

Late Holocene environmental change and the anthropization of the highlands of Santo Antão Island, Cabo Verde

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Abstract

Cabo Verde was the first tropical archipelago colonized by Europeans. Historians have suggested that the first colonizers initiated archipelago-wide ecosystem degradation, loss of vegetation cover, and erosion. However, the human–environment interactions that led to the archipelago’s current environmental status remain poorly understood. Here, we report the first palaeoecological study of past vegetation change and disturbance regimes for Cabo Verde. We present a 2130-yr old sediment

sequence from a volcanic caldera (Cova de Paúl) located at ~1200 m asl on Santo Antão Island, for which we analyzed fossil pollen, Non-Pollen Palynomorphs (NPPs), charcoal, silica bodies, and grain size distribution. Our analyses do not show evidence of the presence of temperate, tropical or subtropical forests growing on the summits of Santo Antão in pre-human times. The pollen record shows that scrubland and grasslands dominated the highlands and underwent compositional changes ca. 1850 and 1300 cal yr BP. These shifts overlap with erosion phases and are linked to intensified seasonality. Steady rates of sedimentation marked the period 1230 to ca. 350 cal yr BP, but an increase in charcoal concentrations indicate a drying phase. Increases in regional and local fire, peaks of coprophilous fungi and the presence of New World crop pollen (*Zea mays*) are interpreted as the onset of Portuguese settlement of the highlands after 450 BP. Sustained erosion between ca. 400 and 100 BP indicate soil degradation, and the pollen record shows the increase in introduced herbaceous taxa (Rosaceae, *Centaurea*, Verbenaceae) and exotic tree taxa (*e.g.* *Pinus*), while shifting abundances of coprophilous fungi indicate changes in land-use. The record shows stabilization of soils in the last century due to recent afforestation of the highlands. Further palaeoecological studies have the potential to provide further detail of the long-term dynamics of Cabo Verde ecosystems and to inform conservation initiatives.

Keywords Ecological disturbances; Human impacts; Islands; Landscape change; Macaronesia; Palaeoecology

1. Introduction

Oceanic islands were some of the last regions on earth permanently settled by humans (Nogué *et al.* 2017). Their settlement led to major alterations in endemic and native biodiversity (*e.g.* Kirch and Ellison 1994, de Boer *et al.* 2013, Siegel *et al.* 2015, Gosling *et al.* 2017) and involved complex socio-economic and cultural processes (Kirch 2017). In some cases, human impacts were significant even before the islands were permanently settled, due to the introduction of domesticated animals such as goats (*Capra hircus*) as provision for passing ships (Schaefer 2003). Palaeoecology, when integrated with archaeo-historical data, can shed light on the specific impacts of human activities on insular environments, showing the effects of the introduction of taxa and the ecological consequences of land management. Studying millennial-scale sediment records in oceanic islands is relevant to the characterization of disturbance regimes and how the spatial and chronological distribution of disturbance events and processes impact upon island ecosystems (Elmqvist *et al.* 2003, Dearing *et al.* 2006, Froyd and Willis 2008). Thus palaeoecology can provide a long-term perspective to contextualize the socio-ecological challenges (*e.g.* loss of biodiversity, desertification, deforestation, erosion) that oceanic islands are currently facing (Rick *et al.* 2013). Here, we address this challenge within the Macaronesian archipelago of Cabo Verde, focusing on human impacts on the highlands of the Island of Santo Antão (Fig. 1).

Macaronesia is a biogeographical region comprising the Azores, Madeira and the Savage Islands, the Canary Islands, and Cabo Verde. Research in the last decade has sought to reveal how the biodiversity of the Canary Islands and the Azores has responded to Holocene climatic change and to anthropogenic pressures (Fernández-Palacios *et al.* 2016, de Nascimento *et al.* 2016, Nogué *et al.* 2013). Palaeoecological studies have disentangled climate- and human-driven ecosystem disturbance regimes in the Azores (Connor *et al.* 2012, Rull *et al.* 2017), and the analysis of fossil plant and animal remains provides evidence that early human exploitation of Canarian landscapes reached the point of eliminating particular animal and plant species (de Nascimento *et al.* 2009, 2016, Rando

2003, Machado 2007). In addition, historical sources have, for example, documented human-driven deforestation through logging in Madeira (Menezes de Sequeira *et al.* 2007).

Cabo Verde is the only tropical archipelago (14–17° N latitude) of Macaronesia and has a history of socio-ecological crises (famine, mass migration), due to strong climate variability, particularly the occurrence of severe drought (Langworthy and Finan 1997). Our limited knowledge of the human colonization process and subsequent historical developments in Cabo Verde derives from documentary sources. Archaeological studies in the archipelago are still in their infancy, being limited to Santiago (Rodrigues 1997, Sorensen and Evans 2011, Evans *et al.* 2012, 2017), sites surveyed or excavated in São Vicente (Cardoso and Monge Soares 2010) and underwater archaeology. It has been hypothesized that Senegalese and Malian sailors, Mediterranean seafarers in Phoenician times, or Arab sailors in Medieval times, could have made temporary expeditions to the islands (Lobban 1998, Shabaka 2013). However, Cabo Verde was not permanently inhabited by humans until the Portuguese-Genoese colonization, a process that started around 1460 CE (Lindskog and Delaite 1996, Mitchell 2004, Green 2009).

During the 16th century, the archipelago became a central hub in the emerging trans-Atlantic trade system. Due to its strategic location, Portuguese traders used the archipelago as a provisioning point for ships, and it became an integral part of the West African colonies (Green 2009). Around the end of the 16th century, Cabo Verde became progressively isolated as the old trade routes were outcompeted by alternative routes to the New World colonies, and the islands of the Gulf of Guinea became a more popular hub for the slave trade (Garfield 2015). Fragmented population records and historical accounts document the catastrophic consequences of extreme weather events such as hurricanes and long-term droughts that occurred in the 16th, 18th and 19th centuries, and produced famines and epidemics across the archipelago (Patterson 1998). The last great famine suffered in Cabo Verde took place in 1944 CE, but the environmental and socio-economic vulnerabilities of the archipelago continue to create hardship in local communities (Garfield 2015).

Currently, the native plant diversity of Cabo Verde is considered vulnerable to climatic and human-driven environmental disturbances and many endemic species are threatened (Duarte *et al.* 2008,

Romeiras *et al.* 2016). Desertification and land degradation in Cabo Verde have been linked to strong winds, long-term droughts and the denudational effects of torrential monsoon rains, but the human dimension of these processes is still to be assessed from a historical perspective. In response to perceived degradation during the second half of the 20th Century, fast-growing drought-resistant species (*e.g. Prosopis jugliflora*, Agavoideae) have been introduced to protect soils (Lepape 1980). Some of these introductions have shown invasive behavior, spreading at the expense of endemic and other native plant species (MAHOT 2014). Thus, Cabo Verdeans face a trade-off between rapid afforestation to fight erosion and the spread of invasive species such as *Prosopis* that may ultimately endanger endemic flora and generate water management problems by removing ground water (Dzikiti *et al.* 2017). Increased development, mass tourism and economic expansion in Cabo Verde have made conserving its unique biodiversity urgent. Local, regional and international programs are addressing these challenges by designing afforestation and conservation programs. In this context, assessing the long-term natural variability of Cabo Verdean landscapes and their responses to human disturbances and climatic change is key to facing these socio-ecological challenges in the near future.

1.1 Human-environment interaction hypotheses

The degree to which Cabo Verdean biodiversity has been changed by humans is uncertain. Historical accounts of the resources and vegetation cover of the archipelago during early settlement are scarce, and most visitors who described landscapes and documented the local flora did so after three centuries of human presence (Duarte *et al.* 2017). Based on the available literature, three non-exclusive hypotheses about human-driven ecological processes can be tested:

The first hypothesis assumes the presence of temperate, laurel or tropical forests in the highest elevations of the islands before Portuguese colonization (Heckman 1985). Based on the early accounts of travelers and sailors, several authors suggest that Cabo Verde held abundant forested areas that were over-exploited and destroyed by the first settlers (Lindskog and Delaite 1996, Barone 2005). For instance, there are historical descriptions of Cabo Verde as a green luscious archipelago, but they probably referred to an area of Senegal that went by the same name (Romeiras *et al.* 2014).

The second hypothesis suggests that Cabo Verdean landscapes were mostly open grasslands and scrublands, which suffered great disturbances in the first centuries of settlement due to human impacts. It is argued that permanent human settlement rapidly led to overgrazing and erosion, and that colonial landscape mismanagement caused desertification (Green 2009, Benton 2013, Shabaka 2013). Human-driven environmental degradation could have derived from a lack of interest in creating resilient or self-sustainable human communities in the archipelago (Heckman 1985, Lindskog and Delaite 1996).

Finally, a third hypothesis is framed around historical accounts that considered Cabo Verde's ecosystems to have been mostly barren of vegetation due to persistent arid conditions; according to which the settlers' main challenge was making them inhabitable and productive (Garfield 2015, Williams 2015). From this viewpoint, environmental and climatic conditions have been proposed as sufficient cause for the colonial abandonment of Cabo Verde.

We set out to evaluate these hypotheses through analyses of a 2200-yr old sedimentary sequence from the Cova de Paúl volcanic caldera in the highlands (1300 m asl) of the Island of Santo Antão (Fig. 1). To describe long-term disturbance regimes in vegetation we integrated multiple proxies: fossil pollen, non-pollen palynomorphs (NPPs), charcoal particles, silica bodies (phytoliths and diatoms), and grainsize distributions in order to: (1) characterize the vegetation composition in the highlands of Santo Antão during the past 2200 cal. years, (2) determine the degree of variability and disturbance in pre-human ecosystems, (3) document human impacts and explore the causes and consequences of ecological disturbances in Cabo Verde during the Portuguese Colonial period (1460–1975 CE).

2. Regional Setting

2.1 Climate and vegetation

Cabo Verde is a small archipelago situated 600 km west of the African coast (14–17 °N). The archipelago is geographically divided between Northern (Santo Antão, São Vicente, Santa Luzia, Branco, Raso and São Nicolau), Eastern (Sal, Boa Vista, and Maio) and Southern (Santiago, Fogo, Brava, Grande and Cima) island groups. Volcanic activity caused the emergence of the oldest islands

in the Miocene (ca. 20 Ma) (Fernández-Palacios *et al.* 2011, Ramalho 2011) and the islands remain active, with the most recent eruption in Fogo in 2014–2015 (Earth Observatory, NASA). The islands have a variety of soils, mostly volcanic, and steep topographic gradients (the highest peak is in Fogo, reaching 2829 m asl) that support diverse habitats and microclimates. Cabo Verde lies at the same latitude as the Sahelian arid belt, in the African-Sahelian climatic region. Its climate is tropical oceanic, with low levels of rainfall (annual precipitation ranges 80–300 mm in the coast and 1200–1600 mm in the highlands), concentrated during the wet season (July–October) (White 1983, Duarte and Romeiras 2009). The Intertropical Convergence Zone (ITCZ) has a great influence on the archipelago's climate, as its migration to northern latitudes causes the arrival of monsoon-type rains from the southwest (Duarte and Romeiras 2009). The seasonal variation between monsoon rains and aridity favors soil erosion, as ephemeral streams under heavy precipitation rapidly overflow their banks. In addition, as noted by Charles Darwin (2011, originally published: 1897) when visiting the island of Santiago, soil degradation caused by strong winds hamper soil formation, resulting in a sparse vegetation cover. During the dry season (November–June), *Harmattan* winds (African Easterly Waves) (Leroux and Hall 2009) bring Saharan dust and pollen from the east and increase evapotranspiration (Heckman 1985, Hooghiemstra *et al.* 1986, Langworthy and Finan 1997). Sedimentological studies in Sal Island reveal that almost all aeolian dust deposited in Cabo Verde is Saharan (Rognon *et al.* 1996). However, trade winds from the northeast are humid and provide water in the form of fog condensation in the highlands of the highest islands.

Historical descriptions of Cabo Verdean landscapes vary between those that highlight the aridity of the archipelago and others that stress the presence of resources, vegetation, and goods (Table 1). Inconsistencies between accounts could be explained by the variety of islands visited, the season of the visit and/or by shifts in the early socio-ecological systems that developed on the archipelago. Overall, Cabo Verde has high levels of endemism, including ~ 35 % of vascular plant species (Duarte *et al.* 2008) and 90% of the 28 reptile species, and there is a high diversity of arthropods (Duarte and Romeiras 2009). While the archipelago only holds six endemic bird species, 36 species use the archipelago as a breeding area, leaving deposits of guano on islets (Heckman 1985). The endemic

plant species belong to 27 families, the richest families being the Apiaceae, Asteraceae, Boraginaceae, Brassicaceae, Fabaceae, Plantaginaceae, and Plumbaginaceae. The endemic flora has mostly Macaronesian and Mediterranean affinities (Duarte *et al.* 2008). For example, 40% of the endemics are related to Canarian and Madeiran species (Barone 2005), and the endemic flora of the arid areas has similarities with Saharan and Arabian vegetation (Duarte *et al.* 2008). Within the archipelago, 78% of endemic vascular plant species are currently considered threatened, some of which are critically endangered, and others are thought to have become extinct (e.g. *Fumaria montana* and *Eulophia guineensis*) (Duarte *et al.* 2008, Romeiras *et al.* 2016).

