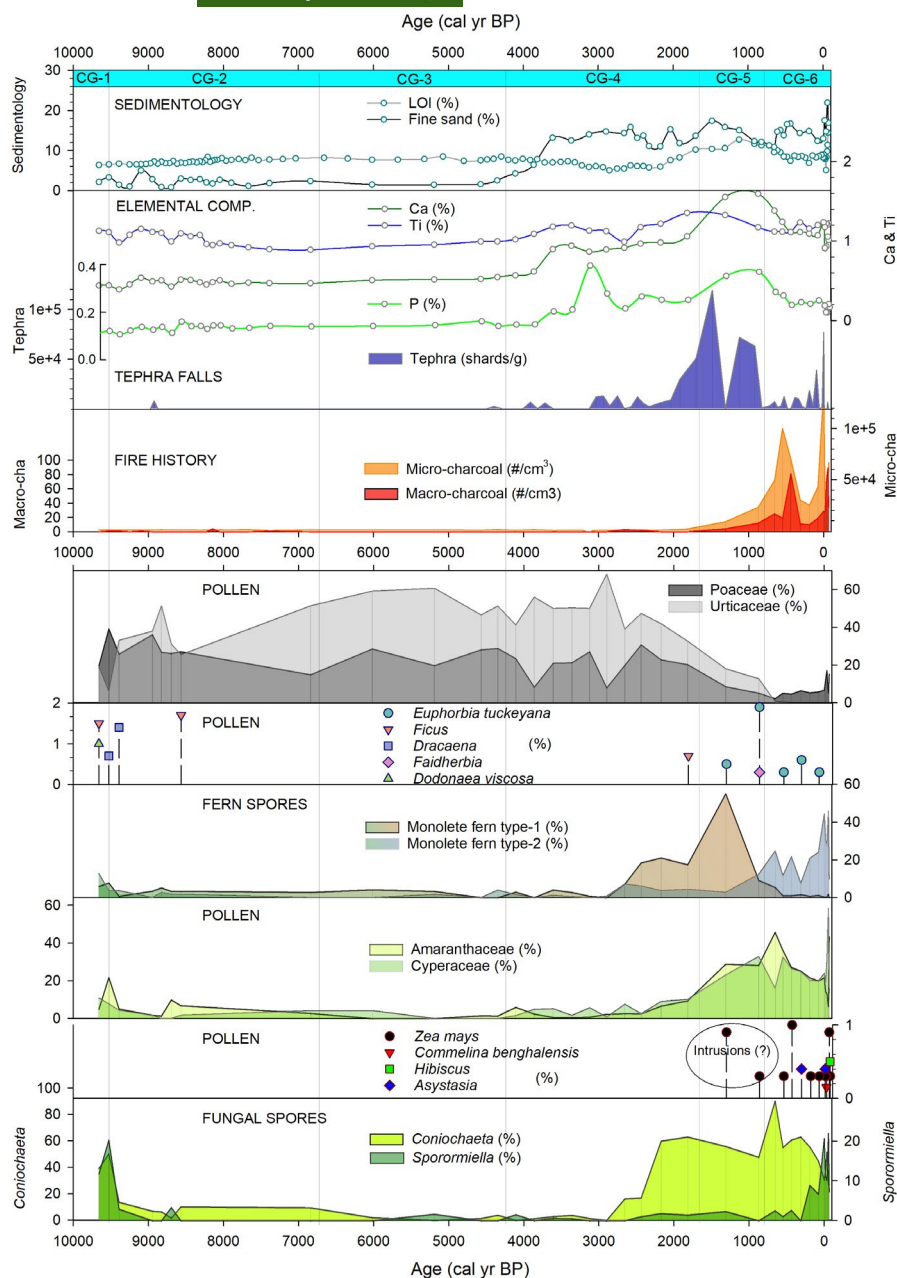


FIGURE 3 Diagram including a selection of indicators of environmental change (proxies) studied in Cova Galinha site, Brava Island, Cabo Verde. Silhouettes are superposed. Fern and fungal spores (NPPs) percentages were calculated over the pollen sum. The label 'intrusions' refers to *Zea mays* pollen grains in levels pre-dating the introduction of this cultivar to the archipelago (see Section 4.1).

(selected morphotypes and shards shown in Figure 2), and tallied these microscopic remains scanning one slide per sample with a microscope equipped with a polarizing lens. In this study, we focused on recording episodes of significant microscopic tephra depositions (defined as >2000 shards per gram of sediment). Episodes of limited deposition of tephra are under this threshold of detection. Characterization of tephra geochemistry and comparison of shard morphology with tephra shards from Fogo Island will be carried out in future studies.

