

## Using multiple palaeoecological indicators to guide biodiversity conservation in tropical dry islands: The case of São Nicolau, Cabo Verde

Alvaro Castilla-Beltrán<sup>a,\*</sup>, Ivani Duarte<sup>b</sup>, Lea de Nascimento<sup>c</sup>, José María Fernández-Palacios<sup>c</sup>, Maria Romeiras<sup>d</sup>, Robert J. Whittaker<sup>e,h</sup>, Margarita Jambrina-Enríquez<sup>f</sup>, Carolina Mallol<sup>f</sup>, Andrew B. Cundy<sup>g</sup>, Mary Edwards<sup>a</sup>, Sandra Nogué<sup>a</sup>

<sup>a</sup> School of Geography and Environmental Science, University of Southampton, Highfield, Southampton SO17 1BJ, United Kingdom

<sup>b</sup> Parque Natural do Monte Gordo, Ministério da Agricultura e Ambiente, Republic of Cabo Verde

<sup>c</sup> Island Ecology and Biogeography Group, Instituto Universitario de Enfermedades Tropicales y Salud Pública de Canarias, Universidad de La Laguna, Spain

<sup>d</sup> Linking Landscape, Environment, Agriculture and Food (LEAF), Instituto Superior de Agronomia (ISA), Universidade de Lisboa, Tapada da Ajuda, 1349-017 Lisboa, Portugal

<sup>e</sup> School of Geography and the Environment, University of Oxford, Oxford OX1 3QY, United Kingdom

<sup>f</sup> Archaeological Micromorphology and Biomarker Research Laboratory, Universidad de La Laguna, Spain

<sup>g</sup> GAU-Radioanalytical, School of Ocean and Earth Science, University of Southampton, National Oceanography Centre (Southampton), Southampton SO14 3ZH, United Kingdom

<sup>h</sup> Center for Macroecology, Evolution and Climate, GLOBE Institute, University of Copenhagen, Copenhagen, Denmark

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### ABSTRACT

Tropical dry islands are currently facing major challenges derived from anthropogenic and climatic pressures. However, their trajectories of environmental change, which could provide relevant information applicable to biodiversity conservation, remain understudied. This is mainly due to poor micro-fossil preservation and irregular sediment deposition. Multi-proxy palaeoecological analyses spanning decades to 1000s of years can add perspective as to how vegetation, fungal communities, and the fauna responded to previous natural and anthropogenic disturbances. In São Nicolau, Cabo Verde, we used palaeoecological methods to analyse a highland soil profile (1000 m asl) dated to 5900 cal yr BP. We analysed how vegetation (abundances in pollen of native and introduced species, and leaf wax *n*-alkanes), ferns and fungal communities (abundance of non-pollen palynomorphs) varied over time in relation to fire (charcoal concentration) and erosion regimes (grain sizes and elemental composition). Between 5000 and 400 cal yr BP the highlands held native woody taxa such as *Euphorbia tuckeyana*, *Dracaena draco* subsp. *caboverdeana*, and *Ficus*, taxa that can be used for future reforestation programmes. From 400 cal yr BP to the present day, replacement of native taxa by introduced and cultivated taxa (*Pinus*, *Eucalyptus*, *Asystasia*, *Opuntia*) has occurred. Vegetation burning and grazing caused loss of vegetation and erosion, acting as conjoined drivers of scrubland degradation. This dataset helps to set historically contextualised restoration goals such as the re-introduction of native species, monitoring of recently introduced species and control of free grazing. This can serve as a model system for the conservation of tropical dry islands' biodiversity.

### 1. Introduction

Anthropogenic activities have been a major driver of environmental degradation in oceanic islands worldwide (Whittaker and Fernández-Palacios, 2007; Whittaker et al., 2017). Tropical dry islands are also especially vulnerable to extreme climatic events such as drought and tropical storms (Hamann, 2004; Holmgren et al., 2006), which are

projected to increase in the next decades (Cai et al., 2014). Studying long-term ecological change in semi-arid environments is challenging due to poor micro-fossil preservation and irregular sediment deposition (Brunelle et al., 2018). However, the understanding of long-term trajectories (i.e. trends of environmental change) is relevant for the management of vulnerable small island populations, especially in the light of increasing anthropogenic impacts and projected global climate

\* Corresponding author at: Geography and Environmental Sciences, Building 44 Room 1077, University of Southampton, Highfield, Southampton SO17 1BJ, United Kingdom.

E-mail address: [a.castilla-beltran@soton.as.uk](mailto:a.castilla-beltran@soton.as.uk) (A. Castilla-Beltrán).

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change (Holmgren et al., 2006). In this context, palaeoecological studies can provide information to determine ecological baselines (e.g. Nogué et al., 2017), past vegetation distributions (e.g. de Nascimento et al., 2009), changes in composition and structure (e.g. Nogué et al., 2013), fire regimes (e.g. McWethy et al., 2009), and long-term ecosystem variability (Froyd and Willis, 2008; Wilmshurst et al., 2013). There are several examples of the application of palaeoecological data to assess relevant conservation strategies in island ecosystems (e.g. Boessenkool et al., 2013; Burney and Burney, 2007). For instance, palaeoecological studies carried out in the Galápagos Islands have also demonstrated the importance of taking a long-term perspective when developing criteria for the designation of non-native/native status of plant taxa (van Leeuwen et al., 2008; Coffey et al., 2011).

Cabo Verde is the only tropical archipelago of the biogeographical region of Macaronesia (the Azores, Madeira, the Salvages, the Canary Islands, and Cabo Verde). Due to the scarcity of historical documents and archaeological research (Evans et al., 2017), little is known about the past abundance, distribution, and variability of endemic vegetation in the archipelago and for example the potential impacts of the drying trend that took place in NW Africa (5500 BP onwards) after the end of the African Humid Period (ca. 9000–5500 BP) (deMenocal et al., 2000). Understanding past ecological change in relation to drying and extreme climatic events is relevant to reduce the uncertainty of island species responses in a changing climate. It is also uncertain how human settlement affected the islands' ecosystems (Romeiras et al., 2014; Castilla-Beltrán et al., 2019). There is currently no evidence of human settlement in Cabo Verde before the arrival of the Portuguese in 1460 CE (490 BP). The first two islands to be settled by Europeans were Santiago and Fogo (Green, 2012). In the case of São Nicolau, historical documents (administrative censuses) suggest that a permanent community was already established by 1580 CE (370 BP) (Patterson, 1988). The presented study site is located in Monte Gordo Natural Park within the highlands of São Nicolau Island. Monte Gordo Natural Park contains the largest remaining fragments of the endemic *Euphorbia tuckeyana* scrubland to be found in the archipelago, as well as endemic species such as *Dracaena draco* subsp. *caboverdeana* and *Sideroxylon marginatum*. In terms of number of endemic species and its size, it is one of the most important of the nine Natural Parks in the archipelago. The Park management plan (MAA/DGA 2008) highlights that the main threats impacting the native vegetation in the park are: the introduction of exotic plants (e.g. *Lantana camara*, *Pinus*, *Eucalyptus*), agricultural practices and grazing, deforestation, and the fragmentation of natural vegetation (MAA/DGA 2008). Because of these impacts, it is believed that taxa such as the endemic *Euphorbia tuckeyana* have been experiencing continuous population decline since human settlement, and in the last decades have been increasingly replaced by invasive species, introduced conifers and *Eucalyptus* (MAA/DGA 2008). However, it is not clear how fast endemic plant populations have declined or which drivers of landscape degradation were at play.

This study will analyse human impact on a dry tropical island and the specific drivers of ecological change associated with anthropogenic activities. Specifically, one of the remaining key knowledge gaps related to the conservation of Cabo Verdean biodiversity and in particular of the Monte Gordo Natural Park is to determine pre-human baselines. Baselines help describing the past diversity of endemic and native plant species for the Natural Park and improve the understanding of plant responses to ecological disturbances in pre- and post-human settlement times. We use a palaeoecological approach to fill this gap and provide new information on past vegetation distribution, composition, and long-term biodiversity variability that will be relevant to inform conservation actions and restoration initiatives for Monte Gordo Natural Park and the native vegetation of the highlands of Cabo Verde (Fig. 1).

In this study, we set out to assess the long-term vegetation dynamics using an integrated multiple-approach analysis: fossil pollen, non-pollen palynomorphs (NPPs), charcoal particles, sediment grain size distributions and elemental composition, and leaf-wax *n*-alkane

biomarkers, from a 190-cm stratigraphic profile excavated within a volcanic caldera from Monte Gordo Natural Park (1000 m asl). Our specific aims are to: 1) characterize biodiversity baselines in the highlands and to determine ecosystem responses to disturbances before the first human arrivals; 2) assess the impacts of land-use on São Nicolau's highland environments, identifying the main drivers of environmental change after human settlement; and 3) suggest potential directions for informed management of Monte Gordo Natural Park in particular, and 4) demonstrate how palaeoecological methods can help to manage dry islands and their natural heritage.

## 2. Material and methods

### 2.1. Study area

#### 2.1.1. Environmental change in Cabo Verde

Cabo Verde is an archipelago formed by ten volcanic islands situated 600 km west of the African mainland (14–17°N, 22.5–25.5° W). It has a tropical dry climate (mean annual temperatures between 20 and 24 °C) marked by low and irregular levels of rainfall (1200–1600 mm in the highlands) which have a monsoon origin (August–October), and Saharan winds (Harmattan) that regularly deposit dust on the islands (Duarte et al., 2008). The archipelago supports a varied flora with high levels of endemism (35% of vascular plants), and its species distributions are shaped by elevational gradients and the effects of moisture brought by northeast trade-winds (Romeiras et al., 2016). Around 92 plant taxa (including several subspecies) are currently considered archipelagic endemics, of which ca. 75% are exclusively distributed in the windward (i.e. Santo Antão, São Vicente, Santa Luzia and São Nicolau) and the leeward (i.e. Santiago, Fogo, and Brava) islands, which are characterized by high mountains, offering a wide range of habitats (Romeiras et al., 2015). According to the IUCN Red List ca. 78% of Cabo Verde's endemic plants are threatened (Romeiras et al., 2016). Forested areas in Cabo Verde are mainly formed by introduced species (e.g. *Prosopis*, *Eucalyptus*, *Pinus*), and scarce endemic and native woodlands are formed by *Phoenix atlantica*, *Faidherbia albida*, *Euphorbia tuckeyana*, and *Dracaena draco* subsp. *caboverdeana* (Romeiras et al., 2014). In addition, some introduced plant species in the archipelago, such as *Furcraea foetida* and *Lantana camara*, are showing invasive behaviour and spreading within the ecological niches of endemic and native plants (Romeiras et al., 2016).