Around 20% of the landscape of Cabo Verde is considered forested (FAO 2005), attributable in the main to afforestation with introduced species (*e.g.* *Prosopis*, *Pinus* spp., *Eucalyptus* spp., *Cupressus* spp.; Barone 2005, MAHOT 2014), while a very small fraction corresponds to native woodlands reintroduced in Serra Malagueta (9.78 ha), Santiago island, and Monte Gordo (6.32 ha), São Nicolau island (GEF/UNEP 2015). Most of these native woodlands are restricted to upland areas of the more mountainous islands, and comprise endemic palm (*Phoenix atlantica*), dragon tree (*Dracaena draco* spp. *caboverdeana*) and other thermophilous plant species, such as *Euphorbia tuckeyana*. The lowlands (0–350 m asl) of the islands are arid or semi-arid, and savannah-like halophilous coastal vegetation dominates up to 80-m elevation in some slopes, with native species such as *Suaeda vermiculata* and *Zygophyllum waterlotii*. The higher elevations (from 350 m asl) hold more species-rich vegetation: sub-humid or humid grasslands and scrublands/heathlands, with endemic species such as *Euphorbia tuckeyana*, *Sideroxylon marginata*, and *Echium vulcanorum* (Duarte and Romeiras 2009). In the eastern islands, halophilous and psammophilous (sand-loving) coastal vegetation is dominant, featuring endemics such as *Cyperus crassipes* and *Lotus brunnei*, as these islands are flat and low (Barone 2005).

Table 1: Historical descriptions of Cabo Verdean landscapes summarised from Romeiras *et al.* 2014 and Green 2009.

Source	Date of observations	Island	Vegetation-economic description
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Diogo Gomes (ca. 1420–1500)	ca. 1460 CE	Santiago	▪ Presence of productive fig trees and Dragon trees ▪ Rich pastures
Duarte Pacheco Pereira (1460–1533)	1505-1508 CE	Santiago	▪ Infertility of the land and scarcity of trees
Martin de Centinera	ca. 1572 CE	–	▪ Good provisioning spot: cows, maize, and other supplies ▪ Overgrazing and tree cutting leading to erosion
Sir Francis Drake (ca. 1540–1596)	ca. 1578 CE	Maio, Fogo	▪ Vineyard cultivation, good quality products ▪ Commodious living
Diego de Flores Valdés	1582 CE	–	▪ Sterile land, total absence of provisions
Sir Francis Drake (ca. 1540–1596)	1585 CE	Santiago	▪ Water running in streams ▪ Many gardens with a great variety of cultivars
William Dampier (1651–1715)	1683 CE	Sal	▪ Unfruitful, absence of trees and grasses ▪ Small shrubby bushes
Willem Adriaan van der Stel (1664–1733)	1699 CE	Santiago	▪ Documented endemic species <i>Lotus jacobeus</i>
Amédée Frézier	1712 CE	São Vicente	▪ Dry landscape except in some valleys ▪ Trees (tamarindos), cotton and citrus trees in valleys ▪ Reference to other endemic trees
George Roberts	1722-1724 CE	All archipelago	▪ Fig trees of São Nicolau exploited for wood ▪ Dragon trees used for medicine in São Nicolau

and Santo Antão

- Palm trees on Sal
- A wide variety of crops in all islands
- Lichens in Maio and Boa Vista

Johan Reinhold Forster	1772 CE		▪ Documented numerous endemic species
Charles Darwin (1809–1882)	1832 CE	Santiago	▪ Atmospheric degradation due to strong winds and dry climate ▪ Accumulation of soils in small pockets
Joseph D. Hooker (1817–1911)	1839 CE	Santiago	▪ Arid flats covered by yellow grass ▪ Weedy species, legumes and sunflowers

2.2 Past regional climatic context

Although no palaeoenvironmental study has been carried out to date on Cabo Verde, climatic variations in Northwestern (NW) Africa likely had an effect on the archipelago (Hooghiemstra *et al.* 1992). NW Africa is characterized by the presence of distinct continental vegetation belts linked to strong precipitation gradients (White 1983, Hooghiemstra *et al.* 1986). Shifts in rainfall regimes linked to ITCZ migration have been proposed as the main drivers of vegetation change in the region during the Holocene (Hooghiemstra *et al.* 1988, 2006). A trend of increasing aridity took place during the mid- and late Holocene in NW Africa, after the termination of the African Humid Period that lasted from 14.8 to ca. 5.5 ka yr BP (deMenocal *et al.* 2000, Hély *et al.* 2009). This transition is thought to have caused vegetation changes in the laurel forest of the Canary Islands (Nogué *et al.* 2013) and has been linked to changes in the NW African monsoon (Hooghiemstra 1989) and the North Atlantic climatic systems (Kuhlmann *et al.* 2014).

Nevertheless, how Holocene climatic changes relate to local vegetation change within NW Africa remains uncertain (Lézine *et al.* 2011, Shanahan *et al.* 2015). Variation in recent precipitation in Cabo

Verde echoes that of the West African Sahel, as both are determined by the intensity of African Monsoon and the African Easterly Waves (Cropper 2013), but drought periods in the last centuries have also significantly differed between the islands and the mainland (Patterson 1998). Palaeoecological data from the mud-belt that accumulates off the mouth of the Senegal River suggests a gradual change towards aridity in the western Sahel since the end of the African Humid Period, with brief humid periods 2900–2500 cal yr BP and punctuated strengthening of the monsoon system around 2100 cal yr BP (Bouimetarhan *et al.* 2009). Mollusk oxygen isotopes reveal a drought-free period in the Senegal area from 1490 to 860 cal yr BP, in contrast to the late 20th century, which was marked by Sahelian droughts in the 1970s (Azzoug *et al.* 2012). High-resolution paleo-records comprising the last 2000 years are still rare in the region, and data from Cabo Verde could help improve regional palaeo-climatic and palaeoecological reconstructions.

3. Materials and Methods

3.1. Study site and coring

We carried out the field research in the volcanic caldera of Cova de Paúl, situated at 1200 m a. s.l. at the highest location of the Rivera de Paúl basin in the Northwest of the island of Santo Antão (779 km²), the northernmost island of Cabo Verde (Figure 1). The study site receives 700 mm of rainfall annually (Heilweil *et al.* 2010). The island is estimated to have emerged ca. 7.6 Ma; the last eruption of the caldera took place 90 ka (Plesner *et al.* 2002), and since then it has progressively filled with sediment. The first fieldwork was undertaken in May 2015. Using a percussion corer, we collected a 320-cm sediment core of 7-cm diameter (named Cova-core) from Cova de Paúl (N17°06.397, W025°03.727), including surface material. This core was composed of eleven drives (segments), each of 30 cm, which were labelled and wrapped in plastic and PVC tubes. After transport to the UK, they were preserved in a cold room at ~ 3°C at the Oxford Long-term Ecology Lab at the University of Oxford. During the second expedition (2018), we opened a trench of 1x1 m to inspect the stratigraphy of the first 180 cm of sediment. We described and measured the sediment layers, and obtained a

second set of samples (every 5 cm) from the stratigraphic profile (named Cova-profile) (Supplementary Fig. 1).

There are intrinsic challenges for palaeoecology in Cabo Verde due to the archipelago's aridity. Permanent accumulation of water is extremely rare, as evaporation exceeds precipitation throughout the year (Duarte and Romeiras 2009), and oxidising conditions likely cause the destruction of palynomorphs. There is no standing water in the Cova de Paúl caldera nowadays, but its location ensures abundant humidity throughout the year due to the condensation of clouds brought by the trade winds. The diameter of the caldera is around 0.5 km, and it is currently used for the cultivation of several crops, including corn (*Zea mays*) and potato (*Solanum tuberosum*), and for grazing of cows (*Bos taurus*), donkeys (*Equus asinus*), and goats (*Capra hircus*). The walls of the caldera are covered by introduced tree taxa such as *Pinus*, *Acacia*, *Cedrus*, and *Grevillea*. We selected the lowest point in the caldera, and avoided coring in the active agricultural land. The site is subject to deposition of material from the steep caldera walls (up to 100 m high) due to erosion.

3.2 Dating and Sedimentology

3.2.1 Dating

We obtained 9 Accelerator Mass Spectrometry (AMS) C-14 dates of charcoal, bulk sediments, macro-fossils, and humic acid extractions from 14 Chrono Centre, Belfast, UK, to create an age–depth model using Bacon, a software based on Bayesian statistics that combines radiocarbon dating and other sources of information such as sedimentology (Blaauw and Christen 2011, 2013).

3.2.2 Grain size distribution and zonation

To calculate the distribution of coarse material throughout the core (Cova-core) we weighed a set of 80 1-cm³ samples and sieved them through a 1.0-mm mesh. The remaining material was weighed, and percentages of material larger than 1.0 mm were calculated. We noted the number of clasts larger than 1.0 cm (gravel) and 3.0 cm (pebbles).

To calculate the grain-size distribution of the material <1mm, we used the sieved sediment of 47 samples taken at 8-cm intervals, and at 4-cm intervals in areas of interest (Cova-core). We introduced fractions of the samples in a Mastersizer Hydro, using soil settings for non-spherical grains. The Mastersizer was programmed to carry out 5 measurements, for 20 seconds each. Results were accepted once the standard deviation of DX10, DX50 (median) and DX90 microns fractions was equal to or below 0.5, 0.3 and 0.5, respectively. Results were reported as median grain size values and as percentages of clay, silt, and sand.

Due to the characteristics of the sedimentary core (*e.g.* low preservation of pollen), the zonation was performed using the lithological changes derived from the Grain size distribution data. This allowed us to recognise a number of zones in the record based on data-visualization, placing boundaries in levels with clear lithological changes, such as sharp increases and decreases in grain size.

3.2.3 Loss on ignition

We used a set of 56 1-cm³ samples from the Cova-core, taken at 8-cm intervals, and at 4-cm intervals in areas of interest, for loss-on-ignition analysis (LOI) (Dean 1974, Heiri *et al.* 2001). Samples were weighed in a high-precision scale, then dried in an oven at 50°C for 24 hours. We burned them in a laboratory furnace at 550°C for four hours and at 1000°C for two hours. Samples were weighed after the drying process and the two burnings, and moisture content and LOI were calculated. We used LOI 550°C value as a proxy for organic content.

3.3 Pollen and Non-Pollen Palynomorphs (NPPs)

To analyze pollen and NPPs a set of 72 2-cm³ samples were taken at an average of 4-cm increments throughout the core (Cova-core) and processed at Oxford University. Two *Lycopodium* tablets were added (batch nr 3862), before following a standard preparation procedure using KOH, HCl, and acetolysis mixture (Erdtman 2013). Palynomorphs were floated by using heavy liquid (Sodium polytungstate) at 1.9 gravity. Slides were mounted using glycerine. Pollen grains and NPPs were counted at 400x magnification and diverse types were photographed at 1000x magnification.

To identify the pollen grains we used a reference collection of 25 endemic species collected by the authors in Cabo Verde in 2015, and Beug (2004) and Gosling *et al.* (2013) pollen keys. Pollen was counted until a minimum of 150 exotic *Lycopodium* spores was reached: counts were of 206 pollen grains on average. Levels in which pollen was extremely scarce (less than 10 pollen grains per 1000 *Lycopodium*) were considered barren, and there were 5 levels with very low pollen concentration (counts from 50 to 110 grains). Due to the presence of potentially contaminant pollen grains (*e.g.* *Alnus*, *Betula*, *Abies-Picea* type), we replicated the preparation of 5 samples at the University of Southampton (Figure 2a). This strongly suggests that the presence of these pollen types was not related to contamination. All pollen grains were included in the pollen sum, including herbs, trees and shrubs, potential wetland taxa (Cyperaceae) due to the existence of terrestrial species of this family in Cabo Verde, potential long-distance pollen grains due to the uncertainty of their local origin, and unidentified grains as an unspecified part of the regional vegetation.

We counted NPPs alongside pollen (Figure 2b). We used the following literature for identification focused on Africa: La Serna and Dominguez (2003), Gelorini *et al.* (2011), and Van Geel *et al.* (2003). In slides with a high concentration of NPPs, they were counted until a sum of 300 items was reached, and the number of pollen grains recorded until that moment was noted down. We express NPP percentages in relation to the total number of pollen grains counted when the NPP counting was finalized, allowing percentages that go above 100%. We divided potential coprophilous fungal types into two groups, following Cugny *et al.* (2012) and Gelorini *et al.* (2011): obligate coprophilous (*Sporormiella*, *Podospora*, *Sordaria*,) and non-obligate coprophilous (*Coniochaeta*, *Cercophora*, *Gelasinospora cf. cratophora*, *Delitschia* spp.).