2.7 | Zonation and ordination analyses

We used Tilia software to establish a zonation by performing stratigraphically constrained CONISS analysis (Grimm, 1993)

resulting in six zones (Table S2). We carried out Canonical Correspondence Analysis (CCA) using the R Vegan package (Oksanen et al., 2013) to assess the influence of six environmental drivers on vegetation change (pollen percentage values). The following proxies were chosen to represent environmental variables: LOI % for organic matter, macro-charcoal particles per cm^3 for local fire, concentrations of obligate coprophilous fungal spores per cm^3 for abundance of herbivores, percentage of sand for erosion, tephra shard concentrations per gram of sediment for significant volcanic ash falls, and the elemental ratio Fe/Mn for the occurrence of soil reducing conditions (Croudace & Rothwell, 2015). We performed two separate Detrended Correspondence Analyses (DCA) in R, Vegan package, using pollen and NPP percentages, to assess turnover in vegetation and fungal/fern communities separately.



3 | RESULTS

3.1 | Zones CG-1, CG-2 & CG-3: 220–110 cm (9700–4100 cal yr BP)

The age–depth model produced using Bacon (Blaauw & Christen, 2013) suggests that the 220 cm of sediments in Cova Galinha caldera comprise the time period between 9700 cal yr BP and the present day (Figure S1). In the deepest zones (CG-1, CG-2 & CG-3), sediments deposited are silt-dominated (mean 83% silt content), with moderate amounts of clay (mean 13.1%) and limited sand inputs (mean 3.3%) (Figure 3). Organic matter varies in this section from 6.0 to 8.5%. Major elemental components are iron (Fe, mean 8.2%) and silicon (Si, 12–17%), with low proportions of titanium (Ti, mean 1%) but peaks of aluminium (up to 8.2%) (Figure S1). The Fe/Mn ratio shows steadily decreasing values in this period, from 23.8 to 16.85 (Figure S5). Poaceae (mean 26.7%) and Urticaceae (mean 39%) are the dominant components of the pollen assemblage. There is also a moderate presence of Asteraceae (mean 7.3%), Cyperaceae (mean 2.8) and *Plantago* (mean 4.8), and occurrence of Campanulaceae, *Lavandula* (type 1), *Ficus*, *Dodonaea viscosa* and *Dracaena* pollen (Figure S2). Fungal spore assemblages are dominated by *Lycogala/Urocystis* (mean 111.6%), *Fusarium* (mean 5.5%), *Glomus* (mean 4.5%) and *Chaetomium* (mean 1.5%), with the presence of *Curvularia intermedia*. Obligate coprophilous fungi (*Sporormiella*, *Cercophora*, *Sordaria*) show high abundance c. 9700–9500 cal yr BP (up to 20.3% *Sporormiella*) (Figure S3). Pollen most likely transported by trade winds (Hooghiemstra et al., 2006; Ritchie et al., 1985) is present in these sections, including *Pinus*, *Juniperus*, *Morella*, *Corylus*, *Quercus* and *Betula*. Charcoal particle concentrations are stable and low, with an average of 641 micro-charcoal particles per cm³, and 0.2 macro-charcoal particles per cm³ (Figure 3).

3.2 | Zone CG-4: 110–65 cm (4100–1800 cal yr BP)

Sediments of zone CG-4 (deposited between c. 4100 and 1800 cal yr BP), are rich in sand (mean 21.3%), with decreasing silt (minimum value of 68.7%) and clay percentages (min. value of 2.9%). Organic matter proportions show a decrease down to 5.5% until level 80 cm (c. 2700 cal yr BP), and then show a sharp rise until level 60 cm up to 10.4% (between 2700 and 1500 cal yr BP). Proportions of calcium (Ca) and titanium (Ti) progressively increase (up to 1 and 1.3% respectively) in this section. The pollen assemblage is characterized by the enlarged proportion of Urticaceae (mean 47.6%) and a reduction of Poaceae (mean 20%). Pollen of Convolvulaceae, *Lotus*, *Ficus*, Primulaceae and Caryophyllaceae is also present in low proportions (<1%). The proportion of degraded (unidentifiable) pollen grains increase to an average of 14%, and most grains show signs of degradation. Spores of *Lycogala-Urocystis* decrease (mean 50%), and above level 80 cm (c. 2700 cal yr BP) monolete psilate fern spores and *Coniochaeta* spores increase (up to 18.1 and 59.9%, respectively) (Figure S3). Significant deposition of tephra particles are

documented between levels 85 and 60 cm (after c. 3000 cal yr BP, with highest values at c. 1800 cal yr BP; 50,700 shards per cm³), yet charcoal concentrations show no significant increase in relation to deeper zones.

