University of Southampton

Faculty of Environmental and Life Sciences
School of Geography and Environmental Science

Tracing human impacts on the islands of Cabo Verde: Palaeoecology for the conservation of island ecosystems in southern Macaronesia

By
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Thesis for the degree of doctor of philosophy
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Abstract

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Doctor of philosophy (PhD)

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Oceanic island ecosystems are exceptional due to their isolation; island species typically exhibit high levels of endemism and small population sizes, which make them especially vulnerable to anthropogenic pressures. Loss of biodiversity has been especially severe on islands during the last several centuries, often associated with human-driven biological invasions and direct impact via land use. In this context, the conservation and restoration of island ecosystems is urgent, yet historical information on long-term environmental trends remain scarce. Palaeoecological evidence can provide insights on how island ecosystems responded to diverse natural and human-driven disturbances through centuries and millennia. In this PhD thesis, long-term environmental changes in the highlands of three islands of Cabo Verde islands (Santo Antão, São Nicolau, Brava) are investigated to determine how vegetation (pollen, phytoliths, leaf wax n-alkanes) and ferns and fungal communities (non-pollen palynomorphs) varied over time in response to the occurrence of fires (charcoal concentration), depositions of volcanic ash (tephra) and erosion pulses (grain sizes and elemental composition).

In Santo Antão and São Nicolau, pre-human ecosystems consisted of grasslands and woody scrublands and showed limited variation in composition linked to naturally occurring disturbances such as wildfires and erosion pulses between 2,000 and 500 cal yr BP. São Nicolau's highlands held abundant woody vegetation incuding *Euphorbia tuckeyana, Ficus* and *Dracaena draco* subsp. *cavoberdeana*. In Brava, the regional drying trend after 4,000 cal yr BP was associated with increased local erosion but had limited impacts on highland grassland vegetation. In contrast, the expansion of fern-rich woody scrubland was likely triggered by volcanic ash deposition after 1,800 and 650 cal yr BP. Human impacts after Portuguese settlement (1460 CE) generated multiple disturbances in all studied islands, including increases in fires, deforestation and the introduction of exogenous species. This led to chronic and persistent disturbances, such as soil degradation and erosion, and the decrease of native vegetation cover in favour of introduced species. The resulting island histories of environmental change described in this thesis are used as guidelines to set historically contextualised management goals. These new palaeoenvironmental discoveries can contribute to the restoration of scrublands and woodlands, soil management, fire prevention and the monitoring and eradication of introduced species.

‘Sodade, sodade,

Sodade dessa minha terra, São Nicolau’

From ‘Sodade’, song composed by Armando Zeferino Soares

Famously interpreted by Cesaria Évora

‘Sodade is a feeling that is granted a special kind of mysticism and romance in the CapeVerdean psyche. It (…) embodies the collective socio-historic landscape of Cape Verde. Sodade is described as a deep emotional state of nostalgic longing, vague and constant desire for something intangible, or a turning towards the past or towards the future’

Definition by April Goltz

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Research Thesis: Declaration of Authorship

Print name: Alvaro Castilla-Beltrán

Title of thesis: *Tracing human impacts on the islands of Cabo Verde: Palaeoecology for the conservation of island ecosystems in southern Macaronesia*. I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research. I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
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Chapter 1 Introduction and overview

1.1 Thesis aim

This PhD thesis investigates the Holocene environmental change in Cabo Verde (from ca. 10,000 cal yr BP until the present day), a tropical archipelago of Macaronesia situated in the Eastern Atlantic Ocean, by using multiple palaeoecological methods. The overall aim of this thesis is to assess the responses of highland ecosystems to natural disturbances in pre-human times, and anthropogenic impacts after human colonization, and to explore the value of these results for guiding biodiversity conservation. Incorporating the theoretical foundations of resilience theory (Hodgson et al., 2015) and socio-ecological systems (Folke, 2006), multiple palaeoenvironmental proxies are studied to reveal changes in vegetation cover (fossil pollen, fern spores, *n*-alkanes), communities of decomposers (fungal spores), fire-history (micro- and macro-charcoal particles) and erosion regimes (sedimentological analyses). The results of this work characterise ecological baselines, providing a historical benchmark from which to inform restoration and conservation initiatives in Cabo Verde and Macaronesia.

While there is a considerable body of knowledge related to the biogeography of Macaronesia and Cabo Verde (e.g. Fernández-Palacios et al., 2011; Freitas et al., 2019), far less is known about the ecological change over time, and how humans have shaped island ecosystems (but see Connor et al., 2012; Fernández-Palacios et al., 2017; de Nascimento et al., 2020). Many of Cabo Verde´s ecosystems, including marine and terrestrial, are currently under pressure from anthropogenic and natural factors such as overgrazing and the occurrence of extreme weather events. The highlands (800 to 2900 m asl) have been of special interest for conservation action due to their high habitat diversity and species richness (Romeiras et al., 2016). This thesis aims to open a new aspect of knowledge about the environmental history of Cabo Verde by investigating the long-term environmental change of highland ecosystems.

1.2 Research questions

The research questions address Holocene environmental change, human impacts and biodiversity management in Cabo Verde.

RQ1 What was the ecological state of the highland ecosystems of Cabo Verde during the Holocene and what was their natural variability?

RQ1.1 Is there evidence of a pre-historic human habitation of Cabo Verde?

RQ1.2 Did Cabo Verde support laurel, Mediterranean or tropical forests in the past?

RQ1.3 What were the drivers of landscape change before human settlement?

RQ2 How has human settlement and the emergence of socio-ecological systems impacted highland landscapes in Cabo Verde?

RQ3 What insights can palaeoecological research offer to guide biological conservation and ecological management in Cabo Verde?

1.3 Research workflow

This thesis is the product of three fieldwork campaigns (2015, 2018, 2019) and laboratory analyses of multiple proxies of environmental change in sediments of volcanic Calderas in three different islands of Cabo Verde. Figure 1 illustrates the research workflow and strategy divided in three stages, highlighting relationships between analytical methods and research outcomes.

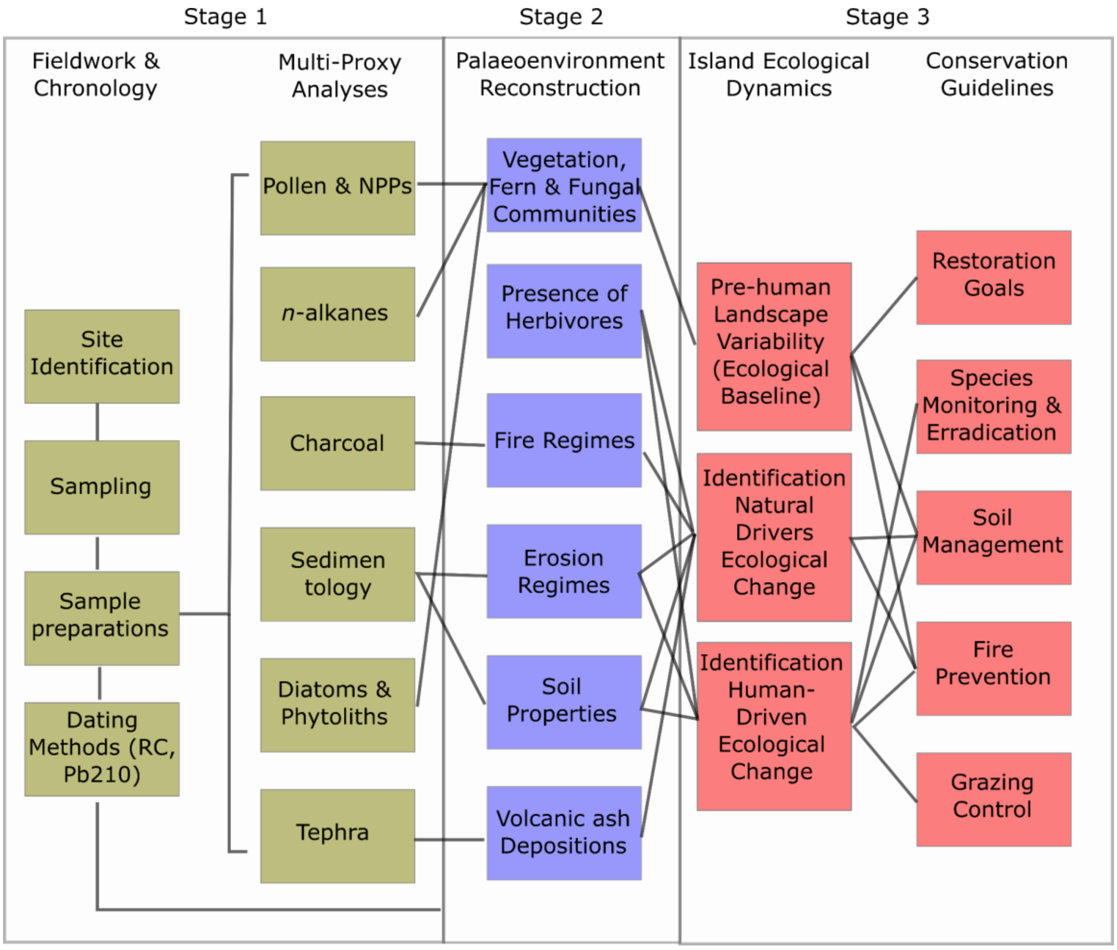

Figure 1.1: Flow chart of the main analytical and interpretative steps followed in this thesis. Acronyms: Radiocarbon (RC), Non-pollen palynomorphs (NPPs), Loss on Ignition (LOI), X-Ray Fluorescence (XRF).

Chapter 2 Theoretical Background

2.1 Oceanic islands: Past, present and future

The study of islands has been at the forefront of the understanding of biological processes since the works of Alexander von Humboldt and Charles Darwin (Whittaker et al., 2017). The field of Island biogeography is focused on the understanding of processes of colonization, evolution and extinction within islands and archipelagos. Isolation is considered the most influential factor in making islands biodiversity hotspots, and it contributes to the emergence of 'naïve' ecosystems, characterized by species with insular adaptations and low population sizes, vulnerable to natural and human pressures (Whitaker & Fernández-Palacios, 2007; Wood et al., 2017). For instance, biological invasions, which account for most of the reductions in the native biodiversity, are especially damaging in oceanic islands (Froyd and Willis, 2008) due to cascading effects related to the extinction of keystone species (Burney & Flannery, 2005). Long-term approaches at different temporal scales are vital to understand the natural history of islands: at a geological scale (Millions of years), the study of island lifecycles can reveal how islands developed and reached maturity as biodiversity hotspots (Whittaker et al., 2008; 2017), while assessing ecological change at the centennial and millennial-scale is pivotal to understand how they were impacted by natural and anthropogenic disturbances (Birks, 2019; Nogué et al., 2017).

The influence of the ocean as a buffer from extreme climates and reduced species competition due to isolation have made islands an ideal refuge for species that have become extinct on continents (Whittaker & Fernádez-Palacios, 2017). Therefore, islands are considered paradigms of ecological stability in the past (McArthur & Wilson, 1967). Palaeoecological research on islands has indeed demonstrated that in many cases island ecosystems throughout the Holocene were relatively stable in composition until human colonization (Birks, 2019). However, drastic contrasts between natural (no human presence) and cultural (ecosystems subject to human impact) landscapes have been documented in islands worldwide (Rick et al., 2013). When looking into the development of socio-ecological systems in islands, the dominant narratives have taken root in biology and considered islands as laboratories (Kirch, 2017), and human impacts as direct cause of ecological catastrophes (Hunt, 2007). But not all island histories are cautionary tales about societal collapse due to unsustainable socio-economic development (Rick et al., 2013). The view of humans as an ever-destructive force of island landscape ecology has been challenged by evidence pointing at the human enhancement of island ecosystems through tree planting and soil protection with terracing in different geographical contexts. The core concept of islands as cultural microcosms is now challenged due to increasing evidence of archipelago-wide networks of interaction (including exchange of materials and species translocations) in the Caribbean and the Pacific (Hofman et al., 2014; Kirch, 2017). These developments add new dimensions to the study of insular and archipelagic socio-ecological systems and demonstrate the need to understand their complex dynamics by integrating disciplines such as geography, ecology, biogeography, and archaeology.

Today, it is increasingly accepted in the scientific community that global human alteration of land, ocean and of atmospheric composition has caused the Earth system to enter a new epoch: the Anthropocene (Crutzen & Stroermer, 2000; Steffen et al., 2015; Lewis & Maslin, 2015). While there is still debate around when was the onset of the Anthropocene, its effects are evident in the form of a human-driven ‘extinction crisis’, with rates up to 1000 times higher than baseline conditions (Mace et al., 2005; Tershy et al., 2015). Islands greatly contribute to global biodiversity (*e.g.* 17% of flowering plants) in relation to their size (5.3% Erath land area). Losses of biodiversity and cultural heritage (*e.g.* languages) are especially severe in islands (Tershy et al., 2015). There is, therefore, an urgent need to preserve biodiversity in threatened island environments, and to actively manage social and ecological processes to reach sustainability in these unique settings. The discipline of palaeoecology can contribute to these efforts by providing insights into long-term environmental change with which to contextualize pressing socio-ecological challenges.

2.2 The principles of Palaeoecology

Documentary evidence and modern instrumental records of environmental change, such as satellite data, are limited to the last few centuries or decades, respectively (Dearing et al., 2006). To assess ecological change at the millennial and geological scale it is necessary to study our planet's fossil record. Palaeoecology is the study of past environments from fossil and sub-fossil evidence by using a range of analytical techniques (Birks & Birks, 1980) and is critical to developing insights into landscape change over longer time-scales. Sequential changes in diverse sediment-based proxies of environmental status provide data on environmental change and human-environment interactions at decadal, century and millennial scales. Chronologies established via diverse dating techniques (*e.g.* radiocarbon dating) are used to model the timing and rates of sediment deposition in a particular site and combinations of sediment-based evidence are investigated in reference to a chronological model. The main limitations of the study of sediment records are differential proxy preservation, chronological uncertainties and proxy-dependent biases (Dearing et al., 2006). The integration of multiple proxy evidence, and of records from different sites, requires careful interpretation and needs to be integrated to modern ecological observations, archaeo-historical evidence and geographical data to fully use of their potential as evidence of ecological and social processes (Dearing et al., 2006).

2.3 Complexity and ecological change: concepts for the study of island ecosystems

Long-term data about past environmental dynamics is useful to assess temporal and spatial patterns of ecological change linked to climatic fluctuations, human influence and internal ecosystem dynamics (Dearing et al., 2006). Four main ecological concepts essential for the assessment of island ecosystem change through time are used here: resilience, ecological thresholds, disturbance regimes, and ecological baselines.

2.3.1 Resilience

The concept of ecological resilience was introduced to ecology by Holling (2001), and is nowadays broadly applied in studies of ecological and social systems. It refers to the persistence or change of an ecosystem in relation to alternative states (Andersen et al., 2008). The resilience approach to the study of an ecosystem is based on monitoring ecological change through time, and analysing its ability to resist exogenous disturbances without switching to other states (resistance), and by assessing the time it needs to recover after perturbations (resilience) (Hodgson et al., 2015). This distinction between the two types of resilience was used by Herbert et al., (1999), who studied the resilience of a mountain native rain forest in the island of Kokee, Hawaii by assessing damage and recovery processes. They concluded that resistance and resilience of forest plots were inversely correlated, meaning that more resistant areas of the forest (that are normally less affected by hurricane activity) would take more time to recover to baseline conditions once impacted. The concept of resilience has proven fertile in long-term ecology throught the comparison of trends of degradation and recovery of similar ecosystems. Cole et al., (2014) used palaeoecological datasets (fossil pollen records) to explore the resilience of tropical forests after diverse disturbances in four tropical regions: Africa, Central America, South America and Asia. Meaningful differences in rates of recovery were identified: generally, forests recoverd faster from larger infrequent disturbances such as tropical storms, and slower to human-driven disturbances such as fires and land use. Forests in Central America and Africa showed faster recovery rates than those in Asia. Also, the results of their meta-analysis suggest that forests that were exposed to more natural and human-driven disturbances in the past showed increased resilience in the present (Cole et al., 2014).

2.3.2 Ecological thresholds

Identifying regime shifts, that is, fundamental reconfiguration of an ecosystem between alternative states, is central to understand the long-term history of an ecosystem (Anderden et al., 2008). When a system switches to another ecosystem state, it can be said that an ecological threshold has been crossed. These regime shifts have been documented after large external perturbations (Dearing et al., 2015), but they can also be caused by the system's internal dynamics, this is, the interactions of ecosystem components such as vegetation and fauna (van Langevelde et al., 2003). The rate of change of an ecosystem and its drivers or the interplay between gradual and rapid changes can cause an ecosystem to cross a threshold (Folke, 2006). For instance, the perfect storm model (Dearing et al., 2012) illustrates how long-term slow, irregular fast, and unpredictable disturbance pulses can have combined effects that produce a system to cross a threshold into alternate ecosystem states. The study of African savannahs revealed that internal system dynamics can generate the crossing of thresholds between grass-dominated and woodland-dominated regimes (van Langevelde et al., 2003). Threshold crossing is, in this case, the product of long-term complex interactions between savannah biotic and abiotic components: a decreasing number of herbivores can cause increases in woody vegetation, and a boundary can be crossed towards a wooded landscape. However, encroachmentd of woody vegetation augments the probability of wildfires, which can make the system cross another threshold to grass-dominated savannahs (van Langevelde et al., 2003).

2.3.3 Ecological disturbances

Ecological disturbance regimes are the combination of biological (e.g. disease) and abiotic (e.g. drought) forces that bring about change in an ecosystem by shifting biodiversity abundance and spatial configuration (Paine, 2012). The natural disturbance regimes that affect ecosystems work via pulses (events) of diverse magnitude, spatial distribution, frequency and duration (Elmqvist et al., 2003) and can generate positive and negative feedback loops in an ecosystem (Fig. 2.1). Such feedback loops are changes in a system in which a variable (e.g. erosion) responds to a driver (e.g. vegetation loss), amplifying or reducing the original change. Positive feedback would entail increased erosion leading to loss of vegetation cover, which would, in turn, leads to more erosion, etc. (Dearing et al., 2010; 2015). Human impacts in an ecosystem, such as deforestation, often lower the resilience of ecosystems to natural and human disturbances (Paine et al., 1998). For instance, anthropogenic preassures can transform disturbance pulses into chronic disturbances and create positive feedbacks between these impacts, generating compounded disturbances (Bengtsson et al., 2003). Observing changes in the dry forest of the island of Guadaloupe (Lesser Antilles, Caribbean) Imbert and Portecop (2008) assessed the interaction of recurrent anthropogenic pressures (such as deforestation for charcoal production) and natural stressors (e.g. hurricanes). Based on 10-yr monitoring of floristic composition they concluded that forest recovery from natural stressors such as hurricanes is delayed by the occurrence of chronic and persistent disturbances like multi-annual droughts and deforestation.

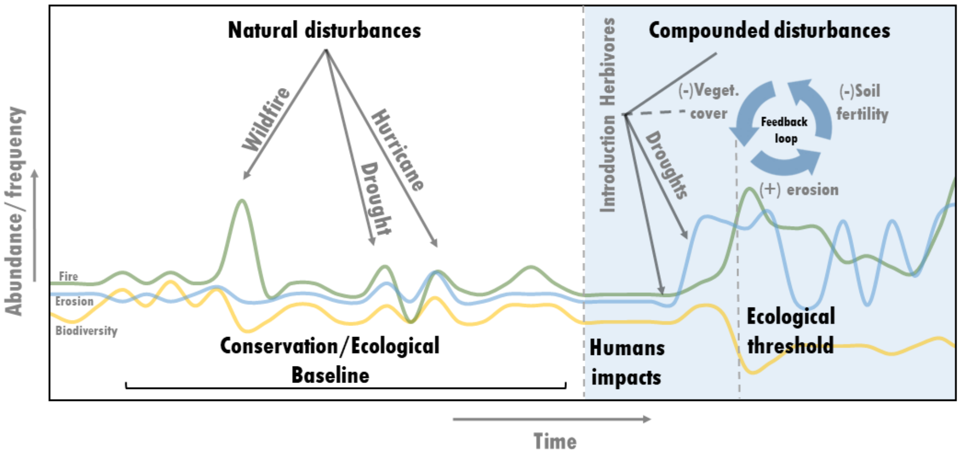

Figure 2.1: Conceptual diagram of Resilience theory in a theoretical model of human-impacts on an oceanic island. Time passes from left to right. The model highlights the role of natural pulse disturbances and feedback loops between natural and anthropogenic (compounded) disturbances, leading to the crossing of ecological thresholds.

2.3.4 Socio-ecological systems

A socio-ecological system is composed of human and natural components that interact and co-evolve through time and space, so they can be considered bio-geo-physical units (Pogue et al., 2015). The human dimension should be considered as integrative to an ecosystem so that complex processes of interaction between societies and environments can be identified (Folke, 2006). Diverse theoretical approaches and guidelines for understanding of human-environment interactions have been proposed, including the complex adaptive systems framework (Levin, 1998; 1992), the human ecodynamics framework (McGlade, 1995; Fitzhugh et al., 2019) and historical ecology (Balée, 2006). These frameworks share a conception of humans as decision-makers that respond to, but also affect, natural systems (Levin, 1998). A multifaceted and dynamic conception of the role humans in SES is aimed at revising the view of humanity as a unidirectional force that drives ecosystems from species-rich environments to degraded, homogeneous landscapes with low diversity (Balée, 2006). Instead, the integrated study of archaeo-historical and ecological threads of evidence is used to assess how complex cultural practices can produce multiple transformations in ecosystems, from degradation to restoration

(Balée, 2006). A long-term perspective is thus essential to gain an understanding of present-day socio-ecological states and future challenges (Dearing et al., 2010).

The integration of insights from complex adaptive systems and historical ecology frameworks in archaeological and palaeoecological studies aims to generate a new understanding of the landscape as a product of historical social and ecological transformations (Gaillard et al., 2009). For instance, study of the landscapes of the Amazonian delta islands is revealing that indigenous societies carried out intensive transformation of local landscapes for millennia. Some of their practices could be implemented nowadays to enhance and sustain the production of resources for local communities (Schaan, 2010; Rostain, 2016). Scientists are finding evidence of the spread of woody domesticated species in the whole Amazonian basin, revealing that modern tree communities in the Amazon are in part a product of direct and indirect human landscape modification (Levis et al., 2017).

2.4 Human impacts on islands: a socio-ecological system approach

Islands often have limited resources in comparison to mainland settings, meaning that their environmental limits more easily transgressed by humans. Initial stages of human settlement in island ecosystems frequently caused environmental degradation (Whitaker & Fernández-Palacios 2007; Wood et al., 2017). This is linked to the arrival of new species (e.g. commensal taxa that travel with humans, domesticates…), which compete with and exert direct predation on native species, unleashing cascade effects through trophic levels (Burney & Flannery, 2005). While human-mediated species introductions in islands may have in some cases 'balanced' the local loss of biodiversity, from a planetary perspective this represents a dramatic loss of biodiversity (Vellend, 2017). In addition, biodiversity loss goes hand-in-hand with biophysical (or biogeomorphic) effects, as the biota has direct links with physical aspects of the environment, including soil integrity and biogeochemistry (Fei et al., 2014; Leppard, 2017). For instance, composition of plant communities determines soil properties through root structure, and loss or change of vegetation cover after human settlement can limit the capacity of soils to resist eroding forces, leading to soil degradation through erosion (Berendse et al., 2015). Furthermore, the introduction of animal species such as ungulates produces the erosion of topsoils, a process that causes disruptions in nutrient cycling, often leading to favourable conditions for the spread of invasive species (Leppard, 2017). The ramifying biophysical impacts of first human colonization in previously uninhabited islands can impose severe constraints in the development of island societies and their sustainability (Leppard, 2017): for instance soil degradation (loss of soil itself or of soil fertility) and loss of vegetation cover could render island ecosystems more vulnerable to extreme weather events.

Limited ecological knowledge and lack of suitable management strategies have led humans to generate depletion of natural resources and species extinctions (Lindskog & Delaite, 1996), after which collapse episodes or landscape abandonment follows (see Romero et al., 1999). An important factor was the development of cultural practices that were not appropriate to achieve sustainability on islands. However, in some cases, human societies can develop coping mechanisms through observation, and are incentivised by this to put in place resource management strategies, such as in some Pacific islands (Johannes, 2002). This can generate long-term co-evolution of social and environmental systems that reach relative equilibriums, as conservation measures are designed to prevent future crises (Berkes & Turner, 2006). Research into the socio-ecological systems of the Galápagos islands shows a sequence of stages with evolving socio-ecological interactions concerning increasing environmental knowledge and implementation of management strategies: during the first three centuries of settlement (1535-1832 CE) extractive exploitation and introduction of alien mammal species led to the scarcity of resources, urging settlers to attempt to monopolise resources in permanent villages (Gonzalez et al., 2008). A second cycle (1832- 1959) was characterised by agricultural expansion in the highlands, but also the creation of protected areas as a response to the increasing pressure on threatened species. A third cycle (1959-1998) took place with the rise of nature tourism, generating chaotic and uncoordinated proliferation of conservation initiatives that took no consideration of local inhabitants. This created a situation of social conflict between conservation institutions and land-owners, and the increase of tourism led to even more immigration and overexploitation of fisheries (Gonzalez et al., 2008). This case study shows how changing cultural practices, knowledge and priorities can generate new stages of socio-ecological interaction.