All identified pollen and NPPs were plotted in pollen diagrams using TILIA software, version 2.0.1 (Grimm 1993).

3.4 Charcoal

For analysis of macro-charcoal, a set of 100 2-cm³ samples, collected at an average of 4-cm resolution throughout the Cova-core, were sieved through a 180-µm mesh. Macro-charcoal pieces larger than

180 μm were counted. Micro-charcoal was quantified by counting opaque, black angular pieces between 5 and 100 μm , alongside *Lycopodium* spores, until the total of both sums was >200 (Fisinger and Tinner 2005). The concentration of micro-charcoal was calculated in relation to the known concentration of *Lycopodium*. The aim of analysing macro- and micro-charcoal together was to discriminate signals of local fire (within the caldera) and regional fires (from the rest of the island or blown in from mainland Africa).

3.5 Silica bodies: Diatoms, chrysophytes, and phytoliths

For the analysis of silica bodies, 40 2-cm³ samples were collected at an average of 8-cm resolution along the Cova-core. Samples were processed using HCl and H₂O₂ solutions. Prepared samples were mounted using Naphrax™. For diatom classification, we used a variety of diatom literature (Krammer and Lange-Bertalot 1999a, 1999b, 2000, 2004), and for phytolith identification we used Piperno (2006). In slides with high concentrations of diatoms, we counted until a sum of 250 was reached, and in slides with low concentration, until a sum of 150 was completed. We counted chrysophytes alongside diatoms. Morphologically diagnostic phytoliths were scarce and mostly belonged to Poaceae (Bilobites, Saddles, Rondels, Trapezoid and Bulliform morphotypes) and we counted them alongside diatoms (average sum, 112 phytoliths) (Figure 2c).

5.7 Ordination analysis

To explore the influence of environmental variables on the distribution of pollen types we performed Canonical Correspondence Analysis (CCA) in R (R Development Core Team) using the *vegan* package. We used pollen percentage data expressed as a percentage of the pollen sum and four environmental variables defined from other proxies with similar resolution studied within the record: regional fire regime (micro-charcoal particles per cm³), local fire regime (macro-charcoal particles per cm³), erosion (percentage of material larger than 1 mm per cm³), and presence of herbivores (percentage of coprophilous fungi in relation to the pollen sum).

4. Results

4.1 Sedimentology (grain size distribution) and zonation

Sedimentological analyses (grain size distribution) provided a continuous dataset. The zonation was performed following changes in the lithology (based on grain size distribution data) of the sedimentary sequence. We identified 6 zones through sedimentology levels 305, 250, 160, 100, and 50 cm. Zones were labelled COVA-1 to COVA-6 (Table 3).

In zone COVA-1, the sediments were mainly composed of silt (mean = 74.3%). Clay (mean = 3.8%) and organic content (10.0%) were higher than in the rest of the record, and the mean of the median grain sizes per sample was 20.1 μm . The percentage of sand (mean = 29.1%) and the mean of the median grain size (35.5 μm) increased in zone COVA-2, peaking around 300 and 260 cm. Some gravel was present in this section of the core, and organic content decreased to around 8.5%. In zone COVA-3, silt percentage and organic content returned to levels equivalent to those of COVA-1 and mean of the median grain size decreased slightly. In the uppermost part of zone COVA-3, the mean organic content of sediments slightly decreased (to ~ 9%), and mean grain sizes (mean = 26.9 μm) increased moderately. In zones COVA-4 and COVA-5, the sediments were characterized by large shifts in grain size and the presence of gravel and rocks. They were mainly composed of sand (mean = 62.9 and 59.4%), and median grain sizes increased, reaching values up to 477 μm . Organic content of the sediment was the lowest in the record (mean = 6.4 %). The final section of the record displayed increased percentages of silt (around 55%).

4.2 Chronology

We obtained a total of 9 AMS C-14 dates for Cova-core and Cova-profile (Table 2). We produced an age–depth model using the Bacon calibration program (Blaauw and Christen 2013). We accepted the radiocarbon dates at 320 cm (charcoal), 269 cm (bulk sediment), 251 cm (bulk sediment), and 41 cm (macrofossils). We excluded the following dates: 180 cm (bulk sediment), 172 cm (bulk sediment), 130 cm (humic acid extractions), 112 cm (bulk sediment), 110 cm (bulk sediment) (Figure 3, Table 2). The rejected radiocarbon dates attest to erosion processes between 180 and 110cm, which produced a mix of old and contemporaneous carbon, as old material was re-worked and entered the sediment sequence; they were considered outliers. We set a prior accumulation mean of 10yr/cm

(following Bacon's suggestion to lower it from default mean value 20yr/cm), and defined sections of rapid accumulation of materials or 'slumping' characterized by >30% of material >1mm. We used the median values of the 95% confidence intervals calculated by Bacon to interpret the record (Table 3). However, strong evidence of first human land-use (*Zea mays* pollen) is in accordance with the minimum values of the 95% confidence intervals; we use this set of values to explain the first anthropization processes of the highlands.

Table 2: Radiocarbon dates and sample specific data from the Cova de Paúl sediments. In bold, dates that were used for the age–depth model. F14C (fraction modern carbon) value is reported in ages between CE 1950 and the present.

Depth	Core/profile	Material	Uncalibrated Age	Error	Calibrated range (95% confidence interval BP)
41 cm	Cova-core	Macrofossils	F14C: 1.1252	0.0038	-7 – -45
110 cm	Cova-core	Bulk sediment	1564	23	1526 – 1404
112 cm	Cova-core	Bulk sediment	1819	51	1871 – 1686
130cm	Cova-profile	Humic acid extractions	1531	26	1597 – 1394
172 cm	Cova-core	Bulk sediment	1607	26	1552 – 1473
180 cm	Cova-core	Bulk sediment	1474	31	1407 – 1307
251 cm	Cova-core	Bulk sediment	1265	14	1263 – 1181
269 cm	Cova-core	Bulk sediment	1533	29	1424 – 1355

320 cm	Cova-core	Charcoal	2170	30	2308 – 2219
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Table 3: Lithological zones for the Cova de Paul record including chronological data, lithological characterizations and number of pollen samples. Date with an asterisk indicate that they were interpreted using the minimum age estimates of the 95% confidence interval, reported in parenthesis.

Zone	Depth interval	Time interval	Time period (using median value of 95% confidence interval)	Lithological characterization based on grain size distribution	N pollen samples
COVA-6	50-0	100 yr	100 cal yr BP– present	Uniform silt/sand sedimentation	9
COVA-5	100-50	~ 150 yr	260–100 cal yr BP	Highest grain sizes, sand-dominated, rocks and gravel	3
COVA-4	165-100	~ 250 yr	500*(~350)–260 cal yr BP	Increase in grain size, sand-dominated, sections with gravel	4
COVA-3	250-165	~ 800 yr	1230–500* cal yr BP	Uniform sedimentation, silt-dominated	14
COVA-2	305-250	670 yr	1900–1230 cal yr BP	Increases in grain size (peaks in levels 300cm, 260cm)	8
COVA-1	320-305	230 yr	2130–1900 cal yr BP	Uniform sedimentation, silt-	4

				dominated	
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4.3 Pollen and Non-Pollen Palynomorphs

Pollen taxa from local and regional origin, and wind-transported pollen from NW Africa, and potentially even from the Iberian Peninsula (Hooghiemstra et al., 1986), were recorded (Supplementary table 1). Four sections of the core were barren of palynomorphs: 270–245cm, 165–140 cm, 120–190cm and 70–55 cm.

4.3.1 Pollen

The pollen assemblage of zone COVA-1 was dominated by Asteraceae tubuliflorae (up to 43%), Asteraceae liguliflorae (up to 34%) and Poaceae (up to 40%), and it also contained some of the highest levels of Brassicaceae (13%) and Apiaceae (12%) (Figure 4). *Artemisia*, Cannabaceae, *Rumex*, *Pinus* and *Morella-Corylus* were present (~ 1%). Cyperaceae and Amaranthaceae (often associated) appeared in zone COVA-2, peaking at levels 304 and 272 cm (up to 25%). Lamiaceae, *Acacia*, *Picea*, *Alnus*, *Betula*, *Convolvulus*, Euphorbiaceae, Moraceae and *Ilex* were present in low percentages (~ 1%).

Zone COVA-3 was characterized by the dominance of Asteraceae tubuliflorae (up to ~ 80%) and Poaceae (up to ~32%) and a decrease in Asteraceae liguliflorae. *Cirsium*-type, *Centaurea*, Solanaceae, type CV-4, Oleaceae, and Sapotaceae-type were recorded as new taxa. The uppermost part of COVA-3 was characterized by an increase in *Pinus* pollen (up to 10%), which was then continuously present in the record. The last sample of the zone showed increases in *Centaurea*, *Cirsium*-type, and Rosaceae (between 5 and 12%). The first pollen of *Zea mays* occurred at 172 cm. *Juglans*, *Quercus*, *Salix* and Fabaceae were also present in this zone, and there was a sustained decrease in Brassicaceae and Apiaceae pollen.

In zone COVA-4, Cyperaceae, Amaranthaceae and *Artemisia* showed a gradual increase and Asteraceae tubuliflorae a gradual decrease. CV-4 pollen was more abundant in this zone (up to 5%), and *Acacia* pollen had a sustained presence. Grains of Lamiaceae and Cerealia were present. The

almost total absence of Cyperaceae and Amaranthaceae grains, and the decline of Poaceae characterized zone COVA-5, as well as the drastic increase of Verbenaceae (up to ~ 36%), and the presence of *Cirsium*-type (up to 7%). Cerealia, *Juglans*, Oleaceae, Urticaceae, Ericaceae, and *Carex* were recorded as new taxa. *Morella-Corylus*, Euphorbiaceae, and Fabaceae had highest levels in the record in this zone. Asteraceae liguliflorae peaked at 72 cm (77%), and *Artemisia* increased at 48 cm (13%). Zone COVA-6 was dominated by Cyperaceae, Amaranthaceae, and *Artemisia* pollen. *Pinus* had stable representation (~ 5%), and *Acacia* and Cerealia were present. Most taxa present in COVA-4 and 5 were absent in this last zone.

4.3.2 Non-Pollen Palynomorphs

NPPs were scarce in section COVA-1. The best represented types were *Coniochaeta*, *Sordaria*, *Podospora*, *Gelasinospora* cf. *cratophora*, *Glomus* sp., *Curvularia*, monolete and trilete fern spores, *Lycogala*, *Ganoderma*, and *Althernari* (Figure 5). Section COVA-2 was characterized by an increase in number and diversity of NPPs. We recorded *Cercophora*, *Sporormiella*, *Apiosodaria*, *Diporotheca*, *Delitschia* spp., types CVf-1, CVf-2, *Tetraploa*, *Spegazzinia*, *Rosellinia*, CVf-3, CVf-4, Pteridaceae spores, *Bactrodesmium*, *Xylaraceae*, *Rhythidospora*, and *Fusarium*. All NPPs of COVA-1 and 2 were present in the first section of COVA-3, but generally in minor quantities. The last section of COVA-3 was characterized by an increase in *Coniochaeta*, *Cercophora*, *Gelasinospora* cf. *Cratophora*, *Diporotheca*, Hyphopodia of *Gaeumannomyces* and CVf-5 types, which presented some of the highest levels of the record, peaking at level 192cm. In contrast, there were few fern spores.

COVA-4 was characterised by a gradual increase in *Sporormiella*, *Diporotheca* and *Delitschia* spp. *Phragmidium* was recorded as a new taxon. Zone COVA-5 was characterized by a dramatic increase in a total number of spores mainly due to the predominance of type CVf-1, and by the decrease or absence of most of the rest of the assemblage. Monolete fern spores also increased. The last sample of this zone (48 cm) showed an assemblage equivalent to zone COVA-4, with an increase in *Glomus* spores. Zone COVA-6 (50–0 cm) was characterized by the dominance of the full coprophilous assemblage (*Coniochaeta*, *Sordaria*, *Podospora*, *Gelasinospora* cf. *cratophora*, *Sporormiella*,

Apiosodaria, *Diporotheca*, *Delitschia* spp.) the presence of *Rosellinia*, and a decrease in monolete and trilete fern spores, in contrast to an increase in Pteridaceae (fern) spores.