3.3 | Zone CG-5: 65–50 cm (1800–650 cal yr BP)

Significant episodes of tephra deposition are documented between 65 and 50 cm (c. 1800–650 cal yr BP), the highest concentration reaching 63,055/g c. 1000 cal yr BP. Sediments contain high proportions of sand (mean 27.2%). Organic matter content reaches its highest levels in the record (up to 12.7%). Proportions of calcium (Ca) and titanium (Ti) also show the highest values of the record (1.3 and 1.4% respectively). Charcoal concentrations increase up to 49,420 micro-charcoal particles/cm³, and up to 6 macro-charcoal particles/cm³. Pollen of the previously dominant Urticaceae and Poaceae steadily decrease (down to 5.2 and 12.7% respectively), while proportions of Cyperaceae and Amaranthaceae show marked increases (up to 32.8 and 28.8%, respectively). Pollen of the woody species *Euphorbia tuckeyana* (up to 1.9%) occurs for the first time in the record and there is limited presence of *Faidherbia albida* pollen, and peaks of Monolete psilate (type 1, up to 55%), *Davallia* fern spores, and of fungal spores of wood-rotting *Bactrodesmium* (up to 2.7%). This zone is also characterized by a high concentration of well-preserved phytoliths (Figure S4), most of which belonged to the morphotypes blocky polygonal, tabular, and Poaceae long cells (bulliform and elongated serrated/sinuate). Minimal percentages of globular echinate phytoliths are indicative of the presence of *Phoenix atlantica* in the island, potentially blown uphill from the coastal areas, a common feature of the Cova de Paúl record in Santo Antão (Castilla-Beltrán et al., 2019). Pollen of the crop *Zea mays* and agricultural weed phytoliths identified as *Commelina benghalensis* are also marginally present (Eichhorn et al., 2010).

3.4 | Zone CG-6: 50–0 cm (650 cal yr BP–the present)

Sediments of zone CG-6, deposited between c. 650 cal yr BP and the present-day) are dominated by increasing proportions of sand (up to 39.26%; the highest value of the record) and decrease in organic matter (except for the uppermost sample: active soil). Tephra shards deposited or re-worked due to erosion are present, especially between levels 50 cm and 20 cm (650–100 cal yr BP). Proportions of aluminium (Al) and silicon (Si) show increases (up to 5.9 and 14.7%, respectively). Charcoal concentrations are the highest in the record (mean 20 macro-charcoal particles/cm³, and mean 55,689 micro-charcoal particles/cm³). The palynomorph assemblage is dominated by Amaranthaceae (mean 24.9%), Cyperaceae (mean 25.9%), Asteraceae tubuliflorae (mean 19.3%) and Brassicaceae (mean 9.1%). There is a sustained presence of *Zea mays* pollen, and pollen of introduced taxa (*Cerealia*, *Ipomoea*, *Hibiscus*, *Commelina benghalensis*,

Asystasia, *Portulaca* types 1&2) and of the native/endemic herbs and shrubs *Artemisia* and *Lavandula* (type-2). Obligate coprophilous fungi (*Sporormiella*, *Cercophora*, *Sordaria* and *Podospora*) show increases after level 40 cm (c. 300 cal yr BP), reaching maximum values for the core in level 20 cm (100 cal yr BP: *Sporormiella* peak of 20.7%). A new assemblage of fern spores including Pterideaceae, *Anthoceros*, Monolete psilate type-2 and *Ophioglossum* becomes dominant. Phytoliths of *Commelina benghalensis* are continually present (Figure S4), Poaceae short-cells become more abundant, and new morphotypes potentially characteristic of the Fabaceae family (e.g., anticlinal epidermal) occur especially after level 20 cm (1950 CE).

3.5 | Ordination analyses

The resulting CCA and DCA ordination plots show how constrained and unconstrained ordination analyses separate soil profile samples in two-dimensional statistical spaces based on pollen and NPP percentage data (DCA), and pollen percentage and six selected environmental variables (CCA) (Figures 4 and 5). CCA axis-1 explained 72% of the variance of the pollen data (eigenvalue 0.46) and CCA axis-2 explained 10% (eigenvalue 0.06), with a permutation test score (F Pr(> F)) of 0.001, indicating an statistically significant result. Environmental variables of erosion, organic matter and local fire show a strong correlation with the negative side of CCA axis-1 (correlation scores: -0.73, -0.51 and -0.78, respectively), and soil reducing conditions shows a strong relationship with the positive values of CCA axis-2 (correlation score: 0.45). Pollen DCA eigenvalues are 0.42 (axis-1), and 0.07 (axis-2), while NPP DCA eigenvalues are 0.43

(axis-1), and 0.18 (axis-2). In the pollen DCA, samples dated between 1800 cal yr BP and the present show a strong correlation with the positive side of DCA axis-1, while samples dated 9700–1800 cal yr BP are strongly correlated with the negative side of DCA axis-2.