2.5 Island palaeoecology and conservation

Assessment of the interactions between nature and society is allowing great advances in the management of socio-ecological systems, including conservation and ecological management (Folke et al., 2002). Knowledge and ecological understanding are key to conservation. Incorporating lessons from past accomplishments and failures to manage the environment is one of the main mechanisms in environmental management and sustainable development (Berkes & Turner, 2006). However, legacies and memories can be lost after generations, and traditional ecological analytical techniques cannot trace socio-ecological change over long time-scales (Froyd & Willis, 2008). In this context, palaeoecological data are useful for conservation, as they can provide a long-term ecological understanding to be integrated as a component to the set of considerations for conservation initiatives.

Conservation practices have traditionally been based on the idea of static, idealized natural ecosystems untouched by humans (Froyd & Willis, 2008). However, the current extinction and climate crises have emphasised a paradox in the conservation of biodiversity in our world: our attempts to preserve biodiversity is at odds with the increasing recognition that the planet´s environments are always in flux (Gillson, 2015). A biodiversity, conservation or ecological baseline can be defined as a description or characterization of a landscape condition before a particular change or impact, to be used as a reference for conservation-rehabilitation initiatives (Dearing et al., 2006). The knowledge of the long-term development of a landscape is useful for the restoration of ecosystems, as understanding the dynamics of past ecosystem states allows to restore 'authentic' landscapes (Balée, 2006; Willis et al., 2005; 2007; 2010; Nogué et al., 2017). As relationships between climate and human-dominated landscapes are complex, ecosystem management and conservation need to be based on a long-term understanding of system dynamics in response to human and climate change impacts (Dearing et al., 2006). Baselines can refer to a single past state (pre-human vs. human-dominated environment) (Fig. 2.1) or address changes after more than one type of disturbance (multiple baselines), including natural perturbations and cultural change (Nogué et al., 2017).

The last decades have seen increasing efforts of palaeoecologists to highlight the conservation value of the insights provided by their studies (Birks, 2019). For instance, long-term ecology can help contextualize views of desirable 'pristine' or 'natural' ecosystem states, and restoring degraded ecosystems consists of bringing the ecosystem to a state that exhibits desirable characteristics. In oceanic islands, human impacts have had distinctive effects through time, and characterising prehistoric cultural landscapes is pivotal to identify processes that have led to undesirable landscape states (Nogué et al., 2017). For instance, palaeoecological studies on Poor Knight Island, New Zealand, indicate that the current dominant *Metrosideros* forest reprsents an altered state, as pre-human vegetation was characterised by *Podocarpus* and palms (Wilmshurst et al., 2014). This ecological transformation took place after different episodes of human settlement and colonization (Maori and European), meaning that there are multiple baselines to be considered when taking ecological restoration action (Nogué et al., 2017). Similarly, the study of the historical ecology of the Caribbean islands has revealed evidence of overexploitation of resources since the first Archaic Age settlement (~7000 BP), indicating that humans degraded local ecosystems throughout the Mid and Late-Holocene (Fitzpatrick & Keegan, 2007). European settlement after AD1492 added a new layer of impacts on top of previous human pressures on terrestrial and marine ecosystems (Fitzpatrick & Keegan, 2007). Characterising ecological baselines can also reveal ecosystem changes that form an integral part of the natural variability of an ecosystem ('historical range of variability'), meaning that ecosystems that seem degraded should not be the target of restoration actions (Froyd & Willis, 2008; Birks, 2019). The main contributions of palaeoecological data as a factual basis for conservation evaluation criteria in islands are presented in Table 2.1.

Table 2.1: Conservation evaluation criteria offered by palaeoecological data in islands.

Conservation-evaluation critera (after Birks, 2019)	**Relevance in oceanic island contexts**
Assessing fragility (degree of resilience to environmental change) of an ecosystem	The fragility of an island ecosystem can increase due to the extinction of keystone species and changing biophysical factors linked with species invasions such as soil erosion (e.g. Ficetola et al., 2018).
Assessing the native/non-native status and history of particular taxa	Ascertaining the native/non-native status of plant taxa has proven vital for island conservation initiatives (e.g. van Leeuwen et al., 2008; Burney & Burney, 2007).
Establishing baseline reference conditions	Island with long histories of human settlement can have developed diverse stages of human-dominated landscapes (Nogué et al., 2017).
Development of landscape-scale management plans in response to fires and human impacts	While fire can be part of the natural variability of some islands, human settlement generally increases fire frequency in islands
Providing a historical perspective on socio-ecological systems	Past human adaptations to island life and the ecological consequences of landscape management can provide alternatives to unsustainable land use strategies.
Deciphering the origin of landscapes mosaics concerning past disturbances	Current landscape mosaics in islands can comprise combinations of native and introduced species, which may be the product of species competition after episodes of disturbance, for example. Elucidating their historical development is key to assessing if they are a desirable feature of island ecosystems.

Chapter 3 Study Setting

3.1 Macaronesia: Biogeography and human settlement

Macaronesia, from the Greek words *makarios* (happy or blessed), and *nessos* (islands) is a biogeographic region situated in the NE Atlantic Ocean formed by five volcanic archipelagos situated west from NW Africa and the Iberian Peninsula: Azores, Madeira, the Salvaegens, Canary Islands, and Cabo Verde (Fernández-Palacios et al*.,* 2011). These archipelagos are characterised by their high terrestrial and marine biodiversity, and they share characteristic flora and fauna (Freitas et al., 2019). Azores, Madeira and the Canary Islands all preserve laurel forests remnant from the dominant continental forests in the Cenozoic (Fernández-Palacios et al., 2016), and it is unknown if Cabo Verde could have supported this relic forest in the past, as the absence of laurel forests from the present-day islands could have been caused by human impacts (Heckman, 1985; Barone 2006). Currently, Cabo Verde is described as representing a biogeographical middle ground between Macaronesia and mainland Africa (Freitas et al., 2009).

The human colonization of Macaronesia took place in three main waves: a North African migration to the Canary Islands started around 2000 BP (Rando et al., 2008), an early settlement of Azones ca. 1290 CE (Rull et al., 2017), and the European (Castilian, Portuguese and Genoese) settlement of Azores, the Canary Islands, Madeira (1420-1430 CE), and finally Cabo Verde (1456-1460 CE). In the Canary Islands, the early arrival of the Guanche population led to profound impacts on island biodiversity including the extinction of animal (Rando et al., 2008) and plant species (de Nascimento et al., 2009; 2020) (Table 3.1). Indigenous impacts were extensive, mainly due to the introduction of goats, sheep, pigs and rodents, and after the Castilians conquered the islands extensive agricultural activity resulted on the fragmentation of native laurel forests in Tenerife, which almost disappeared in Gran Canaria (Fernández-Palacios et al., 2011; de Nascimento et al., 2020). Laurel forest fragmentation also took place in the Azores due to colonial land use. Currently, the islands that preserve the most intact laurel forests are La Gomera and Madeira. While palaeoecological research and archeo-historical studies are producing a wealth of information about long-term environmental change in Macaronesia, the archipelago of Cabo Verde remains largely understudied, mainly due to the intrinsic challenges of carrying our palaeoenvironmental research in dry environments.

Table 3.1: Evidence of human impacts in Azores, Madeira and the Canary islands (after Connor et al., 2012).

Archipelago	**Island**	**First human settlement**	**First human impacts**	**Evidence**	**Source**
Azores	Flores	~530 BP	ca 400 BP, *Juniperus* decrease, introduced and cultivar taxa	Pollen, Charcoal, NPPs	Connor et al., 2012
	Pico	~530 BP			
	São Miguel	~530 BP	1500 BP, forest replacement, cultivation, grazing	Pollen, charcoal, NPPs	Rull et al., 2017
Madeira	Madeira	~ 530 BP	Deforestation	Royal decrees	Menezes de Sequeira et al., 2007
Canary Islands	Tenerife	~2500 BP	1500 BP, decrease *Quercus* and *Carpinus,* fire	Pollen and charcoal	de Nascimento et al., 2009
	La Gomera	~2500 BP	Between 3100-1800 BP, fire, grazing	Charcoal, NPPs	Nogué et al., 2013
	Gran Canaria	~2500 BP	ca. 2300 BP, fire, forest opening	Pollen, charcoal	de Nascimento et al., 2016

3.2 Cabo Verde: climate and biogeography

Cabo Verde is the only tropical archipelago in Macaronesia. It remained uninhabited by humans until 1460 CE when it became the first European territory in the tropics (Evans et al., 2017). It is situated 600 km west of the African coast that can be divided between Northern (Santo Antão, São Vicente, and São Nicolãu), Eastern (Sal, Boa Vista, and Maio) and Southern (Santiago, Fogo, and Brãva) island groups (Fig. 3.1). Cabo Verde is at the same latitude of the Sahelian arid belt, but its climate is tropical oceanic, with low levels of rainfall concentrated during the wet season (July-October). The Intertropical Convergence Zone (ITCZ) has a great influence on the archipelago's climate, as its migration to north latitudes causes the arrival of monsoon-type rains from the southwest (Duarte & Romeiras, 2009). The seasonal variation between monsoon rains and aridity favours soil erosion; streams are ephemeral and run after heavy precipitation. Barren landscapes predominate, and during the dry season, Harmattan winds (African Easterly Waves) bring Saharan dust from the east, and its dryness can increase evapotranspiration rates (Heckman, 1985).

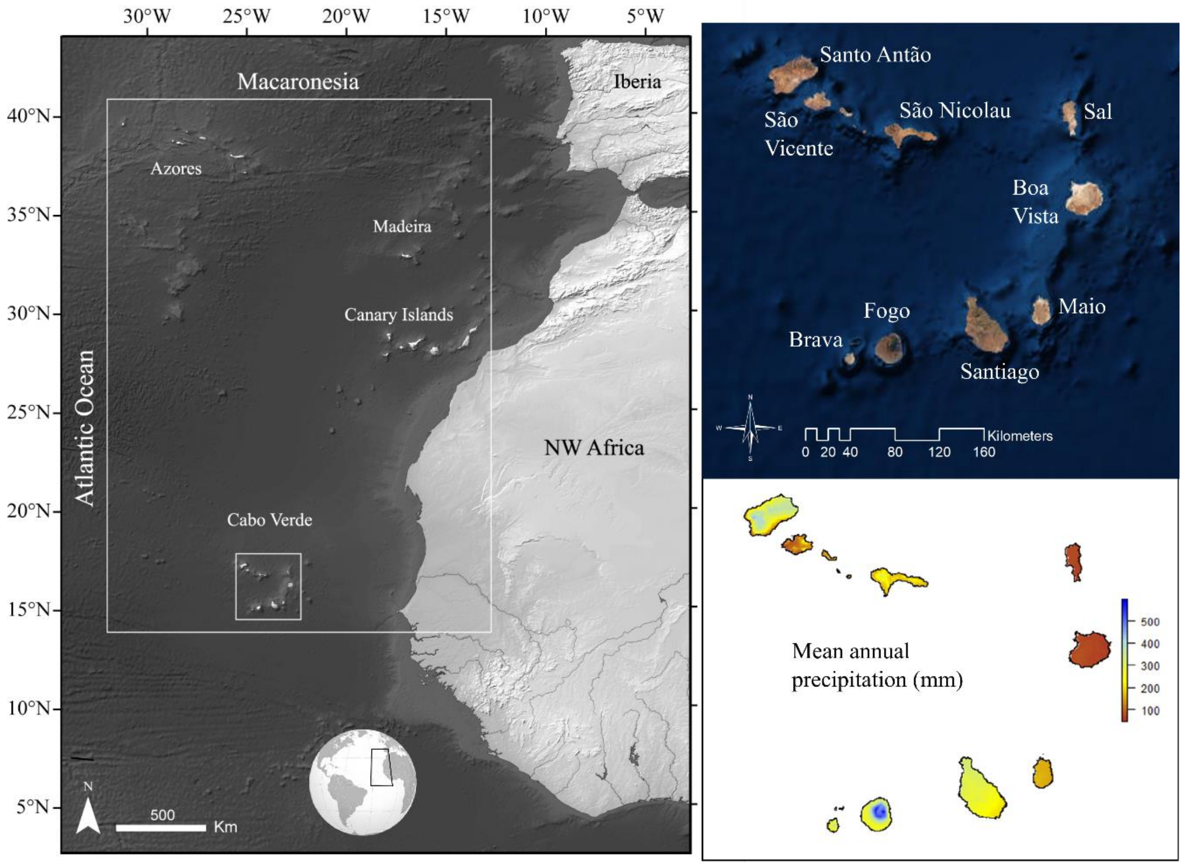

Figure 3.1: Location of Cabo Verde within the region of Macaronesia (left pannel) and maps of elevation, precipitation and temperature (right pannels). Map of Macaronesia created with raster data from maps from Natural Earth: https://www.naturalearthdata.com/. Precipitation map adapted from GADM: https://gadm.org.

Cabo Verdean islands support diverse habitats and local climates (Duarte & Romeiras, 2009). Trade winds from the northeast are humid and provide water in the form of fog condensation on the highlands. There is a spatially heterogeneous flora, with high levels endemism (Table 3.2). The endemic flora of Cabo Verde has mostly Macaronesian and Mediterranean affinities; 40% of the endemics related to Canarian and Madeiran species (Barone, 2005), and the native flora of its arid areas has similarities with Saharian and Arabian vegetation (Duarte et al., 2008). In the archipelago, 78% of endemic vascular plants are currently considered threatened, some of which are critically endangered, and others are thought to have become extinct (Romeiras et al., 2016). Sub-humid or humid grasslands and scrublands/heathlands dominate mid and high elevations. Most native woodlands are now restricted to upland areas in mountainous islands, including '*Ficus* and *Sideroxylon* Woodlands', '*Faidherbia* savannahs', and 'other arborescent communities', formed by *Dracaena caboverdeana, Phoenix atlantica, Tamarix senegalensis* and 'shrub vegetation'(Neto et al., 2020). The lowlands are arid and halophilous coastal vegetation is dominant.

Table 3.2: Features of Cabo Verde islands (after Duarte et al., 2008). Demographic data from Wolfram-Alpha, historical data from Patterson (1988) and Green (2012).

Island	**Area (km^2)**	**Altitude (m)**	**Permanent human population (2015)**	**Endemic taxa (exclusive endemics)**	**Earliest documentary evidence of permanent settlement**
Santo Antão	779	1979	40,547	47 (11)	1580 CE
São Vicente	227	725	76,107	35 (1)	1623 CE
Santa Luzia	35	395	0	10 (0)	-
São Nicolau	343	1304	12,769	46 (8)	1580 CE
Sal	216	406	35,000	15 (1)	1650 CE
Boavista	631	387	8,554	14 (0)	1567 CE
Maio	269	436	6,980	11 (0)	1505 CE
Santiago	991	1392	272,312	38 (3)	1462 CE
Fogo	476	2,829	37,200	38 (7)	1580 CE
Brava	64	976	5,971	25 (0)	1580 CE

3.3 Holocene regional climate and landscape change

Climate and precipitation in Cabo Verde are determined by the oscillations of the West African Monsoon (Duarte & Romeiras, 2009). Changes in the latitude of the Intertropical Convergence Zone have led to different monsoon regimes though the Holocene in Northern Africa, shaping vegetation in the Sahara region and Cabo Verde via the expansion and contraction of biomes reflecting monsoonal moisture fluctuations (Pausata et al., 2020; Neto et al., 2020). A major displacement of the African monsoon northward in the early Holocene is known as an African Humid Period (AHP), the last one recorded taking place between ca. 12,000–5,000 yr BP. After the last AHP, regional conditions became dryer in a process that has been hypothesised to be regionally progressive from north to south, but that was abrupt from the local perspective (Pausata et al., 2020). This has been assessed by the study of near-shore marine records in the Senegal region, which reveal sharp decreases in precipitation after 4,000 ca yr BP, as well as increases in the deposition of Saharan dust after 3,500 and 200 cal yr BP (deMenocal et al., 2000; Tierny et al., 2017; Mulitza et al., 2010). The responses of the landscapes of Cabo Verde to such climatic events are still to be assessed, but it has been hypothesised that processes of vegetation expansion in wet periods and contraction in dry periods have shaped the current landscape configuration (Neto et al., 2020). Furthermore, the role of climate and natural environmental disturbances is still to be disentangled from human-driven landscape disturbances in this archipelago.

3.3.1 Human settlement and socio-ecological systems in Cabo Verde

Current knowledge suggests that Cabo Verde was not permanently inhabited by humans until the Portuguese-Genoese colonization, a process that started around 1460 CE (Mitchell, 2004; Green, 2012). During the late fifteenth and most of the sixteenth century, the archipelago became a central hub in the emerging trans-Atlantic trade system; due to its strategic location, Portuguese traders used the islands as a provisioning point for ships and as a slave trade centre, and it became an integral part of the West African colonies (Green, 2012; Caney, 2011). Fragmented population records and historical accounts reveal the demographic consequences of the highly variable nature of Cabo Verde´s climate, including extreme weather events and long-term droughts that were linked to the occurrence of famines and epidemics (Patterson, 1998) (Fig. 3.2). At the end of the sixteenth century, Cabo Verde became progressively isolated as the old trade routes were outcompeted by ones to the New World colonies and the islands of the Gulf of Guinea (Garfield, 2015). The year 1944 CE saw the last great famine suffered in Cabo Verde, but the environmental and socio-economic vulnerabilities of the archipelago continue to create hardship in local communities. Currently, population sizes of islands such as Brava and São Nicolau are following a downward trajectory, while others (Santiago, Sal, São Vicente) are experiencing exponential increases due to ongoing urban expansion.

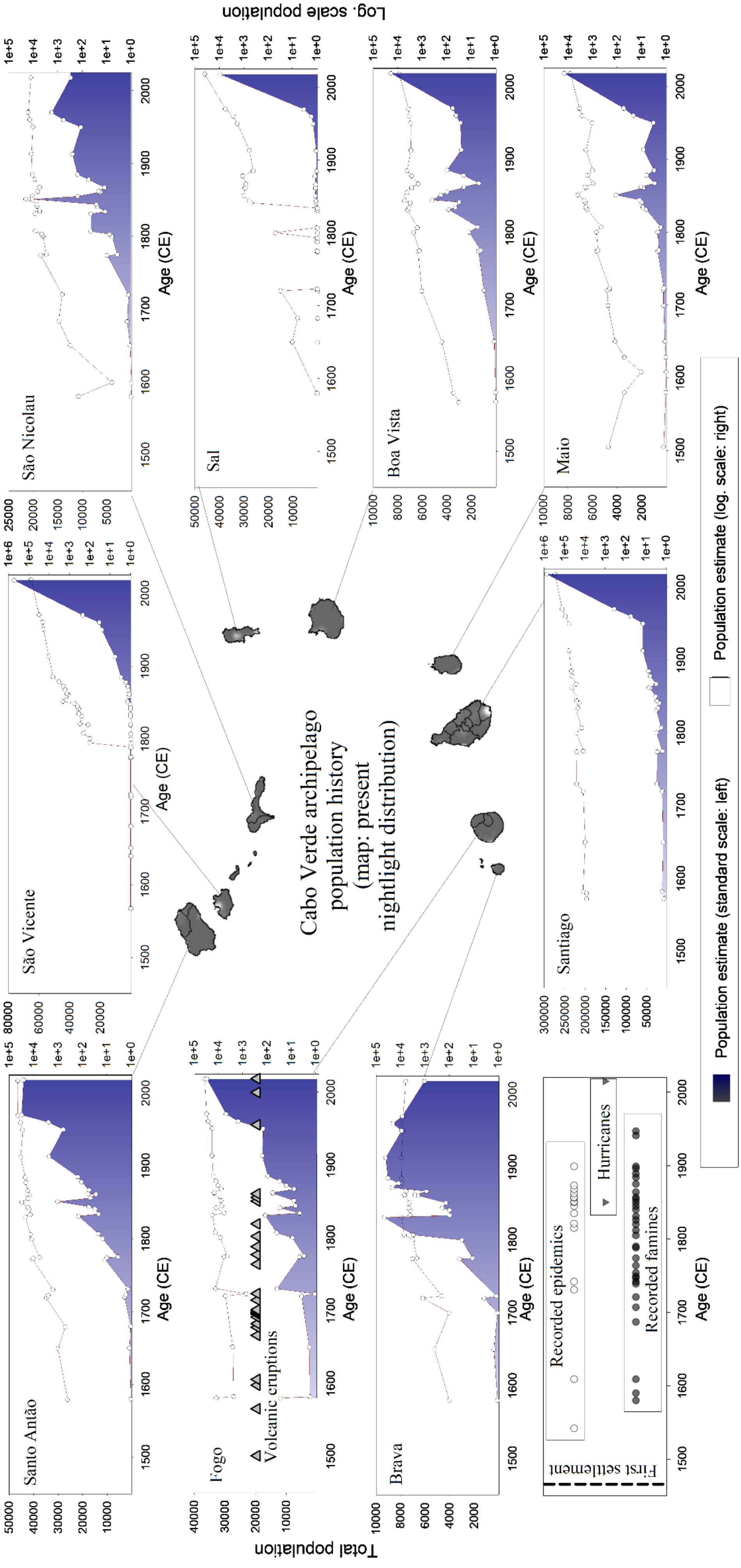
Cabo Verde archipelago population history (map: present nightlight distribution)
Santo Antão
São Vicente
São Nicolau
Sal
Boa Vista
Maio
Santiago
Fogo
Brava
Volcanic eruptions
Recorded epidemics
Hurricanes
Recorded famines
First settlement
Total population
Log. scale population
Age (CE)
1500
1600
1700
1800
1900
2000
1e+0
1e+1
1e+2
1e+3
1e+4
1e+5
1e+6
Population estimate (standard scale: left)
Population estimate (log. scale: right)

Figure 3.2: Population history of Cabo Verde per island, based on historical records including instances of recorded famines, epidemics, hurricanes (Patterson, 1988) and volcanic eruptions (Ribeiro, 1960). The degree of blue shading of the population curve represents the reliability of population estimates, as earlier population records (pale blue) are less precise. Map of present-day nightlight distribution adapted from GADM https://gadm.org.

3.3.2 Current socio-ecological challenges in Cabo Verde

The lack of long-term palaeoecological studies in the area prevents an in-depth understanding of how local ecosystems have responded to human and natural perturbations through time. Currently, Cabo Verde faces environmental threats such as soil degradation, desertification, overexploitation, and the spread of invasive species (MAHOT, 2014; GEF/UNEP, 2015):

Desertification and soil erosion: Desertification and soil erosion have been linked to long-term droughts and colonial mismanagement, and it is considered one of the main ecological threats in Cabo Verde. In the face of projected climate change, this problem could be accentuated all over the archipelago (Baptista et al*.,* 2015).

Resource overexploitation: Historical sources mention the exploitation of endemic woody species, such as *Ficus sp.* (Romeiras et al., 2014). In addition, the arrival and spread of grazers like goats and cows is proposed as one of the main drivers of ecological disturbance in Cabo Verde (Lindskog & Delaite, 1996).

Spread of Invasive Species: Reforestation programs have introduced species such as American Mesquite (*Prosopis jugliflora*), which has shown invasive behaviour, creating negative pressures on local tree species such as the Tarrafe (*Tamarix senegalensis*) and endemic palm (*Phoenix atlantica*) (MAHOT, 2014). In most islands, introduced sickle bush (*Espinho-catchupa*) and agave (*Furcraea foetida*) have occupied large areas at the expense of local species. The loss of endangered and endemic species would be extremely negative for the uniqueness and balance of the ecosystems of Cabo Verde (Romeiras et al., 2016) and would be highly detrimental to the growing development of local ecotourism.

3.3.3 Study sites and intrinsic challenges for Palaeoecology in Cabo Verde

Paleoenvironmental reconstructions have provided new perspectives of environmental change since the early 20th century. However, most of these studies have been performed in temperate and tropical environments, and a major research geographical gap exists in arid and semi-arid lands. Due to their aridity, the islands of Cabo Verde lack permanent natural standing water (*e.g.* lakes) making paleoecological research challenging. Lack of perennial lakes means that sediment deposition can be highly irregular, often producing fragmentary records due to challenging preservation conditions for proxies such as pollen (Brunelle et al., 2018). Even when wetlands or small lakes are present, episodes of periodic desiccation and oscillating water-tables are linked to oxidation processes that can destroy bio-proxies (Carrión et al., 2009). Two main factors are necessary to carry out paleoecological studies in semi-arid islands: relatively steady deposition of sediment in a basin, and abundant humidity for the preservation of bio-proxies such as fossil pollen. Fortunately, volcanic calderas in the humid highlands act as sediment traps, showing stratified deposits accumulated throughout millennia. In this thesis, volcanic calderas in the humid highlands of Cabo Verde are the targeted study sites. We visited and sampled a total of seven sites in five different islands. After initial assessment of the potential of these sites to achieve a successful palaeoenvironmental reconstruction (Table 3.3) we seleced the three most promising study sites located in the highlands of two northern (Santo Antão, São Nicolau) and one in the southern islands of Cabo Verde (Brava), raging between 800 and 1200 m asl (Fig. 3.3).