There is an agreement among scholars that the Cabo Verde archipelago has undergone extensive changes in the last six centuries. Cabo Verde was permanently settled by humans after 1460 CE when Portuguese and Genoese settlers established a colony in Santiago Island (Green, 2012). It was the first European colony in the tropics. Since then, the history of Cabo Verde has been marked by socio-ecological crises: it became a colonial hub for the slave trade in the 16th century, but it was outcompeted in the 17th century by Brazil and the Gulf of Guinea colonies (Romeiras et al., 2014). According to Patterson (1988) and Green (2012), the socio-ecological crises could be related to the occurrence of extreme weather events, long-term droughts and subsequent famines and epidemics in Cabo Verde.

The extent and nature of human impacts upon the native flora and fauna of Cabo Verde remain to be assessed. Some authors propose that the islands were mostly barren before Portuguese settlement and that humans made them inhabitable by introducing exogenous flora and fauna (Garfield, 2015). However, others consider that Cabo Verdean biomes probably suffered intense impacts after human settlement due to logging, land clearing, and overgrazing that caused desertification and the almost total disappearance of endemic woodlands (Lindskog and Delaite, 1996). A first palaeoecological study carried out by Castilla-Beltrán et al. (2019) in the neighbouring island of Santo Antão, which covered the past 2200 years, has shed light on these questions. Fossil pollen time-series complemented with charcoal and sedimentology analyses showed that the main human impacts in the

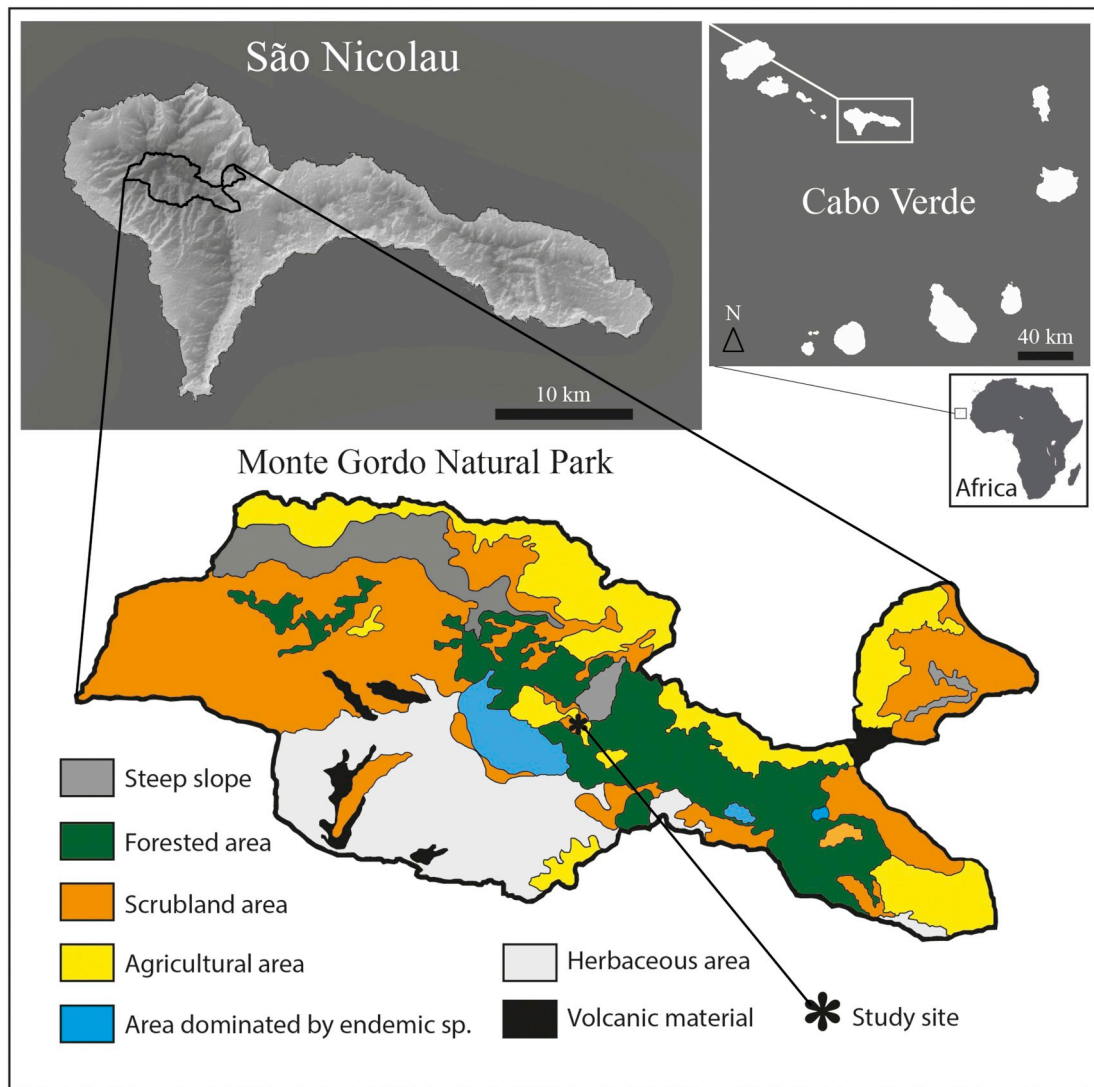


Fig. 1. Elevation map of São Nicolau (modified after USGS) and land-cover map of Monte Gordo Natural Park (vegetation map based on MAA/DGA 2008, p. 81).

highlands of Santo Antão were the increase of fires, sustained erosion, episodes of land abandonment, and the spread of invasive species. More studies in the archipelago will serve to assess the effects of human impact on different ecosystems.

#### 2.1.2. The Monte Gordo Natural Park, São Nicolau island

São Nicolau is an island of volcanic origin with a total area of 388 km<sup>2</sup> and a population of ca. 13,000 people. The island is believed to have emerged in the Early Pliocene (Troll et al., 2015). The Monte Gordo Natural Park, created in 2003, comprises the most important humid mountain ecosystems of São Nicolau. It extends over 952 ha and is inhabited by ca. 2300 people. The Park receives around 1500 visitors a year and is one of the preferred destinations for eco-tourism in Cabo Verde. Within it, there are significant populations of endemic species such as: *Asteriscus smithii*, *Echium stenosphon* subsp. *glabrescens*, *Diplotaxis gracilis*, *Lotus arborescens*, *Dracaena draco* subsp. *caboverdeana*, *Periploca chevalieri*, and some of the largest populations of *Euphorbia tuckeyana* in the archipelago (1.5 ha) alongside those of Santo Antão, with specimens that reach 2.5 m in height (MAA-DGA, 2008). The presence of these species is thought to reflect the local vegetation composition before human colonization (MAA-DGA, 2008).

Nowadays, Monte Gordo also holds an extensive afforested area planted in the 20th century, mainly comprising introduced planted species (e.g. *Pinus canariensis*, *P. halepensis*, *P. radiata*, *P. pinaster*,

*Eucalyptus camaldulensis* and *Cupressus*) (MAA-GDA 2008). Other exotic naturalized species have shown invasive behaviour in the park, mainly *Lantana camara*, *Leucaena leucocephala* and *Furcraea foetida*, which continue to spread at the expense of endemic and native species (MAA-GDA 2008). The uncontrolled spread of *Lantana camara* and *Leucaena leucocephala* is considered to be contributing to one of the main threats to the Natural Park, wildfires; for example, *Lantana camara* can cover large areas and cause encroachment, providing extra fuel (MAA/DNA 2008). In addition, tropical storms have had profound impacts by removing trees and bushes and increasing soil erosion: the impact of Hurricane Freddy in 2015 destroyed some forest plantations that were situated over 1000 m asl (Jenkins et al., 2017).

Finally, the main conservation management actions currently being implemented within the Natural Park are the monitoring of threatened species (e.g. *Asteriscus smithii* – local name “marcela do Gordo”), the removal of invasive species (e.g. *Furcraea foetida*) in the forested areas, the recovery of threatened endemic species (e.g. *Sideroxylon marginatum*), and education programmes in local schools. In the short-term, the main objectives of the Natural Park are to protect endangered species and control invasive ones, preserve soils and aquifers and achieve an equilibrium between the natural landscape and sustainable development by local inhabitants, thereby also improving conditions for the practice of eco-tourism (MAA/DNA 2008).

## 2.2. Fieldwork and soil profile sampling

We carried out fieldwork in São Nicolau Island Monte Gordo Natural Park in June 2018, visiting its three volcanic calderas (numbered 1 to 3) situated 900 m (Caldera-1), 1000 m (Caldera-2 or Calderinha) and 1050 m asl (Caldera-3, with potential for further studies) (Fig. 1). We selected Calderinha as a study site due to its moderate size (ca. 50 m in diameter) and sparse cultivation, as well as its less pronounced slopes. The walls of the caldera are terraced, and residents from nearby villages cultivate crops such as maize (*Zea mays*) and sweet potato (*Ipomoea batatas*). We opened a 1 × 1 m trench in the centre of the caldera to record and sample a stratigraphic profile (Fig. 1). We documented stratigraphic features according to texture and colour throughout the 190-cm profile (Supplementary Fig. 1). We collected a sample of ca. 30 g of sediment every 5 cm, by using stainless steel tools, and placed them in individual sealed plastic bags. The samples were transported to the University of Southampton and stored in a cold room at 4 °C.