4 | DISCUSSION

4.1 | Taphonomical processes and the interpretation of soil biostratigraphy

Palaeoecological research in dry islands is challenging due to the lack of permanent water mires that preserve microfossils in water-logged conditions. As a consequence we have limited understanding of long-term ecological dynamics in these locations. Dry sediment archives such as volcanic calderas are the alternative, yet they are more likely to be affected by interrupted sedimentation and uneven and discontinuous preservation of microfossils (Brunelle et al., 2018; Carrión et al., 2009). However, we demonstrate that sites such as this highland volcanic caldera hold a diversity of forms of palaeoenvironmental information. Past environmental change can be reconstructed through the integration and nuanced interpretation of multiple proxies extracted from stratigraphically oriented sediments in soil profiles. Soils are not inert, and taphonomical and soil-formation processes affect micro-fossil preservation and mobility within the sediment matrix (Horrocks & D'Costa, 2003). In the Cova Galinha soil profile there were sections barren of palynomorphs, and some horizons composed of high proportions of sand contained pollen grains affected by degradation processes, probably due to

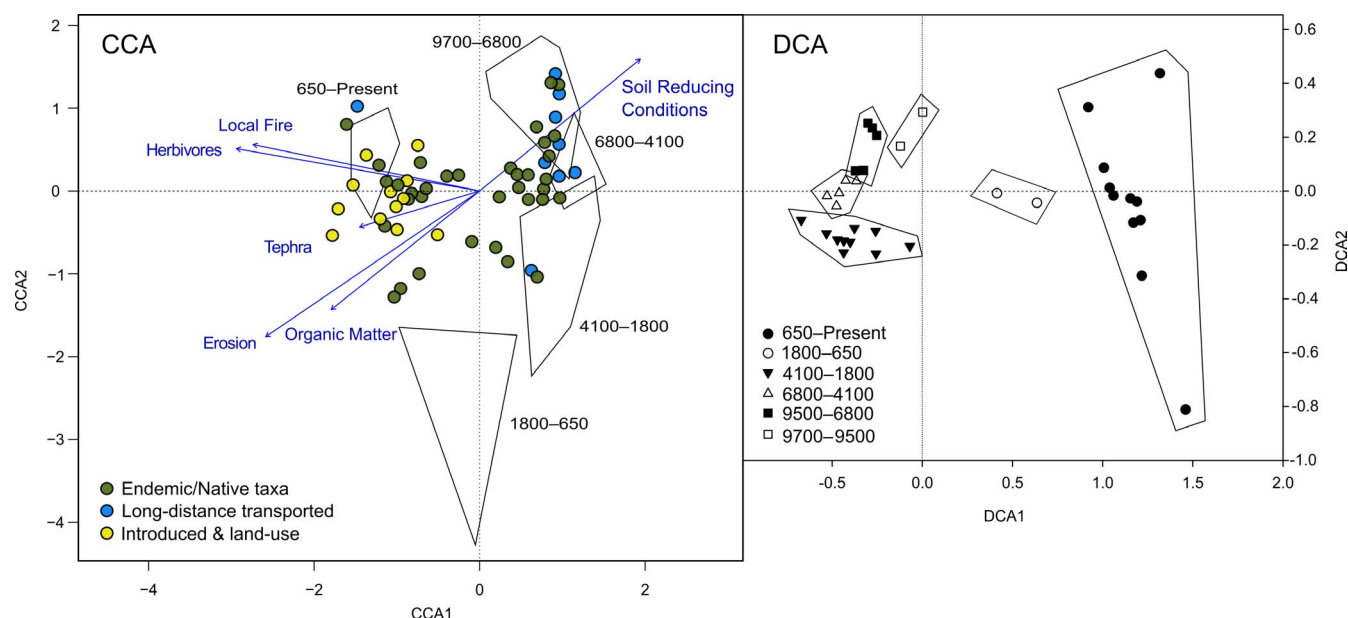
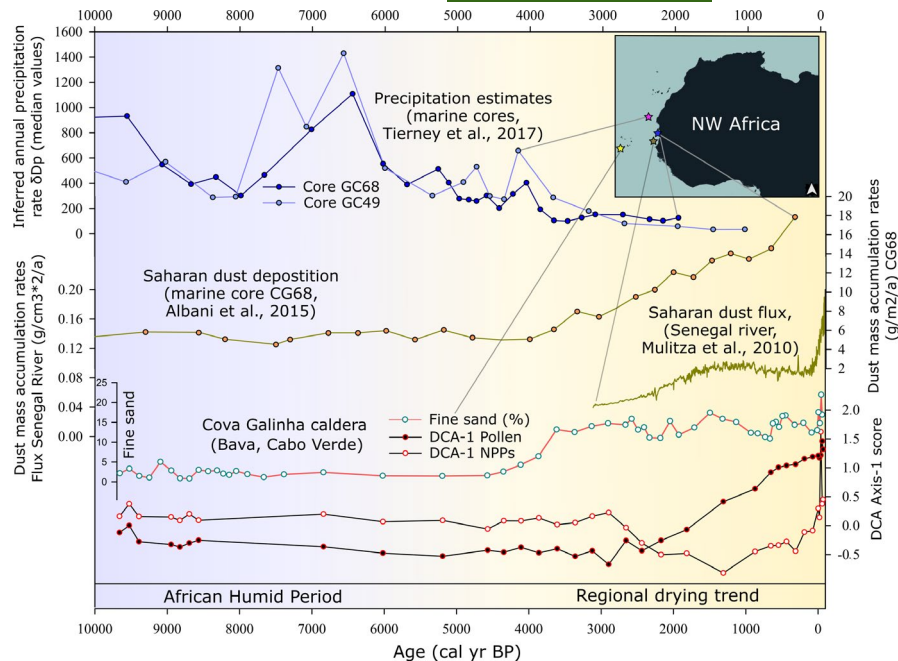