Table 3.3: Summary table of all sites visited and sample in Cabo Verde, including notes on sediment characterisation and palynomorph preservation.

Island	**Site name**	**Altitude**	**Depth**	**Sediment characterisation**	**Notes**
Santo Antão	Cova de Paúl	1200m asl	Core: 320cm	See chapter 4	See chapter 4
			Profile: 180cm	See chapter 4	See chapter 4
São Nicolau	Calderinha	1000m asl	190cm	See chapter 5	See chapter 5
São Nicolau	Caldera-3	1050m asl	250cm	Abundant sandy and gravel layers	Poor pollen preservation in sandy layers, potentially good in silt layers
Brava	Cova Galinha	810m asl	220cm	See chapter 6	See chapter 6
Brava	Fondo Mato	758m asl	250cm	Mostly sandy and gravel layers, with some silty ones	Poor pollen preservation in sandy layers, potentially good in silt layers
Fogo	Ka Nazio	1010m asl	200cm	Abundant sandy layers	Poor pollen preservation in bottom metre, abundance of phytoliths
Santiago	Aguas Grandes	687m asl	160cm	Abundant sandy layers	Potentially good pollen preservation

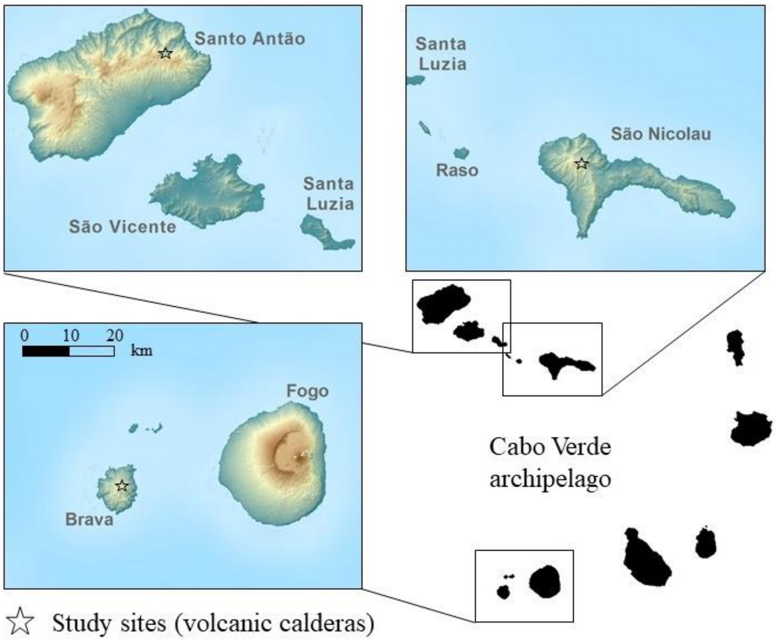

Figure 3.3: Elevation maps of Cabo Verde islands with studied palaeoecological sites (highland volcanic calderas) indicated with stars. Elevation maps adapted from USGS 2016, https://eros.usgs.gov

Chapter 4 Late Holocene environmental change and the anthropization of the highlands of Santo Antão Island, Cabo Verde

Castilla-Beltrán, A., de Nascimento, L., Fernández-Palacios, J. M., Fonville, T., Whittaker, R. J., Edwards, M., & Nogué, S. (2019). Late Holocene environmental change and the anthropization of the highlands of Santo Antão Island, Cabo Verde. Palaeogeography, Palaeoclimatology, Palaeoecology, 524, 101-117.

4.1 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.

4.2 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 & 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 & 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. 4.1).

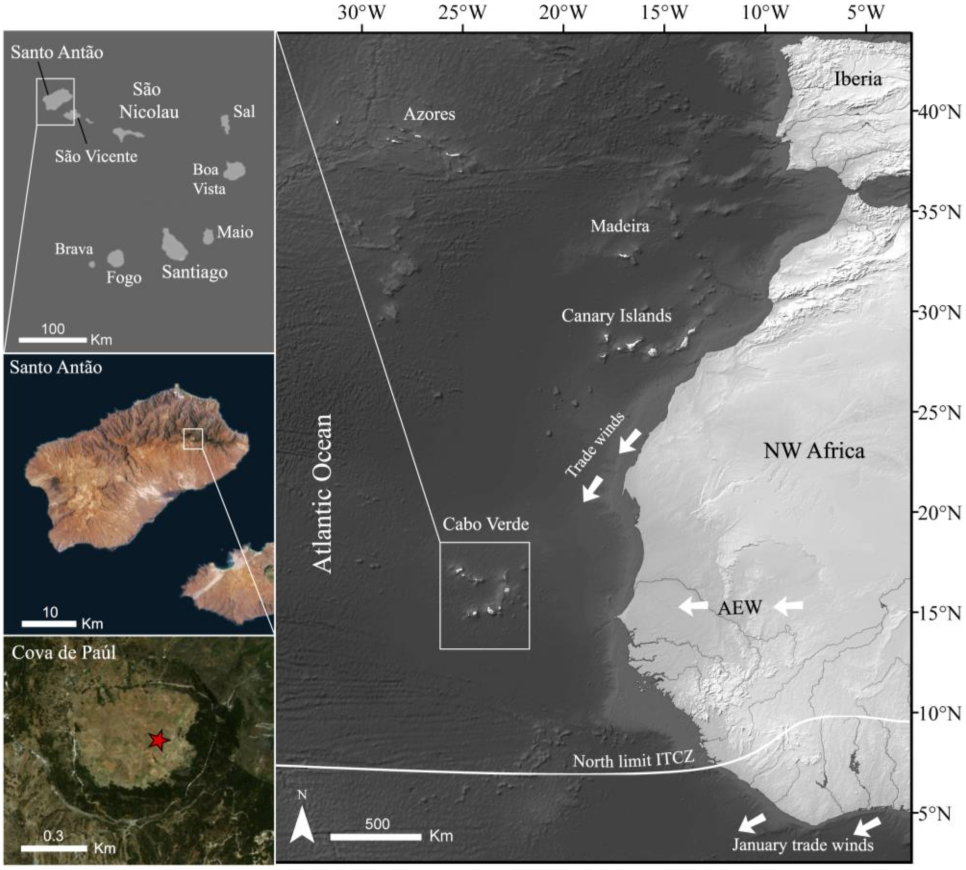

Figure 4.1: Maps of Macaronesia including trade winds (AEW stands for African Easterly Waves) and the northern limit of the ITZC, Cabo Verde and the location of Cova de Paúl coring site, Santo Antão. Raster data from maps from Natural Earth: https://www.naturalearthdata.com/ and ArcMap (ESRI, 2016).

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 & 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 & Evans, 2011; Evans et al., 2012; 2017), sites surveyed or excavated in São Vicente (Cardoso & 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 & Delaite, 1996; Mitchell, 2004; Green, 2012).

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, 2012). 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.

4.2.1 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 & 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, 2012; 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 & 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. 4.1). 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).

4.3 Regional setting

4.3.1 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 & 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 & 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 & Hall, 2009) bring Saharan dust and pollen from the east and increase evapotranspiration (Heckman, 1985; Hooghiemstra et al., 1986; Langworthy & 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

4.1). 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 & 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 & 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 4.1: Historical descriptions of Cabo Verdean landscapes summarised from Romeiras et al., (2014) and Green (2012).

Source	**Date of observations**	**Island**	**Vegetation-economic description**

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 *Lotus jacobeus*
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

4.3.2 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, 1988). 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, 1988) and the North Atlantic climatic systems (Kuhlmann et al., 2004).

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.

4.4 Materials and Methods

4.4.1 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 km^2), the northernmost island of Cabo Verde (Fig. 4.1). 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., 2003), 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 ~ 3ºC 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) (Fig. S1).

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 & 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 (S*olanum 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.

4.4.2 Dating and Sedimentology

4.4.2.1 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 & Christen 2011; 2013).

4.4.2.2 Grain size distribution and zonation

To calculate the distribution of coarse material throughout the core (Cova-core) we weighed a set of 80 1-cm^3 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.

4.4.2.3 Loss on ignition

We used a set of 56 1-cm^3 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.

4.4.3 Pollen and Non-Pollen Palynomorphs (NPPs)

To analyze pollen and NPPs a set of 72 2-cm^3 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 (Fig. 4.2). 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 (Fig. 4.3). We used the following literature for identification focused on Africa: La Serna & 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., (2010) 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).

Figure 4.2: Pollen: Selected pollen grains documented in Cova de Paúl sediments. All scale bars are 10 µm. a. Apiaceae, b. Brassicaceae, c. Agavoideae, d. Euphorbiaceae, e., f. *Acacia*-types, g. Sapotaceae-type, h. CV-4, i. Cannabaceae, j. *Juglans,* k. *Zea mays*, l. Cerealia, 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. *Convolvulu*s, ab. Solanaceae, ac. *Carex* ad. *Ilex*, ae. *Alnus*, af. *Morella-Corylus*, ag. *Quercus*.

4.4.4 Charcoal

For analysis of macro-charcoal, a set of 100 2-cm^3 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 & 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).

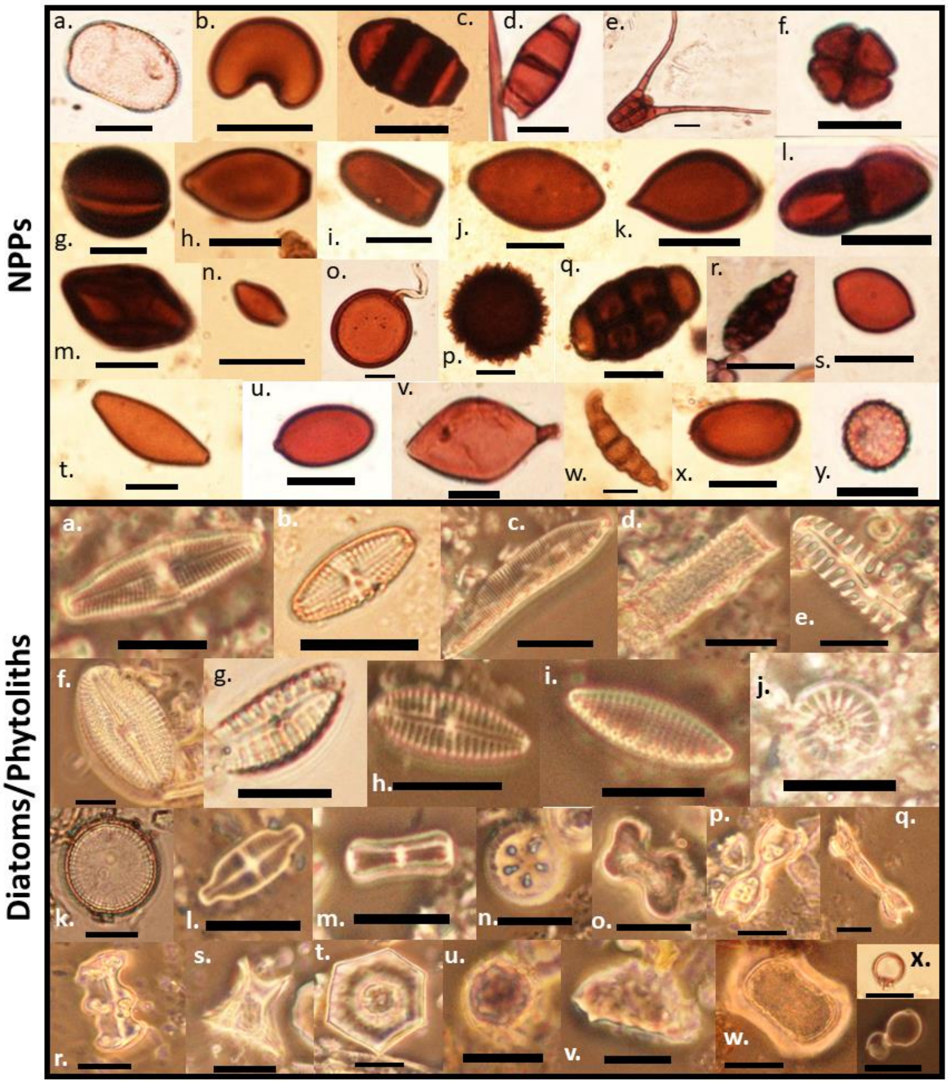

Figure 4.3: **NPPs**: Selected NPPs documented in Cova de Paúl record. All scale bars are 10 µm. a. CVf-23 (HdV 149), b. CVf-5, c. *Bactrodesmium,* d. *Curvularia intermedia,* e. *Tetraploa* sp., f. *Spegazzinia tessarthra,* g. *Coniochaeta,* h. *Cercophora,* i. *Sporormiella,* j. *Sordaria,* k. CVf-3 (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. *Nitzchia 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. Echinate, v. Conical echinate, w. Saddle *cf*. Cloridoid, x. *Chrysophyte* stomatocysts.

4.4.5 Silica bodies: Diatoms, chrysophytes, and phytoliths

For the analysis of silica bodies, 40 2-cm^3 samples were collected at an average of 8-cm resolution along the Cova-core. Samples were processed using HCl and H_2O_2 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) (Fig. 4.3).

4.4.6 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 cm^3), local fire regime (macro-charcoal particles per cm^3), erosion (percentage of material larger than 1 mm per cm^3), and presence of herbivores (percentage of coprophilous fungi in relation to the pollen sum).

4.5 Results

4.5.1 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.

In zone COVA-1, the sediments were mainly composed of silt (mean =74.3%). Clay (mean n = 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 20.1µm. The percentage of sand (mean = 29.1%) and the mean of the median grain size (35.5µm) 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 = 26.9µm) 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%).

4.5.2 Chronology

We obtained a total of 9 AMS C-14 dates for Cova-core and Cova-profile (Table 4.2). We produced an age–depth model using the Bacon calibration program (Blaauw & 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) (Fig. 4.4, Table 4.2). 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 4.3). However, strong evidence of first human land-use (*Zea mays* pollen, Fig S2) 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 4.2: 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 Age 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**

Table 4.3 Lithological zones for the Cova de Paúl 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-dominated	4

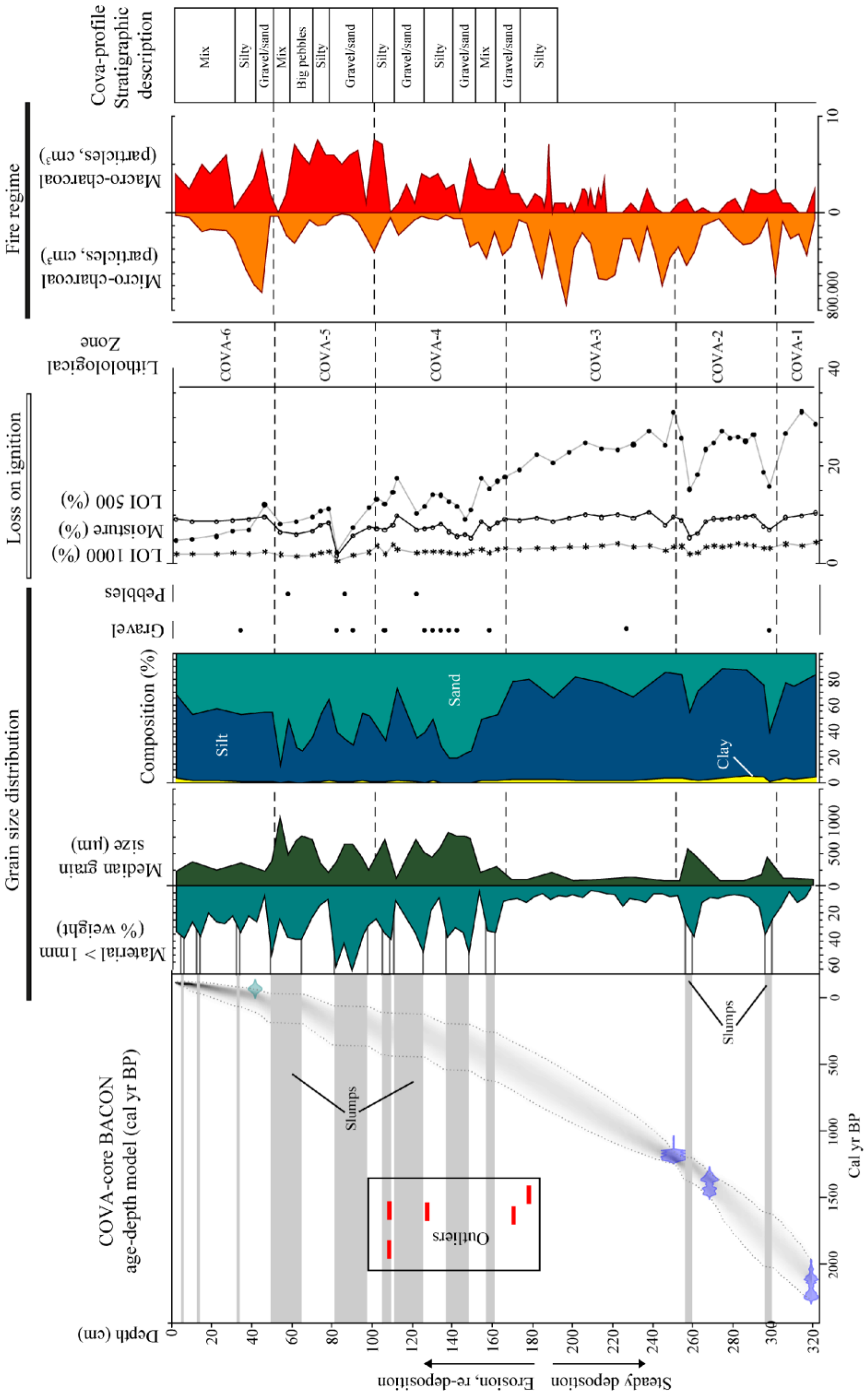

Figure 4.4: Stratigraphic diagram showing age–depth model, charcoal abundance and sedimentology of Cova de Paúl record, Santo Antão. Age–depth model produced with Bacon (Blaauw & Christen, 2013; Fig. S3). Grey area shows 95% confidence intervals based on calibrated C14 dates. Horizontal grey bands indicate 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.

4.5.3 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. Four sections of the core were barren of palynomorphs: 270–245cm, 165–140 cm, 120–190cm and 70–55 cm.

4.5.3.1 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%) (Fig. 4.5). *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%).

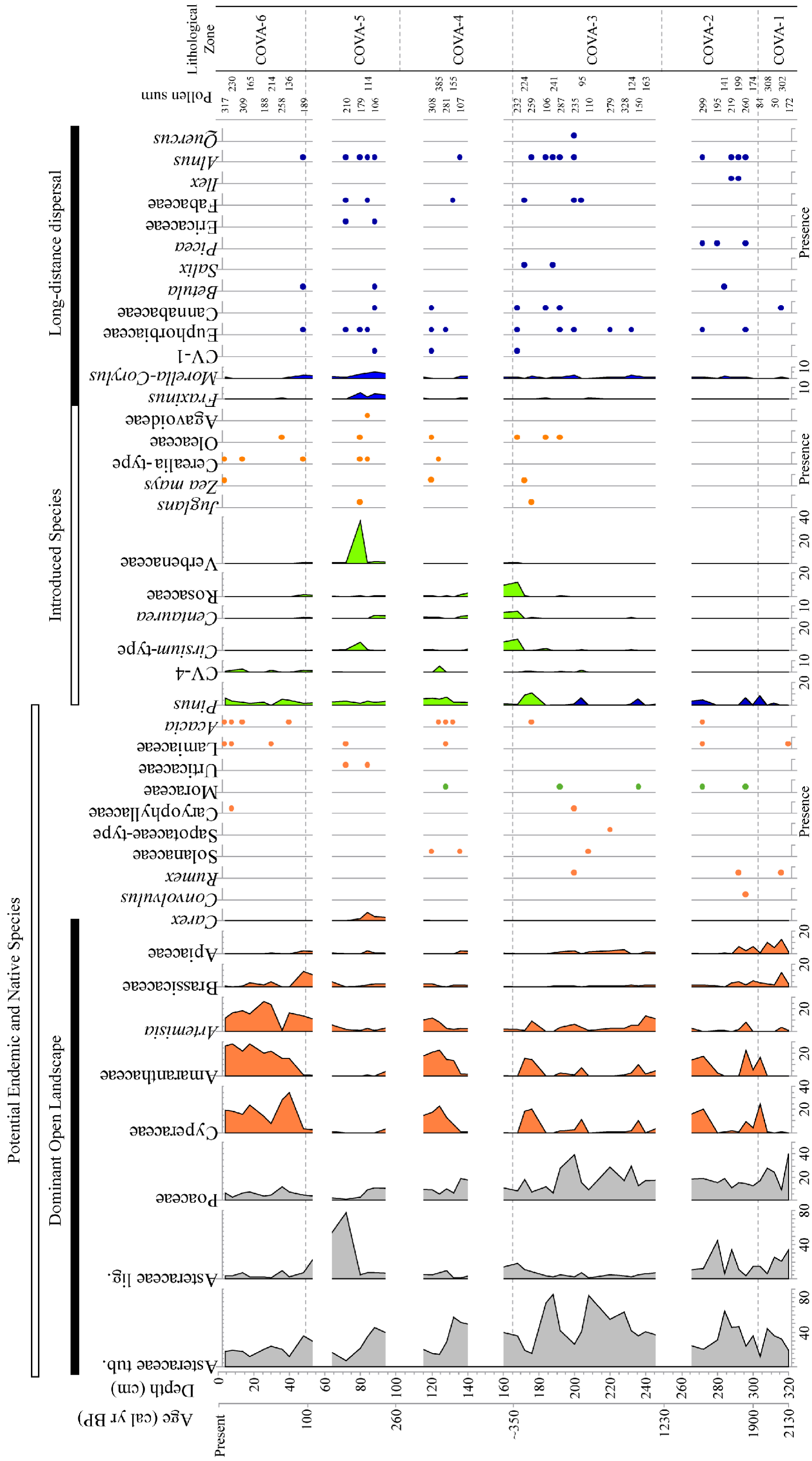

Figure 4.5: Stratigraphic diagram showing pollen percentages of Cova de Paúl record, Santo Antão. Pollen sum includes all taxa. Presence of rare types (values < 1%) plotted with dots. Horizontal white bars placed in sections in which pollen was not found or was not adequately preserved.

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* occured 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.

4.5.3.2 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* (Fig. 4.6). 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.

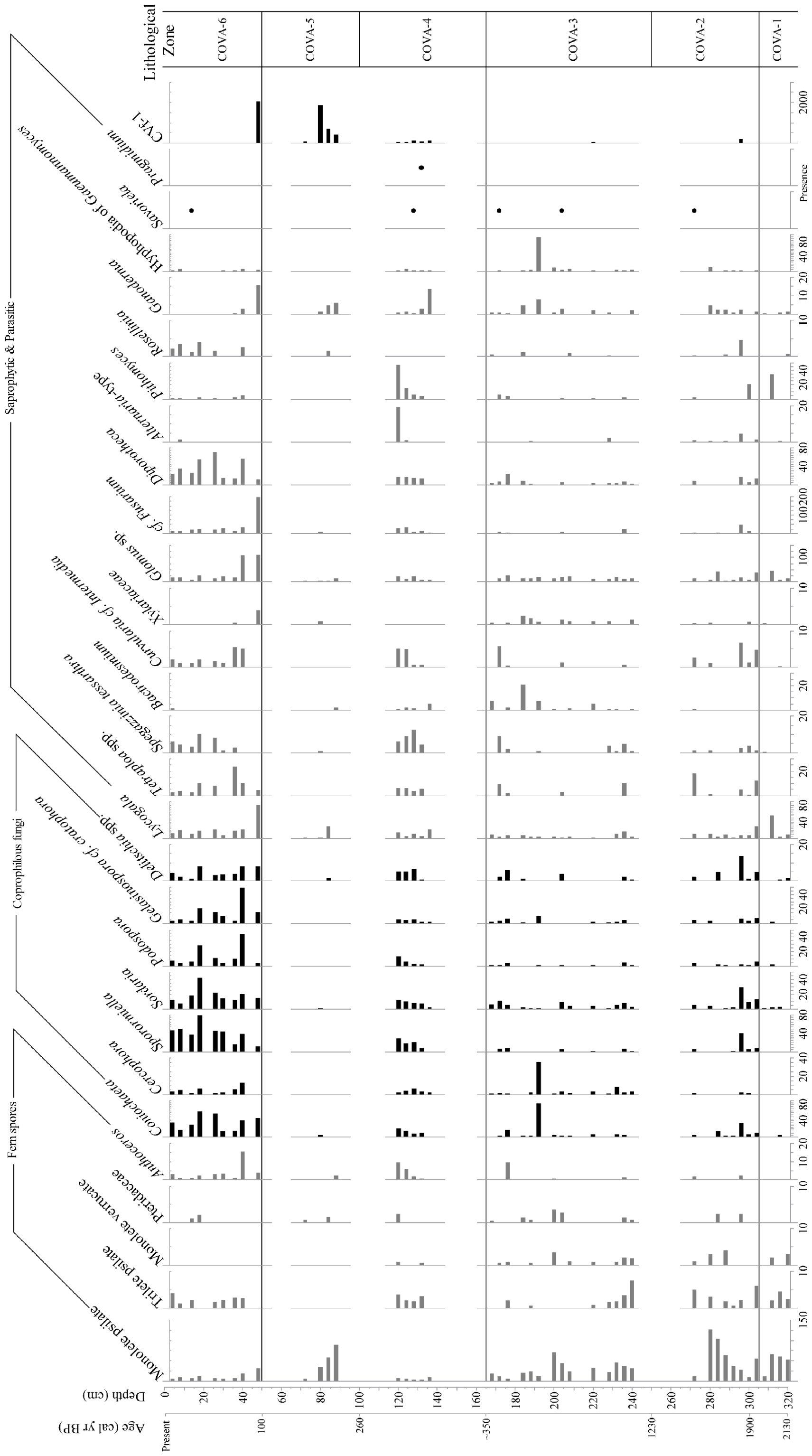

Figure 4.6: Stratigraphic diagram of non-pollen palynomorph (NPPs) percentages of Cova de Paúl record, Santo Antão, including fern and fungal spores. Percentages calculated in relation to the pollen sum.