4.4 Silica bodies:

4.4.1 Diatoms

In the diatom record, section COVA-1 was dominated by the diatom species *Navicula mutica* (avg. 71%) (Figure 6). It had moderate levels of *Hantzschia amphioxys* (avg. 16%) and *Navicula contenta* was present. Zone COVA-2 featured an increase in *Fragilaria virescens*, *Hantzschia amphioxys*, *Gomphonema angustum*, *Pinnularia borealis*, *Nitzschia amphibia* and *Diploneis parma*, the presence of *Orthoseira* and the highest numbers of *Chrysophyte* stomatocysts. A progressive decline of *Navicula mutica* characterized zone COVA-3, as well as an increase in *Fragilaria virescens* (up to 40%), *Achnantes undulorostrata*, *Pinnularia borealis*, *Diploneis parma* and the sustained presence of *Cymbella alpina*. There were lower concentrations of diatoms in the uppermost levels of zone COVA-3, so sums were low (~150 diatoms). Here, and in zone COVA-4, there was a clear dominance of *Fragilaria virescens* (between 30 and 60%), the sustained presence of *Nitzschia amphibia*, and an increase in *Amphora lybica*. COVA-4 showed the highest peaks of *Cymbella alpina* (up to 16%). COVA-5 featured the presence of *Epithemia*, and COVA-6 showed a progressive increase in *Hantzschia amphioxys* (up to 45%) and a decrease in *Aulacoseira*.

4.4.2 Phytoliths

The phytoliths identified in the record belong mostly to the family Poaceae (rondels, saddles, bilobites, bulliforms and wavy trapezoids), and small percentages (around 5 %) belong to Cyperaceae. There was, notably, a minimal presence of palm (echinate) phytoliths in zones COVA-3 and 4. An increase in wavy trapezoid cells (up to 29%), often associated with agricultural landscapes, occurred at the end of COVA-3 and continued in subsequent zones.

4.5 Charcoal

Zones COVA-1 and COVA-2 were characterized by discontinuous macro-charcoal at low abundances and moderate levels of micro-charcoal ($\sim 20,000$ per cm^3) (Figure 2). The first section of zone COVA-3 was characterized by an increase in concentrations of micro-charcoal (up to $74,000$ per cm^3) and low presence of macro-charcoal (avg. $1/\text{cm}^3$), while its uppermost part was characterized by high concentrations of macro- (up to 7 particles per cm^3 in level 187cm) and micro-charcoal (avg. $25,000/\text{cm}^3$). Micro-charcoal levels decreased in zone COVA-4 and COVA-5 (average $14,712/\text{cm}^3$ and $7,848/\text{cm}^3$) while macro-charcoal levels increased (average $3.1/\text{cm}^3$ and $3.75/\text{cm}^3$). The last levels of COVA-5 showed a decrease in micro- and macro-charcoal, but COVA-6 was characterized by high levels of macro- and micro-charcoal.

4.6 Canonical Correspondence Analysis

The plot of the CCA shows the two most important gradients of pollen associations that are best explained by a linear combination of the four environmental variables (Figure 7). Axis 1 accounted for 53% of explained variance (eigenvalue 0.28) and Axis 2 accounted for 33% (eigenvalue 0.16). The analysis reveals a close negative relationship between position on axis 1 and the presence of herbivores (correlation score -0.92), whereas position on axis 2 is positively related to increased evidence of regional fires and reduced local fires and erosion (correlation scores of -0.95 and -0.71 respectively). Taxa such as *Convolvulus*, Cyperaceae, Amaranthaceae, *Artemisia* and *Acacia* are associated with evidence of increased herbivory. Samples that plot with these taxa correspond to anthropization phases of the highlands (*e.g.* levels 176cm, 120cm, 40–14cm). Increased evidence of local fires and erosion corresponds with increases in taxa such as Cerealia, *Carex*, Verbenaceae and Ericaceae, which plot in the bottom-right of the graph. These pollen types with high negative axis 2 scores were abundant in samples within levels 88–80cm (that plot with the taxa), characterized by high grain sizes and increased macro-charcoal concentrations. Taxa such as Sapotaceae-type, *Rumex* and *Quercus* are associated with evidence of regional fires but limited local fires and erosion, and with low levels of herbivore activity. Samples that plot with these taxa (upper-right quadrant of the graph) are representative of the pre-human landscape (*e.g.* levels 320–280cm). Taxa that plot in the

centre of the ordination, such as Rosaceae, Fabaceae, Asteraceae and Brassicaceae, do not exhibit much variation corresponding with the tested environmental variables.

5. Discussion

Palaeoecological studies provide relevant information on the pre-human natural variability of insular ecosystems by identifying species turnover and disturbance regimes – the distribution of pulse (intermittent) disturbances acting on an ecosystem through time – and their impact on local environments (Elmqvist *et al.* 2003, Dearing *et al.* 2006). Moreover, palaeoecological studies have also provided information on how human settlements and the associated land management have changed the dynamics of ecosystem disturbances on oceanic islands worldwide (Mack and D’Antonio 1998, Nogué *et al.* 2017). Anthropogenic ecosystem degradation, including the spread of invasive species (Reaser *et al.* 2007, Ficetola *et al.* 2018), has been linked to the loss of resilience of ecosystems, whereby natural pulse disturbances, which typically occurred intermittently, give way to chronic disturbances (with near-continuous disturbance episodes) of ecosystems (Paine *et al.* 1998, Bengtson *et al.* 2003).

In the absence of lakes in Cabo Verde, volcanic calderas have proved to be good natural sediment traps preserving palaeoecological proxies such as fossil pollen. The multi-proxy analysis from Santo Antão volcanic caldera enabled us to analyse the disturbance regimes pre- and post- Portuguese colonization and to hypothesise relationships between erosion, fire history, and ecological succession processes (*e.g.* Ejarque *et al.* 2015, Castilla-Beltrán *et al.* 2018).

The process of permanent settlement of the nine inhabited islands of Cabo Verde lasted at least half a century (1460–1510 CE; Green 2012). The exact date of the first establishment of a permanent community in Santo Antão is unknown, but it is safe to assume that it had taken place by 1550 CE, as estimates based on historical documents (administrative censuses) estimated a population of 400 inhabitants in the island by 1580 CE (Patterson 1988). Difficulties in dating zones COVA-3 and COVA-4 of the Cova de Paúl record do not allow us to confidently ascertain the specific timing of

human impact within Santo Antão's highland environments. We interpret as indicators of potential European anthropogenic changes the peaks in non-obligate coprophilous fungal spores, the occurrence of new pollen types (including the presence of crop pollen *Zea mays*, supplementary figure 2), and the increase in macro-charcoal concentrations in levels 192–160cmMaize (*Zea mays*) is thought to have been brought to Cabo Verde from Brazil between 1500 and 1550 CE (its first mention in historical sources is from Santiago Island ca. 1535 CE), and experimentation with these cultivars became common throughout the archipelago (Miracle 1965, Moran 1982, Green 2009). The median age estimates within the 95% confidence interval of our age-depth model (760–500 BP) are too early for New World crops to have arrived in Cabo Verde. We therefore use the minimum age estimates within the 95% confidence interval, ca. 500–350 cal yr BP (1450–1600 CE), which yield plausible ages in accordance to the biostratigraphy. We report these ages as circa (ca.) cal yr BP to highlight the chronological uncertainties within this section of the record.

The following sections discuss the environmental reconstruction for Santo Antão in detail and the contribution of our results to understanding 1) Late Holocene environmental change and disturbance regimes (COVA1-3) and 2) Anthropization processes after human settlement (COVA4-6).

5.1 Late Holocene open grasslands/scrublands and erosion phases (COVA-1, 2): 2130-1230 cal yr BP

Our results show that pre-human environmental conditions in the highlands of Cabo Verde covering the period from 2130 to 1230 cal yr BP comprise periods of disturbance and phases of erosion with seasonally wet environments (ca. 1850 and 1300 cal yr BP). During the period from 2150 to 1900 cal yr BP (zone COVA-1), the volcanic caldera supported an open landscape composed of scrubland and grasslands dominated by Asteraceae, Poaceae, Brassicaceae, and Apiaceae taxa (Fig. 3). Moreover, the NPP assemblage at this time also indicates the presence of a fern-rich landscape with low herbivore presence (low levels of coprophilous fungi). Low concentrations of micro- and macro-charcoal indicate that local and regional fires were scarce. The dominance of the diatom *Navicula mutica* suggests moderately saline soils (Van Dam *et al.* 1994).

Levels characterized by an increase in median grain size (300 and 260 μ m) suggest that the caldera underwent processes of erosion concentrated in two main periods: ca.1850 and 1300 cal yr BP (zone COVA-2). Deposits were more mineralogenic in these periods and included gravel. Such erosion phases might indicate pulse disturbances linked to extreme weather events, such as tropical storms, which are known to have been typical in Cabo Verde during the past few centuries (Patterson 1998), or multi-year periods with greater than average precipitation. The increase in pollen percentages of Cyperaceae and Amaranthaceae might indicate that halophilous vegetation and sedges grew in the mountain slopes and within the caldera, indicating moist local conditions. The CCA analysis reveals the potential association of these taxa with the presence of native fauna (*e.g.* lizards, nesting birds) as indicated by the moderate increases in coprophilous fungal spores (*Cercophora*, *Sporormiella*, *Apiosodaria*, *Delitschia* spp., *Gelasinospora cratophora*) (Wood *et al.* 2011). It is likely that vertebrate populations would have benefited from an increased availability of moisture in the highlands. In addition, the increase in the diversity of parasitic and saprophytic fungal communities could indicate the increase in plant biomass and/or arrival of new plant taxa in the highlands; for instance, *Tetraploa* is usually a parasite of Cyperaceae plants, while *Spegazzinia* and *Curvularia* infect grasses (Gelorini *et al.* 2011). The rising percentages of *Fragilaria virescens* and *Aulacoseira granulata*, diatoms of wetter soils and standing water, during the erosion pulses, suggests that seasonal ephemeral wetlands formed occasionally on Cova de Paúl. High levels of *Chrysophyte* stomatocysts indicate that wetland vegetation grew near the site when conditions were optimal.

Within a regional setting, erosion periods observed in Cova could be linked with enhanced fluvial deposition indicative of intensified monsoons in the Senegal region. For example, rapidly fluctuating fluxes of pollen, dinoflagellate cysts, fresh water algae, and plant cuticles in the sediment deposits of the Senegal River (960 km from Cova de Paúl) at ca. 2150 cal yr BP were interpreted as an increase in sedimentation rates produced by flash flood events (Bouimetarhan *et al.* 2009). Moreover, while no precise chronology exists for the Lake Guiers record in Senegal (ca. 1000 km from Cova de Paúl), phytoliths that show the development of swamp grasses are estimated to have occurred around 2000 BP (Alexandré *et al.* 1997). Chronological uncertainties at all localities may explain the slight

asynchrony between Cabo Verdean and Sahelian indicators of extreme weather disturbances (~300 years). It is also possible that in a period of enhanced regional variability, driven by changes in the northward extent of the ICTZ, both areas were affected but there was real short-term asynchrony. Finally, at the continental scale, high-resolution palaeoenvironmental records in Cameroon (central Africa) show that the period between ca. 2500 and 2000 yr BP was relatively dry, with an increase in seasonality, which led to erosion and forest retreat (Maley and Brenac 1997). In Cabo Verde, the development of seasonal wetlands and erosion could indicate punctuated phases of pronounced seasonality caused by intensified monsoon systems alternating with intensified dry seasons.

5.2 System stabilization and first evidence of anthropization (zone COVA-3): 1230 -ca. 300 cal yr BP

The sedimentation regime in Cova de Paúl became stable from 1230 (median value of the 95% confidence interval) to ca. 350 cal yr BP (minimum value of the 95% confidence interval) (zone COVA-3) and was characterized by silt-dominated deposition. Vegetation growing within the caldera during this period showed a progressive increase in Asteraceae and Poaceae, indicating the continuity of an open landscape of scrubland and grasslands, enriched with the sporadic presence of Solanaceae, CV-4, and Oleaceae. An increase in fungal spores of *Bactrodesmium*, found in wood and bark (Gelorini *et al.* 2011), indicates woody vegetation was present. Very low values of Sapotaceae-type pollen could indicate the local scarce presence of the endemic tree *Sideroxylon marginata*. A general decrease in abundance of fern spores indicates less moisture availability, and a rise of regional fires is reflected in higher levels of micro-charcoal. Indeed, CAA analysis suggests an association between regional fire regimes and pollen types dominant in this period. Overall, these results support an interpretation of increasing dryness. The diatom assemblage adds information on moisture patterns: for example, increases in *Cymbella alpina*, *Amphora pediculum*, *Pinnularia borealis*, and *Diploneis parma* and their replacement of *Navicula mutica* suggests a seasonally wet environment as these species tolerate wet-to-dry conditions. Based on ecological indicator scores tabulated in Van Dam *et al.* (1994), this assemblage could also indicate less saline soils.