FIGURE 4 CCA and DCA plots of the Cova Galinha record, Brava Island, Cabo Verde, using pollen percentage data (DCA), as well as concentrations of obligate coprophilous fungi for herbivore presence, LOI (%) for organic matter, find sand (%) for erosion, tephra shard concentrations for ash falls and Fe/Mn ratio for soil reducing conditions (CCA). In both plots, numbers and polygons indicate the age of the samples, and as can be seen, both the constrained (CCA) and unconstrained (DCA) analyses separate out the samples clearly into arcs of increasing age within the two-axes space.

FIGURE 5 Paleoenvironmental trends from marine cores taken along the Senegal coast (cores GC68 & GC49: Collins et al., 2013; Tierney et al., 2017 and Albani et al., 2015, core GeoB9501: Mulitza, Heslop, Pittauerova, Fischer, Meyer, Stuut, Zabel, et al., 2010, data downloaded from NOAA and PANGEA) in comparison with erosion indicators, axis-1 scores of two DCA analyses (pollen and NPPs) as proxies of vegetation and fungal community turnover in the Cova Galinha site, Brava Island, Cabo Verde. Blue to orange colour gradient represents the transition from moist to dryer conditions in the Sahara.



mechanical weathering and oxidation (Figure S5). In these sections, NPPs showed better preservation potential, and they are useful to assess continuity or change in local environmental conditions. The process of incorporation of micro-fossils into the soil matrix can be complex: for instance, *Zea mays* and agricultural weed phytoliths identified as *Commelina benghalensis* (Eichhorn et al., 2010), taxa introduced by humans after 435 BP (Moran, 1982), were registered in small percentages in sections dated to before first human arrival. In the context of the Cova Galinha site, the stratigraphic position of these pollen grains underneath the anthropic agricultural soil horizons (c. 10 cm) supports the interpretation that their presence is due to limited microfossil intrusions through leaching, root percolation or herbivore trampling.

Sediment mixing and redeposition can also affect soil stratigraphic sequences: for instance, our age–depth model shows two inverted radiocarbon dates (195 cm: UBA-42111 and 170 cm: SUERC-92975) that coincide with peaks in aluminium (Al) and silicon (Figure S1). Sediment mixing and reworking could also explain why Pb-210 analysis failed to yield accurate chronological control in the more recently deposited sediments – while surface activities of Pb-210 are clearly enriched over likely supported or background activities (approximated here by Pb-214 activity), the Pb-210 activity–depth profile does not show the near-exponential decline with depth expected in uniformly accreting sediment sequences (Figure S6). Instead, it fluctuates with Pb-214 activity, indicating that the vertical distribution of Pb-210 is controlled by input on reworked sediment particles and by variations in sediment composition, rather than by direct atmospheric fallout (Cundy & Stewart, 2004). Even with the constraints of working in a dry environment, the clear-cut biostratigraphic patterns found in Cova Galinha caldera sediments provide unique insights into environmental change in Brava, and our age–depth model successfully provides a chronological framework to discuss natural and human-driven disturbance regimes in Brava.