## 2.3. Dating, sediment granulometric analysis, and sediment organic content

To develop an age-depth model we obtained eight AMS radiocarbon assays from the sediment profile, dating bulk sediment, charcoal, and charcoal/wood (Table 1). These were complemented with Pb-210 and Cs-137 dates on bulk sediments from the uppermost (near-surface) section of the sediment profile. We report our results using Before Present (BP), 'present' being 1950 CE by definition, so negative dates indicate years after 1950, and Present-day refers to 2018, the date of our fieldwork.

Pb-210 and Cs-137 activities in bulk sediments were determined by gamma spectrometric analysis, using HPGe well-type detectors (Cundy et al., 2006; Gaki-Papanastassiou et al., 2011). Detectors were calibrated against a mixed radionuclide standard solution, which was used to prepare a source of identical counting geometry to that of the samples. Gamma spectra were analysed and individual radionuclides quantified using Fitzpeaks spectral deconvolution software (JF Computing Services, Faringdon, UK). Detection limits were 0.001–0.002 Bq/g.

The elemental composition of the sediment was analysed with a hand-held X-ray Fluorescence (XRF) device (de Lima et al., 2019), model Niton XL3T GOLDD. In total, 38, 2 cm<sup>3</sup> dry samples (taken at 5 cm intervals) were analysed, using a test-stand. The hand-held XRF carried out one 160-second measurement per sample, using the instrument 'mining' setting. The results are reported in the proportion of elements above the limit of detection (0.0001%).

To calculate grain size distributions, we analysed the same set of 38 2 cm<sup>3</sup> samples (taken at 5 cm intervals) in a Mastersizer Hydro (Malvern). The Mastersizer was programmed to measure soil settings for non-spherical grains, carrying out 5 measurements per sample, of 20 s each. Results were accepted once the standard deviation of the three fractions (Dx10, Dx50, and Dx90) was equal to or below 0.5, 0.3

**Table 1**

Radiocarbon dates for the Calderinha record, São Nicolau Island. Dates in bold are the ones used for the final age-depth model.

Laboratory ID	Depth	Material dated	Age	Calibrated age
SUERC-87009	60 cm	Charcoal & wood	1609 ± 37	1594–1405 cal yr BP
SUERC-87008	70 cm	Bulk sediment	2661 ± 35	2845–2744 cal yr BP
SUERC-87004	80 cm	Bulk sediment	2999 ± 37	3336–3066 cal yr BP
SUERC-87003	105 cm	Bulk sediment	2868 ± 37	3140–2872 cal yr BP
SUERC-87002	<b>115 cm</b>	<b>Charcoal</b>	<b>501 ± 35</b>	<b>624–500 cal yr BP</b>
SUERC-87001	125 cm	Bulk sediment	3161 ± 37	3456–3257 cal yr BP
UBA-38690	135 cm	Bulk sediment	4517 ± 28	5303–5051 cal yr BP
UBA-38473	185 cm	Bulk sediment lipid extractions	5120 ± 33	5934–5179 cal yr BP

and 0.5, respectively. Results are reported as proportions of clay, silt, and sand, and as median grain size values (Dx50) (Prins and Weltje, 1999).

To calculate the sediment organic content, we carried out loss on ignition (LOI) (Heiri et al., 2001) analysis of 38 2 cm<sup>3</sup> samples taken every 5 cm. We dried the samples at 100 °C for 24 h in previously weighted crucibles and weighed the dry sample using a high precision scale. Samples were then burned in a furnace at 550 °C for 4 h and weighed again. LOI was calculated and used as a proxy for organic content.

## 2.4. Pollen and NPPs

For analysis of pollen and non-pollen palynomorphs (NPPs), we processed 38 2 cm<sup>3</sup> samples (taken at 5 cm intervals) by following standard procedures (Erdtman, 2013). For pollen identification, we used our Cabo Verde and Canary Islands reference collection (Supplementary Table 1), as well as African pollen atlases, including Gosling et al. (2013) and Schüler and Hemp (2016). All pollen grains were included in the pollen sum: including potential long-distance, herbaceous, wetland, and unidentified taxa, to achieve a broad overview of local and regional vegetation, including unspecified vegetation (Fig. 2, see Supplementary Table 2 for total pollen and NPP sums). We carried out stratigraphically constrained CONISS analysis using pollen percentage data in Tillia software (Grimm, 1993). We recognized four main pollen zones (Supplementary Table 3).

## 2.5. Charcoal

For analysis of macro-charcoal, we processed 38 2 cm<sup>3</sup> samples (taken at 5 cm intervals). We sieved the sediment using a 180 µm mesh and counted charcoal fragments in a petri dish using a low magnification microscope. For analysis of micro-charcoal, we counted black opaque particles between 10 and 100 µm alongside exotic *Lycopodium* until the sum of both categories reached > 200, and then calculated micro-charcoal concentrations (Finsinger and Tinner, 2005).

## 2.6. n-Alkane analysis

We analysed and quantified the n-alkane fraction at the Archaeological Micromorphology and Biomarker Research Laboratory (University of La Laguna, Spain). We selected a set of 10 samples for wax lipid analysis at an average of 20 cm intervals, to compare n-alkane distributions in the four zones of the profile (see Appendix 1 for preparation and quantification methods, Gas Chromatograph settings and compound identification procedures).

We used average chain length (ACL) as a proxy for the predominance of a terrigenous vs. an aquatic source of organic matter:  $ACL_{23-31} = \sum(C_i * [C_i]) / \sum[C_i]_{23 < i < 31}$  (Pancost et al., 2002). We calculated a *Paq* index following Ficken et al., (2000):  $(C_{23} + C_{25}) / (C_{23} + C_{25} + C_{29} + C_{31})$  to ascertain the relative contribution of plants adapted to humid environments (index values > 0.1), and the long-chain n-alkane ratio  $C_{31}/C_{29} + C_{31}$  to distinguish local predominance of woody ( $C_{29}$  dominant) vs. herbaceous ( $C_{31}$  dominant) vegetation (Ortiz et al., 2016). Odd over even predominance (OEP):  $(C_{27} + C_{29} + C_{31}) / (C_{26} + C_{28} + C_{30})$  (Hoefs et al., 2002), was calculated to test its correlation with long-chain n-alkane ratios as a potential indicator of post-depositional alteration of fossil n-alkanes. The n-alkane concentration is expressed as µg of individual compound per gram of dry sediment (µg/gds).

## 2.7. Ordination analysis

Canonical correspondence analysis of pollen and NPP assemblages was carried out in R using the *Vegan* package to assess the influence of five environmental drivers on local vegetation expressed as pollen percentages. Environmental variables (drivers) were: 1) grazing, to

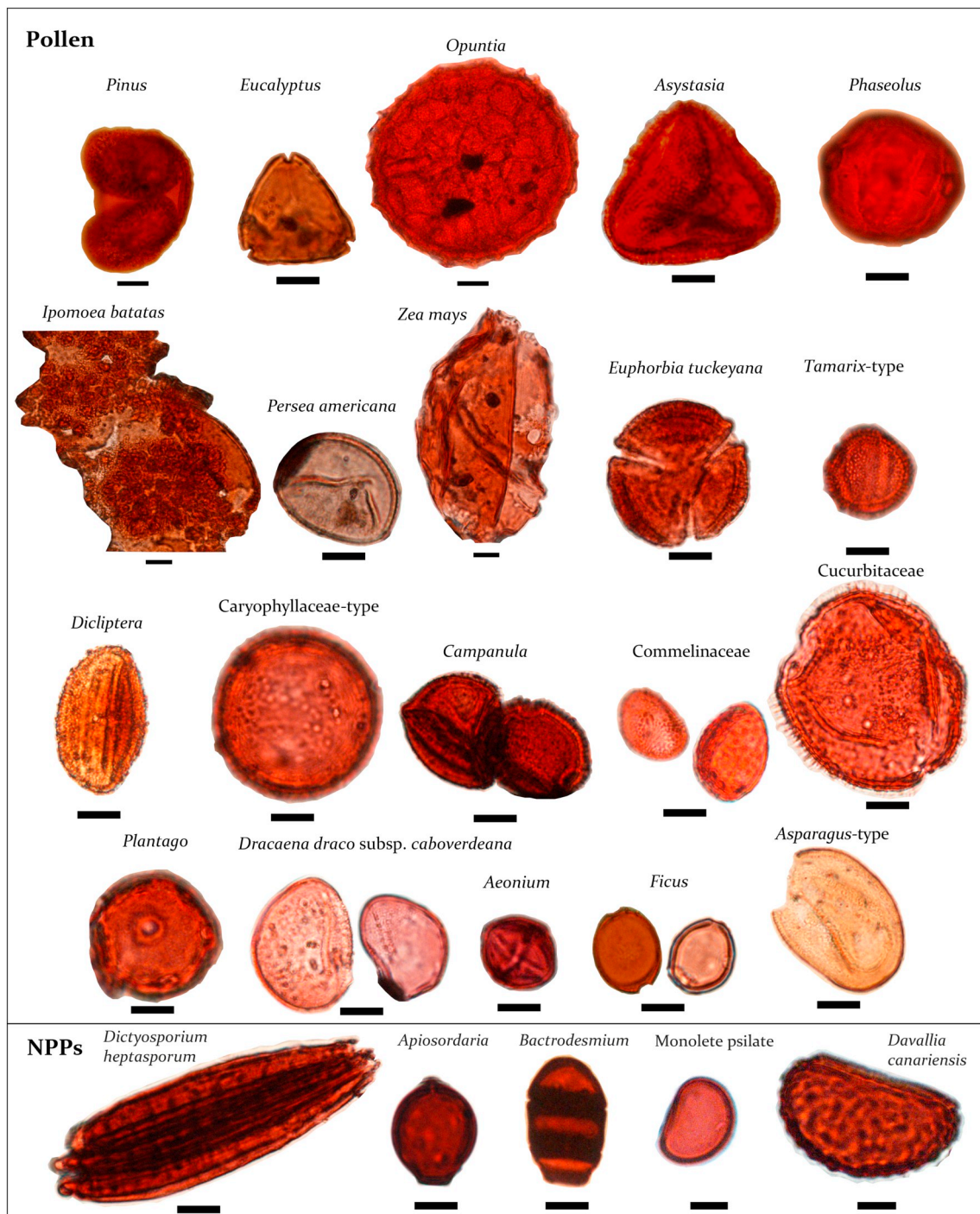


Fig. 2. Selected pollen grains and non-pollen palynomorphs of the Calderinha record, São Nicolau, Cabo Verde.