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.

4.5.4 Silica bodies

4.5.4.1 Diatoms

In the diatom record, section COVA-1 was dominated by the diatom species *Navicula mutica* (avg. 71%) (Fig. 4.7). 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, Nitzchia 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 *Nitzchia 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.*

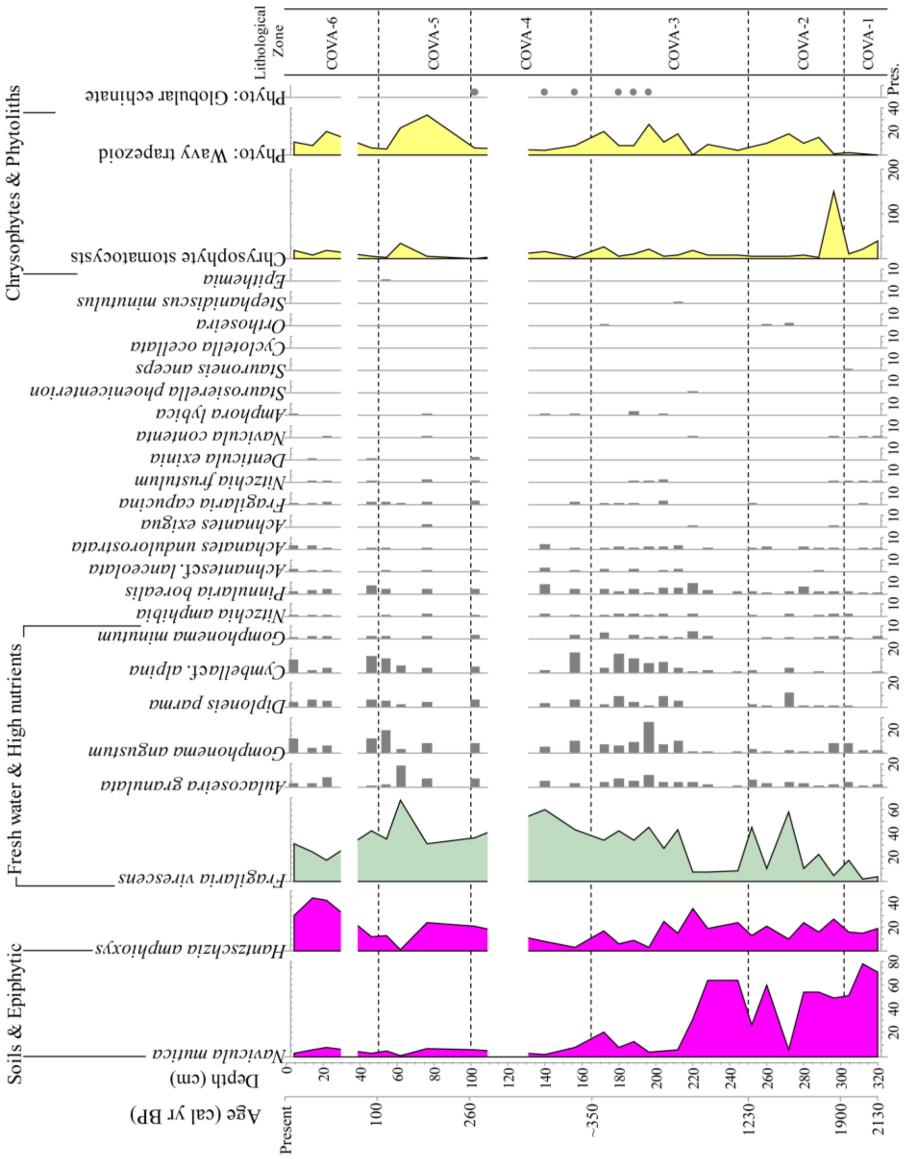

Figure 4.7: Stratigraphic diagram showing diatom percentages of Cova de Paúl record, Santo Antão. We used silhouettes to highlight the three dominant diatom species, and bars for the rest of the assemblage. Percentages of Crysophytes and selected phytoliths are shown in relation to diatom sum.

4.5.4.2 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.

4.5.5 Charcoal

Zones COVA-1 and COVA-2 were characterized by discontinuous macro-charcoal at low abundances and moderate levels of micro-charcoal (~20,000 per cm^3) (Fig. 4.4). 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. $1/cm^3$), 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. $25{,}000/cm^3$). Micro-charcoal levels decreased in zone COVA-4 and COVA-5 (average $14{,}712/cm^3$ and $7{,}848/cm^3$) while macro-charcoal levels increased (average $3.1/cm^3$ and $3.75/cm^3$). 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.

4.5.6 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 (Fig. 4.8). 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.

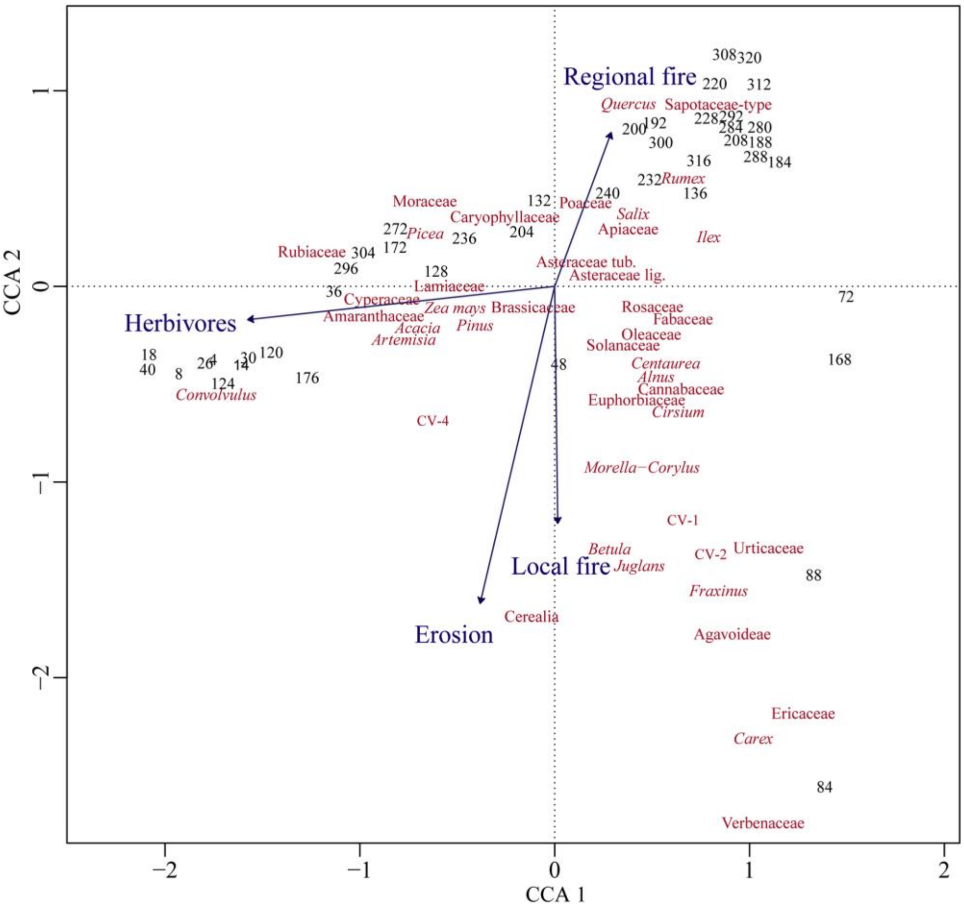

Figure 4.8: Canonical Correspondence Analysis plot of pollen types (red), core levels (black) with four environmental variables (dark blue) of Cova de Paúl record, Santo Antão. We used pollen percentage data expressed as a percentage of the pollen sum and four environmental variables for the analysis: 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).

4.6 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 & 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*, Figure S2), 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, 2012), 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).

4.6.1 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. 4.5). 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 260cm) 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* c*ratophora*) (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 & Brenac, 1998). 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.

4.6.2 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 cm^3) 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.

4.6.3 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 (Fig. S1).

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.

4.6.4 Long-distance vs. local vegetation signals

As the pollen diagram shows (Fig. 4.5) 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 & 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.

4.6.5 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.

4.7 Discussion

This first palaeoenvironmental study covering the past 2130 yr for Cabo Verde has generated the following main conclusions: There were 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. Sporomiella*) 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.

Chapter 5 Using multiple palaeoecological indicators to guide biodiversity conservation in tropical dry islands: The case of São Nicolau, Cabo Verde

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5.1 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 5000–400 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.

5.2 Introduction

Anthropogenic activities have been a major driver of environmental degradation in oceanic islands worldwide (Whittaker & 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 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 & 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 & 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/DCA, 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. 5.1).

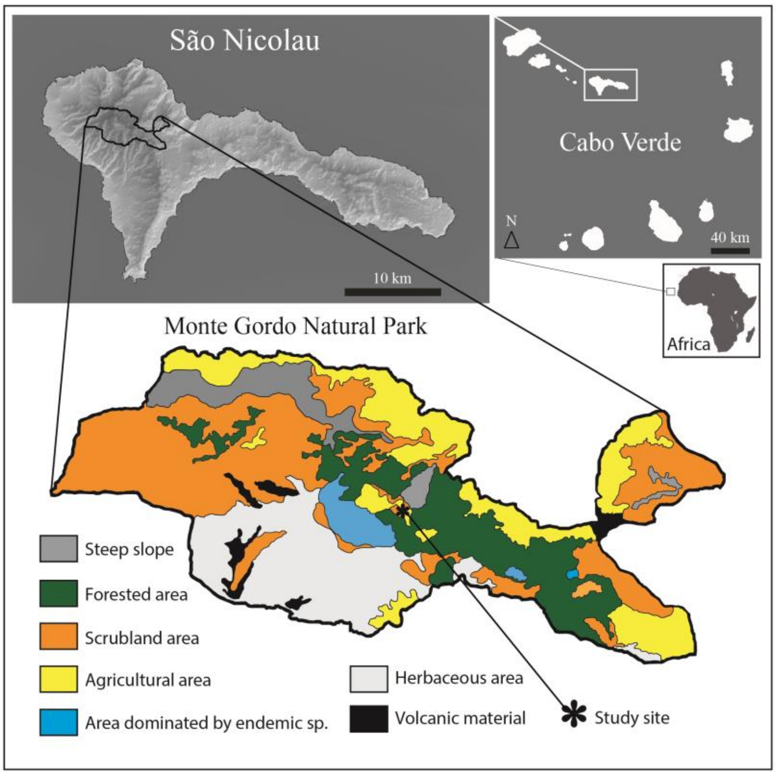


Figure 5.1 Elevation map of São Nicolau (modified after USGS) and land-cover map of Monte Gordo Natural Park (vegetation map based on MAA-DGA 2008, p. 81).

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.

5.3 Material and methods

5.3.1 Study area

5.3.1.1 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 ºN, 22.5–25.5º W). It has a tropical dry climate (mean annual temperatures between 20 and 24ºC) marked by low and irregular levels of rainfall (1200–1600mm 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 & 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 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.

5.3.1.2 The Monte Gordo Natural Park, São Nicolau island

São Nicolau is an island of volcanic origin with a total area of 388 km^2 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 stenosiphon* 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 hectares) alongside those of Santo Antão*,* with specimens that reach 2.5 meters 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-DGA, 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-DGA, 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-DGA, 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 programs 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-DGA, 2008).

5.3.2 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. 5.1). 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 1x1 m trench in the centre of the caldera to record and sample a stratigraphic profile (Fig. 5.1). We documented stratigraphic features according to texture and colour throughout the 190-cm profile (Fig. S4). 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.

5.3.3 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 5.1). 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 AD 1950 by definition, so negative dates indicate years after 1950, and Present-day refers to 2018, the date of our fieldwork.

Table 5.1: 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	60cm	Charcoal & wood	1609 ± 37	1594–1405 cal yr BP
SUERC-87008	70cm	Bulk sediment	2661 ± 35	2845–2744 cal yr BP
SUERC-87004	80cm	Bulk sediment	2999 ± 37	3336–3066 cal yr BP
SUERC-87003	105cm	Bulk sediment	2868 ± 37	3140–2872 cal yr BP
SUERC-87002	**115cm**	**Charcoal**	**501 ± 35**	**624–500 cal yr BP**
SUERC-87001	**125cm**	**Bulk sediment**	**3161 ± 37**	**3456–3257 cal yr BP**
UBA-38690	**135cm**	**Bulk sediment**	**4517 ± 28**	**5303–5051 cal yr BP**
UBA-38473	**185cm**	**Bulk sediment lipid extractions**	**5120 ± 33**	**5934–5179 cal yr BP**

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, 2cm^3 dry samples (taken at 5cm 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 2cm^3 samples (taken at 5cm 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 seconds 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 and 0.5, respectively. Results are reported as proportions of clay, silt, and sand, and as median grain size values (Dx50) (Prins & Weltje, 1999).

To calculate the sediment organic content, we carried out loss on ignition (LOI) (Heiri et al., 2001) analysis of 38 2cm^3 samples taken every 5 cm. We dried the samples at 100°C for 24 hours 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 four hours and weighed again. LOI was calculated and used as a proxy for organic content.

5.3.4 Pollen and NPPs

For analysis of pollen and non-pollen palynomorphs (NPPs), we processed 38 2cm^3 samples (taken at 5cm intervals) by following standard procedures (Erdtman, 2013). For pollen identification, we used our Cabo Verde and Canary Islands reference collection (Table S1), as well as African pollen atlases, including Gosling et al., (2013) and Schüler & 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. 5.2, see Table S2 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 (Table S3).

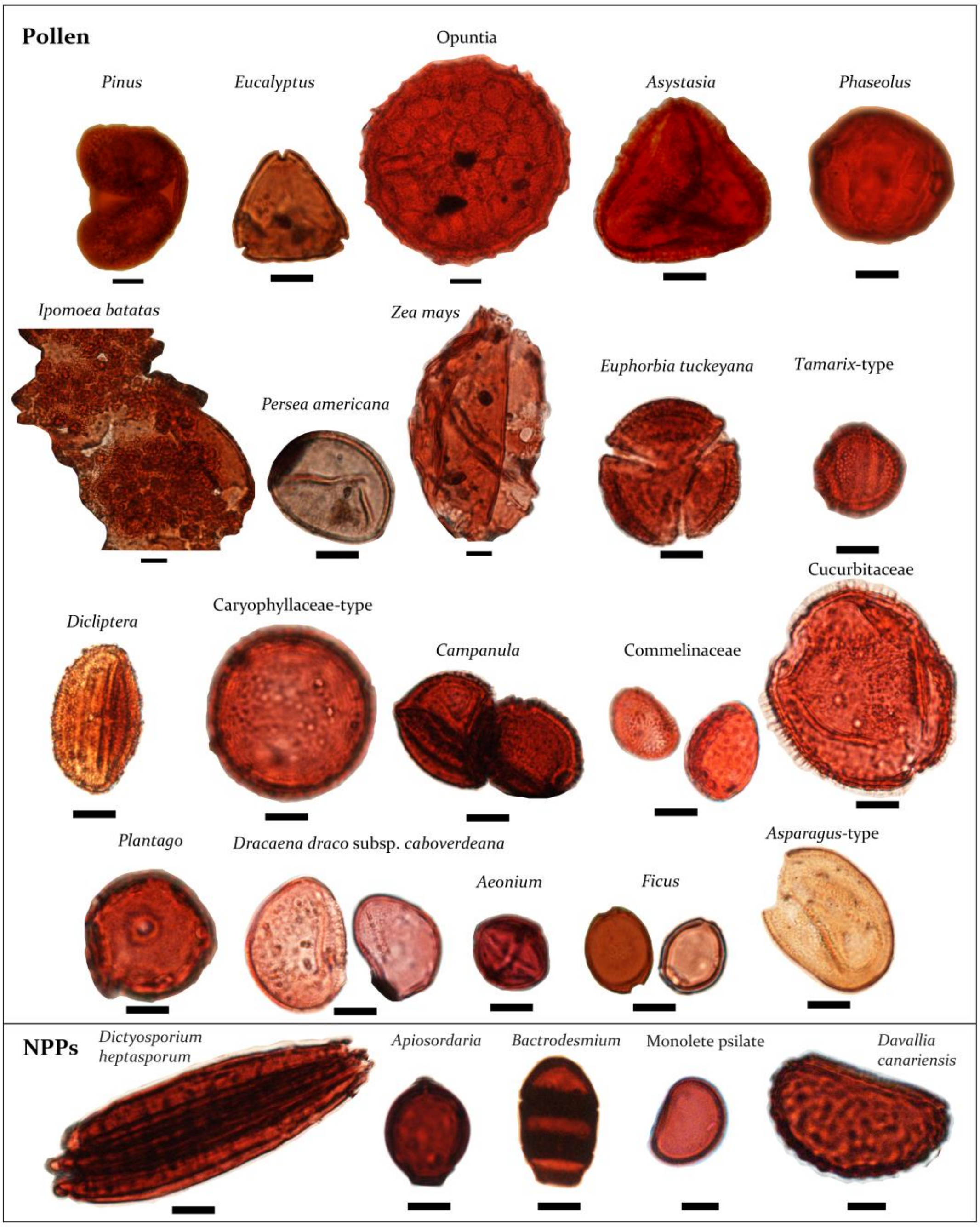


Figure 5.2: Selected pollen grains and Non-Pollen Palynomorphs of the Calderinha record, São Nicolau, Cabo Verde.

5.3.5 Charcoal

For analysis of macro-charcoal, we processed 38 2cm^3 samples (taken at 5cm 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 & Tinner, 2005).

5.3.6 *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 20cm intervals, to compare *n*-alkane distributions in the four zones of the profile (see Appendix B 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: $ACL_{23\text{-}31}$=∑(Ci*[Ci]) /∑[Ci]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 rations 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).

5.3.7 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 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 cm^3) to assess impacts of fires beyond the immediate catchment, 3) local fire (abundance of macro-charcoal particles per cm^3) to explore impacts of fire in the local setting, 4) erosion (median grain size, Dx50) 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.

5.4 Results and Palaeoecological reconstruction

5.4.1 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 180cm. The main elements/compounds identified in the sediment were Silicon Dioxide (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 µg in zone Cld-3 to a minimum of 0.13 µg/gds in Cld-4. *n*-Alkanes had chain lengths ranging from *n*-C_{23} to *n*-$C_{31,}$ and were always dominated by long carbon chains with a strong odd/even carbon number preference: *n*-C_{29} in the middle and bottom sections of the profile (zones Cld-1 to -4), and *n*-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= <0.36) suggests that changes in the *n*-alkane patterns were mainly controlled by changes in vegetation, and not by post-sedimentary alteration effects (Buggle et al., 2010). These findings are further interpreted in sections 3.3, 3.4 and 3.5.

5.4.2 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 inwashed 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 (0-50cm), most recently deposited section of the record, as this technique has proven successful in mixed alluvial and colluvial sediment sequences elsewhere (e.g. Cundy & Stewart, 2004). To develop a chronological model for the record, we first calculated two alternative C-14 chronological models (see Appendix C, Fig. S5 and FigS6 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. 5.3).

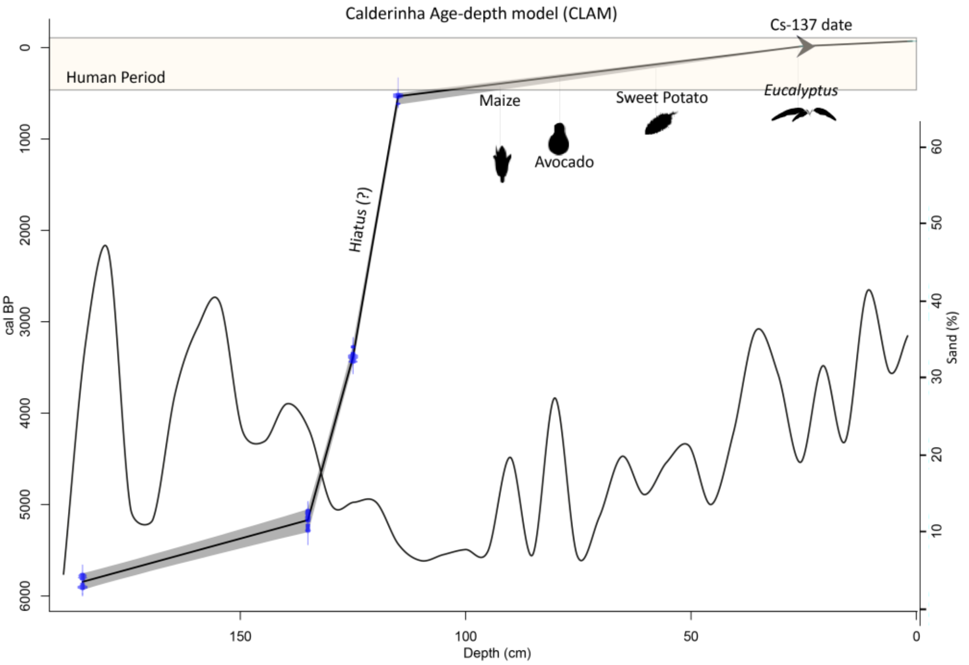


Figure 5.3: Age–depth model of the Calderinha record (grey line, calibrated RC dates in blue), São Nicolau Island, and its validation against granulometric data (sand content percentage, curve) and first occurrence of pollen from cultivated species (silhouettes). The period of human settlement is highlighted in yellow (~400 cal yr BP– the present day).

5.4.3 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 µm) low in Titanium content (Fig. 5.4). 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 & 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 & DeLaune, 2012). The low concentration of micro-charcoal particles (average 1330 /cm^3) and the near absence of macro-charcoal particles indicates that very few fires occurred from 5900 to 4900 in comparison with 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^3). 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. 5.5). 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 25–64%) spores, which are produced by fungi in wood and bark (Gelorini et al., 2011; La Serna-Ramos & Domínguez-Santana, 2003), and *Glomus* type (184% in level 195 cm), associated with erosion (Fig. 5.6) (van Geel et al., 2003). The presence of woody vegetation is also supported by *n*-alkane dominant chains nC_{29} (long-chain *n*-alkane ratio between 0.6 and 0.7). We interpret this period as characterised 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).

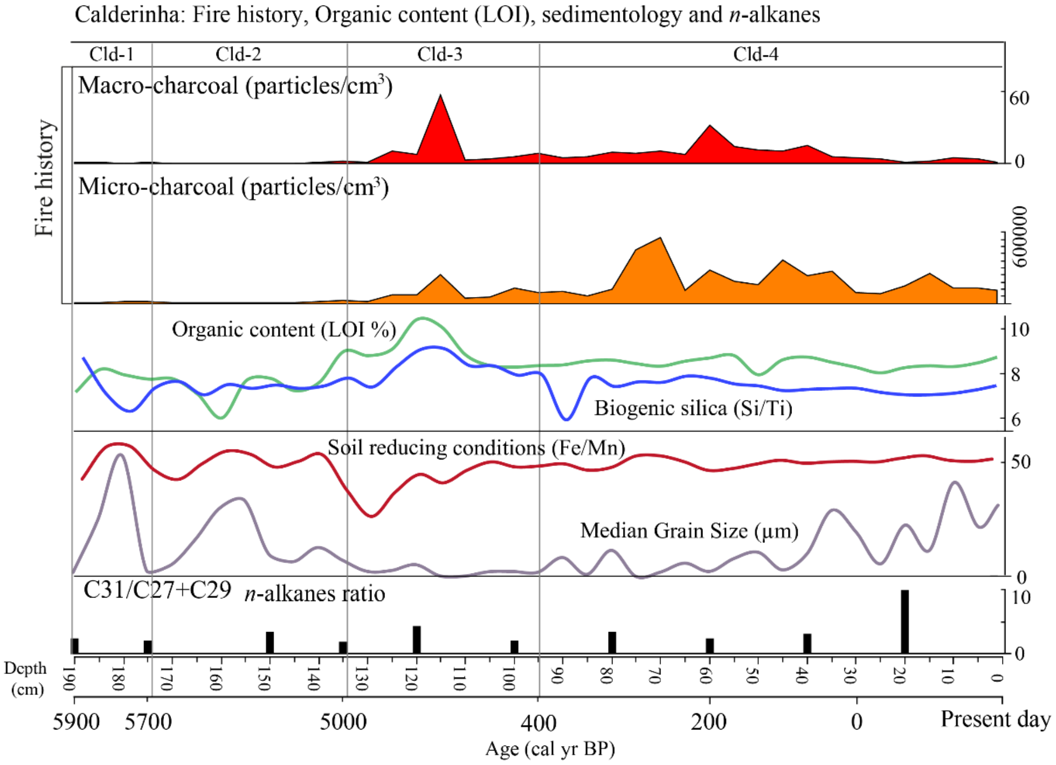


Figure 5.4: Stratigraphic diagram of the Calderinha record, São Nicolau Island, showing fire-history, sedimentology and n-alkane long-chain distributions.