4.2 | Erosion, vegetation and regional climatic change

The Early and Middle Holocene periods in Northern Africa are defined by the occurrence of the most recent African Humid Period (AHP: 12,000–5000 yr BP), which was characterized by increased precipitation and vegetation cover across the entire Saharan region (deMenocal et al., 2000; Pausata et al., 2020). Our pollen data suggest that c. 10,000 years ago, Brava's highlands supported an open landscape dominated by Poaceae, Urticaceae (likely *Forsskaolea procrifolia* and *Forsskaolea viridis*, endemic and native to Brava respectively), Cyperaceae and *Plantago major*. The limited presence of pollen grains of woody species *Dodonaea viscosa*, *Ficus* (*Ficus sycomorus* and *Ficus sur*, species with African biogeographic affinities) and *Dracaena draco* subsp. *caboverdeana* (very scarce in Brava in the present, see Arechavaleta Hernández et al., 2005) suggests that these species were native to Brava (Figure 3). This reconstruction is strengthened by consideration of the NPP assemblage, which is dominated by saprophytic fungi that thrive in grasslands. Low concentrations of charcoal particles indicate the likely absence of local and regional fires, probably due to the prevailing humid conditions and scarcity of fuel. The presence of coprophilous fungal spores (e.g. *Sporormiella*, *Podospora*) indicates that the island may have supported significant populations of native fauna. In the absence of alternative evidence such as faunal fossils or *seda*DNA, we hypothesize that native reptiles and bird communities could have produced faecal matter that sustained these fungal communities. Long-distance transported pollen taxa are not considered part of Cabo Verde's flora, as their ecological requirements are not matched by the current environmental conditions, but it cannot be ruled out that taxa from the Canaries (e.g. *Juniperus*, *Morella*, *Pinus*) were once native to Cabo Verde.

During the AHP interval in Brava (9700–5000 cal yr BP), variation in the elemental composition of the sediments may reflect

increased precipitation, but there is no strong evidence of inwash events, indicating that erosion rates were relatively stable. Leaf-wax data from marine cores off the Senegal coast 750 km east of Brava (GC68 & GC44) indicate abundant precipitation between 8000 and 6000 cal yr BP (Collins et al., 2013; Tierney et al., 2017) (Figure 5). Notably, CCA analysis (Figure 4) shows an association between samples from this period and the Fe/Mn ratio (positively correlated with CCA axes 1 and 2, biplot scores of 0.55 and 0.45, respectively), indicating soil reducing conditions. This could be related to episodes of waterlogging. We found similar results in a previous palaeoecological study from the island of São Nicolau (190 km north of Brava; 1000 m asl), which showed soil reducing conditions between 6000 and 5000 cal yr BP (Castilla-Beltrán et al., 2020).

At around 4000 cal yr BP there was a significant change in lithology in the Cova Galinha caldera, with a sharp increase in sand content, indicative of local erosion. Dust concentrations from marine core GC68 indicate increased Saharan sediment input after 4000 cal yr BP, suggesting that Brava's erosion signal (dated with a 95% confidence interval between 4583–3587 cal yr BP) could be roughly synchronous with that of the Senegal region (Figure 5). Increased aeolian transport of materials from the continent could explain increases in calcium (Ca), potassium (K) and phosphorous (P) in Brava's soils (Figure 3), as these are abundant elements in Saharan dust (Møberg et al., 1991). The expansion of the Sahara desert, which became a source of wind-transported dust material, coupled with intensified seasonality due to changes in the monsoon system, could explain the increased erosion in the highlands of Brava: stronger seasonal variation between long dry seasons and short and intense monsoon rains would favour soil denudation. For instance, two pulses of erosion on the island of Santo Antão (Cabo Verde) between 2000 and 1700 cal yr BP may be related to flash-floods linked to extreme weather events (Castilla-Beltrán et al., 2019). Similar events have been recorded from sites on the Senegal coast around 2150 cal yr BP (Bouimetarhan et al., 2009).

In more northern latitudes, the end of the AHP led to changes in Macaronesian laurel forest communities. The fossil pollen data from the summit of Garajonay National Park in La Gomera (1266 m asl) show a progressive increase of the comparatively xerophilous taxa *Morella faya* and *Erica* at approximately 5000 years BP relative to levels of other laurel forest taxa, while fire incidence increased after 3100 cal yr BP (Nogué et al., 2013). In contrast, in the island of São Nicolau, Cabo Verde, vegetation showed relative stability between 4500 and 1000 cal yr BP; there was a prevalence of fern-rich wooded landscapes, and such vegetation would have protected the highland soils (Castilla-Beltrán et al., 2020). Our data suggest that in Brava, vegetation change was nuanced in this period. Changes in the DCA axis-1 scores of pollen show that vegetation was experiencing changes after c. 3000 cal yr BP (Figure 4): an with increased dominance of Urticaceae and presence of *Lotus* (*Lotus purpureus* is recorded in Brava in the present) and *Lavandula* (perennial shrubs *Lavandula coronopifolia* or *Lavandula dentata*, both currently present in Brava). However, variable pollen preservation (increase in the proportion of unidentifiable pollen grains due to mechanical weathering

and oxidation) could be hampering our understanding of vegetation change in this period.