assess the impact of the introduction of livestock in the island (abundance of coprophilous fungi, % over pollen sum. Notice that this variable was excluded from the NPPS CCA to avoid redundancy), 2) regional fire (abundance of micro-charcoal particles per  $\text{cm}^3$ ) to assess impacts of fires beyond the immediate catchment, 3) local fire (abundance of macro-charcoal particles per  $\text{cm}^3$ ) to explore impacts of fire in the local setting, 4) erosion (median grain size,  $\text{D}_{x50}$ ) to assess impact of deposition of coarse material from local and regional sources, 5) soil reducing conditions (based on the ratio of Fe/Mn), which reflect processes of soil oxidation or reduction, potentially related to rapid soil burial and flooding, 6) organic matter (LOI %) to assess the ecological influence of increased organic matter in soils.

### 3. Results and palaeoecological reconstruction

#### 3.1. Sediment composition and *n*-alkanes

The sediments of Calderinha are dominated by silts, with an average content of 63%, reaching a minimum of 45% in level 180 cm. The main elements/compounds identified in the sediment were silicon dioxide ( $\text{SiO}_2$ , average 24%), silicon (Si, 11%), iron (Fe, 9%), and aluminium (Al, 4%). The concentration of *n*-alkanes varied throughout the profile, from a maximum of 1.72  $\mu\text{g}$  in zone Cld-3 to a minimum of 0.13  $\mu\text{g}/\text{gds}$  in Cld-4. *n*-Alkanes had chain lengths ranging from *n*- $\text{C}_{23}$  to *n*- $\text{C}_{31}$ , and were always dominated by long carbon chains with a strong odd/even

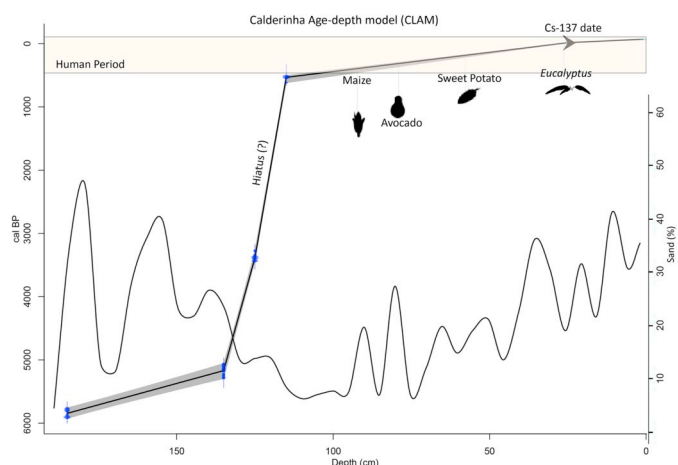
carbon number preference:  $n\text{-C}_{29}$  in the middle and bottom sections of the profile (zones Cld-1 to -4), and  $n\text{-C}_{31}$  in the top (zone Cld-4). The ranges of ACL, Paq and OEP varied between 30.11 and 28.79, 0.15 and 0.01, and 14.71 and 6.00, respectively. A low correlation coefficient obtained between  $C_{31}/C_{29} + C_{31}$  ratio and OEP ( $R^2 \leq 0.36$ ) suggests that changes in the  $n$ -alkane patterns were mainly controlled by changes in vegetation, and not by post-sedimentary alteration effects (Bugge et al., 2010). These findings are further interpreted in Sections 3.3, 3.4 and 3.5.

### 3.2. Chronological models

Obtaining a radiocarbon (RC) chronology from a sediment profile formed in dry tropical environments poses several challenges. First, the preservation of organic material, particularly in the form of macrofossils, can be very limited. Second, in a caldera setup, erosional processes depositing in washed or colluvial material may interrupt slower phases of sedimentation. Third, in the case of highland calderas in Cabo Verde, the local landscape is used for low-intensity agriculture, and some level of bioturbation through land preparation for planting, or the pulling of roots for clearing the land, is to be expected and may have occurred since settlement (after 400 BP). We used Pb-210 and Cs-137 dating to verify the chronology in the uppermost (0–50 cm), most recently deposited section of the record, as this technique has proven successful in mixed alluvial and colluvial sediment sequences elsewhere (e.g. Cundy and Stewart, 2004). To develop a chronological model for the record, we first calculated two alternative C-14 chronological models (see Appendix 2 and Supplementary Fig. 2 for details of the alternative age-depth models), and validated them against sedimentological data (sand %), biostratigraphic markers (pollen data) and Pb-210 and Cs-137 dating. We selected the model that best explains the data (model B, CLAM), and ran a final model adding a calendar date based on Cs-137 dating (Fig. 3).

### 3.3. Evidence of the end of the African Humid Period (5900–4900 cal yr BP, zones Cld-1 & Cld-2)

The period between 5900 and 4900 cal yr BP (zones Cld-1 & Cld-2) was characterized by rapid coarse sediment deposition, the minimal occurrence of fire and poor palynomorph preservation. Sediments of zone Cld-1 (190–175 cm) are characterized by alternations between silty and sandy deposits (median grain size 27  $\mu\text{m}$ ) low in Titanium



**Fig. 3.** Age-depth model of the Calderinha record (grey line, calibrated RC dates in blue), São Nicolau Island, and its validation against granulometric data (sand content percentage, curve) and first occurrence of pollen from cultivated species (silhouettes). The period of human settlement is highlighted in yellow (~400 cal yr BP–the present day). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

content (Fig. 4). Sand peaks occur in levels 185 and 180 cm (37 and 49% 5800–5700 cal yr BP), as opposed to silt-rich deposits in levels 190 cm and 175 cm, and organic content varied between 7.1 and 8.5%. High values of the ratio Fe/Mn indicate anoxic and reducing conditions (Corella et al., 2012; Croudace and Rothwell, 2015). The reddish colour of the sediments can also be a product of reducing conditions, which in turn is related to soil seasonal flooding (Cundy et al., 2006; Pezeshki and DeLaune, 2012). The low concentration of micro-charcoal particles (average 1330/cm<sup>3</sup>) and the near absence of macro-charcoal particles indicates that very few fires occurred from 5900 to 4900 in comparison to modern periods. Probably, due to moist regional and local conditions or sparse vegetation. In this zone, the pollen concentration is low (average 53 grains/cm<sup>3</sup>). The scarcity of pollen could be related to preservation conditions and/or to the low levels of local pollen production. Pollen of local endemic and native plants, such as Poaceae, Asteraceae, Brassicaceae, *Euphorbia tuckeyana*, *Ficus*, *Plantago* is present in this section (Fig. 5). In addition, potential long-distance dispersal pollen types (*Alnus*, *Rumex*, *Betula*, *Morella-Corylus*, *Quercus*, *Juniperus*) increased through zone Cld-1, with a peak in level 175 cm, potentially transported by North-eastern trade winds. These pollen types likely came from the Mediterranean and the African continent (see Hooghiemstra et al., 2006 for a synthesis of long-distance transport studies based on ocean cores in the region), and have also been documented in sediments from the neighbouring island of Santo Antão (Castilla-Beltrán et al., 2019). The NPP assemblage is dominated by *Lycogala*-type (ranging from 90 to 292%) and *Dyctiosporium heptasporum* (from 25 to 64%) spores, which are produced by fungi in wood and bark (Gelorini et al., 2011; La Serna-Ramos and Domínguez-Santana, 2003), and *Glomus* type (184% in level 195 cm), associated with erosion (Fig. 6) (van Geel et al., 2003). The presence of woody vegetation is also supported by  $n$ -alkane dominant chains  $n\text{C}_{29}$  (long-chain  $n$ -alkane ratio between 0.6 and 0.7). We interpret this period as characterized by an open landscape with the scarce presence of woody species, during which rapid deposition of coarse material occurred. This could have been produced by strong trade winds, the occurrence of tropical storms and/or drier conditions associated with the end of the African Humid Period (ca. 5500 BP).

Erosion processes evidenced in Cld-1 continued in Cld-2 (174–136 cm, 5700–5000 cal yr BP): sediments are sand-rich, with peaks in levels 160 (39%) and 155 cm (42%), the Fe/Mn ratio is also high between 160 and 140 cm. Peaks in the ratio Ti/Ca (levels 170 cm and 140 cm) indicate episodes of increased detrital input (Croudace and Rothwell, 2015). Increasing values of SiO<sub>2</sub> in zone Cld-2 (up to 24%) could be associated with an increase of Saharan dust arrival episodes, as a drying trend in the Saharan region was taking place between 5.5 and 3 ka BP (deMenocal et al., 2000; Kröpelin et al., 2008). Increase in the long-chain  $n$ -alkane ratio to 1.3 (level 150 cm) may indicate an opening of the landscape linked to erosion. While the scarcity of pollen prevented a full analysis, the NPP assemblage in level 145 cm mirrors that of zone Cld-1, showing continuity in the local ecology.