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 & Rothwell, 2015). Increasing values of SiO_2 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 5.5–3 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.

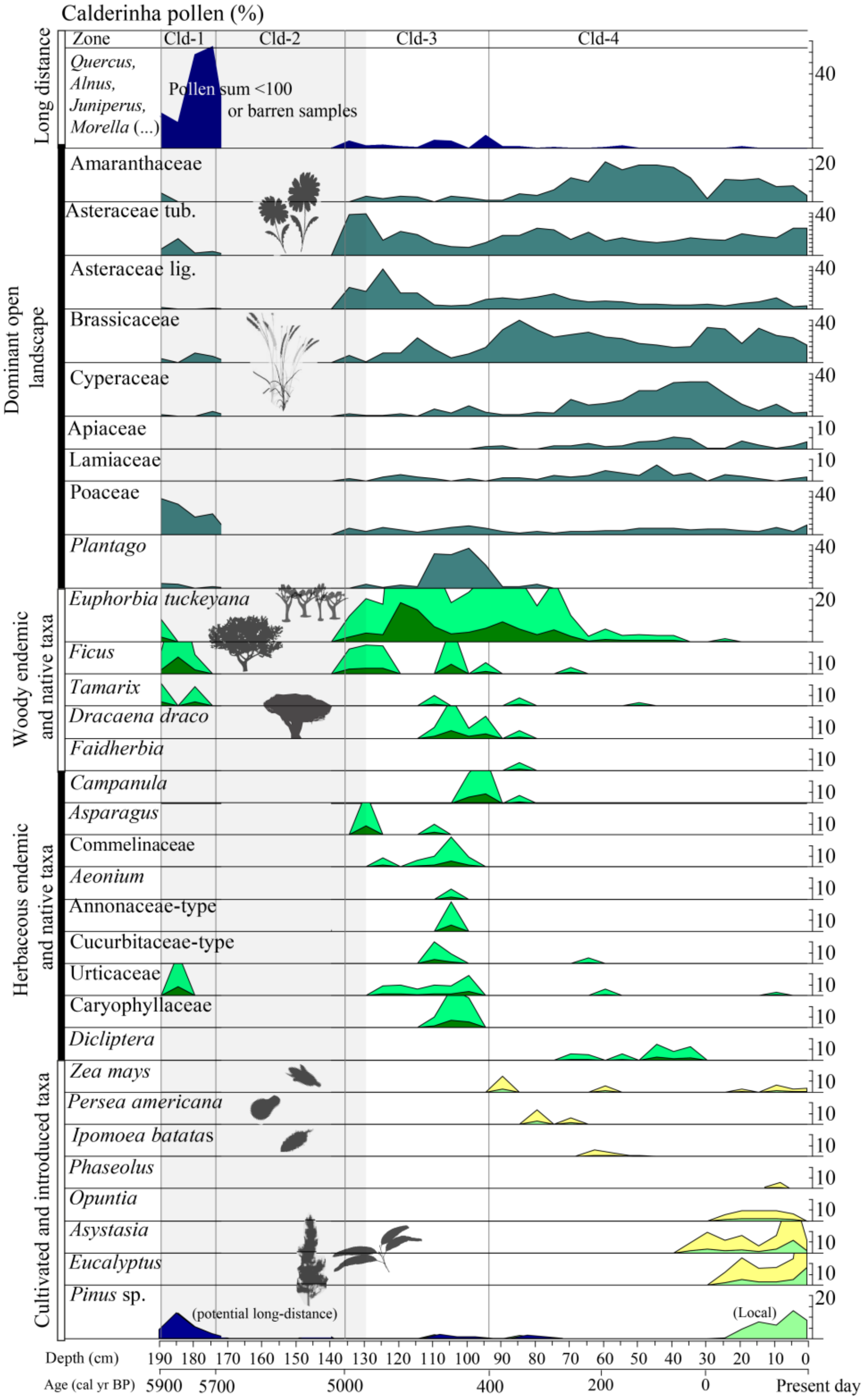


Figure 5.5: Stratigraphic diagram of the Calderniha record, São Nicolau Island, showing pollen percentages. Exageration curves (light green and yellow) x10.

5.4.4 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 (Fig. 5.4 and 5.5). First, clay proportions increased, peaking at level 115 cm (29%, highest in the record) and macro-charcoal (57 particles/cm^3 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 & Rothwell, 2015). The sharp increase in macro-charcoal 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 monolete psilate fern spores and spores from the epiphytic *Davallia canariensis* (ranging from 217–701 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 7–9%). 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.

5.4.5 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 per cm^3 (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. 5.6).

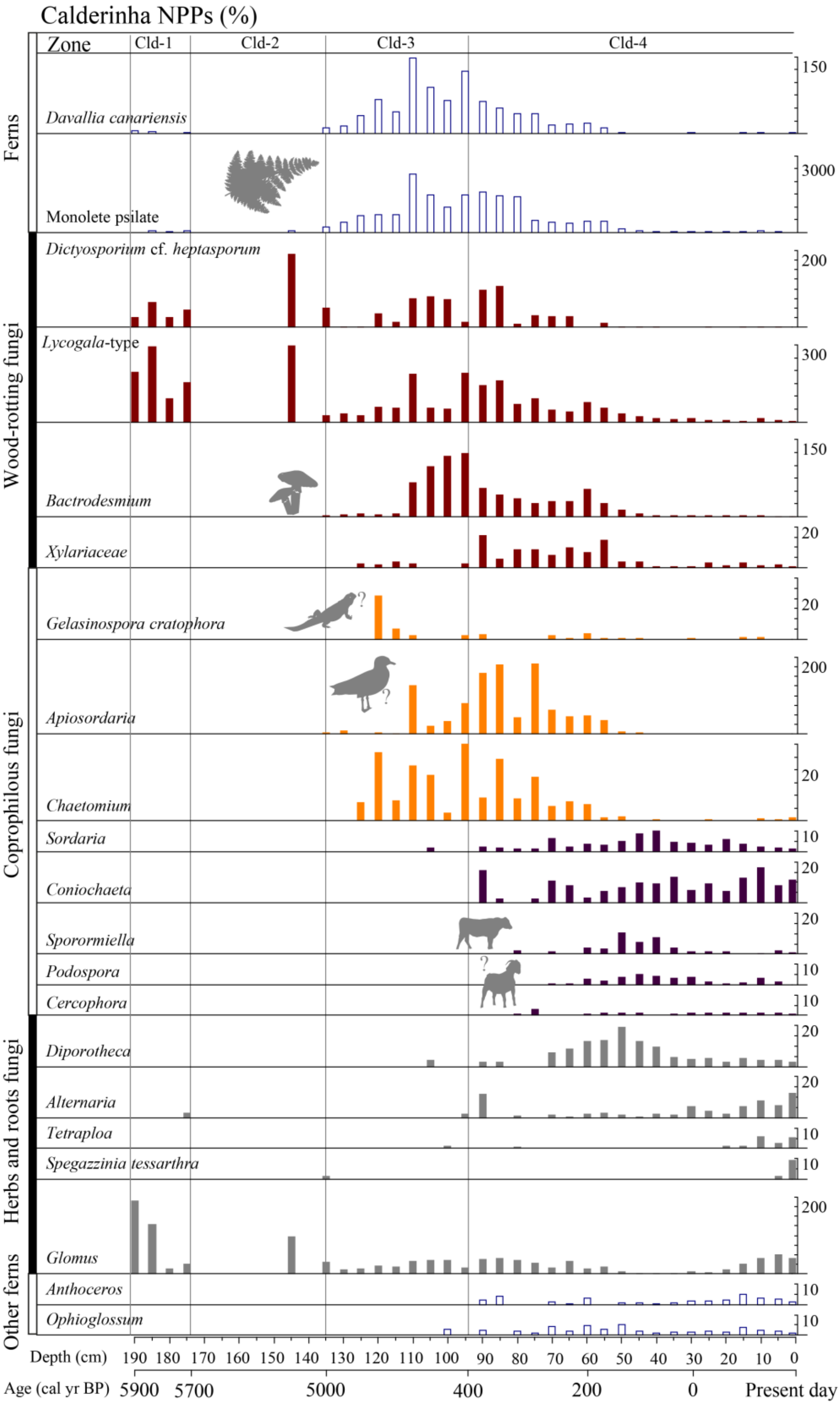


Figure 5.6: Stratigraphic diagram of the Calderinha record, São Nicolau Island, showing Non-Pollen Palynomorph percentages in relation to the pollen sum.

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 agriculture and grazing activities took place. The highest concentrations of micro-charcoal occurred in this period (93,276 particles/cm^3). Macro-charcoal fragments peak at ca. 280 cal yr BP (level 60 cm, 31 particles/cm^3) 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 (*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_{29} peaks associated with woody taxa, to dominant C_{31} 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 program 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 to 13–8%) and *Eucalyptus* pollen (2.6–8.2%), and the decrease of open landscape taxa such as Amaranthaceae and Cyperaceae. The presence of 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 µm) 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.

5.4.6 Canonical correspondence analysis

The two plots shown in Fig 5.7 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.

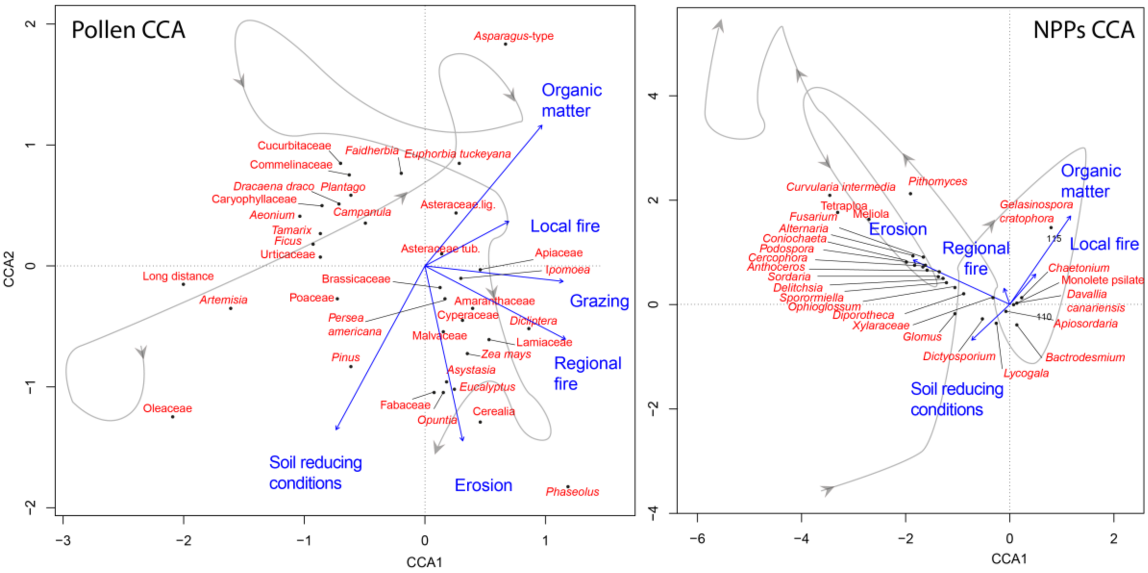


Figure 5.7: Canonical Correspondence Analysis (CCA) using pollen (left panel) and NPPs (right panel) data of the Calderniha record, São Nicolau Island. Six environmental variables were used: Abundance of organic matter (OM %), Local and Regional fire (macro- and micro-charcoal), Grazing (coprophilous 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

5.5 Discussion: implications for conservation

5.5.1 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 paleoenvironmental data: the long-term response of ecosystems to fire and erosion regimes, and the specific human impacts that have taken place since Portuguese settlement.

5.5.1.1 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; Forsskaolea procridifolia; Paronychia illecebroides; Polycarpaea 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 has a low dispersability index value, meaning that it is only recorded when the plant is 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 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 (Romerias 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.

5.5.1.2 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. –5,500 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.

5.5.2 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 5.2. 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.

Table 5.2 Summary of insights derived from palaeoecological data for conservation and livelihoods in Monte Gordo Natural Park, São Nicolau.

Conservation challenge based on Paleo evidence	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 & Burney, 2016). Future studies might yield insights on past abundance of other important endemic species such as *Sideroxylon marginatum*.
Potential establishment (100 years ago) of introduced taxa such as *Asystasia* and *Opuntia* (?)	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, *Opuntia dillenii* and *O. maxima* are considered invasive species.
Ancient fire potentially related	Charcoal particles	Avoiding fuel loading, especially	According to our fire data fire has been present at least for the last millennium

to scrubland encroachment		added by spreading invasive species	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 *Eucalyptus*. 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.

5.5.2.1 Restoration in a human-dominated landscape

Palaeoeocological 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 & 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 sycomorus* 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 & Mehta, 2006; see Campbell-Hunt, 2014 for case-studies in New Zealand).

5.5.2.2 Monitoring and eradication

The identification of Acanthaceae (*Asystasia*) and *Opuntia* pollen (Fig. 5.2) 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).

5.5.2.3 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.

5.5.2.4 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 & Willis, 2008). This can help improve outreach material and give new tools for education programs by adding a temporal dimension to what has been called ‘sense of place’ (Burney & 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.

5.6 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 characterise 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.

Chapter 6 Effects of Holocene climate change, volcanism and mass migration on the ecosystem of a small dry island (Brava, Cabo Verde)

Castilla-Beltrán, A. de Nascimento, L., Fernández-Palacios, J.M. Whittaker, R.J., Romeiras, M., Cundy, A.B., Edwards, M. Nogué, S. (under review) Effects of Holocene climate change, volcanism and mass migration on the ecosystem of a small dry island (Brava, Cabo Verde). Journal of Biogeography.

6.1 Abstract

Aim: Small islands are the miner´s canary of humankind’s impacts on global biodiversity. Loss of species, habitat fragmentation and soil degradation are especially pressing challenges in dry volcanic archipelagos with steep topography. Brava Island (Cabo Verde) is an excellent system to approach global challenges such as assessing the integrated impacts of global drying, volcanic eruptions, and human mass migrations in a constrained environment. We aim to identify the consequences of these global-to-local and co-occurring environmental disturbances on a small dry oceanic island.

Location: Brava Island, Republic of Cabo Verde.

Taxon: Terrestrial vegetation and fungi.

Methods: We use palaeoecological analyses applied to a caldera soil profile dated back to 9,700 cal yr BP. Analyses include pollen (vegetation history), NPPs (changes in fern and fungal communities), grain size distribution, loss-on-ignition and geochemistry (sedimentology and erosion regimes), microscopic tephra shards (volcanic ash depositions) and charcoal (fire regimes).

Results: We assess how a regional drying trend after 4,000 cal yr BP caused increased erosion but had limited immediate impacts on highland grassland vegetation. The expansion of fern-rich woody scrubland was contemporaneous with significant depositions of volcanic ash and erosion between 1,800 and 650 cal yr BP. The mass migration of human population from Fogo Island c. 1680 CE in response to volcanic hazards on that island led to the rapid introduction of exogenous plants and grazers, the rise of fires and decrease of native vegetation in Brava.

Main conclusions: Regional climate change was a driver of erosion since the Mid-Holocene in Brava, but did not have an immediate influence on highland vegetation. Our results indicate a potential role of tephra depositions as a driver of vegetation change. Inter-island mass migration after volcanic events in Fogo Island ca. 1680 CE triggered land-use change and intensification, causing a reduction of native vegetation in Brava.

6.2 Introduction

Oceanic islands globally have undergone extinctions and habitat fragmentation since human settlement (Whittaker et al., 2017), and have been defined as the frontline sites of humankind's greatest challenges (Baldaccino & Niles, 2011). The contrast of ecological change before and after human arrival is informative of the degree of human pressure after settlement, and how this interacted with pre-existing disturbance regimes (Dearing et al., 2006; Paine et al., 1998). Dry islands are especially vulnerable to environmental disturbances such as an increase in extreme weather events and periods of drought (Holmgren et al., 2006), which can interact with, and aggravate, human impacts. It is thought that the legacy of centuries of colonial land mismanagement in Cabo Verde, a tropical archipelago in the eastern Atlantic Ocean, has led to the loss of soils and habitats after continued land-use (Lindskog & Delaite, 1996; Norder et al., 2020). However, the role of volcanic hazards and climate fluctuations in these ecological changes remains to be assessed. For instance, volcanic eruptions can impact human societies by causing migrations and land-use shifts, as well as chemical, biological, and even climatic alterations (Payne & Egan, 2019). Studying these multi-scalar and potentially co-occurring disturbances and their socio-ecological effects may provide a much needed historical perspective on landscape degradation. This is pivotal to: (i) understanding the effects of environmental change at multiple scales in a reduced ecological/socio-ecological system; (ii) improving conservation guidance on island biodiversity (Nogué et al., 2017); and (iii) planning responses to future crises.

Cabo Verde comprises 10 volcanic islands and 3 islets in the African-Sahelian climatic region (Fig. 6.1). In islands with steep topography (Santo Antão, São Nicolau, Santiago, Fogo and Brava), elevation has a strong influence on temperature (mean annual temperatures vary between 23 and 26 ºC at sea level and 17–20 ºC in the highlands) and moisture (Duarte et al., 2008). Cabo Verde's flora exhibit different regional affinities: plants from the arid lowlands show similarities with tropical Africa, while mountainous vegetation show close relationships with plants from other Macaronesian archipelagos (Freitas et al., 2019). Over the last two decades, the Cabo Verde vascular plants have become more threatened, mostly as a consequence of the increase in exotic species, habitat degradation and human disturbance (Romeiras et al., 2016). Over centuries and millennia, regional climatic fluctuations driven by the oscillations of the West African Monsoon are thought to be determinant in shaping natural vegetation composition and distribution in Cabo Verde by processes of expansion and contraction of vegetation (Neto et al., 2020). During the last African Humid Period (AHP: 12,000–5,000 yr BP), the African monsoon migrated to the north, leading to higher precipitation in the Saharan region. After this phase, regional conditions became dry, leading to the present Sahara (Pausata et al., 2020). Near-shore marine records in the Senegal region reveal sharp decreases in precipitation after 4,000 cal yr BP, as well as increases in the deposition of Saharan dust after 3,500 and after 200 cal yr BP (Mulitza et al., 2010; Tierny et al., 2017). After Portuguese settlement (1460 CE), ecosystems in the northern islands of Cabo Verde were transformed by direct and indirect anthropogenic disturbances (Castilla-Beltrán et al., 2019; 2020). In recorded history, episodes of socio-ecological distress in Cabo Verde were caused by volcanic eruptions, hurricanes and multi-annual droughts, which are thought to have de-stabilised colonial socio-ecological systems (Garfield, 2015; Green, 2012; Heckman, 1985; Lindskog and Delaite, 1996; Patterson, 1988).

Brava (Portuguese for ‘wild’) is a small island (64 km^2) with a maximum elevation of 976 m asl, and is regarded as one of the most fertile of Cabo Verde, earning it the title of the ‘Garden Island’. It is one of the geologically youngest of the archipelago, having formed ca. 3 Ma, and shares its volcanic base with Fogo Island (Madeira et al., 2010). Brava harbours some of the most diverse vegetation of Cabo Verde and the highest total plant species richness, with 239 species, and second-highest endemic floral species density, with 25 taxa, but due to its small size has received little attention regarding conservation initiatives (Duarte et al., 2008). Brava’s north-facing highlands (700–960 m) are favourable for the occurrence of humid local climates by the capturing of cloud moisture (Correia, 1996). Currently, it is estimated that 13% of Brava’s land area is wooded, much of it by introduced taxa such as *Prosopis juliflora*, *Grevillea robusta*, and *Cupressus lusitanica*. Native vegetation is under great pressure due to the grazing of cows, donkeys and goats (GEF/UNEP, 2015). Brava’s neighbouring islands, Santiago and Fogo, were the first to be significantly settled by Europeans (ca. 1460 and 1470 CE, respectively), but it is estimated that Brava remained only marginally inhabited until ca. 1680 CE, when ‘many families’ from Fogo fled to take refuge on Brava after an earthquake and a major volcanic eruption (Correia, 2000; Mitchell-Thomè, 1981; Ribeiro, 1960) (Table S4). Here, we present multiple palaeoecological analyses to show how ecosystems and soils in Brava developed in the last 10,000 yr in response to global-to-local and potentially co-occurring environmental changes, including regional drying, within-archipelago volcanism and inter-island human migration.

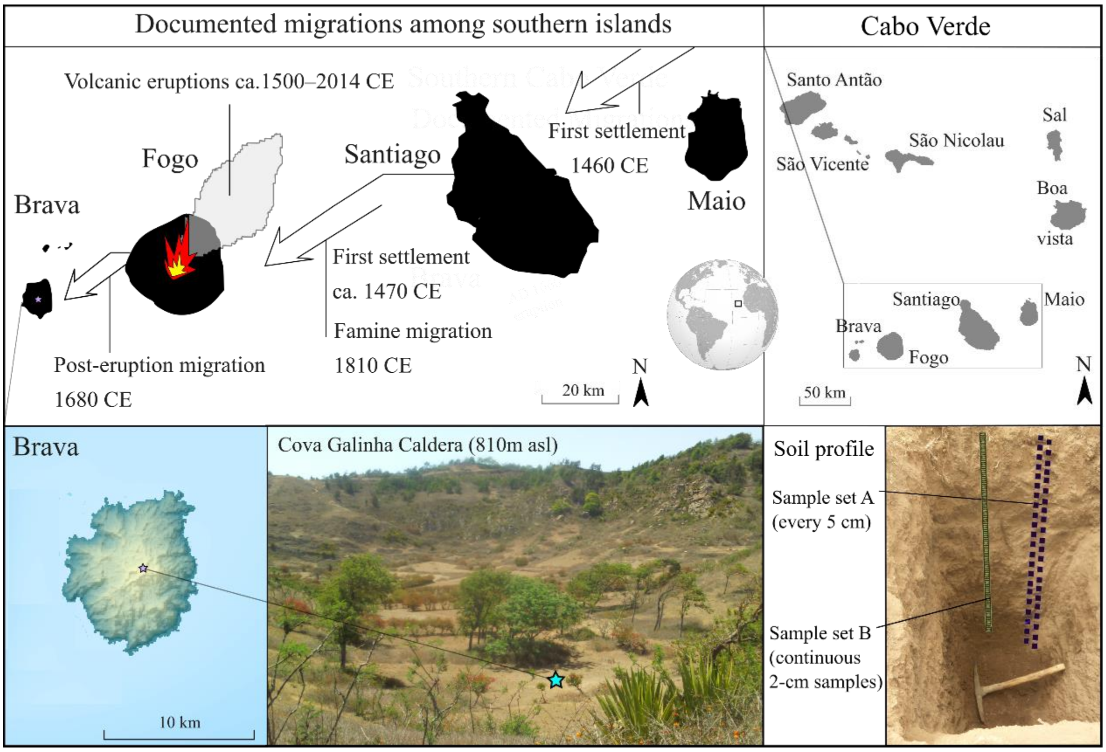


Figure 6.1: Maps of Cabo Verde with information of documented migrations between southern islands. Topographic map of Brava modified after Danielson & Gesch (2011). Pictures of Cova Galinha caldera and the studied soil profile (modified to show sampling strategy) taken by the authors.

6.3 Material and methods

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

6.3.1 Fieldwork and sample collection

In May 2019, we visited Brava Island and selected the Cova Galinha (CG) caldera based on its high elevation (higher calderas show good micro-fossil preservation due to increased humidity) and small size, as smaller calderas often hold fewer rocks and gravels, which is better for micro-fossil preservation. CG is situated at 810 m asl (14º51’26.2’’N, 24º42’09.5’’W) and is currently used for low-intensity agriculture, mostly of maize (*Zea mays*), and cattle grazing. We opened a 2 x 1 m trench in the centre of the caldera, and collected a set of samples of ca. 30 g of sediment every 5 cm (sample set A), and a set of contiguous 2 cm^3 block samples (sample set B) (Fig. 6.1). We placed the samples in sealed plastic bags. The samples were transported to the University of Southampton and stored in a cold room at +4 ºC within the School of Geography and Environmental Science.