The lack of evidence of erosion or extreme weather events from ca. 1230 to ca. 350 cal yr BP (zone COVA-3) in the Cova de Paúl record suggests a geomorphically stable period; in this period there was

little vegetation change. This finding is compatible with palaeoclimatic evidence derived from oxygen-isotopic ratios from fossil shells in the Saloum Delta, Senegal (ca. 1050 km from our site), indicating a drought-free, climatically stable period between ca. 1500 and 900 BP (Azzoug *et al.* 2012). The stabilization of local conditions could be linked to the emergence of regional semiarid (Sahelian) conditions from ca. 2000 yr BP onwards (Lezine 1989, Alexandré *et al.* 1997), without periods of intensified monsoon that have a disruptive erosive effect.

A close examination of the record between 192 and 165 cm (zone COVA-3, ca. 500–350 cal yr BP, based on minimum values of 95% confidence intervals) reveals a succession of changes in the palynomorph assemblage, charcoal, and sedimentology that may reflect the first human impacts within the landscape. First, the highest peak of spores of *Coniochaeta*, *Cercophora* and *Gelasinospora cf. cratophora*, non-obligate coprophilous fungi, in level 192 cm, could indicate local presence of livestock dung in the caldera. Two other spore types, *Gaeumannomyces* and CVf-5, and the diatom type *Cymbella alpina* (typical of moist soils with high nutrients) also peak at this level, which suggests a change in local soil conditions, potentially associated with the arrival of domesticated herbivores. In addition, a high concentration of micro-charcoal (mean = 25,990 per cm³) and the first peak in macro-charcoal was documented at level 187 cm. The pollen record shows changes around this depth; *Zea mays* was identified at level 172 cm. In level 168 cm, increases in *Cirsium*-type, *Centaurea*, and Rosaceae are related to the proliferation of previously rare or newly introduced plants in the caldera.

5.3 Colonial landscapes, chronic disturbances, and highland afforestation (Zone COVA-4, 5, 6): ca. 350 cal. yr BP-present

From ca. 350 to 250 cal yr BP (zone COVA-4), our record shows human-induced environmental changes in the highlands of Santo Antão, such as the introduction of new taxa (*e.g.* Rosaceae and *Pinus*), the pressure of introduced herbivores on local vegetation, and vegetation removal for agricultural activities. The deposition of high quantities of sandy material from the caldera walls and slopes, starting in level 165 cm (ca. 350 cal yr BP), indicates the onset of a long phase marked by erosion. We interpret this section of the record as the occurrence of multiple disturbances, such as

overgrazing and vegetation burning, which together with physical disturbances (*e.g.* extreme weather conditions in the 17th and 18th centuries) caused the washing away of highland soils. These factors merged to form a chronic disturbance. Deposits of coarse material, including gravel and pebbles, also indicate a fast rate of sedimentation. The lower concentrations of micro-charcoal (while macro-charcoal levels were high), could mean that the regional background levels of microscopic and volatile charcoal particles were mixed in larger quantities of sediment each year (Sup. Figure 1).

Lower organic content reflects the high mineral content of the sediments. Most samples lacked diatoms, as algae would either not have survived the arid conditions or, if they did, were not preserved. The levels with some preservation show dominance of *Fragilaria virescens*, indicating the intermittent formation of ephemeral seasonal ponds. In these environmental conditions, levels with good preservation of palynomorphs show the progressive formation of marshy grasslands, as indicated by increases in Cyperaceae and Amaranthaceae pollen. Cerealia pollen suggests the establishment of locally cultivated fields. Furthermore, there was afforestation of the highlands with native and alien species, as evidenced by the rising levels of *Pinus* and *Acacia*. Human activities in the caldera included herding of large domestic herbivores, as indicated by the progressive increase in *Sporormiella* and *Podospora* fungal spores, and in the rest of the coprophilous fungal assemblage.

NPPs and pollen in the period between 250 and 100 cal yr BP (COVA-5) show change in land-use linked to the lack of livestock in the highlands. This is indicated by the absence of coprophilous fungal spores in the NPP record. In addition, a new pollen assemblage dominated by Verbenaceae, Asteraceae liguliflorae, *Carex*, *Cirsium*-type, and Urticaceae, and the presence of Agavoideae suggests arid conditions and the succession of invasive and native ruderals in disturbed soils. This shift could indicate responses to the effects of decadal droughts in the island during the 18th century, as historical sources remark that in times of hunger and epidemics in islands like Santo Antão, often almost all domestic animals were killed (Patterson 1998). The increase in long-distance pollen provides support for a reduction of local vegetation biomass caused by arid conditions and soil degradation.

Finally, during the last 150 yr (zone COVA-6, 100 cal yr BP-present), afforestation efforts reflected in the increase in *Pinus* and *Acacia* pollen achieved the relative stabilization of local soils, which led to the reduction of soil in-wash and produced a silt-dominated soil matrix. The caldera was used for agricultural and livestock herding activities. Land preparation for economic activities is evidenced by peaks in *Glomus* spores, fungi that grow on exposed roots of vegetation, and *Artemisia* pollen, potentially from the endemic *Artemisia gorgonum*, which are commonly ruderal. Seasonally moist local conditions are indicated by the Cyperaceae in the pollen record and the dominance of *Hantzschia amphioxys* and *Fragilaria virescens* diatoms. Taxa that expanded at the onset of the anthropization process (Rosaceae, *Cirsium*-type) disappeared from the record. Long-distance pollen was mostly absent, probably masked by increased local pollen rain.

5.4 Long-distance vs. local vegetation signals

As the pollen diagram shows (Fig. 3) our analysis revealed a pollen assemblage component that we attribute to long-distance transport, due to the absence of these taxa in Cabo Verde today (Arechavaleta *et al.* 2005). The presence of a long-distance pollen component (*e.g.* *Abies-Picea*, *Ilex*, *Betula*, *Alnus*) likely reflects the transport of pollen by the trade winds. Accordingly, our initial interpretation is that pollen of these taxa were transported by winds from Europe, North Africa and the Canary Islands (Hoooghiemstra *et al.* 2006) and deposited from the clouds that accumulate along the NW façade of the Ribera do Paúl. This assemblage is almost constant throughout the record and its presence is likely a reflection of the low pollen production of the Cabo Verde vegetation, due to low plant biomass and the dominance of entomophilous strategies in the native flora, as has been shown for some Canarian vegetation types (de Nascimento *et al.* 2015). In addition, other common pollen types, such as Cyperaceae, could have also been transported from West African savannahs and Sahelian areas by wind (Hooghiemstra and Agwu 1986). However, there are several species of endemic *Carex* in Cabo Verde and the abundance of this pollen type in the record, as well as the presence of Cyperaceae phytoliths, suggest that Cyperaceae pollen was mostly produced by local vegetation.

A complementary hypothesis is that some these taxa were locally present, but in small numbers. For instance, in the pre-human period (2130-ca. 400 BP), the occurrence of *Acacia* and Sapotaceae-type and Moraceae pollen could indicate the local presence of the endemic trees *Acacia caboverdeana*, *Sideroxylon marginata* and *Ficus sycomorus* spp. *gnaphalocarpa*. Future expeditions to the islands will enable a comparison with reference pollen material. It could also be hypothesized that Canarian or North African taxa such as *Pinus*, *Morella*, or *Corylus* might have been brought by migrating birds in pre-human times, developing communities in the cloud belt of Ribera do Paúl. This option seems less likely, but it could be explored by assessing other local records. In addition, the increased presence of *Juglans*, *Fraxinus* and Ericaceae, if produced by local plants, could reflect experimentation with exogenous plants for agriculture, afforestation and medicinal purposes (Romeiras *et al.* 2011). Failure of some of these taxa to adapt to local environmental conditions could explain their absence from the present-day Cabo Verdean landscapes.

5.5 Hypotheses testing

In this study, we set out to test three main hypotheses about human-driven ecological processes in Cabo Verde:

Our results suggest that no substantial thermophilous, temperate or laurel forests existed in the highlands of Santo Antão during the last 2130 years. Small percentages of pollen of potentially endemic taxa suggest the rare local presence of endemic trees. The presence of European, Canarian and North African forest taxa in low amounts within the pollen record is most likely explained by long-distance transport, but this should be further scrutinized in future palaeoecological studies. If present at lower elevations, forest formations did not produce sufficient amounts of microfossils to be observed in the caldera deposits.

We confirm that dynamic mosaics of grassland and scrubland were continuously present in the highlands, as indicated by the fossil pollen assemblages. These vegetation communities, as well as communities of decomposers and locally occurring diatoms, responded to shifts between different climatic conditions during the late Holocene, likely influenced by variable migrations of the ITCZ,

particularly around 1850 and 1300 cal yr BP. These phases of intensified seasonality and monsoon activities could have been similar to pulse disturbances recorded in the region of the Senegal River around 2100 cal yr. BP (Bouimetarhan *et al.* 2009). From 1230 cal yr BP to ca. 350 cal yr BP, the progressive development of an arid phase saw an increase in regional fires in the highlands of Santo Antão.

Our results showed that the highlands of Santo Antão were not barren of vegetation. On the contrary, we have shown evidence of how early settlements transformed the local landscapes. Anthropization processes consisted of the introduction of livestock, followed by the use of fire for land clearing, the establishment of agricultural lands, the expansion of introduced weedy vegetation and sustained erosion. Human and herbivore pressures on the landscape likely left soils unprotected, and the occurrence of extreme climatic conditions during the 17th, 18th and 19th centuries caused soils to be washed away. Periods of marked change in fungal and vegetation communities indicate a discontinuity in animal husbandry activities. Increases in arboreal pollen in anthropic phases reflect early and recent human attempts to afforest parts of the island with introduced species.

6. Conclusions

This first palaeoenvironmental study covering the past 2130 yr for Cabo Verde has generated the following main conclusions: There was no evidence of temperate, tropical or subtropical forests in pre-human times: instead, scrubland and grassland taxa were present. We identified erosion phases in the oldest part of the record that could be linked to intensified monsoonal activity and increased seasonality ca. 1850 and 1300 cal yr. BP. In contrast, from 1230 cal yr BP to ca. 350 cal yr BP sedimentation became stable, and increased charcoal concentrations suggest a drying phase. After the Portuguese settlement of the highlands the pollen record showed an increase in weedy and introduced herbaceous (*e.g.* Rosaceae, *Centaurea*, Verbenaceae) and tree taxa (*e.g.* *Pinus*). Shifting abundances of coprophilous fungi (*e.g.* *Sporormiella*) indicated stark changes in land-use around the 19th century, while the record showed relative stabilization of soils in the 20th century until the present due to afforestation of the highlands.

Finally, our work is indicative of the complexity of human–environment relationships and ecological disturbance regimes in island ecosystems, and in particular in the island of Santo Antão. Further research using palaeoecological proxies here and in other volcanic calderas will help reveal the relationships between human actions, climatic changes, and local environmental variation in the whole archipelago. Long-term datasets provide information on past distributions of endemic vegetation communities that are relevant to inform conservation actions. Such work could encourage education-based initiatives that show that local landscapes and biodiversity can be valued as natural and cultural heritage worth conserving.

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Figure captions

Figure 1: Maps of Macaronesia including trade winds (AEW stands for African Easterly Waves) and the northern limit of the ITZC, Cabo Verde and the location of Cova de Paúl coring site, Santo Antão. Raster data from maps from Natural Earth: <https://www.naturalearthdata.com/> and ArcMap (ESRI 2016).

Figure 2:

Pollen: Selected pollen grains documented in Cova de Paúl sediments. All scale bars are 10 µm. a. Apiaceae, b. Brassicaceae, c. Agavoideae, d. Lamiaceae, e., f. *Acacia*, g. Sapotaceae-type, h. CV-4, i. Cannabaceae, j. *Juglans*, k. *Zea mays*, l. Cerealina, m. *Centaurea*, n. *Cirsium*-type, o. Rosaceae, p. Oleaceae, q. CV-1, r. *Fraxinus*, s. CV-2, t. Fabaceae-type, u. Ericaceae, v. Urticaceae, w. Verbenaceae, x. *Rumex*, y. *Abies-Picea*, z. *Betula*, aa. *Convolvulus*, ab. Solanaceae, ac. *Carex* ad. *Ilex*, ae. *Alnus*, af. *Morella-Corylus*, ag. *Quercus*.

NPPs: Selected NPPs documented in Cova de Paúl record. All scale bars are 10 µm. a. CVf-23 (HdV 149), b. CVf-5, c. *Bactrodesmium*, d. *Curvularia intermedia*, e. *Tetraploa* sp., f. *Spegazzinia tessarthra*, g. *Coniochaeta*, h. *Cercophora*, i. *Sporormiella*, j. *Sordaria*, k. CVf-3 (OU-119), l. *Delitschia* spp., m. *Diporotheca* spp., n. CVf-1, o. *Glomus* sp., p. CVf-2, q. *Pithomyces*, r. *Alternaria*, s. *Chaetomium*, t., u. Sordariaceae (HdV-55), v. CVf-4, w. *Meliola* sp., x. CVf-24, y. CVf-21 (cf. HdV-86).