### 3.4. Mid- to Late-Holocene ecological change (5000–410 cal yr BP, zone Cld-3)

The period between 5000 and 410 cal yr BP (zone Cld-3, 135–95 cm) was characterized by an abrupt deceleration in sediment accumulation (mostly of silt and clay deposits with high organic content) and/or a sedimentation hiatus, increase in fire occurrence and a woody scrubland landscape characterized by the abundant presence of endemic and native taxa (Figs. 4 and 5). First, clay proportions increased, peaking at level 115 cm (29%, highest in the record) and macro-charcoal (57 particles/cm<sup>3</sup> in level 115 cm) and organic content (11.5% in level 120 cm) reached the maximum values recorded. The ratio of Si/Ti reached its highest values in this period, indicating peak inputs of biogenic silica due to increased levels of organic matter (Croudace and Rothwell, 2015). The sharp increase in macro-charcoal

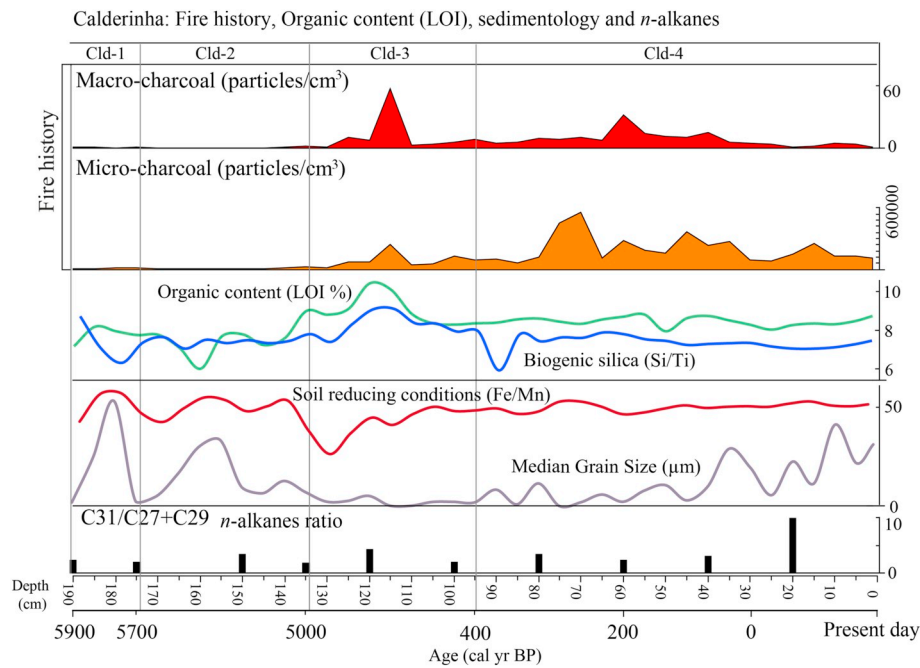


Fig. 4. Stratigraphic diagram of the Calderinha record, São Nicolau Island, showing fire-history, sedimentology and *n*-alkane long-chain distributions.

indicates local fires due to a drying trend or an increase in fuel biomass. It coincides with increases in micro-charcoal levels in the neighbouring island of Santo Antão between 1100 and ca. 500 cal yr BP (Castilla-Beltrán et al., 2019). Presence of the non-obligate coprophilous and saprophytic fungi *Chaetomium* (up to 27%) and *Gelasinospora cratophora* (up to 21%) could indicate the presence of local fauna (lizards, migratory or nesting birds), or be related to the increase in decomposing organic matter. An increase in monolet psilate fern spores and spores from the epiphytic *Davallia canariensis* (ranging from 217 to 701 and 10–66% over pollen sum respectively) reveals a fern-rich landscape. The pollen record indicates the dominance of highland scrubland with high percentages of Asteraceae pollen (47% in level 125 cm) and an increasing percentage of *Euphorbia tuckeyana* (peaking at 18% in level 120 cm). Presence of *Ficus* pollen suggests the presence of native trees *Ficus sycomorus* subsp. *gnaphalocarpa* and/or *Ficus sur*.

Sediments of zone Cld-3 after level 115 cm are characterized by lower grain sizes (median grain size 7.8 µm) and very low sand deposition (between 7 and 9%). Peaks in clay percentages occur in levels 110 cm and 95 cm, yet organic content decreased (up to 8.5%) in relation to the previous section. The pollen assemblage in this zone is characterized by high percentages of pollen produced by taxa that thrive in humid and disturbed soils like *Plantago* (ranging from 22% to 37%) and Cyperaceae (10% in level 100). *Paq* index values are highest in this section (0.15), suggesting increased leaf-wax contribution of plants adapted to humid environments, likely a mixture of terrestrial and aquatic macrophytes (Ficken et al., 2000). The first appearance of *Dracaena draco* subsp. *caboverdeana* pollen (ranging from 1 to 3.7%) and the presence of Cucurbitaceae, Caryophyllaceae, Urticaceae, Commelinaceae, *Asparagus*, *Campanula* and *Tamarix*-type indicate the presence of varied endemic and native flora. The emergence of these taxa could be related to better pollen preservation due to more clay content and lower sand content. Wood and bark fungi thrived in this environment; this is indicated by the increase in *Bactrodesmium* (ranging 66–124%), *Dictyosporium heptasporum* (average 60%), and *Xylariaceae*. In addition, the presence of the coprophilous fungi *Apiosodaria* supports the presence of local fauna. In summary, our multiple lines of evidence suggest that in zone Cld-3, environmental conditions favoured the establishment of a fern-rich wooded landscape in which taxa such as *Euphorbia tuckeyana*, *Ficus* and *Dracaena draco* subsp. *caboverdeana*

could have created closed scrubland canopies under which ferns and decomposers were present.

### 3.5. Human-driven disturbances in São Nicolau (410 cal yr BP–present day, zone Cld-4)

The period between ca. 410 cal yr BP and the present day (Zone Cld-4, 94–0 cm, 410 cal yr BP–present day) was characterized by a rapid sedimentation rate (1.5–2 yr/cm for the latter part of this period, based on Pb-210 and Cs-137 dating), increased erosion and stable organic content (between 9.3 and 8%). Direct human landscape modification is evidenced in the record in the form of anthropogenic fires, cultivation, grazing and the introduction of alien species.

In zone Cld-4 sand-rich (21 and 29% in levels 90 cm and 80 cm) and clay-rich (23 and 25% 85 cm and 75 cm) sediments alternated until level 75 cm (380 cal yr BP). Level 90 cm scores lowest in Si/Ti ratio, indicating the lowest biogenic silica in the record. This evidence suggests variable environmental conditions linked to phases of erosion. Micro-charcoal levels increased in density to 75,781/cm<sup>3</sup> (level 75 cm), indicating the occurrence of fires in other parts of the island or the local burning of fine fuels such as grasses. The pollen assemblage is characterized by the highest values of Brassicaceae (average 31%), the increase of *Campanula jacobaea* (up to 4% in level 95 cm), a decrease in *Euphorbia tuckeyana* from 9% to 3%, and the presence of *Faidherbia albida*. These data suggest a decrease in woody vegetation and the dominance of taxa that tolerated disturbances and more arid conditions. In addition, there is direct evidence of local cultivation based on the presence of *Zea mays* (level 90 cm) and *Persea americana* (level 80 cm) pollen; indicating that these levels date to the colonization period, as the Portuguese brought these cultivars from the New World in the late 15th and early 16th century (Green, 2012). The NPP assemblage confirms the evidence of human landscape modification: there was an increase in coprophilous fungi *Cercophora* and *Sordaria* and *Apiosordaria* (average 141%), most likely due to the first introduction of livestock. The decrease in fungal spores of taxa that live in wood and bark, as well as of fern spores, supports the interpretation of an opening of the landscape under more arid conditions (Fig. 6).

From 380 to 75 cal yr BP (levels 74–25 cm) a complete substitution of the local endemic-rich landscape by an open grassland linked to