6.3.2 Dating methods

To develop a first chronological model of the Cova Galinha site we obtained 10 bulk sediment and one macrofossil sample AMS radiocarbon (RC) date(s) in the Belfast and SUERC Radiocarbon laboratories (Table 6.1). We also carried out Pb-210 and Cs-137 analysis in the top metre of the core using sample set A, to achieve precise chronological control of sediment deposits in the last 200 yr. These analyses were undertaken in the GAU-Radioanalytical Laboratories at the National Oceanography Centre (Southampton), using gamma spectrometric analysis in HPGe well-type detectors (Cundy et al., 2006). We used Bacon in RStudio (Blaauw & Christen, 2013) to calculate the age–depth model based on all dates and defining level 20 cm as post- CE 1952 based on the sharp increase in Cs-137 and two ‘post-bomb’ RC dates (Fig. S7).

Table 6.1: Radiocarbon dates of the Cova Galinha site, Brava Island, Cabo Verde, and their calibration. 14C enrichment value is reported in ages between 1950 CE and the present.

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

Granulometry, elemental composition and Loss on Ignition analyses

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

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

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

6.3.3 Pollen and non-pollen palynomorph analyses

To determine vegetation, fern and fungal community changes, and assess the presence of herbivores, we processed 44 2 cm^3 samples from set A for pollen and NPP analyses following standard procedures (after Erdtman, 2013) and adding *Lycopodium* exotic spore for calculating concentrations. We used a high-power microscope to identify palynomorphs at x40 and x100 magnification and consulted African pollen atlases (e.g. Gosling et al., 2013) and our Cabo Verde and Canary Islands reference collections to identify pollen grains. NPP literature was used to identify fungal and fern spores (Gelorini et al., 2011; van Geel et al., 2003). All pollen grains were included in the calculation of the total pollen sum and categorised as local (endemic and native taxa to Cabo Verde), introduced, long-distance transported, or unidentifiable (mostly too damaged to identify). The latter was included in the sum to account for unidentified vegetation. We counted in a maximum of four microscope slides per level, a minimum of 250 pollen grains in samples with abundant pollen (section 55–0cm), a minimum of 100 grains in the rest of the record, and included counts over 50 pollen grains in the section with scarcer pollen abundance (section 115–195cm). The pollen and NPP data are presented as percentages over the pollen sum.

6.3.4 Macro- and micro-charcoal

For macro-charcoal quantification we used 44 2 cm^2 samples from sampling set A (taken every 5 cm), and sieved the material through a 180-micron sieve. We used a low-power microscope to count charcoal fragments. We performed micro-charcoal quantification in pollen-slides by counting angular opaque particles between 10 and 180 microns alongside exotic *Lycopodium* until reaching a sum over 200 items and then calculating micro-charcoal concentrations.

6.3.5 Silica structures: phytoliths and tephra

For phytolith and tephra analyses, we used a dry ashing sample preparation (Parr et al., 2001) with sample set B. We sieved the samples through 10 and 180-micron sieves. We tested density separation using sodium polytungstate at density 2.5 sg in ten samples, which resulted in the flotation of more than 50% of the material. As a cost-effective alternative, we followed recommendations of Lenfter & Boyd (1998) for sandy sediments, directly mounting microscope slides using Canada balsam, a method we previously used for diatom and phytolith analysis in Cabo Verde (Castilla-Beltrán et al., 2019). We used phytolith literature (e.g. Piperno, 2006) for their identification. We spiked the samples with a known quantity of exotic *Lycopodium* spores to calculate the concentration of phytoliths and tephra shards (selected morphotypes and shards shown in Fig. 6.2) and quantified these microscopic remains, scanning one slide per sample, with a microscope equipped with a polarising lens. In this study, we focused on recording episodes of significant microscopic tephra depositions (defined as >2,000 shards per gram of sediment). Episodes of limited deposition of tephra are under this threshold of detection. Characterisation of tephra geochemistry and comparison of shard morphology with tephra shards from Fogo Island will be carried out in future studies.

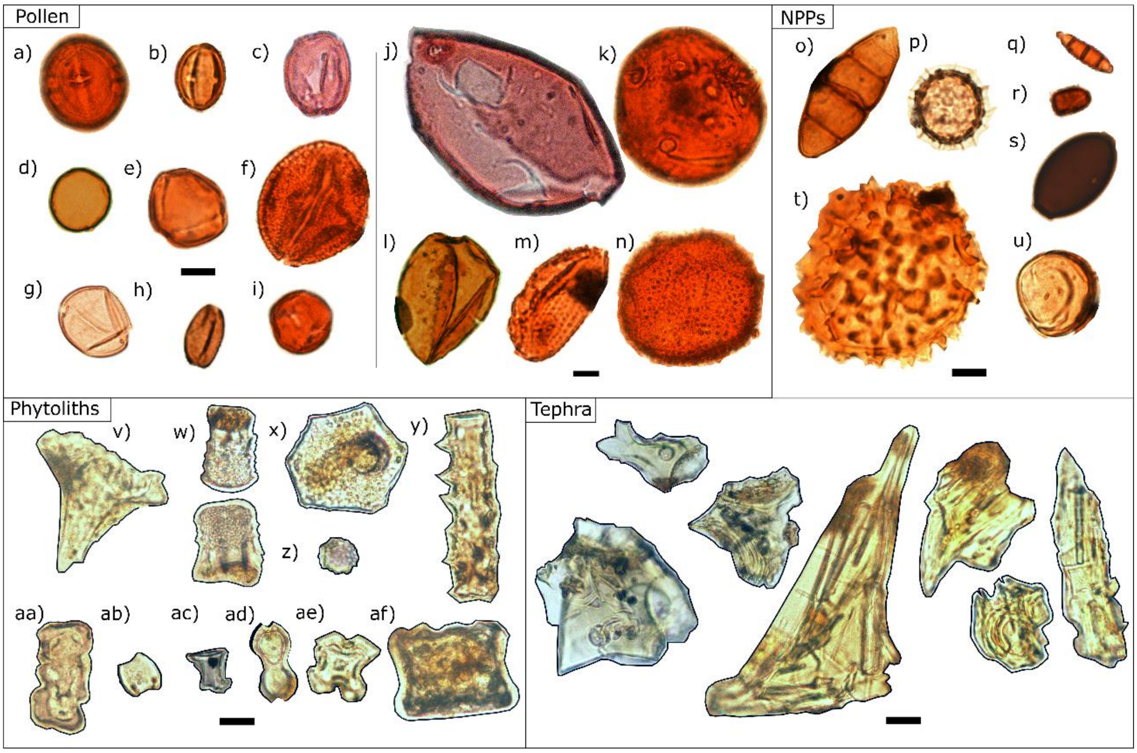


Figure 6.2 Selected microfossils documented in the Cova Galinha site, Brava Island, Cabo Verde. Pollen: a) *Dodonaea viscosa*, b) Primulaceae-type, c) cf. *Dracaena*-type, d) Urticaceae, e) *Lavandula*, f) *Euphorbia tuckeyana*, g) *Ficus*-1, h) *Ficus*-2, i) *Portulaca*-1, j) *Zea mays*, k) *Ipomoea*, l) Cerealia, m) *Commelina benghalensis*, n) *Portulaca*-2. NPPs: o)

Alternaria, p) *Lycogala-Urocystis*, q) *Fusarium*, r) *Sporormiella*, s) *Podospora*, t) *Anthoceros*, u) Monolete psilate-2. Phytoliths: v) Hair-cell, w) Maranthaceae (*Commelina benghalensis*), x) Cyperaceae, y) Elongated echinate z) Globular echinate (*Phoenix*), aa) Wavy trapezoid, ab) Saddle, ac) Rondel, ad) Bilobate cf. Chloridoidea, ae) Cross var. 1 (*Zea mays*), af) Rondel crown-top (*Zea mays*). Tephra: Selected shards from core section 70–30cm.

6.3.6 Zonation and Ordination analyses

We used Tilia software to establish a zonation by performing stratigraphically constrained CONISS analysis (Grimm, 1993; resulting in zones in Table S5). We carried out Canonical Correspondence Analysis (CCA) using RStudio's Vegan package to assess the influence of six environmental drivers on vegetation change. The following proxies were chosen to represent environmental variables: LOI % for organic matter (OM), macro-charcoal particles per cm^3 for local fire, percentage of obligate coprophilous fungal spores over the total pollen sum for herbivores, percentage of sand for erosion, tephra shards per gram of sediment for significant volcanic ash falls, and the ratio of Fe/Mn for the occurrence of soil reducing conditions. We performed two separate Detrended Correspondence Analyses (DCA) in RStudio, Vegan package (Oksanen et al., 2013), using pollen and NPP percentages, to assess turnover in vegetation and fungal/fern communities.

6.4 Results

6.4.1 Zones CG-1, CG-2 & CG-3: 9,700-4,100 cal yr BP

Between 9700 and 4,100 cal yr BP (zones CG-1, CG-2 & CG-3) sediment deposits in CG caldera were silt-dominated (mean 83% silt content), with moderate amounts of clay (mean. 13.1%) and limited sand inputs (mean 3.3%) (Fig. 6.3). There were limited proportions of organic matter, which followed an increasing trend (from 6.0 to 8.5%). Major elemental components in these deposits were iron (Fe, mean 8.2%) and silicon (Si, 12–17%), with low proportions of titanium (Ti, mean 1%) but peaks of aluminium content (up to 8.2%). Peaks in aluminium (Al) and silicon and increases in sand deposition could relate to inverted radiocarbon assays observed between levels 195 and 170 cm of the soil profile (Fig. S7). The Fe/Mn ratio shows steadily decreasing values in this period, from 23.8 to 16.85. Notably, CCA analysis shows an association between samples from this period and the Fe/Mn ratio, which are positively correlated with axes 1 and 2 of the CCA (biplot scores of 0.57 and 0.53 respectively) (Fig. 6.4). Poaceae (mean 26.7%) and Urticaceae (mean 39%) were the dominant components of the pollen assemblage. There was also a moderate presence of Asteraceae (mean 7.3%), Cyperaceae (mean 2.8) and *Plantago* (mean 4.8), and occurrence of Campanulaceae, *Lavandula* (type 1), *Ficus*, *Dodonaea viscosa* and *Dracaena* pollen (Fig. S8). Fungal communities were dominated by *Lycogala/Urocystis* (mean 111.6%), *Fusarium* (mean 5.5%)*, Glomus* (mean 4.5%) and *Chaetomium* (mean 1.5%), with the presence of *Curvularia intermedia*. Obligate coprophilous fungi (*Sporormiella*, *Cercophora*, *Sordaria*) show high abundance ca. 9,700–9,500 cal yr BP (up to 20.3% *Sporormiella*) (Fig. S9). Pollen most likely transported by trade winds was abundant in this period, including *Pinus*, *Juniperus*, *Morella*, *Corylus*, *Quercus*, and *Betula* (Ritchie et al., 1985; Hooghiemstra et al., 2006). Most of these taxa are not considered part of Cabo Verde's flora, as their ecological requirements are not matched by the current environmental conditions, but it cannot be ruled out that taxa from the Canaries (e.g. *Juniper, Morella, Pinus*) were once native to Cabo Verde. Charcoal particle concentrations were stable and very limited, with an average of 641 micro-charcoal particles per cm^3, and 0.2 macro-charcoal particles per cm^3 (Fig. 6.3).

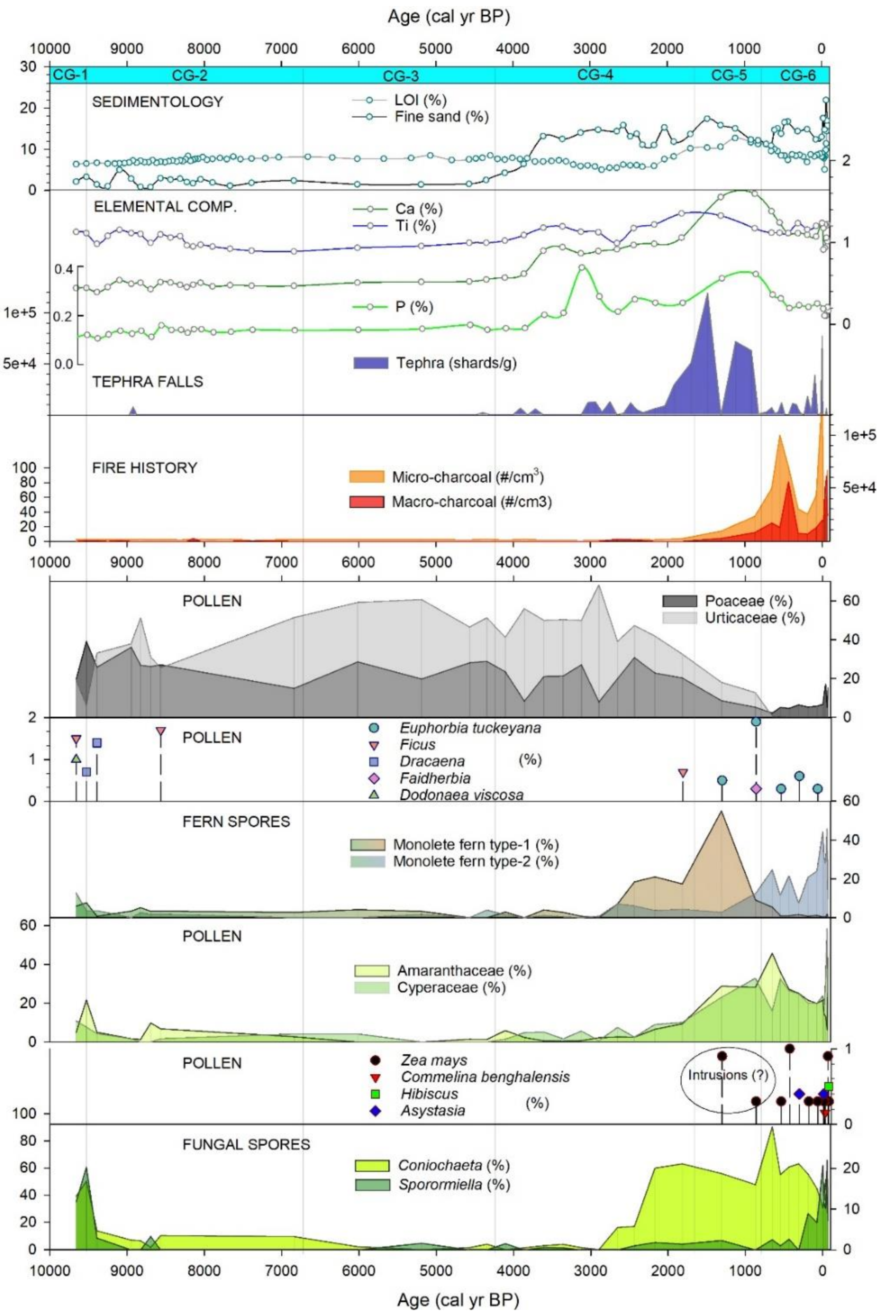


Figure 6.3: Diagram including a selection of indicators of environmental change (proxies) studied in Cova Galinha site, Brava Island, Cabo Verde. Silhouettes are superposed. Fern and fungal spores (NPPs) percentages calculated over the pollen sum. The label 'intrusions' refers to Zea mays pollen grains in levels pre-dating the introduction of this cultivar to the archipelago (see section 3.3).

6.4.2 Zone CG-4: 4,100–1,800 cal yr BP

Sediments deposits between 4,100 and 1,800 cal yr BP (zone CG-4) in the Cova Galinha caldera were rich in sand (mean 21.3%), with decreasing silt percentages (minimum value of 68.7%) and clay (min. value of 2.9%). Organic matter proportions decreased until ca. 2,700 cal yr BP (down to 5.5%), and then experienced a sharp rise between 2,700 and 1,500 cal yr BP (up to 10.4%).

Proportions of calcium (Ca) and titanium (Ti) increased (up to 1 and 1.3% respectively). The pollen assemblage was characterised by the enlarged proportion of Urticaceae (mean 47.6%) and a reduction of Poaceae (mean 20%). Pollen of Convolvulaceae, *Lotus*, *Ficus*, Primulaceae and Caryophyllaceae was also present in low proportions (<1%). The proportion of degraded (unidentifiable) pollen grains increased to an average of 14%. Spores of *Lycogala-Urocystis* decreased (mean 50%), and after 2,700 cal yr BP, monolete psilate fern spores and *Coniochaeta* spores increased (up to 18.1 and 59.9% respectively) (Fig. S9). Changes in the DCA axis-1 scores of pollen and NPPs show that the assemblages were already experiencing a transition within this period after 3,000 cal yr BP (Fig. 6.4). Episodes of significant deposition of tephra particles occurred especially after 3,000 cal yr BP, with highest values at ca. 1,800 cal yr BP (50,700 shards per cm^3), yet charcoal concentrations showed no significant change. CCA analysis does not suggest a strong association between samples in this period and tephra depositions, as samples score positive values in CCA axis-1, while tephra as an environmental variable exhibits a negative relationship to this axis (Fig. 6.4).

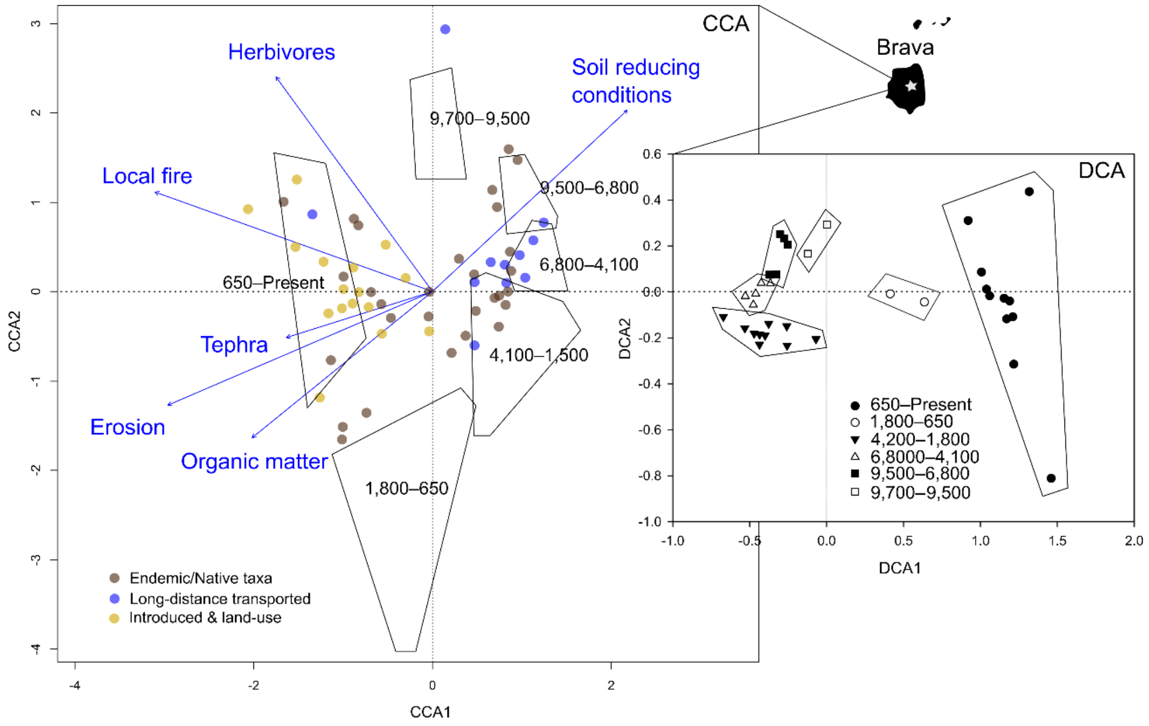


Figure 6.4: CCA and DCA plots of Cova Galinha record, Brava Island, Cabo Verde, using pollen percentage data. Polygons indicate the areas where samples plot. CCA axis-1 explained 71% of the variance (eigenvalue 0.42) and CCA axis-2 explained 11% (eigenvalue 0.06). Variables of Erosion, Organic Matter and Fire show a strong correlation with the negative side of CCA axis-1 (correlation scores: -0.78, -0.53 and -0.82 respectively), and Herbivores and Soil reducing conditions show a strong relationship with the positive values of CCA axis-2 (correlation scores: 0.63, 0.53 respectively). DCA eigenvalues 0.42 (axis-1), and 0.07 (axis-2).

6.4.3 Zone CG-5: 1,800-650 cal yr BP

Significant episodes of tephra deposition took place in the CG caldera ca. 1,800–650 cal yr BP (the highest concentration was 63,055/g ca. 1000 cal yr BP), and deposits contained high proportions of sand (mean 27.2%). Organic matter content reached its highest levels in the record (up to 12.7%). Proportions of calcium (Ca) and titanium (Ti) also showed the highest values of the record (1.3 and 1.4% respectively). Charcoal concentrations experienced progressive increases (up to 49,420 micro-charcoal particles/cm^3, and up to 6 macro-charcoal particles/cm^3). Pollen of the previously dominant Urticaceae and Poaceae steadily decreased (down to 5.2 and 12.7% respectively), while proportions of Cyperaceae and Amaranthaceae showed marked increases (up to 32.8 and 28.8%, respectively). Pollen of woody species *Euphorbia tuckeyana* (up to 1.9%) occurred for the first time in the record and there was the limited presence of *Faidherbia albida* pollen, and peaks of Monolete psilate (type 1, up to 55%), *Davallia* fern spores, and of fungal spores of wood-rotting *Bactrodesmium* (up to 2.7%). This period was also characterised by a high concentration of well-preserved phytoliths, most of which belonged to the morphotypes blocky polygonal, tabular, and Poaceae long cells (Bulliform and Elongated serrated/sinuate). Minimal percentages of globular echinate phytoliths are indicative of the presence of *Phoenix atlantica* in the island, potentially blown uphill from the coastal areas, a common feature with the Cova record in Santo Antão (Castilla-Beltrán et al., 2019).

We also found the presence of pollen from economic *Zea mays* and agricultural weed phytoliths identified as *Commelina benghalensis* (Eichhorn et al., 2010), both taxa introduced by humans after 500 BP. In previous work, the presence of *Zea mays* pollen has been used to validate alternative chronological models and interpreted as biostratigraphic markers of human settlement (Castilla-Beltrán et al., 2019; 2020). In the context of the Cova Galinha site, the proximity between these pollen grains and anthropic agricultural soil horizons (ca. 10cm) supports the interpretation that their presence is due to limited microfossil intrusions through leaching and root percolation in this soil layer. Samples dating from this period and taxa such as *Euphorbia tuckeyana* plot in the bottom left of the CCA graph, where the most influential environmental variable are organic matter and erosion (axis-1 correlation scores: -0.78, -0.53), showing a strong negative association with the soil reducing conditions (Fig. 6.4).

6.4.4 Zone CG-6: 650 cal yr BP–the present

Sediments deposited between 650 cal yr BP and the present-day in Cova Galinha are dominated by increasing proportions of sand (up to 39.26%; highest of the record) and decrease in organic matter (except for the uppermost sample: active soil). Significant events of tephra deposition or re-deposition due to erosion occurred especially between 650 and 100 cal yr BP. Proportions of aluminium (Al) and silicon (Si) showed increases (up to 5.9 and 14.7% respectively). Charcoal concentrations were the highest in the record (mean 20 macro-charcoal particles/cm^3, and mean 55,689 micro-charcoal particles/cm^3). The palynomorph assemblage became dominated by Amaranthaceae (mean 24.9%), Cyperaceae (mean 25.9%), Asteraceae tubuliflorae (mean 19.3 %) and Brassicaceae (mean 9.1%). There was sustained presence of *Zea mays* pollen, and there was the presence of pollen of introduced taxa Cerealia, *Ipomoea*, *Hibiscus*, *Commelina benghalensis*, *Asystasia*, *Portulaca* (types 1&2), and of native/endemic shrubs *Artemisia* and *Lavandula* (type-2) pollen. Obligate coprophilous fungi (*Sporormiella, Cercophora, Sordaria* and *Podospora*) showed increases after 300 cal yr BP, reaching maximum values for the core ca. 100 cal yr BP (e.g. *Sporormiella* peak of 20.7%). A new assemblage of fern spores including Pterideaceae, *Anthoceros*, Monolete psilate type-2 and *Ophioglossum* became dominant. Phytoliths of *Commelina benghalensis* were continually present (Fig. S10), Poaceae short-cells became more abundant, and new morphotypes potentially characteristic of the Fabaceae family (*e.g.* Puzzle skin) occurred especially after -10 cal yr BP (1960 CE).

The DCA axis-1 indicates increased rates of change in pollen and NPPs assemblage after 300 cal yr BP, and especially after -10 cal yr BP (Fig. 6.4). Samples dated after 650 cal yr BP plot in the left quadrants of the CCA graph, and those dated after 300 cal yr BP show positive CC2 scores, which supports a positive association with herbivores and local fire incidence (Fig. 6.4).