Diatoms/Phytoliths: Selected diatoms and phytoliths documented in Cova de Paúl record. All scale bars are 10 µm. a., b. *Navicula mutica*, c. *Hantzschia amphioxys*, d. *Aulacoseira granulata*, e. *Pinnularia borealis*, f. *Diploneis parma*, g. *Cymbella alpina*, h. *Gomphonema minutum*, i. *Nitzschia amphibia*, j. *Stephanidiscus minutulus*, k. *Orthoseira*, l. *Achnantes exigua*, m. *Navicula contenta*, n. *Cyclostephanos* aff. *ocellata*, o. Bilobite cf. *Panicoid*, p. Bilobite, cf. *Cloridoid*, q. Bilobite cf. *Aristoideae*, r. Wavy trapezoid, s. Rondel, t. Cyperaceae cell, u. Echinete, v. Conical echinate, w. Saddle cf. *Cloridoid*, x. *Chrysophyte* stomatocysts.

Figure 3: Stratigraphic diagram showing age–depth model, charcoal abundance and sedimentology of Cova de Paúl record, Santo Antão. Age–depth model produced with Bacon (Blaauw and Christen 2013). Grey area shows 95% confidence intervals based on calibrated C14 dates. Horizontal grey bands indicate sections of fast sediment deposition (‘slumps’) based on sedimentology data. Red lines indicate the Age and depth of RC dates rejected for the model, based on inversions. Composite of Grain size distribution: Clay (%) in yellow, Silt (%) in blue, Sand (%) in green.

Figure 4: Stratigraphic diagram showing pollen percentages of Cova de Paúl record, Santo Antão. Pollen sum includes all taxa. Presence of rare types (values < 1%) plotted with dots. Horizontal white bars placed in sections in which pollen was not found or was not adequately preserved.

Figure 5: Stratigraphic diagram of non-pollen palynomorph (NPPs) percentages of Cova de Paúl record, Santo Antão, including fern and fungal spores. Percentages calculated in relation to the pollen sum.

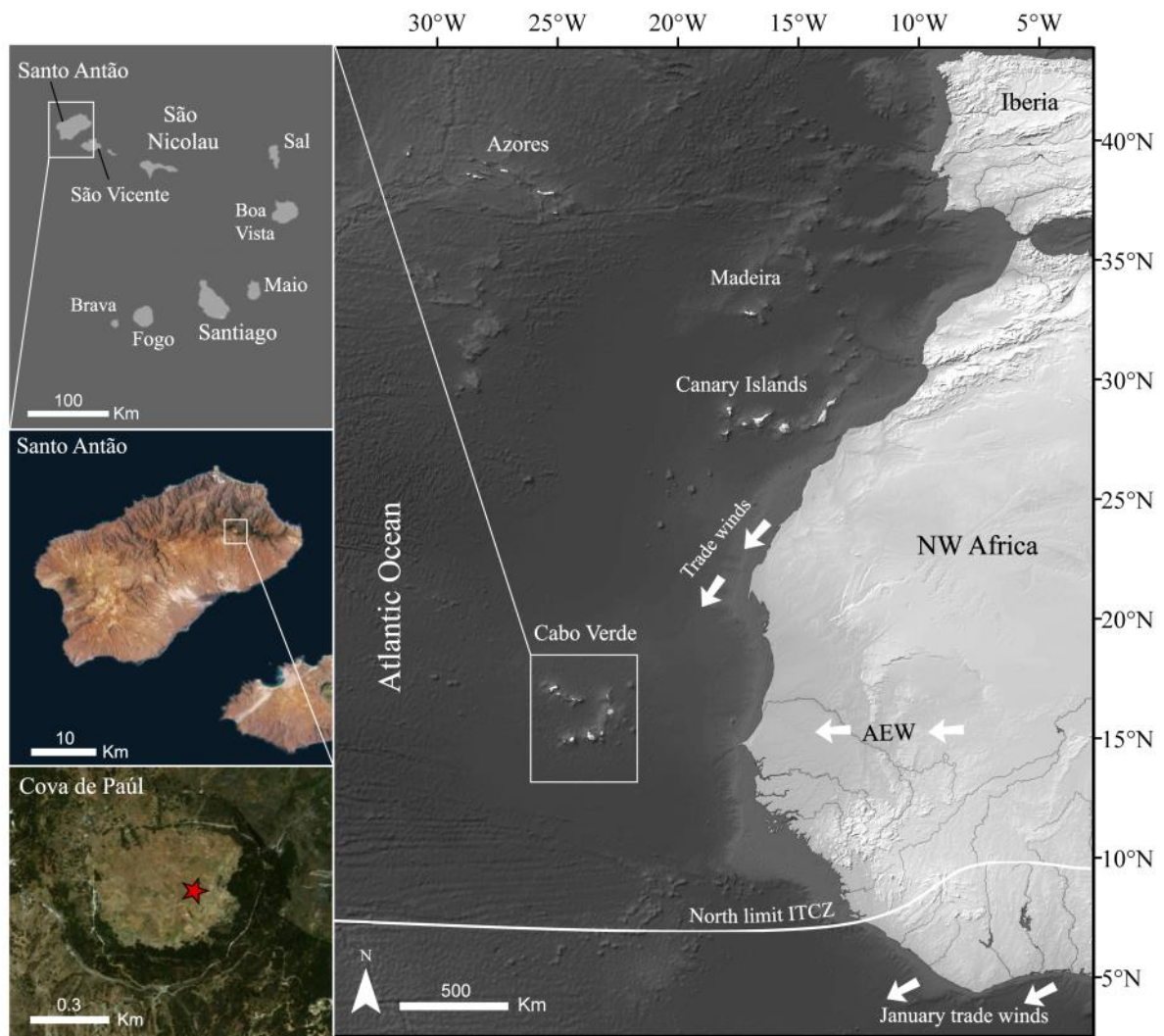
Figure 6: Stratigraphic diagram showing diatom percentages of Cova de Paúl record, Santo Antão. We used silhouettes to highlight the three dominant diatom species, and bars for the rest of the assemblage. Percentages of Crysophytes and selected phytoliths are shown in relation to diatom sum.

Figure 7: Canonical Correspondence Analysis plot of pollen types (red), core levels (black) with four environmental variables (dark blue) of Cova de Paúl record, Santo Antão. We used pollen percentage data expressed as a percentage of the pollen sum and four environmental variables for the analysis: regional fire regime (micro-charcoal particles per cm³), local fire regime (macro-charcoal particles per cm³), erosion (percentage of material larger than 1 mm per cm³), and presence of herbivores (percentage of coprophilous fungi in relation to the pollen sum).

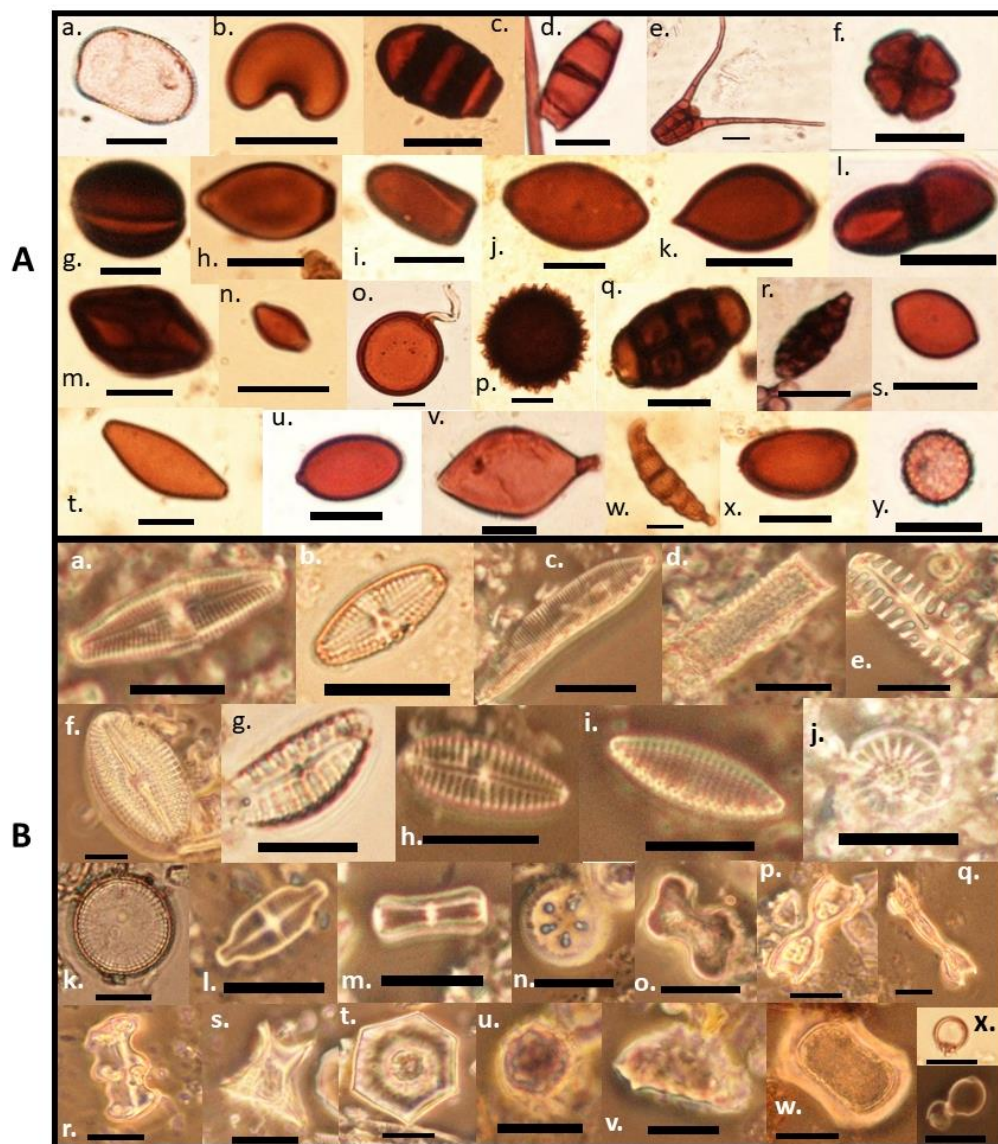
Supplementary figure 1: Stratigraphic diagrams of the soil profile (Cova-profile) and the core (Cova-core) of Cova de Paúl, Santo Antão. Right panels show the stratigraphy of the soil profile, including sediment descriptions, the sampling strategy (one sample every 5cm), and the sample taken for radiocarbon dating. Right panels show the Grain size distribution of Cova-core (bars) and micro-charcoal influx (curve).