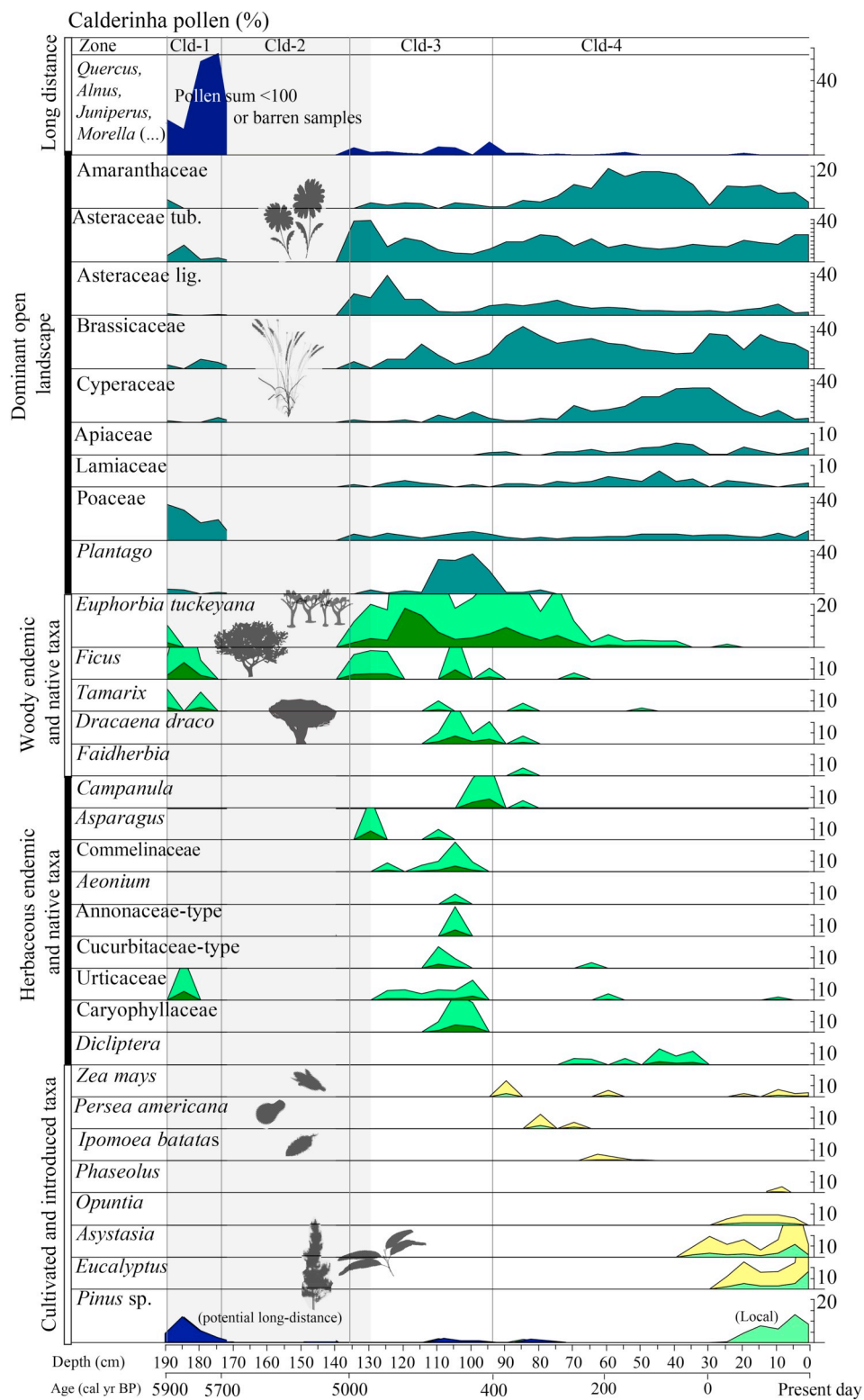


Fig. 5. Stratigraphic diagram of the Calderinha record, São Nicolau Island, showing pollen percentages. Exaggeration curves (light green and yellow) x10. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

agriculture and grazing activities took place. The highest concentrations of micro-charcoal occurred in this period (93,276 particles/cm<sup>3</sup>). Macro-charcoal peak at ca. 280 cal yr BP (level 60 cm, 31 particles/cm<sup>3</sup>) indicating a clearing of vegetation in the lowlands, after which macro-charcoal levels decreased. Sand deposition increased in this zone, peaking in levels 35 cm (38%) and 30 cm (33%). Increases in

Amaranthaceae (11–17%) and Cyperaceae (16–32%) suggest open landscapes that benefited from seasonally moist soils. In contrast, fern spores and wood-fungi decrease to minimum levels. Local agricultural activities are evidenced by the presence of pollen of *Zea mays* and *Ipomoea batatas*, and abundant obligate coprophilous fungi (*Sporormiella* and *Podospora*) and non-obligate coprophilous fungi



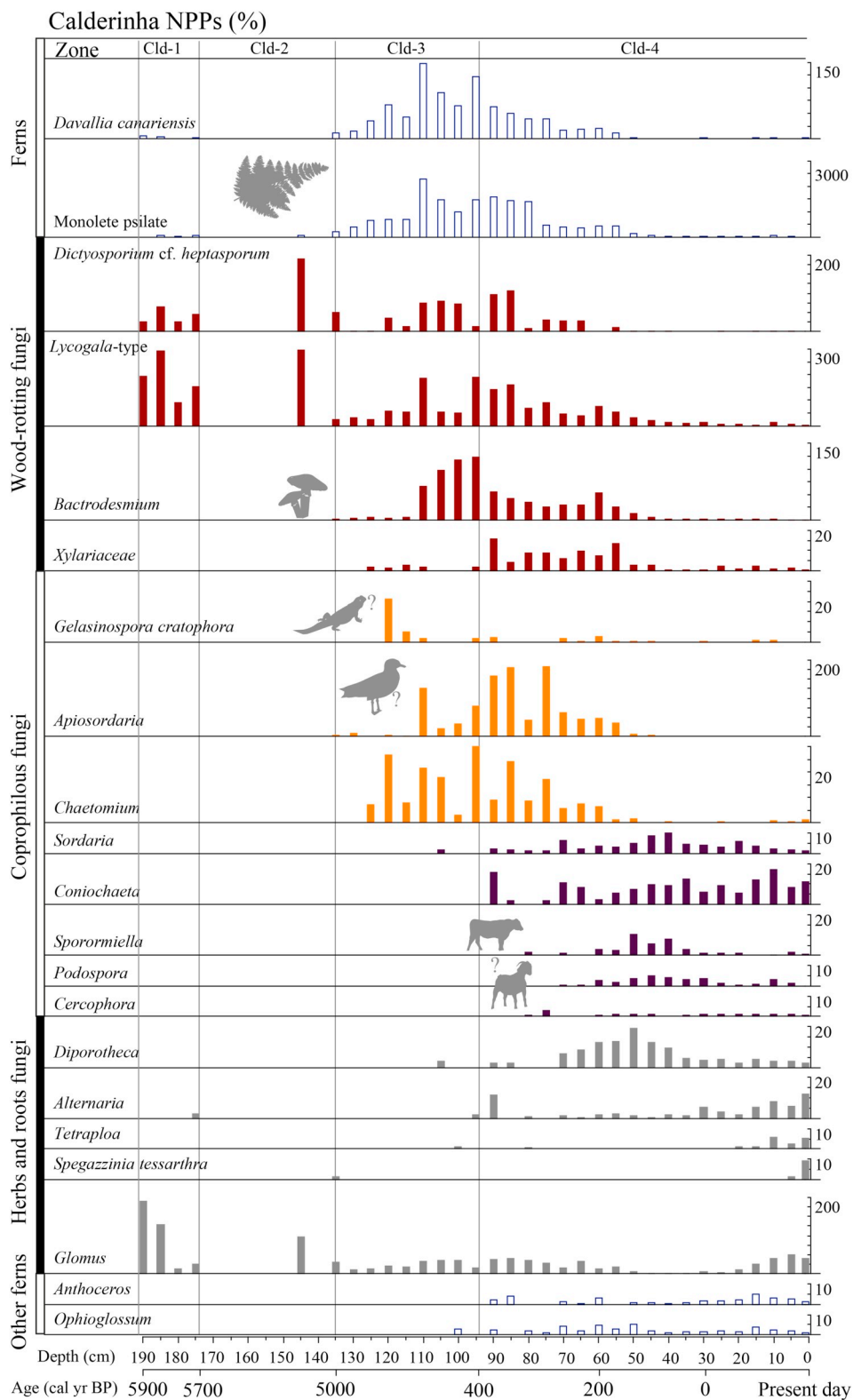
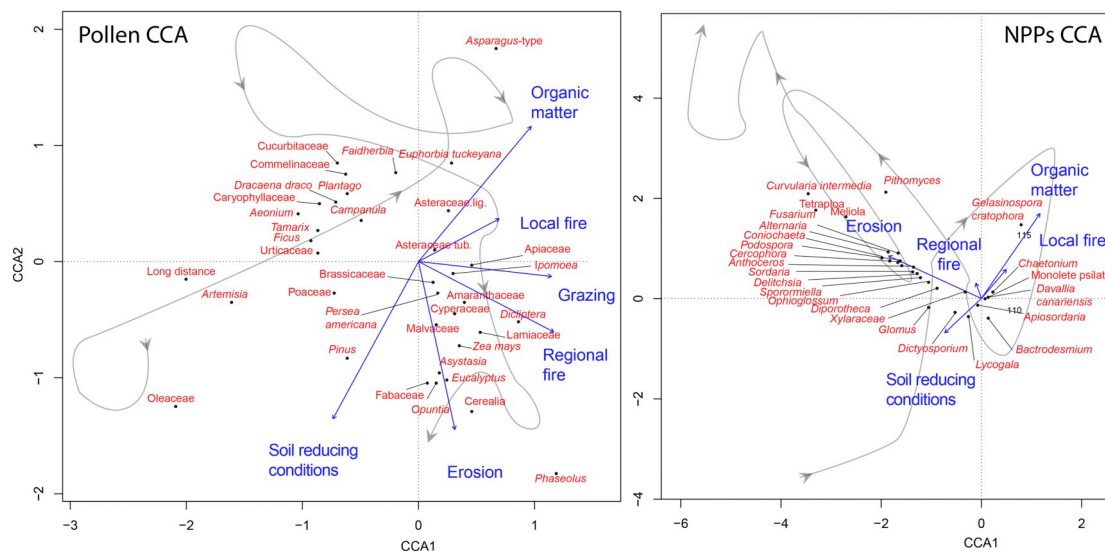


Fig. 6. Stratigraphic diagram of the Calderinha record, São Nicolau Island, showing non-pollen palynomorph percentages in relation to the pollen sum.

(*Delitschia* and *Coniochaeta*). The occurrence of native taxa such as *Dicliptera*-type (1–2%) indicates the spread of these weeds in disturbed environments. Such landscape change is also evident from a switch in *n*-alkane leaf waxes from dominant C<sub>29</sub> peaks associated with woody taxa, to dominant C<sub>31</sub> peaks associated with herbaceous taxa, supporting our interpretation that woody vegetation was cleared from the interior of the caldera.

Between –13 cal yr BP and the present day (24–0 cm,) intense landscape modification is indicated, caused by an afforestation programme to protect local soils that started ca 1950, and the abandonment of the highest points of the park by local residents. Afforestation is indicated by the increasing quantities of *Pinus* (ranging between 4.5 and 13–8%) and *Eucalyptus* pollen (2.6–8.2%), and the decrease of open landscape taxa such as *Amaranthaceae* and *Cyperaceae*. The presence of



**Fig. 7.** Canonical correspondence analysis (CCA) using pollen (left panel) and NPPs (right panel) data of the Calderinha record, São Nicolau Island. Six environmental variables were used: Abundance of organic matter (OM %), Local and Regional fire (macro- and micro-charcoal), Grazing (coprophilous fungal spores, not used in NPPs CCA), Erosion (median grain size) and soil reducing conditions (Fe/Mn). Grey line unites sample depths from bottom to top of the soil profile.

taxa such as *Asystasia* (Acanthaceae) and *Opuntia* indicate the presence of introduced cultivated herbaceous taxa. The decrease of charcoal and coprophilous fungal spore abundance attests to the depopulation of the highlands and decrease of grazing activities. Nevertheless, the increase in *Glomus* spores (11–39%) the median grain sizes (average 33  $\mu\text{m}$ ) and sand percentages (average 34%) indicate that local soils are still experiencing erosion, potentially related to the abandonment of agricultural terraces (directly observed in the field) within the highland Calderas and also related to the impacts of tropical storms such as hurricane Freddy in 2015.