6.5 Discussion

6.5.1 Erosion, vegetation and regional climatic change

The Early and Middle Holocene periods in Northern Africa were defined by the occurrence of the most recent African Humid Period (AHP, 12,000–5,000 yr BP), which was characterised by increased precipitation and vegetation cover in the entire Saharan region (deMenocal et al., 2000; Pausata et al., 2020). Our pollen data suggest that 10,000 years ago, Brava´s highlands supported an open landscape dominated by Poaceae, Urticaceae (likely *Forsskaolea procridifolia* and *Forsskaolea viridis*, endemic and native to Brava respectively), Cyperaceae and *Plantago major*. The limited presence of pollen grains of woody species *Dodonaea viscosa*, *Ficus* (*Ficus sycomorus* and *Ficus sur*; species with African biogeographic affinities) and *Dracaena draco* subsp. *caboverdeana* (species not recorded in Brava in the present, see Arechavaleta et al., 2005) suggests that these species were native to Brava (Fig. 6.3). This reconstruction is strengthened by consideration of the NPP assemblage, which is dominated by saprophytic fungi that thrive in grasslands. Low concentrations of charcoal particles indicate the likely absence of local and regional fires, probably due to the prevailing humid conditions. The abundance of coprophilous fungal spores (e.g. *Sporormiella, Podospora*) indicate that the island may have supported significant populations of native fauna. In the absence of alternative evidence such as faunal fossils or *seda*DNA, we hypothesize that native reptiles and bird communities could have produced faecal matter that sustained these fungal communities.

During the AHP interval on Brava (9,700–5,000 cal yr BP), variation in the elemental composition of the sediments may reflect increased precipitation, but there is no strong evidence of inwash events, indicating that erosion rates were relatively stable. Leaf-wax data from marine cores off the Senegal coast 750 km east of Brava (GC68 & GC44) indicate abundant precipitation between 8,000 and 6,000 cal yr BP (Tierney et al., 2017) (Fig. 6.5). Soil reducing conditions during this period in Brava are evidenced by high values in the Fe/Mn element ratio and could be related to episodes of waterlogging. We found similar results in a previous palaeoecological study from the island of São Nicolau (190 km north of Brava; 1000 m asl), which showed soil reducing conditions between 6,000 and 5,000 cal yr BP (Castilla-Beltrán et al., 2020).

At 4,000 cal yr BP there is an abrupt change in lithology in the Cova Galinha caldera, with a sharp increase in sand content, indicative of local erosion. Dust concentrations from marine core GC68 indicate increased Saharan sediment input shortly after 4,000 cal yr BP, strongly suggesting that Brava's erosion signal was synchronous with that of the Senegal region (Fig. 6.5). Increased aeolian transport of materials from the continent could explain increases in calcium (Ca), potassium (K) and phosphorous (P) in Brava's soils (Fig. 6.3), as these are abundant in Saharan dust (Møberg et al., 1991). The browning of the Sahara, coupled with intensified seasonality due to changes in the monsoon system, explain the increased erosion in the highlands of Brava: stronger seasonal variation between long dry seasons and short and intense monsoon rains would favour soil denudation. For instance, two pulses of erosion on the island of Santo Antão (Cabo Verde) between 2,000 and 1,700 cal yr BP may be related to flash-floods linked to extreme weather events (Castilla-Beltrán et al., 2019). Similar events have been recorded from sites on the Senegal coast around 2,150 cal yr BP (Bouimetarhan et al., 2009).

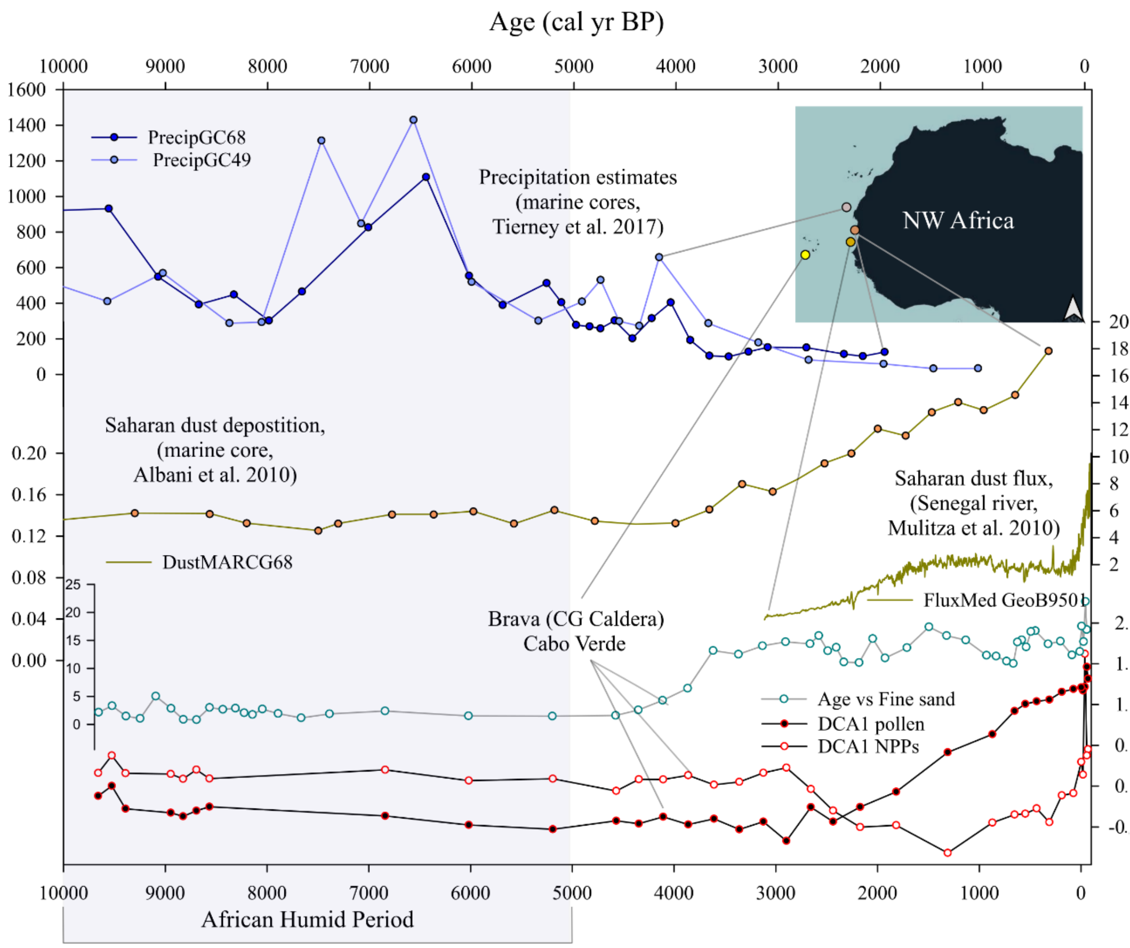


Figure 6.5: Paleoenvironmental trends from marine cores taken along the Senegal coast (cores GC68 & GC49: Tierney et al., 2017 and Albani et al., 2015, core GeoB9501: Mulitza et al., 2010, data downloaded from NOAA and Pangea) in comparison with erosion indicators, axis-1 scores of two DCA analyses (pollen and NPPs, axis-1 eigenvalues 0.42 and 0.43 respectively) as proxies of vegetation and fungal community turnover in the Cova Galinha site, Brava Island, Cabo Verde.

In more northern latitudes, the end of the AHP led to changes in the Macaronesian laurel forest communities. The fossil pollen data from the summit of Garajonay National Park in La Gomera (1266 m asl) show a progressive increase of the comparatively xerophilous taxa *Morella faya* and *Erica* at approximately 5000 years BP in relation to levels of other laurel forest taxa, while fire incidence increased after 3,100 cal yr BP (Nogué et al., 2013). In contrast, in the island of São Nicolau, Cabo Verde, vegetation showed relative stability between 4,500 and 1,000 cal yr BP, with the prevalence of fern-rich wooded landscapes, as vegetation would have protected the highland soils (Castilla-Beltrán et al., 2020). Our data suggest that in Brava, vegetation change was nuanced, as grasslands underwent only subtle changes, with increased dominance of Urticaceae and presence of *Lotus* (*Lotus purpureus* is recorded in Brava in the present) and *Lavandula* (perennial shrubs *Lavandula coronopifolia* or *Lavandula dentate*, both currently present in Brava).

Variable pollen preservation (increase in the proportion of unidentifiable pollen grains) could be hampering our understanding of vegetation change in this period.

Overall, an abrupt change towards more arid conditions at the end of the AHP (Pausata et al., 2020) is linked to increased erosion and dust deposits in Brava (ca. 4,000 cal yr BP), but it caused no major vegetation changes, indicating some degree of ecosystem resilience to regional drying. While rainfall likely decreased in Cabo Verde, cloud condensation in the highlands might have remained a sufficient source of humidity for local vegetation. Increases in turnover of pollen and NPP assemblages in Brava (DCA axis-1) only started changing after 2,500 cal yr BP, and are linked to the expansion of woody vegetation and fern-rich communities (Fig. 6.5).

6.5.2 Vegetation responses to volcanism

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

Abundant depositions of tephra shards took place in Brava especially between 1,800 and 650 cal yr BP. Brava Island has no recorded eruptions in the historical period but the volcano could have erupted in the Late Holocene (Worsley, 2015), meaning that the observed tephra could be of local origin. However, it is also likely that most, if not all, tephra originated from Fogo (highly active in the historical period 450 BP–present) and transported by north-eastern trade-winds (Table S4). The Brava data show that vegetation changed after tephra deposition events. An increase in woody plant taxa and soil organic content suggests an increase in local biomass. For example, there was an increase in the endemic shrub *Euphorbia tuckeyana*, which is well-adapted to thrive in pyroclastic soils. There was a parallel surge of Monolete fern (type-1) spores (up to 50%, the highest levels of the record), and spores of wood-rotting fungi such as *Bactrodesmium* and *Canalisporium* in the record, supporting evidence of an increase in woody taxa. The resulting palynological assemblage shows similarities to endemic-rich scrublands documented in the island of São Nicolau ca. 4,000–400 cal yr BP (Castilla-Beltrán et al., 2020).

In the Azores, volcanic eruptions ca. 5150 cal yr BP led to local vegetation change, including an increase in *Euphorbia* pollen (Connor et al., 2012). We hypothesise that in Brava there was an expansion of local taxa previously limited to rocky margins and cliffs between 1,500 and 500 cal yr BP, a process that may be linked to volcanism. It cannot be excluded that vegetation change primarily responded to a build-up of soil organic matter or to Saharan dust depositions, which also increase soil fertility, as demonstrated in studies in La Palma, Canary Islands (von Suchodoletz et al., 2013). Climatology could have also played a role in this process: palaeoclimatological research in Senegal (ca. 750 km from Cabo Verde) indicates a stable and drought-free period between 1500 and 900 BP (Azzoug et al., 2012). Further research is needed to clarify the relationships between volcanism, vegetation change and climate in Cabo Verde, including processes of tephra re-deposition linked to erosive pulses and the study of independent palaeoclimatic lines of evidence.

6.5.3 Colonial settlement, mass migration and human ecological footprint

From 500 BP to the present day, Brava's highlands underwent significant anthropogenic ecological disturbances due to the arrival of European settlers (the first permanent settlers on the island). The first peak in micro-charcoal concentration, dated ca. 500 cal yr BP, which is accompanied by the presence of *Zea mays* pollen, could indicate the onset of the first stage of human occupation of Brava and Fogo islands. The first introduction of maize in Cabo Verde is documented by historical accounts after 1535 CE (Moran, 1982), meaning that the presence of *Zea mays* pollen in soil layers pre-dating this period could be explained as pollen intrusions through leaching (Fig. 6.3). The first stage of land-use was followed by a change in fern communities through the increase of Pteridaceae, *Anthoceros*, Monolete psilate type-2 and *Ophioglossum*, indicating moderate disturbances.

Around 300 cal yr BP a peak in macro-charcoal coincident with significant tephra fall broadly corresponds with the documented mass migration (the fleeing of 'many families', no further numerical estimates given) from the island of Fogo after earthquakes and volcanic eruptions between 1660–1680 CE (290–270 BP) (Ribeiro, 1960). Volcanism was once again a driver of change in southern Cabo Verde, but this time spurring inter-island human migration and resultant land-use change on Brava. Historical accounts describe how these catastrophic episodes in Fogo led to the abandonment of sterile lands and damaged settlements, triggering migration between islands (Correia, 2000; Ribeiro, 1960). Population estimates for Fogo before the eruption were of 2,500 inhabitants by 1650 CE, so the exodus potentially involved hundreds of people. The impacts of sudden mass settlement in Brava are evident through the increase in obligate coprophilous fungi (e.g. *Sporormiella*), which indicate the presence of abundant livestock in the studied caldera. The woody vegetation present during the period 1,500–500 cal yr BP decreased (*e.g. Euphorbia tuckeyana*) and associated ferns and exogenous species appear within the samples from the caldera, including *Asystasia,* two species of *Portulaca*, and *Commelina benghalensis*. Introduced species plot with herbivore and local fire ecological drivers in the CCA, as their expansion was linked to land use (Fig. 6.4). The topmost samples of the Cova Galinha record (20–1cm) are represented by active unconsolidated soil; pollen of *Hibiscus cannabinus*, the flower emblem of the island, reflects the cultivation of this shrub for textile manufacture (Romeiras et al., 2011). Current environmental assessments of Brava confirm that free grazing by goats and other ungulates is the main threat for local biodiversity (GEF/UNEP, 2015), and tackling this problem would be beneficial for the conservation of threatened plant species and soils.

6.6 Conclusions

The study of sediments from a volcanic caldera in Brava, the smallest inhabited island of Cabo Verde, provides the first characterisation of highland vegetation throughout the Holocene in this island system. It also offers a long-term view of local ecological responses to environmental changes and disturbances originating at coarse regional scales, to those of more local within-archipelagic and within island origins. Pollen evidence suggests that taxa such as *Ficus sur*, *Ficus sycomorus*, *Dodonaea viscosa* and *Dracaena draco* subsp. *caboverdeana* were native to this small dry island before human settlement. While a regional drying trend after 4,000 BP led to increased erosion, grasslands showed limited immediate changes. Turnover of pollen and NPP assemblages increased after 3,000 cal yr BP and are reflected in the expansion of ferns and shrubs that could have been favoured by significant tephra falls and increased Saharan dust deposits. Although the link between tephra and vegetation change requires confirmation, we suggest that both direct (enrichment of soils) or indirect (change in local climate) impacts of tephra falls might have driven vegetation change. Mass-migration from the neighbouring Fogo Island after destructive episodes of volcanic eruptions there (1660–1680 CE) led to the introduction of exogenous taxa and the degradation of the highlands in Brava. Studying long-term environmental change in small islands reveals how major climatic transitions and disturbance episodes impact spatially constrained ecological systems. This is important for the current and future development of guidelines on the protection of island biodiversity and ecosystem services, and for managing future sustainability in islands and archipelagos.

Chapter 7 Discussion

7.1 Overview

Chapter 7 provides an integrative overview of the three case studies presented in this thesis in chapters 4-6: Santo Antão (SA), São Nicolau (SN) and Brava (BR) Islands. It provides a reflection on methodological innovation, the contribution of the research to the understanding of Holocene environmental change and human impacts in Cabo Verde, and its relevance for biodiversity conservation.

7.2 Study methodological innovations and future research

This thesis presents the first palaeoecological research carried out in Cabo Verde, successfully revealing Holocene ecological change in three different islands to provide historically-contextualised conservation goals. We have faced several methodological challenges: Dry conditions prevalent in the Cabo Verde archipelago cause intrinsic difficulties for palaeoecological research, including interrupted sedimentation and uneven and discontinuous preservation of micro-fossils (Brunelle et al., 2018; Carrión et al., 2009). This could be a reason why no palynological work had been conducted in Cabo Verde. This thesis has demonstrated that highland volcanic calderas in these islands hold a diversity of palaeoenvironmental evidence. Site selection is an important first step for palaeoenvironmental reconstructions: larger calderas such as Cova de Paúl (SA, ca. 500m diameter) contain rocky and sandy layers that have shown poor pollen preservation, while smaller calderas (Calderinha, SN, and Cova Galinha, BR, 50–30m diameter) support more continuous palynomorph preservation, although some barren sections were present and some sections contained high percentages of degraded pollen gains (Fig. 7.1). Soil horizons characterised by higher grain sizes, reflecting erosion processes, were more commonly barren of palynomorphs or contained damaged pollen grains due to mechanical degradation (Havinga, 1966) (e.g. the section between 110–60cm in Cova Galinha site, BR). Sections with oxidised sediments also showed poor palynomorph information potentially due to oxidation and microbial attack (Havinga, 1966), as evidenced by the Calderinha, SN, (140–170cm) and Cova Galinha, BR (140–175cm, 200–205cm) sediment records (Fig. 7.1).

A multi-proxy approach, including full analysis of NPP assemblages, micro- and macro-charcoal, silica structures, sedimentology and *n*-alkanes, has proven useful to reconstruct palaeoenvironments in Cabo Verde: for instance, silica structures (phytoliths, diatoms) were present in sections of poor pollen preservation in Cova de Paúl (SA) sediments, and NPPs and *n*-

alkanes were preserved in promising concentrations in sections of poor pollen preservation in Calderinha (SN) (Fig. 7.1). Such integration can compensate for shortcomings of single methods as alternative or complementary proxies of environmental change. For instance fungal spores, phytoliths and *n*-alkane biomarkers can provide insights into the stability or change of environmental conditions in sections with poor pollen preservation. The implementation of complementary cutting-edge methods such as *seda*-DNA in the future could help improve proxy-dependent biases such as low taxonomic resolution. Finally, independent studies of pollen productivity, deposition and preservation in Cabo Verde will help interpret the fossil pollen record in the archipelago (see appendix A).

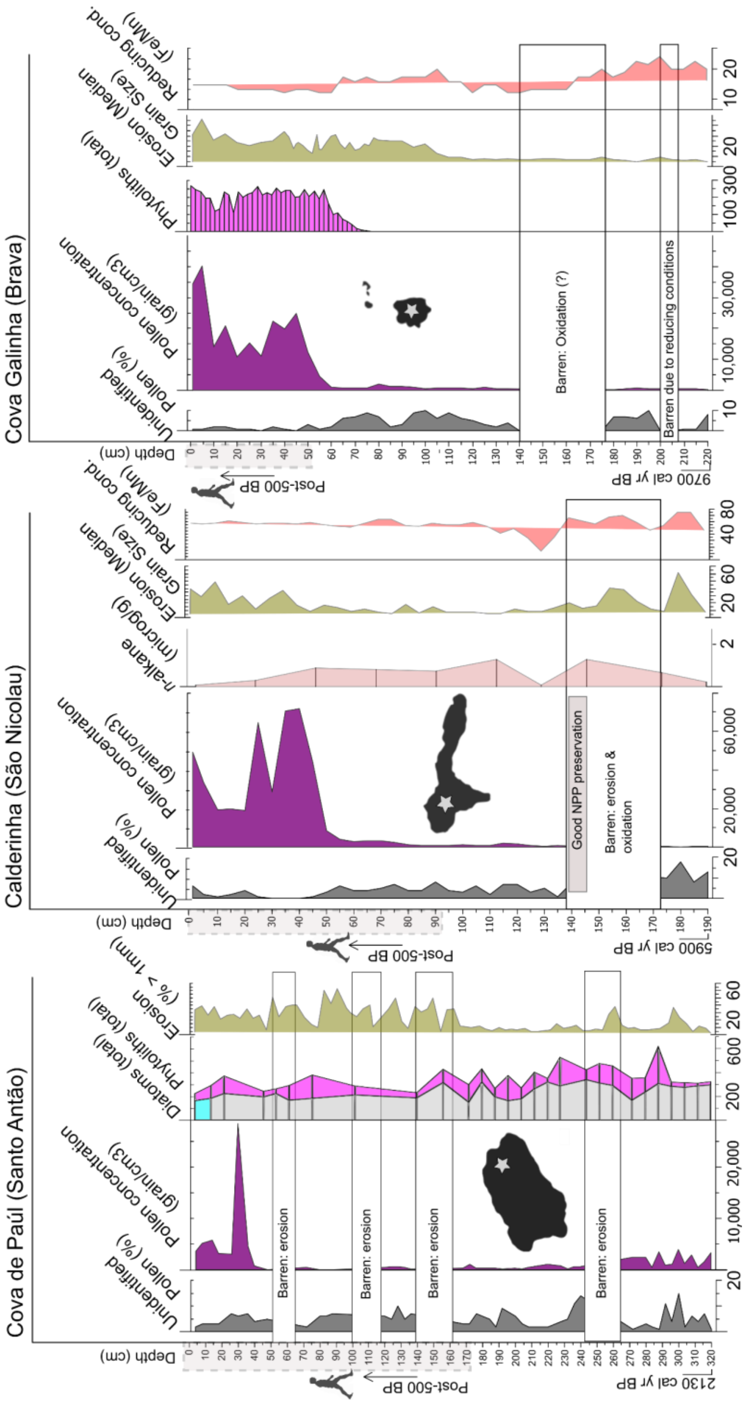


Figure 7.1: Summary taphonomical diagram showing pollen preservation (% unidentifiable pollen), pollen concentration and complementary proxies of three Caldera sites in Cabo Verde: Cova de Paúl (SA), Calderinha (SN) and Cova Galinha (BR).

Processes of sediment mixing (e.g. bioturbation), slumping and redeposition, as well as microfossil percolation, are inherent to soil stratigraphic sequences and must be taken into account to properly interpret biostratigraphic data. These processes can hamper the accurate reconstruction of processes such as short-term ecological successions. For instance, pollen from introduced economic taxa was identified in strata dating to pre-human times (e.g. *Zea mays* in Cova Galinha), which was interpreted as a result of percolation from the neighbouring soil horizons. Research into volcanic soils in New Zealand has shown that pollen percolation rates are discrete (< 0.056 cm per year), concluding that soil sequences are useful as records of environmental change in that region (Horrocks & D’Acosta, 2003). We conclude that studying soil sequences in Cabo Verde is useful to study long-term processes of ecological change such as pre- and post-human arrival, but that further techniques such as soil micromorphology (Nicosia & Stoops, 2017) would be needed to reconstruct shorter-term environmental processes such as land use change and the impact of episodes of extreme weather events.

Buildingstrong chronologies for Cabo Verde paleoenvironmental records has proven a challenging task. Radiocarbon dating is the most common geochronological method used in palaeoecology, but it is not exempt from shortcomings, depending on the sedimentary context and materials dated. The main limitation of using radiocarbon dating in Cabo Verde soil sequences was the scarcity of macrofossils bellow the uppermost soil horizons (generally between level 40cm and the surface) or a significant mass of charcoal to date, meaning that most dates were necessarily done on bulk sediment, a dating material that is most likely to undergo redeposition (Grimm et al., 2009). The inherent challenges of working in soil profiles were also at play, such as soil leaching and mixing processes. For instance, erosion leading to sediment redeposition can produce mixtures of old and contemporaneous carbon in the sediment sequence, producing artificially old ages. In the three case studies, this limitation was overcome by implementing diverse geochronological modelling strategies (e.g. defining sections of rapid depositions or ‘slumps’ based on sedimentological data), and the integration of radiocarbon dating with alternative dating strategies such as Pb-210 and Cs-237, which was successful in providing alternative chronological frameworks for paleoecological reconstruction. We found that incorporating additional sedimentological data such as hiatuses and ‘slumps’ into age-depth models is vital to the interpretation of palaoenvironmental data in such dry sites. In future research, the integration of other independent dating methods such as Optically-Stimulated

Luminescence could help strengthen chronological models, and the application of soil microstratigraphic analysis would be useful to better understand sections subjected to bioturbation, sediment mixing and trampling (Nicosia & Stoops, 2017). The use of tephra as a chronostratigraphic marker, especially in the southern islands of the archipelago, could be explored in future research through chemical characterization of tephra shards, which are expected to be abundant in some soil profiles. The study of tephrochronology and the ecological impacts of volcanism in Cabo Verde will face the challenges of taphonomy and preservation of micro-fossils, of successfully linking tephra records form different sites (Payne & Egan, 2019), and of identifying particular volcanic episodes from a volcano as historically active as Pico do Fogo (Ribeiro, 1969).Finally, a central aspect not directly analysed in the studied sediment sequences was the influence of local climatic changes in the transformation of the ecosystems of Cabo Verde. Variation in rainfall regimes is especially interesting for the study of vegetation change and of socio-ecological resilience in this archipelago. Independent palaeoclimatological proxies, such as hydrogen isotope (δD) of terrestrial plant waxes (C_{28} *n*-alkanoic Acid or *n*-alkanes), could be used in the future to provide a local perspective on the regional change on rainfall regimes studied in marine cores (e.g. Tierney et al., 2017). In particular, the study of the impact of past droughts and other extreme natural phenomena on island socio-ecological systems can provide a long-term perspective of how societies adapted to changing environmental conditions through time in Cabo Verde.

7.3 Research questions, answered

7.3.1 What was the ecological state of the highland ecosystems of Cabo Verde during the Holocene and what was their natural variability?