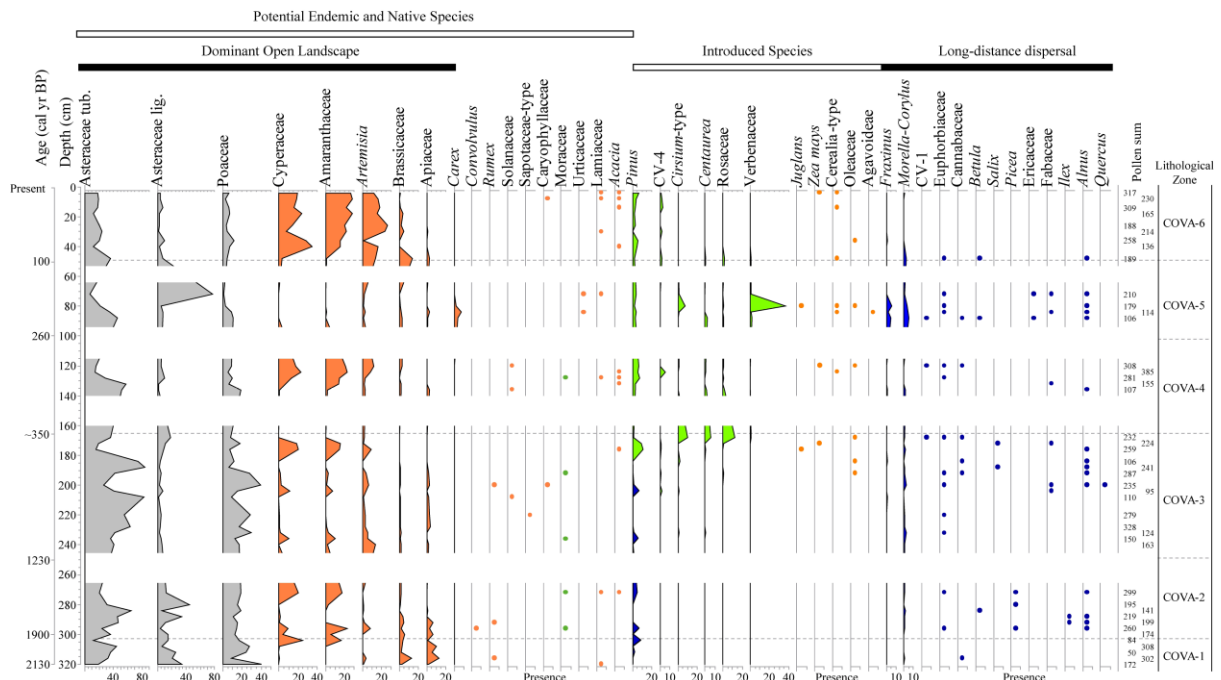
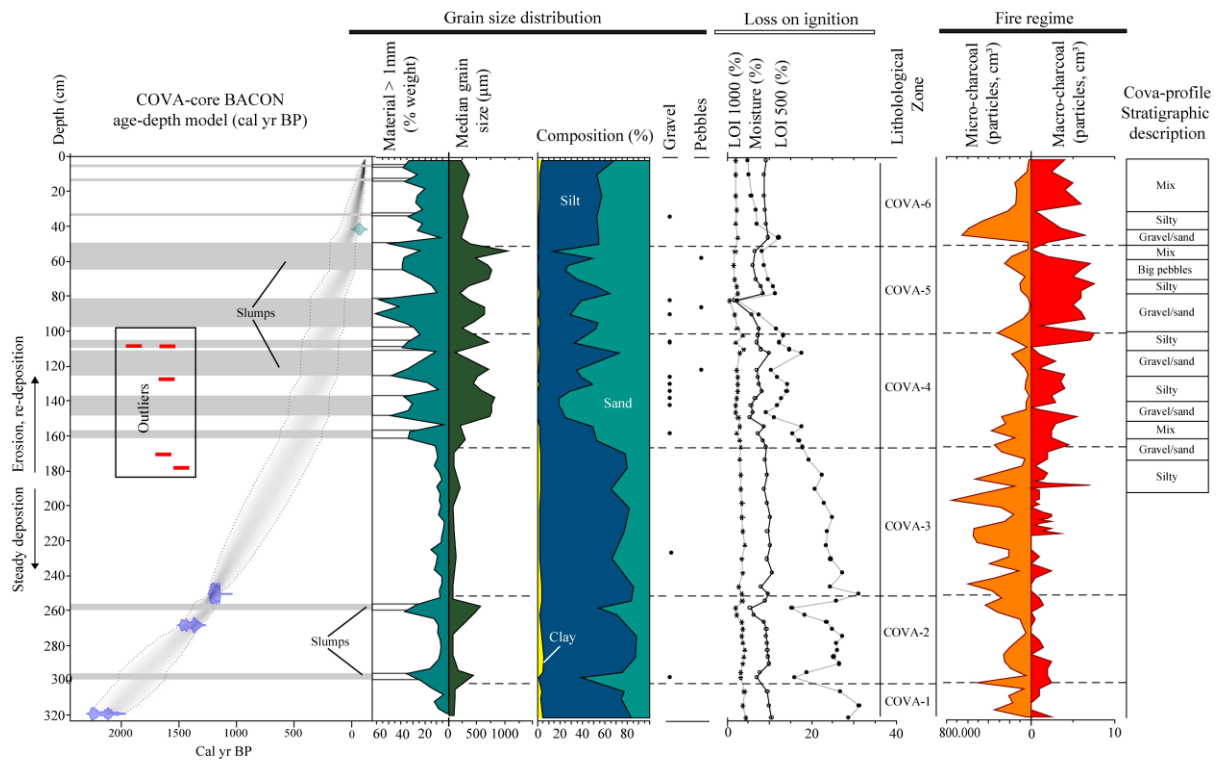
Supplementary figure 2: Photographs of *Zea mays* pollen from COVA-core levels 172 and 120cm (magnification 1000x), Cova de Paúl, Santo Antão. These grains were identified as *Zea mays* based on their diameters ca. 70 μm (note that these are minimum diameter measurement, as grains are folded). Average *Zea mays* grains range between 58 and 99 μm (Sluyter 1997).

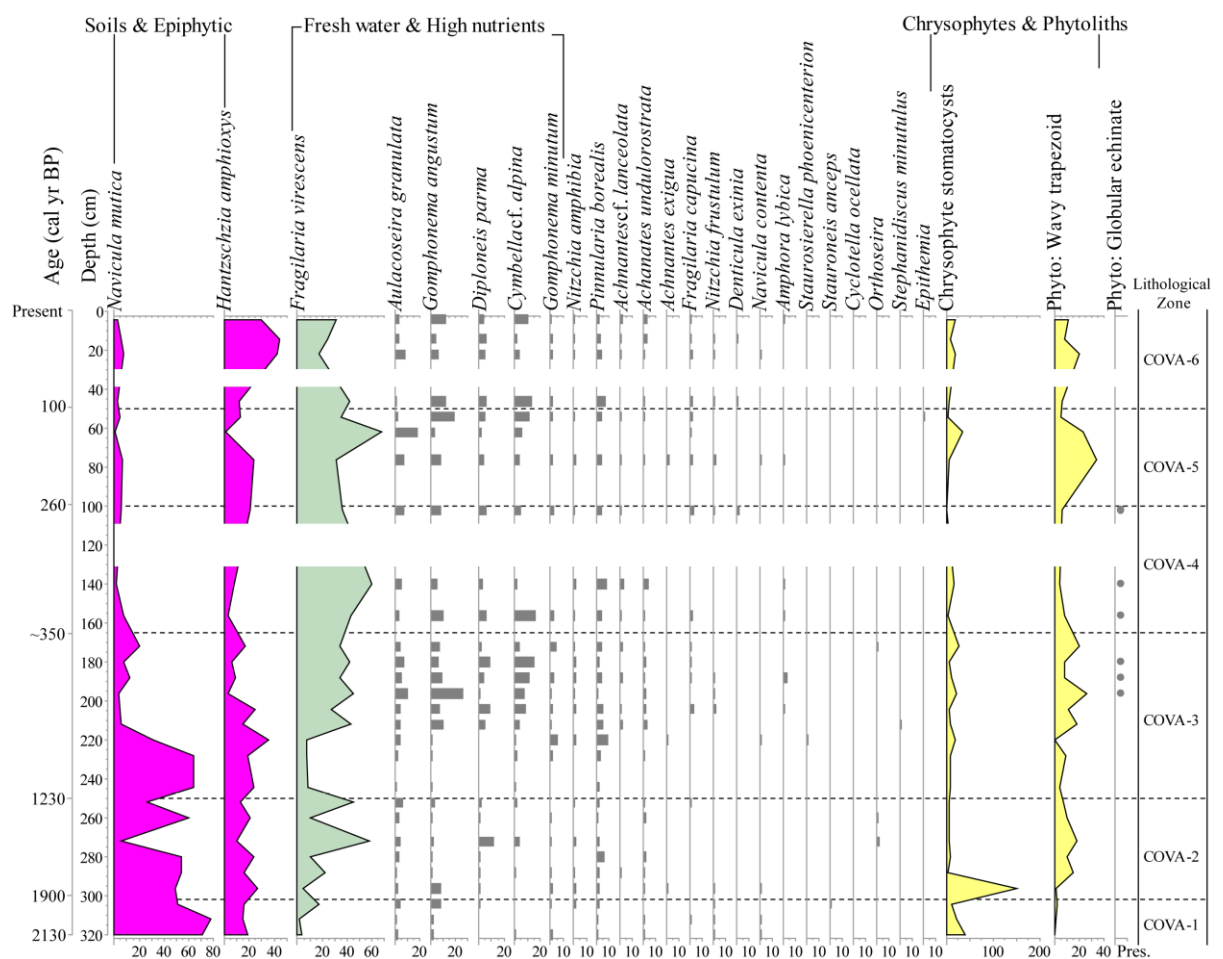
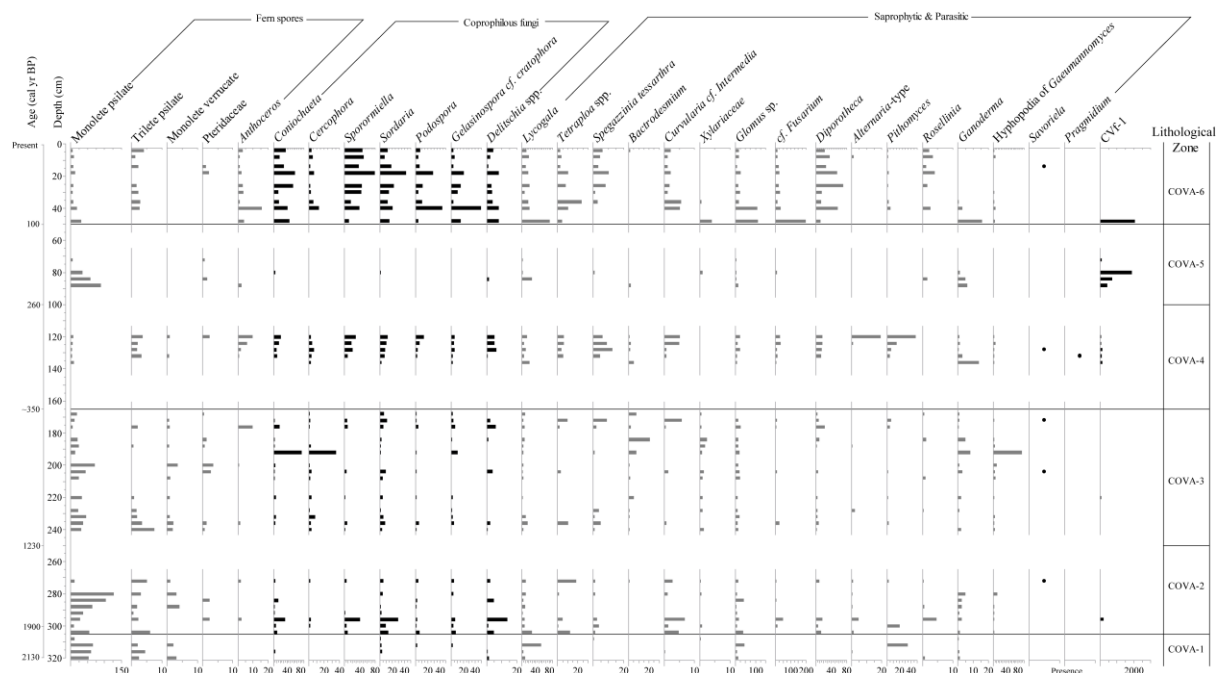
Supplementary figure 3: A: Bacon age–depth model for COVA-core, Cova de Paúl, Santo Antão. Grey area shows 95% confidence intervals based on calibrated C14 dates. Horizontal grey bands indicate sections of fast sediment deposition (‘slumps’) based on sedimentology data (>30% material > 1 mm). B: Markov Chain Monte Carlo iterations for the Bacon model. C: Distribution of accumulation rate D: distribution of memory (the degree of dependence of the accumulation rate of a level in relation to the level above it). E: ‘Ghostplot’ of sedimentation rate per age.