Overall, an abrupt change towards more arid conditions at the end of the AHP (Pausata et al., 2020) could be linked to increased erosion and dust deposits in Brava (c. 4000 cal yr BP), but it caused no major vegetation changes, indicating some degree of ecosystem resilience to regional drying. While rainfall likely decreased in Cabo Verde, cloud condensation in the highlands might have remained a sufficient source of humidity for local vegetation. Increases in turnover of pollen and NPP assemblages in Brava (DCA axis-1) only started changing after 2500 cal yr BP, and are linked to the expansion of woody vegetation and fern-rich communities (Figure 5).

4.3 | Vegetation responses to volcanism

Assessing the relationship between changes in vegetation and the consequences of volcanic activity, such as tephra deposition and tephra domination of soils, is challenging. Volcanic eruptions can have indirect influences in vegetation through a change in local- and micro-climates (increased humidity and/or precipitation) due to augmented aerosol cover during prolonged episodes of volcanism (Payne & Egan, 2019). According to popular knowledge in Cabo Verde, after volcanic eruptions, good years of rain are to be expected ('*Anos bons*' in Creole) (Correia, 1996, 2000). Close examination of meteorological records from the 20th century does not show a robust link between eruptions and change in local climate (Correia, 2000). This cannot be ruled out in previous centuries, however, as the eruptions of Pico do Fogo in the 20th century were of relatively low intensity, duration and frequency. Vegetation change could also be directly linked to the effects of the deposition of tephra layers, which can only constitute a minor ecological disturbance, and can lead to better water retention and enhanced plant growth (Crisafulli et al., 2015). After the eruption of Mount St. Helens (Washington State, USA), woody species benefitted in some areas from limited tephra falls (Zobel & Antos, 2017). Soils that incorporate volcanic ash are rejuvenated and stocked with essential nutrients, such as phosphorous, that are readily accessible to plants (Schlesinger et al., 1998); this also enhances their potential to sequester carbon (Fiantis et al., 2019). But vegetation responses to ash falls are highly variable: on the Eastern Andean flank forest responses to substantial ash fall varied from almost negligible to the expansion of species with pioneering qualities (Loughlin et al., 2018), while in New Zealand, complete revegetation of forests occurred in 200 years after volcanic disturbance (Wilmshurst & McGlone, 1996).

Abundant deposition of tephra shards took place in Brava, especially between 1800 and 650 cal yr BP. Brava Island has no recorded eruptions in the historical period, but the island's volcanic cones may have erupted in the Late Holocene (Worsley, 2015), meaning that the observed tephra could be of local origin or even re-deposited by local erosion. However, it is also likely that most tephra, if not all, originated from Fogo (highly active in the historical period 450 BP–present) and was transported by northeast trade winds (Table S1).



On Brava, vegetation changed after these tephra deposition events. An increase in woody plant taxa and soil organic content could be explained by more abundant local biomass or by soil formation processes. There was an increase in the endemic shrub *Euphorbia tuckeyana*, which is well-adapted to thrive on pyroclastic soils. A parallel increase of *Monolete* fern (type-1) spores (up to 50%, the highest levels of the record) and spores of wood-rotting fungi, such as *Bactrodesmium* and *Canalisporium*, also suggest an increase in woody taxa. The resulting palynological assemblage shows similarities with endemic-rich scrublands documented in the island of São Nicolau c. 4000–400 cal yr BP (Castilla-Beltrán et al., 2020). In the Azores, volcanic eruptions c. 5150 cal yr BP led to local vegetation change, including an increase in *Euphorbia* (Connor et al., 2012). We hypothesize that in Brava there was an expansion of local taxa previously limited to rocky margins and cliffs between 1500 and 500 cal yr BP, a process that may be linked to volcanism. It cannot be excluded that vegetation primarily responded to a build-up of soil organic matter and nutrient availability related to Saharan dust deposition, which also increase soil fertility, as demonstrated in La Palma, Canary Islands (von Suchodoletz et al., 2013). For instance, taxa such as *Euphorbia tuckeyana* plot in the bottom left of the CCA graph, where the most influential environmental variables are organic matter and erosion (axis-1 correlation scores: -0.78 , -0.53) (Figure 4). Climate could have also played a role in this process: palaeoclimatological research in Senegal (c. 770 km from Brava) indicates a stable and drought-free period between 1500 and 900 BP (Azzoug et al., 2012). Further research and integration of palaeoenvironmental records, as well as the study of independent palaeoclimatic lines of evidence could clarify the relationships between volcanism, vegetation change and climate in Cabo Verde.