### 3.6. Canonical correspondence analysis

The two plots shown in Fig. 7 display the results of canonical correspondence analyses (CCA) using pollen and NPP data. They consist of taxa and sample depths (cm) represented in bi-dimensional spaces, which are defined by the two most important compositional gradients (CCA axes 1 and 2) that are explained by linear combinations of the selected environmental variables.

In the CCA of pollen data, axis 1 accounted for 40% of explained variance (eigenvalue 0.28), and showed a positive relationship with Regional Fire and Grazing variables (correlation scores (CS) of 0.58 and 0.57 respectively), being inversely correlated with the Reducing Conditions variable (CS of  $-0.57$ ). Axis 2 accounted for 26% of the variance (eigenvalue 0.15), and had a positive relationship with the Organic Matter variable (CS of 0.58) and a negative correlation with Erosion (CS of  $-0.73$ ) and Reducing Conditions (CS of  $-0.68$ ). Pollen taxa such as *Artemisia*, *Poaceae* and *Pinus*, as well as long-distance taxa, plot in the lower left quadrant, being loosely associated with the Reducing conditions variable, and they are inversely correlated with the Organic Matter variable. Endemic and native taxa such as *Aeonium*, *Ficus*, *Cucurbitaceae*, *Dracaena draco* subsp. *caboverdeana*, *Faidherbia albida*, and samples 110, 105, 100 and 95 cm plot in the top left quadrant of the graph, and are inversely correlated with Erosion, Regional Fire and Grazing. Introduced and cultivated taxa and samples from zone Cld-4 plot in the bottom right quadrant of the plot and are associated with Grazing, Regional Fire and Erosion variables.

In the CCA of NPPs, axis 1 accounted for 55% of explained variance (eigenvalue 0.16), and showed a positive relationship with Organic Matter (CS 0.55), and negative relationships with Erosion (CS  $-0.87$ ). Axis 2 accounted for 22% of the variance (eigenvalue 0.06) and showed

a positive relationship with Erosion (CS 0.4) and Organic Matter (CS 0.8), and a negative relationship with Reducing conditions (CS  $-0.32$ ). Weed fungi such as *Curvularia intermedia*, and *Tetraploa*, fern spores such as *Anthoceros* and *Ophioglossum* and most coprophilous fungi (e.g. *Sporormiella*, *Podospora*, *Sordaria*, *Coniochaeta*) plot in the top left quadrant, and are associated with increased Erosion. Taxa such as *Glomus*, *Dictyosporium heptasporium* and *Lycogala* plot in the bottom left of the plot and are associated with soil reducing conditions and negatively correlated with Organic Matter.

## 4. Discussion: implications for conservation

### 4.1. Highland vegetation composition and the drivers of ecological change

Reconstructions of past vegetation are a first step towards setting conservation and restoration goals (Boessenkool et al., 2013; Barnosky et al., 2017), and in combination with other palaeoecological indicators can fill further knowledge gaps in the long-term ecology of dry tropical islands. For Cabo Verde, we identified two main knowledge gaps related to the management of island biodiversity that can benefit from palaeoenvironmental data: the long-term response of ecosystems to fire and erosion regimes, and the specific human impacts that have taken place since Portuguese settlement.

#### 4.1.1. Biodiversity baselines

Our palaeoecological data provide information on the long-term responses of native ecosystems to fire and erosion regimes (baselines), their pre-human taxonomic composition, and the specific human impacts and related ecosystem changes that took place since Portuguese settlement. Overall, our results show a pre-human landscape (5900–410 cal yr BP) characterized by a high diversity of endemic perennial herbaceous and sub-shrub taxa (e.g. *Aeonium gorgoneum*; *Asparagus squarrosus*; *Forsykaolea procrifidifolia*; *Paronychia illecebroides*; *Polycarpha gayi*; *Campanula jacobaea*) as well as the presence of shrubs and trees including *Euphorbia tuckeyana*, *Ficus*, *Dracaena draco* subsp. *caboverdeana*, and *Tamarix senegalensis*. A modern pollen rain study from Tenerife (Canary Islands) revealed that *Euphorbia* pollen had a low dispersability index value, meaning that it was only recorded when the plant was locally present (de Nascimento et al., 2015). According to this, and based on the Calderinha record showing percentages as high as 18%, we infer that *Euphorbia tuckeyana* was abundantly present in

**Table 2**  
Summary of insights derived from palaeoecological data for conservation and livelihoods in Monte Gordo Natural Park, São Nicolau.

Conservation challenge based on palaeoevidence	Evidence	Conservation action	Considerations regarding livelihoods and future research
Degradation of scrubland and loss of woody taxa since human settlement	Pollen and NPPs	Reforestation using native species reported in this study, associated with removal of identified invasive species	A study to compare economic benefits provided by introduced taxa and native species is needed. The control of invasive species in areas of restored native vegetation could require prolonged labour (see Burney and Burney, 2016). Future studies might yield insights on past abundance of other important endemic species such as <i>Sideroxylon marginatum</i> .
Potential establishment (100 years ago) of introduced taxa such as <i>Asystasia</i> and <i>Opuntia</i> (?)	Pollen	Monitor the spread of these species and study their economic value for local inhabitants.	These species are not (yet) considered invasive in Cabo Verde (MAA/DGA 2008). However, in the Canary Islands, <i>Opuntia dillenii</i> and <i>O. maxima</i> are considered invasive species.
Ancient fire potentially related to scrubland encroachment	Charcoal particles	Avoiding fuel loading, especially added by spreading invasive species	According to our fire data fire has been present at least for the last millennium in the National Park. Conservation action could focus on the recovery of recently burned land, as our data shows that introduced species spread in cleared areas.
Current erosion levels are higher than Late-Holocene baseline levels and an increasing trend	GSD	Use of abandoned and degraded terrace structures for afforestation initiatives	Monitor the response of vegetation and soils to extreme weather events to assess which taxa would offer better soil-protection. For instance, Hurricane Freddy (2015) severely affected slopes that held planted conifers and <i>Eucalyptus</i> . Reforestation with native species could offer more resilient plant cover on slopes vulnerable to strong winds and heavy rainfall.
Grazing as a main driver of loss of vegetation cover and erosion	NPPs, pollen, GSD	Restrict and control grazing activity in areas of endemic and native vegetation, allocating special areas for this activity	A study of local reliance on free-range grazing and of potential alternatives is needed to protect nursing areas for restored vegetation.

the highlands, forming scrublands where epiphytic ferns, and wood-rotting fungal communities might have thrived. Within this woody matrix, the presence of pollen of *Dracaena draco* subsp. *caboverdeana* (endemic Dragon tree) indicates its local abundance. Noteworthy is the presence of *Ficus* pollen until ca. 300 cal yr BP, given that *Ficus* are insect-pollinated and typically are underrepresented in sediments and pollen cores. In the first accounts of the discovery of Santiago Island, Diogo Gomes described the presence of productive fig-trees, and historical sources mention the exploitation of *Ficus* trees in São Nicolau in the 18th century (Romeiras et al., 2014), but Gomes did not clarify if they were African species or the introduced Mediterranean species *Ficus carica*. Our analyses suggest that *Ficus sur* (currently very rare in São Nicolau) and/or *Ficus sycomorus* subsp. *gnaphalocarpa* (absent from São Nicolau in the present day), was/were important in the vegetation of São Nicolau's highlands. Although we cannot confirm which *Ficus* species were present in Monte Gordo in the past, we suggest that at least one of these species may have played an important role in preventing soil erosion during the Late Holocene (as zone Cld-3 has the lowest levels of erosion coinciding with the presence of *Ficus* pollen). *Ficus* trees might have provided sustenance for local fauna such as reptiles, birdlife and invertebrates.

To determine whether there have been faunal changes over time and whether these changes are linked to a specific driver of change or a combination of many, we have used non-pollen palynomorphs (NPPs). NPP data give a perspective on how communities of decomposers developed in relation to vegetation and fauna. Coprophilous fungal communities experienced multiple shifts, especially between two assemblages: *Apiosordaria*, *Chaetomium* and *Gelasinophora cratophora* dominant in zone Cld-3 and declining in zone Cld-4, and *Sporormiella*, *Podospora*, *Sordaria*, *Delitschia* and *Coniochaeta*, which are only recorded after Portuguese settlement 400 BP onwards (zone Cld-4). The first group could potentially be linked to distinctive endemic fauna (birds, reptiles), which were displaced by the loss of habitat and the grazing pressure of livestock introduced by humans. However, this requires further testing, potentially through sedaDNA analyses, or the analysis of fossil bones and ancient coprolites (e.g. Wood et al., 2012). Finally, the abundance of ferns such as *Davallia canariensis*, which are epiphytic, as well as wood-rotting fungi (e.g. *Bactrodesmium*, *Dyctiosporium heptasporum*), confirm the picture of a humid wooded landscape between 5000 and 410 cal yr BP. As the long-distance pollen assemblage is

known to be transported by trade winds in North-west Africa (Hooghiemstra et al., 2006), we interpret taxa such as *Juniperus*, *Corylus*, *Morella*, *Pinus* (in pre-human times) and *Quercus* as not locally available until further evidence (e.g. macro-fossils) can suggest the contrary.