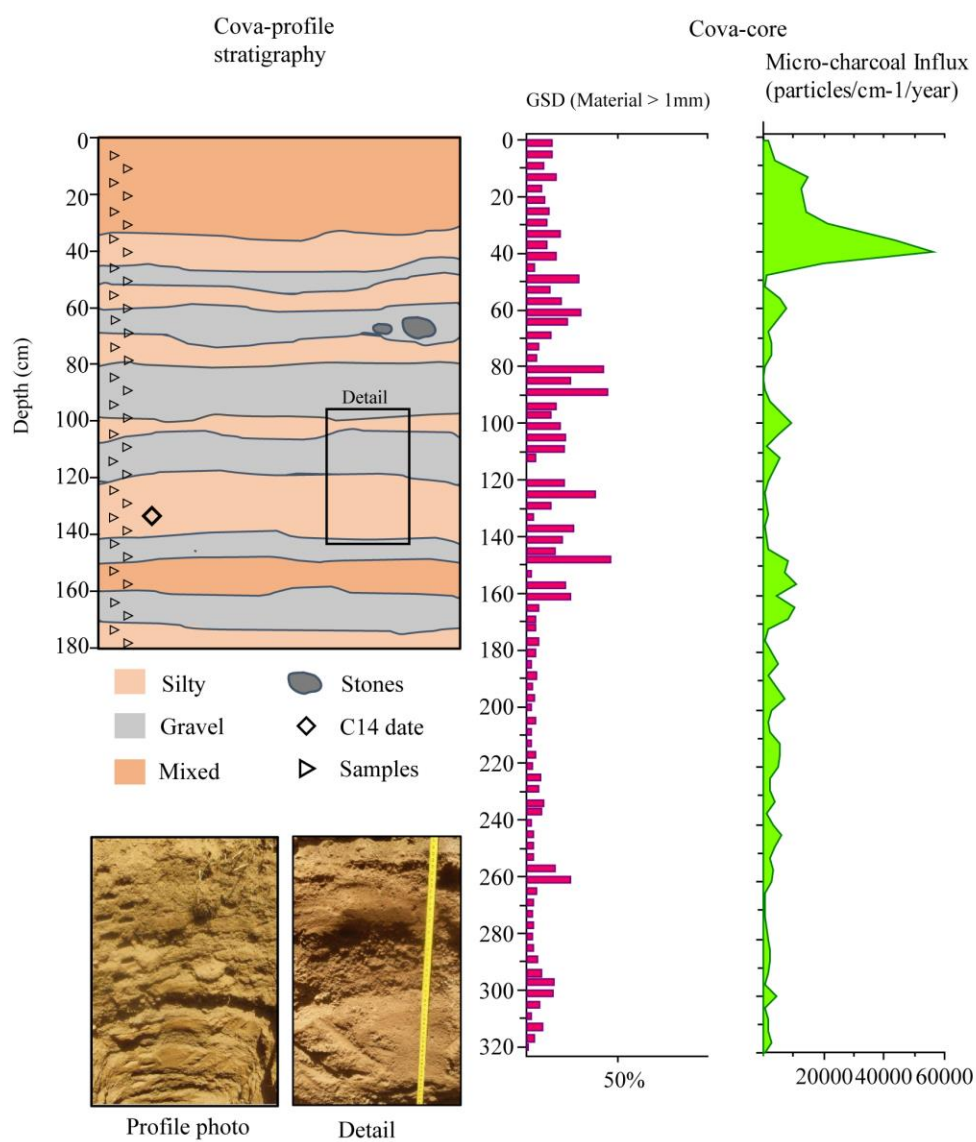




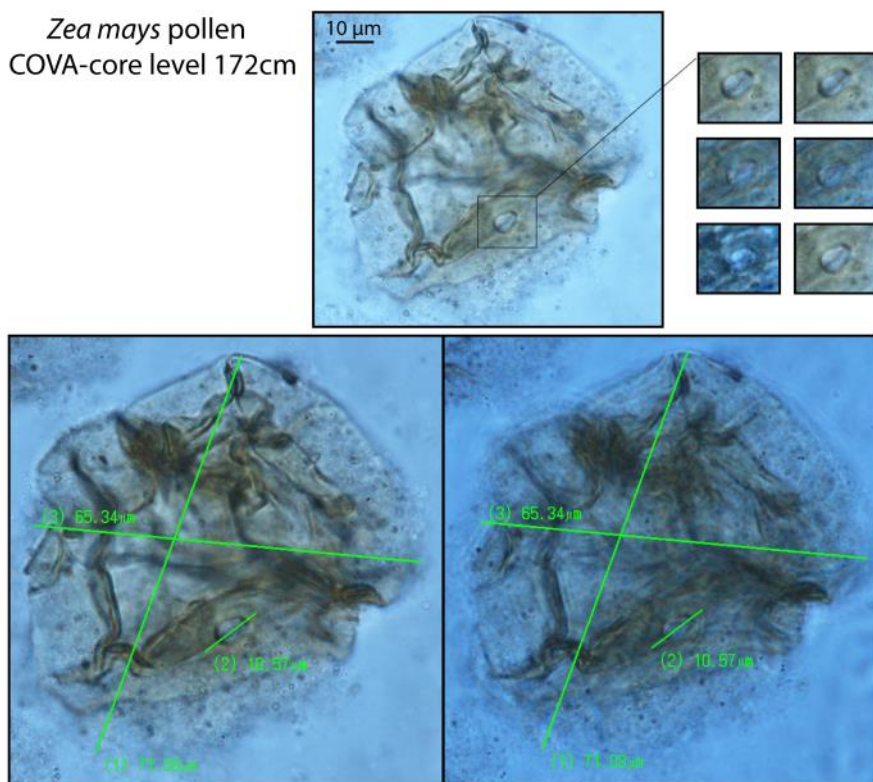




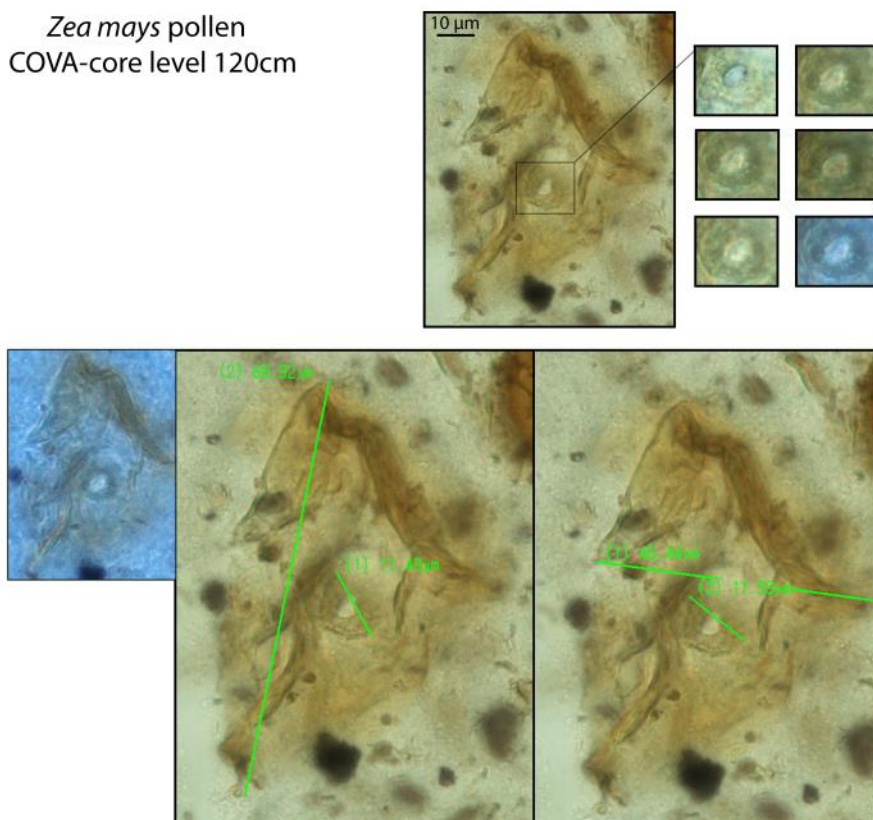


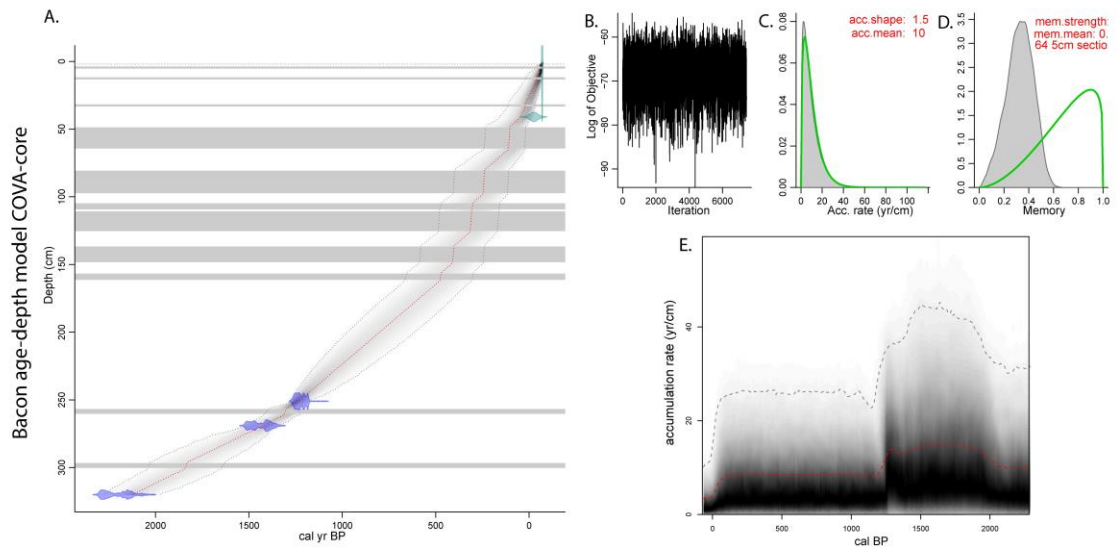


Zea mays pollen
COVA-core level 172cm



Zea mays pollen
COVA-core level 120cm





Supplementary Table 1: Pollen families identified the Cova de Paúl record indicating number of endemic, native and introduced species that exist in Cabo Verde (based on Arechavaleta *et al.* 2005 and Rivas-Martínez *et al.* 2017).

Pollen Family/genus	N. of endemic plant spp.	N. of native (non-endemic) or probably native plant spp.	N. of introduced or probably introduced plant spp.
<i>Abies-Picea</i>	X	X	X
Agavoideae	X	X	2 (<i>e.g. Agave sisalana</i>)
<i>Alnus</i>	X	X	X
Amaranthaceae	X	3 (<i>e.g. Aerva javanica</i>)	18 (<i>e.g. Amaranthus hybridus</i>)
Apiaceae	6 (<i>e.g. Melanoselinum bischoffii</i>)	X	7 (<i>e.g. Anethum graveolens</i>)
Asteraceae	17 (<i>e.g. Artemisia gorgonum</i>)	11 (<i>e.g. Blumea viscosa</i>)	38 (<i>e.g. Ambrosia maritima</i>)
<i>Betula</i>	X	X	X
Brassicaceae	12 (<i>e.g. Diplotaxis antoniensis</i>)	6 (<i>e.g. Cakile maritima</i>)	9 (<i>e.g. Brassica nigra</i>)
Cannabaceae	X	X	X
Caryophyllaceae	2 (<i>e.g. Polycarpaea gayi</i>)	2 (<i>e.g. Polycarpaea nivea</i>)	5 (<i>e.g. Arenaria leptoclados</i>)
Chenopodiaceae	1, <i>Suaeda caboverdeana</i>	7 (<i>e.g. Arthrocnemum franzi</i>)	3 (<i>e.g. Atriplex halimus</i>)
Cyperaceae	2. (<i>e.g. Carex antoniensis</i>)	15 (<i>e.g. Cyperus amabilis</i>)	19. (<i>e.g. Eleocharis geniculata</i>)
Ericaceae	X	X	X
Euphorbiaceae	1, <i>Euphorbia tuckeyana</i>	8 (<i>e.g. Andrachne telephioides</i>)	17 (<i>e.g. Acalypha crenata</i>)
Fabaceae (incl. Caesalpiniaceae and Mimosaceae)	10 (<i>e.g. Acacia caboverdeana</i>)	25 (<i>e.g. Faidherbia albida</i>)	53 (<i>e.g. Cajanus cajan</i>)
<i>Fraxinus</i>	X	X	X
<i>Ilex</i>	X	X	X
<i>Juglans</i>	X	X	X

Lamiaceae	2 (e.g. <i>Lavandula rotundifolia</i>)	5 (e.g. <i>Salvia aegyptiaca</i>)	12 (e.g. <i>Hyptis pectinata</i>)
Malvaceae	X	13 (e.g. <i>Abutilon pannosum</i>)	X (e.g. <i>Malvastrum americanum</i>)
Moraceae	X	3 (e.g. <i>Ficus sycomorus</i> ssp. <i>gnaphalocarpa</i>)	1, <i>Ficus carica</i>
<i>Morella-Corylus</i>	X	X	X
Oleaceae	X	X	3 (e.g. <i>Olea europaea</i>)
Pinaceae	X	X	1, <i>Pinus canariensis</i>
Poaceae	4 (e.g. <i>Aristida cardosoi</i>)	64 (e.g. <i>Enteropogon prieuri</i>)	70 (e.g. <i>Cenchrus biflorus</i>)
<i>Quercus</i>	X	X	X
Rosaceae	X	X	3. (e.g. <i>Prunus persica</i>)
Rubiaceae	X	4 (e.g. <i>Kohautia aspera</i>)	8 (e.g. <i>Mitracarpus hirtus</i>)
<i>Rumex</i>	X	1, <i>Rumex vesicarius</i>	3. (e.g. <i>Rumex crispus</i>)
Salicaceae	X	X	1, <i>Salix fragilis</i>
Sapotaceae	1, <i>Sideroxylon marginata</i>	X	X
Solanaceae	1, <i>Withania chevalieri</i>	1, <i>Withania somnifera</i>	26. (e.g. <i>Capsicum baccatum</i>)
Urticaceae	1, <i>Forsskaolea procrudifolia</i>	2 (e.g. <i>Parietaria debilis</i>)	2 (e.g. <i>Laportea aestuans</i>)
Verbenaceae	1, <i>Stachytarpheta fallax</i>	X	4 (e.g. <i>Lantana camara</i>)