4.4 | Colonial settlement, mass migration and human ecological footprint

From 500 BP to the present day, Brava's highlands underwent significant anthropogenic ecological disturbances due to the arrival of European settlers (the first known permanent settlers on the island). The first peak in micro-charcoal concentration, dated c. 500 cal yr BP, which is accompanied by the presence of *Zea mays* pollen, could indicate the onset of the first stage of human occupation of Brava and Fogo islands. This first stage of land use was followed by a change in fern communities through the increase of *Pteridaceae*, *Anthoceros*, *Monolete* psilate type-2 and *Ophioglossum*, indicating moderate disturbances. Around 300 cal yr BP, a peak in macro-charcoal coincident with a significant tephra fall broadly corresponds with the documented mass migrations (the fleeing of 'many families'; no further numerical estimates given) from the island of Fogo after earthquakes and volcanic eruptions between 1660–1680 CE (290–270 BP) (Ribeiro, 1960). Volcanism was once again a driver of change in southern Cabo Verde, but this time spurring inter-island human migration and resultant land use change in Brava. Historical accounts describe how these catastrophic episodes in Fogo led to the

abandonment of sterile lands and damaged settlements, triggering migration between islands (Correia, 2000; Ribeiro, 1960). Population estimates for Fogo before the eruption were of 2500 inhabitants by 1650 CE, so the exodus potentially involved hundreds of people. The impacts of mass settlement in Brava are evident through the increase in obligate coprophilous fungi (e.g. *Sporormiella*), which indicate the presence of abundant livestock in the studied caldera. The woody vegetation present during the period 1500–500 cal yr BP (e.g. *Euphorbia tuckeyana*) and the associated epiphytic ferns (e.g. *Davallia*) drastically decreased. Exogenous species arrived to the caldera, including *Asystasia*, two species of *Portulaca*, and *Commelina benghalensis*. DCA axis-1 indicates increased rates of change in pollen and NPPs assemblages after 300 cal yr BP, and especially during modern times (Figure 4). Samples dated after 300 cal yr BP show positive correlation scores with herbivores and local fire environmental variables (Figure 4). Introduced species also plot with herbivores and local fire ecological drivers in the CCA, as their expansion was linked to land use change (Figure 4).

The topmost samples of the Cova Galinha record (20–1 cm) are represented by active unconsolidated soil; pollen of *Hibiscus cannabinus*, the floral emblem of the island, reflects the cultivation of this shrub for textile manufacture and cattle feeding (Romeiras et al., 2011). Current environmental assessments of Brava confirm that free grazing by goats and other ungulates is the main threat for local biodiversity (GEF/UNEP, 2015), and tackling this problem would be beneficial for the conservation of threatened plant species and soils.

5 | CONCLUSIONS

The study of sediments from a volcanic caldera in Brava, the smallest inhabited island of Cabo Verde, provides the first characterization of highland vegetation throughout the Holocene on this island. It also offers a long-term view of local ecological responses to environmental changes and disturbances originating at regional scales and those with more local, within-archipelago and within-island origins. Pollen evidence suggests that taxa such as *Ficus sur*, *Ficus sycomorus*, *Dodonaea viscosa* and *Dracaena draco* subsp. *caboverdeana* were native to this small dry island before human settlement. While a regional drying trend after 4000 BP led to increased erosion, grasslands showed limited vegetation change. Turnover of pollen and NPP assemblages increased after 3000 cal yr BP and are reflected in the expansion of ferns and shrubs that could have been favoured by significant tephra falls and increased Saharan dust deposits. Although the link between tephra and ecological change requires confirmation, we suggest that both direct (enrichment of soils) or indirect (change in local climate) impacts of tephra falls might have driven shifts in highland vegetation. Mass-migration from the neighbouring Fogo Island after destructive episodes of volcanic eruptions there (1660–1680 CE) led to the introduction of exogenous taxa and the reduction and fragmentation of the native ecosystems in the highlands in Brava. Studying long-term environmental change in small islands

reveals how major climatic transitions and disturbance episodes impact spatially constrained ecological systems. This is key for the current and future development of guidelines on the protection of island biodiversity and ecosystem services, and for managing future sustainability in islands and archipelagos.

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DATA AVAILABILITY STATEMENT

The dataset supporting our findings has been uploaded to the Neotoma Palaeoecology Database (online and open-access: <https://apps.neotomadb.org/explorer/?datasetid=48891>) and can also be requested via email to the corresponding author of this paper.

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BIOSKETCH

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Authors contribution: ACB, SN, JFP, LdN and ME designed and conceptualised the study; ACB collected the samples (May 2019). ACB carried out the analyses under the supervision of: SN, LdN and AC. ACB, SN and ME wrote the first draft and all authors (ACB, LdN, JFP, RW, AC, MR, ME and SN) made substantial contributions to the final article.

SUPPORTING INFORMATION

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

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