#### 4.1.2. Fire history and erosion

Sedimentology and charcoal data provide insights into natural and human-driven disturbances. The analysis of grain size distributions and sediment elemental composition show that erosion, soil reducing conditions, and inputs of detritus occurred at the end of the African Humid Period (ca. 5500 BP). These values could be explained by relatively high levels of precipitation (deMenocal et al., 2000). The occurrence of fire in Monte Gordo Natural Park could be linked with four main factors: an increase of fuel availability, arid conditions, more storms and lightning and direct human land clearing. The first significant local fires documented in the record took place in what is considered pre-human times (between 1000 and 400 cal yr BP), and they likely occurred naturally, made possible by bush encroachment and greater fuel load in the highlands. This was also considered a period of increasing aridity in Northern Africa (deMenocal et al., 2000), and increases in fires in the neighbouring island of Santo Antão (Castilla-Beltrán et al., 2019) coincide with pre-human fire events in São Nicolau. After fire in pre-human times, the local endemic vegetation did not change radically. Continuous regional and local fire, grazing, and erosion define the human-dominated landscapes from 410 cal yr BP onwards and are likely direct drivers of landscape degradation and associated biodiversity change.

#### 4.2. Palaeoecological insights for the conservation of Monte Gordo's natural landscapes

The integration of diverse lines of evidence of long-term environmental change in dry tropical islands, and especially for Monte Gordo Natural Park, is relevant to set informed conservation actions, such as those listed in Table 2. It has been previously highlighted (MAA/DGA 2008) that eradication of invasive species and restoration programmes are two of the main conservation actions needed in Monte Gordo. Here, we will discuss in light of our palaeoecological results' potential species to target for monitoring, eradication, and/or vegetation restoration

programmes. We will also discuss management strategies that incorporate how fire, erosion, and grazing processes impacted local ecology and the relevance of these results for education programmes.

#### 4.2.1. Restoration in a human-dominated landscape

Palaeoecological studies in tropical archipelagos such as Hawaii, the Galápagos Islands, and Mauritius have proven that micro- and macro-fossils can provide adequate data to guide restoration ecology (e.g. van Leeuwen et al., 2008; de Boer, 2014; Burney and Burney, 2007). In our study, palaeoecological data have provided evidence of the ecological importance of woody taxa such as *Euphorbia tuckeyana*, *Ficus*, and *Dracaena draco* subsp. *caboverdeana* for the highland ecosystems of São Nicolau. Our results also provide a new perspective on the potential importance of these species to form suitable habitats for endemic fauna, ferns, and fungal communities, as well as for a diversity of herbaceous species. Restoring the *Euphorbia tuckeyana* cover (this taxon was abundant based on our pollen data) could be beneficial to recover original native and endemic plant and fern communities, and to avoid soil erosion. In addition, we would like to highlight the past presence of a potential native *Ficus* species. Unfortunately, due to lack of reference material, at this stage, we cannot identify using fossil pollen alone the species of *Ficus* that was present in the landscape during pre-human times. Future analysis of the Calderinha fossil *Ficus* pollen with reference material from these two species, (or sedaDNA analysis) could help ascertain which *Ficus* species were present.

Being a human-populated Natural Park (2257 inhabitants), socio-economic variables should be taken into consideration when implementing restoration action by collaborating with stakeholders (Musche et al., 2019). For instance, introduced species (such as conifers) deliver wood for local communities, and this ecosystem service cannot be offered by slow-growing endemic or native species. In contrast, alien taxa could have detrimental impacts by drying and degrading soils. We suggest that re-introduced *Ficus* trees (*Ficus sur* and *Ficus sycamoros* subsp. *gnaphalocarpa*) could offer sustenance to native fauna in the Natural Park. In the short term, *Ficus* could coexist with alien conifers and in the long-term replace them. The restoration of endemic-dominated landscapes could play a key role in the ecotouristic appeal of the park for international and national visitors (Blangy and Mehta, 2006, see Campbell-Hunt, 2014 for case-studies in New Zealand).

#### 4.2.2. Monitoring and eradication

The identification of Acanthaceae (*Asystasia*) and *Opuntia* pollen (Fig. 2) in zone Cld-4 of the record, corresponding to introduced taxa that established locally in the last decades, suggests that these taxa might be in a phase of expansion, especially in abandoned agricultural lands. Land abandonment may indeed play a major role in the spread of these species: in Galápagos, non-actively managed land has acted as centres of establishment and dispersal of introduced species (González et al., 2008). These taxa are not currently considered invasive species in Cabo Verde (MAA/DGA 2008). However, according to our palaeoecological evidence, we suggest that it would be useful to start a monitoring programme to gather data about the speed of their spread and their competition with native taxa. Depending on the monitoring results it might be beneficial to put eradication campaigns in place to control their spread. Future palaeoecological studies could help ascertain if some of these species could have been native to some of Cabo Verde's islands before human arrival, as has been discovered in the Galápagos based on fossil evidence (Coffey et al., 2011; van Leeuwen et al., 2008).

#### 4.2.3. Erosion, grazing, and fire

Natural disturbance regimes in Monte Gordo included phases of erosion (ca. 5500 cal yr BP) and occurrence of fires (between 1000 and 400 cal yr BP). Human impacts and drying conditions with sporadic extreme weather events led to sustained erosion in the last ca. 400 yr, and our data (sedimentation rates and grain size distributions) suggest

that afforestation efforts have not yet reversed this trend. Soil protection and restoration initiatives can go hand in hand with vegetation restoration actions. Monitoring soil fertility, organic matter, erosion, and their link to current vegetation would allow understanding of which type of restoration action will result in better soil protection (Musche et al., 2019).

Island biodiversity can be especially vulnerable to the effects of introduced herbivores (Nogué et al., 2017). For example, sedaDNA and NPPs revealed that introduced rabbits in a sub-Antarctic island caused an increase in erosion rates due to the reduction of endemic vegetation (Ficetola et al., 2018). Rabbit population control measures helped reduce erosion rates to pre-invasion levels in a few years. In arid islands with rugged topography, soil erosion is a major threat for biodiversity and livelihoods. In other Macaronesian islands such as Tenerife, it has been suggested that a superabundance of introduced herbivores played a role in species extinction (e.g. *Quercus*) (de Nascimento et al., 2009). Our data show that grazing has had significant impacts on local vegetation so the control of herding and its delimitation to specific areas would help improve the conditions for native species, and in consequence, reduce soil loss.

Fire is also a main driver of landscape change in Monte Gordo. Our data suggest the occurrence of fire during what is considered the pre-human period. This early evidence of fire might suggest that in pre-human landscapes, increasing aridity, fuel loading, and/or lightning could have led to wildfires. Currently, the risk of fire in the Natural Park might be inherently higher, as the extra fuel added by invasive species such as *Lantana camara* is considered an urgent threat (MAA/DGA 2008). Palaeoecological charcoal records in Tasmania show that fire has been common during the Holocene, yet it has also been identified as a potential driver of species extinction in the present (Cadd et al., 2019). In Tasmania, researchers recommend focusing conservation actions on regions where topography discourages fire spread, such as slopes protected from trade winds (Cadd et al., 2019). Studying the relationships between topography, vegetation encroachment and risk of fire in arid islands could be crucial to avoid loss of biodiversity and select areas of priority conservation action.

#### 4.2.4. Education

Analysing how drivers of environmental change shaped the ecology of islands can offer new narratives that can show the magnitude of change that humans produced, and provide scientific justification of conservation efforts (Froyd and Willis, 2008). This can help improve outreach material and give new tools for education programmes by adding a temporal dimension to what has been called 'sense of place' (Burney and Burney, 2007). Our data can help strengthen the narrative of human impacts in Monte Gordo Natural Park, helping to convey a message urgency and a view of the landscape as a heritage worth preserving.

## 5. Conclusions

This study shows how palaeoecological methods, including multiple lines of evidence (e.g. changes in vegetation, fungal communities, fire and erosion), can reveal long-term information about landscape change in dry tropical islands that can be useful for conservation and restoration. The combination of classical proxies such as pollen, which can be subject to uneven preservation, with molecular and sedimentological information, has the potential to reveal important information about vegetation shifts and drivers of ecosystem change. The analysis of the Calderinha sediment profile (São Nicolau Island) has shown that for the past 5900 years, the landscape of Monte Gordo Natural Park has experienced considerable vegetation changes mainly linked to direct human impacts, but also due to fire and erosion in pre-human times. Our data has also shown land-use change in the highlands, including a first phase of agriculture and regional use of fire, followed by grazing, and finally the spread of introduced species that characterize today's

anthropogenic landscapes. This information may be of value in informing conservation practitioners, to help in setting restoration goals, including the re-introducing of native species (e.g. *Ficus*), and the monitoring and potential eradication of introduced species. In addition, we would like to highlight the importance of conserving soil quality and stability. Finally, we would like to suggest that new palaeoenvironmental studies across the Cabo Verdean islands have potential to reveal how general the trends we have found in the São Nicolau's highlands are, and will thereby allow comparison of different legacies of environmental change with diverse human histories and natural factors for the whole archipelago.

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#### Author statement

ACB, SN, LdN, ME, RW and JFP designed the study; ACB and ID collected the soil samples (June 2018). ACB analysed the sedimentary core under the supervision of: SN, TF, LdN, CM, MJE, AC. All authors made substantial contributions to the writing of the article.

#### CRediT authorship contribution statement

**Alvaro Castilla-Beltrán:**Conceptualization, Investigation, Formal analysis, Writing - original draft.**Ivani Duarte:**Investigation, Writing - original draft.**Lea de Nascimento:**Conceptualization, Writing - original draft.**José María Fernández-Palacios:**Conceptualization, Writing - original draft.**Maria Romeiras:**Writing - original draft.**Robert J. Whittaker:**Conceptualization, Writing - original draft.**Margarita Jambrina-Enríquez:**Writing - original draft, Investigation.**Carolina Mallol:**Writing - original draft.**Andrew B. Cundy:**Writing - original draft, Investigation.**Mary Edwards:**Conceptualization, Writing - original draft.**Sandra Nogué:**Conceptualization, Writing - original draft, Investigation.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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