Assessing long-term ecosystem change is pivotal to understanding the natural variability of oceanic island ecosystems, including the ecological responses to natural disturbances and the role of different ecological drivers of change (Froyd & Willis, 2008). It is also useful in identifying the distribution of ecosystems in the past, and to document episodes of human settlement to complement the archaeo-historical record (de Nascimento et al., 2020; Siegel et al., 2015). Analysing volcanic caldera sediments deposits has provided the first view of Holocene highland vegetation, fern and fungal community changes in Cabo Verde.

7.3.1.1 Is there evidence of a prehistoric inhabitation of Cabo Verde?

It has been hypothesized that humans may have inhabited Cabo Verde before the arrival of Europeans ca. 1460 CE, for example, from visits by Mediterranean or West African sailors

(Lobban, 1998; Shabaka, 2013). Common proxy evidence of human habitation in the palaeoecological record is the increase of coprophilous fungal spore concentrations, peaks in fire indicators and the introduction of cultivars (Birks, 2019). In the three Cabo Verde records, phases with abundant coprophilous fungal spores are documented (e.g. *Sporormiella, Podospora*) in Brava, São Nicolau and Santo Antão islands, and phases of increased fire occurrence in São Nicolau and Santo Antão pre-date 1460 CE. A lack of supporting archaeological evidence and no evidence of introduced crops suggests that these phases were probably caused by natural phenomena: coprophilous fungi could indicate the abundance of native fauna, most likely reptiles or birds (Wood et al., 2012), and increased fire occurrence can reflect natural wildfire variability. This interpretation could be reconsidered if independent evidence of significant pre-historic settlement of the islands is found in the future.

7.3.1.2 Did Cabo Verde support laurel, Mediterranean or tropical forests in the past?

It has been hypothesised that the current absence of Macaronesian forests could be due to the effects of human impacts, which wiped out the last remnants of these forest formations (Heckman, 1985; Barone, 2006). In light of this investigation, it can be affirmed that there is no substantial evidence of laurel, Mediterranean or other from of tropical forest present in Cabo Verde during the Holocene. This affirms the peculiarity of the biogeographic status of Cabo Verde as a part of the region of Macaronesia: it does not share some of the characteristics of the other archipelagos, notably the presence of laurel forests (Freitas et al., 2009).

However, it must be noted that Cabo Verdean pollen assemblages include pollen grains that could indicate the presence of taxa not considered native today, and some belonging to laurel forest communities (e.g. *Morella*, *Pinus*, *Juniperus*, and CV-2, which potentially belongs to *Clethra arborea* in the SA record). European and North African forest taxa also occur in low amounts (*e.g. Quercus, Corylus, Alnus*). Such a mix of pollen from local and within-island catchments and grains from more distant origin occurs in all records. This has been recorded in marine sedimentary cores off West Africa; northeast trade-winds transport pollen from mainland Africa, the Mediterranean and the Canary Islands (Hooghiemstra et al., 2006). These pollen grains are likely observable in the Cabo Verde records due to preservation biases, and to the low pollen production of local vegetation, which can be related to low plant biomass and the dominance of an entomophilous flora, similarl to the Canary Islands (de Nascimento et al., 2015). The long-distance background pollen signal means the native status of these taxa remains uncertain, and further fossil evidence is required to confirm if some type of Mediterranean or laurel forest formation was present locally in Cabo Verde before human settlement. Thus, future studies and the examination of other palaeobiological records (e.g. macro-fossils) could change the present interpretation.

7.3.1.3 What were the drivers of landscape change before human settlement?

Highland ecosystems in Cabo Verde were subject to significant vegetation change before human settlement, exhibiting responses to naturally occurring disturbances such as wildfires and erosion pulses. Natural disturbances affected highland ecosystems, but their transformations were more nuanced than those that occurred after human settlement. The Cabo Verde records show the variable development of grasslands and scrublands, with presence of different degrees of native woody vegetation and associated fern and fungal communities within the three studied islands. Between 10,000–5,000 cal yr BP, Brava´s highlands supported open landscapes dominated by Poaceae and Urticaceae, and in lesser proportions by Cyperaceae, Amaranthaceae, Asteraceae and *Plantago*. Woody species such as *Dodonaea viscosa*, *Ficus* and *Dracaena draco* subsp. *caboverdeana* were present. Between 6,000–5,000 cal yr BP São Nicolau´s highland vegetation was dominated by Poaceae, Asteraceae and Brassicaceae and *Plantago*, with the presence of woody species such as *Euphorbia tuckeyana*, and *Ficus*. Fungal assemblages were characteristic of grasslands (*Lycogalla-Urocystis*, *Curvulatia intermedia),* and there were significant proportions of *Glomus sp*. in both Brava and São Nicolau. *Dictiosporium heptasporium*, a parasitic fungus found in wood and bark (Gelorini et al., 2011), had a significant presence only in São Nicolau.

Rarefaction analysis is useful to show the relative richness of distinct pollen types per sample in different records compensating for the effect of dissimilar pollen counts (Birks & Line, 1992). Rarefied palynological diversity in Brava and São Nicolau islands shows that pollen assemblages exhibited higher diversity during the AHP (10,000–5,000 BP), following a downward trend between 5,000 cal yr BP and the present (Fig. 7.2). In contrast, The Cova de Paúl (SA) exhibits an upward trend in rarefied palynological diversity, which could reflect the fact that it is a younger record limited to the last 2100 yr BP. It must be noted that preservation biases could be affecting the observed pattern, as samples from the top and bottom of the records typically show less palynomorph degradation.

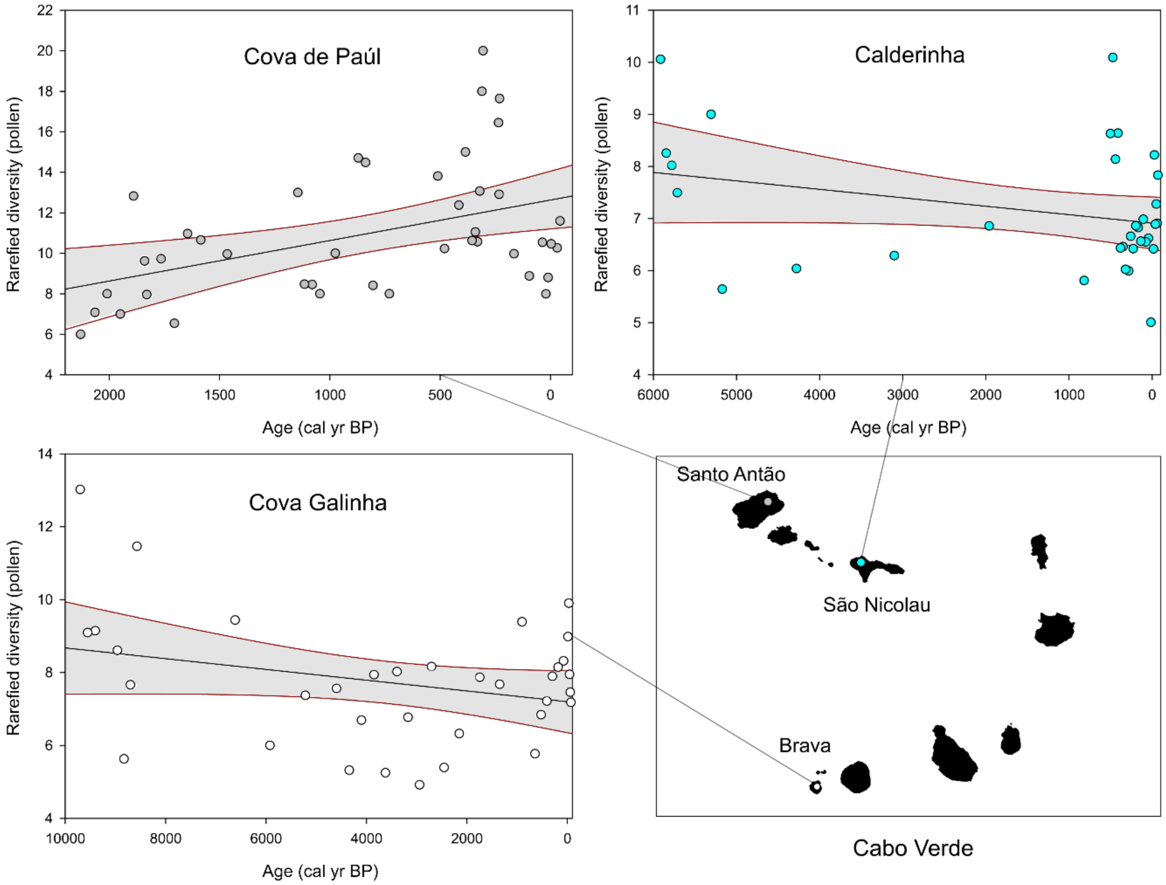


Figure 7.2 Rarefied species diversity of pollen samples through time of three sites in Cabo Verde, Cova de Paúl (SA), Calderinha (SN) and Cova Galinha (BR). Analysis conducted in R studio, Vegan package, using pollen count data of the three sites, method following Birks & Line (1992).

Diverse shifts in Cabo Verde's highland ecosystems were documented during the period between 5,000–500 cal yr BP, which was marked by the end of the AHP and a trend of increasing aridity in the Saharan region. For instance, Detrended Correspondence Analysis (DCA) of all fossil pollen datasets shows significant changes in DCA axis-1 of the records after 2,000 yr cal yr BP (BR), and after 1,000 cal yr BP (SN, SA) (Fig 7.3). The Cova Galinha record (Brava) is useful to assess the response of native grassland vegetation to erosion and tephra falls: vegetation turnover in Brava after 2,000 cal yr BP was linked to increased volcanic ash falls and peaks in soil organic matter and characterised by an increase in the endemic shrub *Euphorbia tuckeyana,* fern spores (monolete psilate type-1) and spores of wood-rotting fungi such as *Bactrodesmium* and *Canalisporium*. In Santo Antão, the period between 1,300–400 cal yr BP was characterised by the occurrence of regional fires and an increase in woody vegetation, indicated by the presence of Sapotaceae and Moraceae pollen (indicating the presence of *Syderoxylon marginata* and *Ficus*), and by peaks of wood-rotting fungi *Bactrodesmium*. There was also a marked change in the diatom assemblages of the Cova de Paúl record (SA), likely associated with changes in soil salinity and/or moisture.

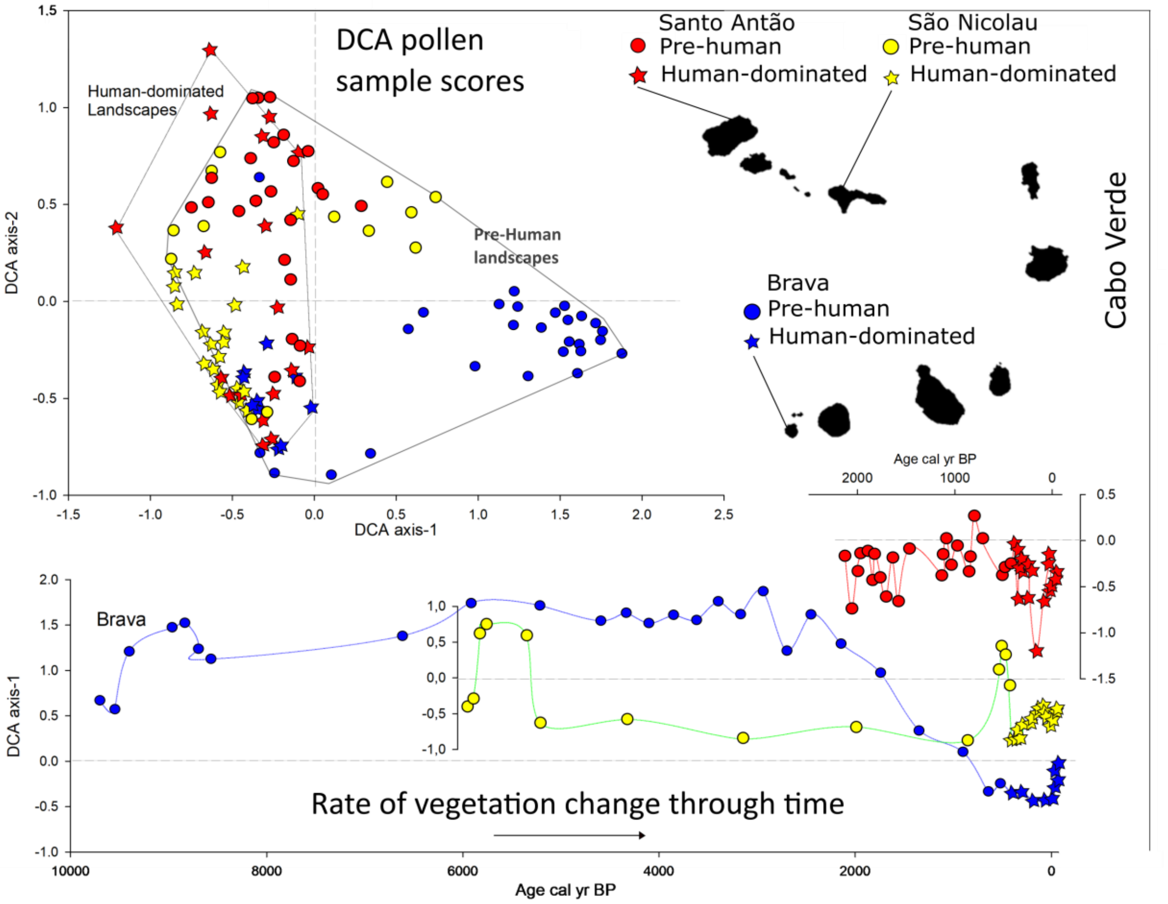


Figure 7.3: Plots showing Detrended Correspondence Analysis (DCA) results using pollen percentages through time of three sites in Cabo Verde: Cova de Paúl (SA), Calderinha (SN) and Cova Galinha (Brava). Eigenvalues: DCA axis.1, 0.48, DCA axis-2, 0.26.

In Calderinha (São Nicolau), the highest abundance of woody native plants was recorded between 3,000–400 cal yr BP, and this period was associated with an increase in local fires. Being the record with highest percentage of woody vegetation cover of all sites studied, Calderinha is useful to examine the natural development of highland woody scrublands and woodlands in Cabo Verde. Vegetation changes following the occurrence of local fire after ca. 1,000 cal yr BP involved an increase in taxonomic diversity, with herbaceous taxa such as *Aeonium*, *Asparagus*, *Campanula* and Cucurbitaceae, as well as woody species such as *Dracaena draco subsp. caboverdeana*, and *Tamarix senegalensis*. A new assemblage of fungal and fern spores revealed changes in faunal and fungal communities associated with vegetation succession in São Nicolau, notably the presence of the non-obligate coprophilous fungi *Apiosordaria*, *Chaetomium* and *Gelasinophora cratophora,* and the abundance of epiphytic ferns (e.g., *Davalia canariensis*) and wood-rotting fungi such as *Bactrodesmium*. The processes that potentially led to the occurrence of natural fires could involve bush encroachment that led to an increase in local fuel (also seen in an increase in organic matter content in sediments between 3,000 and ca. 1,000 cal yr BP), and a trend of increasing aridity and changes in seasonality. The data suggest that after natural fires, the woody scrublands persisted, showing a degree of resilience in the face of burning (Fig. 7.4). In contrast, the introduction of herbivores and presumably direct deforestation by humans led to the rapid decrease in woody taxa, leading to a state of open landscapes between 400–50 cal yr BP.

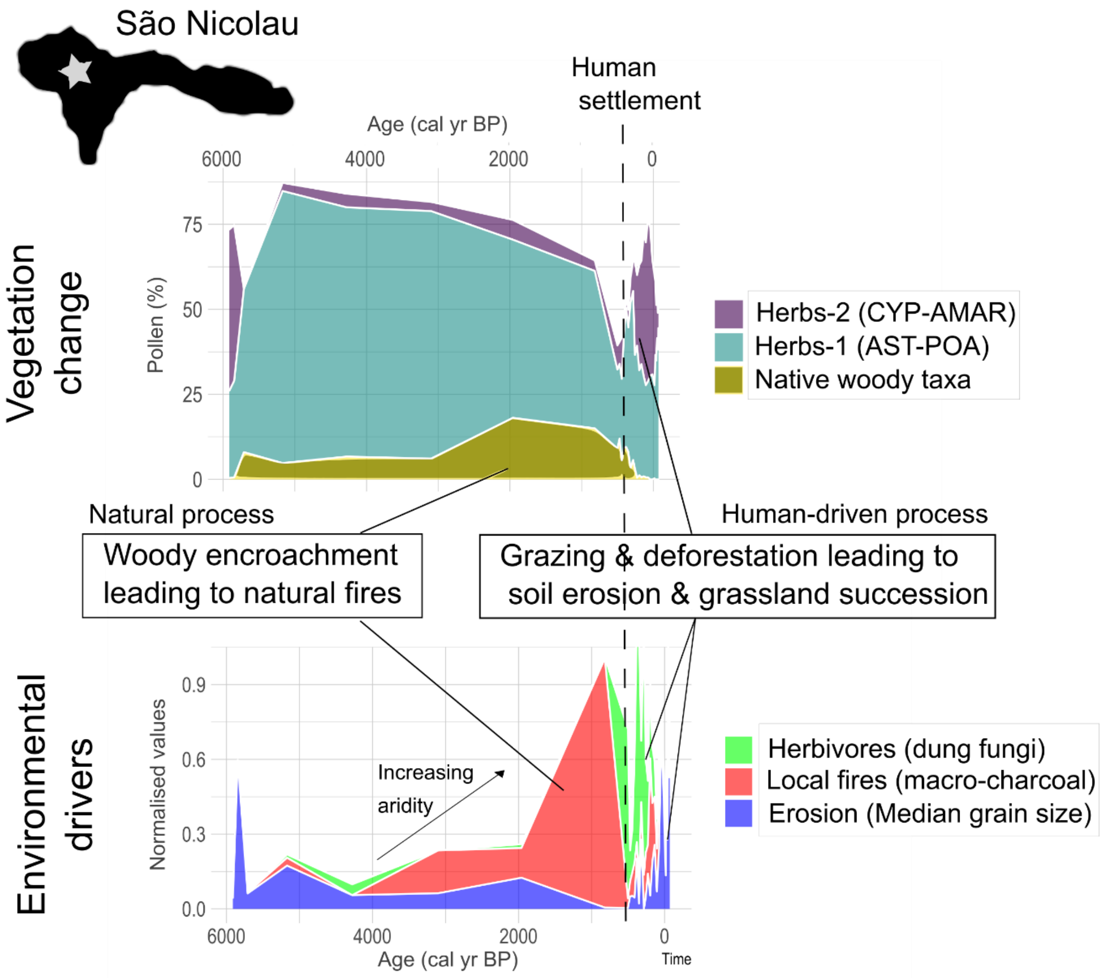


Figure 7.4: landscape-scale natural and human-driven ecological processes in São Nicolau´s highlands based on the variance of woody vegetation and two groups of herbaceous taxa in relation to changes in fire, erosion and grazing regimes. Abbreviations: Asteraceae (AST), Poaceae (POA), Cyperaceae (CYP) and Amaranthaceae (AMAR).

In summary, the Cabo Verde records show a pattern of pre-human ecological variability in response to regional drying, extreme weather events and volcanism. This goes in accordance to palaeoecological research in other Macaronesian archipelagos: for instance, in La Gomera (Canary Islands) laurel forest structural changes were identified in response to increased aridity at the end of the AHP (Nogué et al., 2013). In the Azores, pre-human Holocene vegetation change was also driven by volcanism (major volcanic eruptions ca. 5150 cal yr BP), including phases of vegetation succession and increases in forest cover (Connor et al., 2012).

7.3.2 How has human settlement and the emergence of socio-ecological systems impacted highland landscapes in Cabo Verde?

The environmental history of Cabo Verde since human settlement conforms to a global trend of environmental degradation brought by colonial economic systems in oceanic island environments (Whittaker et al., 2017). Testimonies from early travellers to Cabo Verde, such as Duarte Pacheco Pereira (1505-1508 CE) and Matin de Centinera (ca. 1572 CE) already highlighted the infertility of the land and the damaging effects of grazing and logging in Cabo Verde (Romeiras et al., 2014; Green, 2012). These accounts suggests that resource overexploitation and lack of environmental knowledge were key to these environmental changes (Lindskog & Delaite, 1996).

7.3.2.1 Vegetation change after human settlement

The palaeoecological datasets from Cabo Verde are useful for assessing the effects of anthropogenic landscape perturbations in three distinct islands. Human settlement and the introduction of species exogenous to the archipelago caused rapid and widespread ecological and soil degradation (e.g. reduction of native species and erosion) in Cabo Verde. The three records (SA, SN, BR) document similar processes of landscape anthropization, including the decline of pollen of woody native species (e.g. *Ficus*, *Dracaena draco* and *Euphorbia tuckeyana*), decrease of native grassland taxa such as Poaceae, Asteraceae and Urticaceae, and increases in fungal spores of saprophytic and parasitic species (e.g. *Diporotheca, Tetraploa*) and fern spores associated with land use and disturbance (e.g. *Anthoceros*).

Herbaceous pollen taxa that tended to show the most significant increases in human-dominated landscapes were Cyperaceae and Amaranthaceae, which constituted the matrix of agricultural lands and rangelands. Interestingly, phases of increase in proportion of Cyperaceae and Amaranthaceae pollen were also recorded in pre-human times in SA and SN during short-lived phases of natural disturbance, such as erosion pulses and local fires (Fig. 7.5). After the human settlement of SA and SN, the sustained occurrence of grazing, erosion and fire are associated with the increases of Cyperaceae and Amaranthaceae in herbaceous pollen assemblages. In contrast, Brava´s dominant herbaceous vegetation (Poaceae and Urticaceae) showed a certain degree of resilience in response to increasing erosion after the AHP, but increases in Cyperaceae and Amaranthaceae were identified after volcanic ash falls and changes in soil conditions ca. 1500 cal yr BP, an assemblage that prevailed and after human settlement. Further study of grassland dynamics is needed to ascertain the alternative states of highland grasslands in Cabo Verde and their capacity of recovery after environmental disturbances.

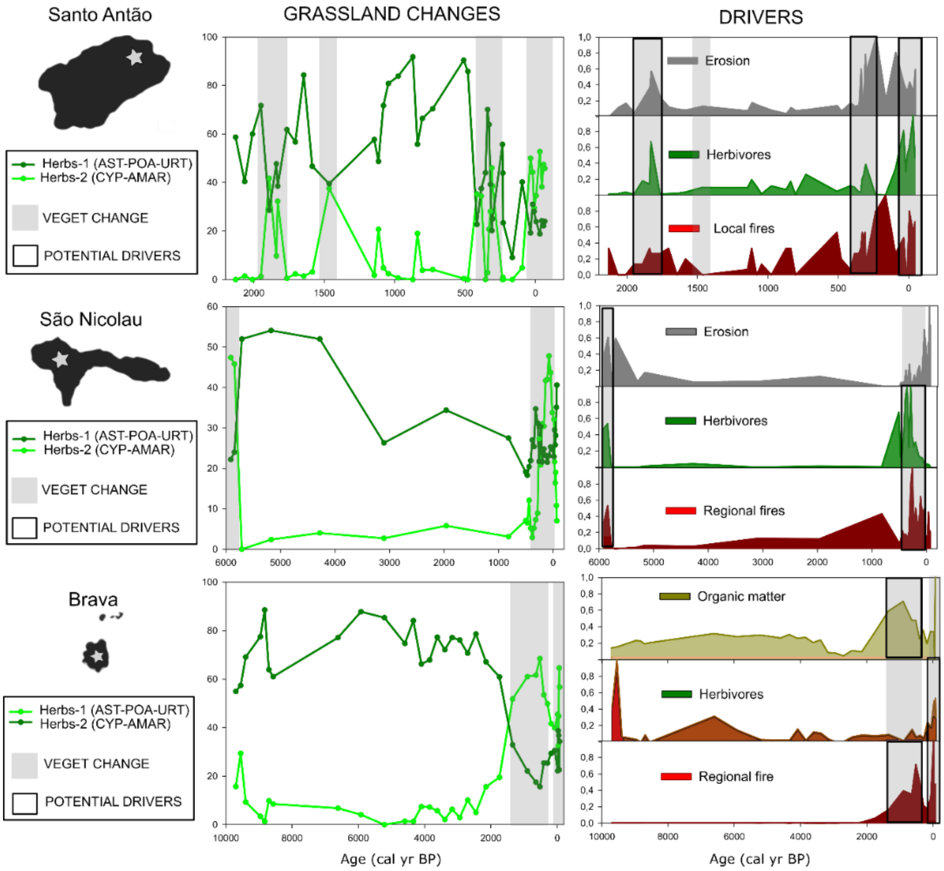


Figure 7.5: Changes in dominant herbaceous vegetation in the three studied sites in Cabo Verde: Cova de Paúl (SA), Calderinha (SN) and Cova Galinha (Brava), with the most likely drivers of vegetation change indicated for each site. Abbreviations: Asteraceae (AST), Poaceae (POA), Urticaceae (URT), Cyperaceae (CYP) and Amaranthaceae (AMAR).

7.3.2.2 Landscape homogenization in Cabo Verde

Landscape homogenization is a phenomenon that has been related to biodiversity loss due to agricultural intensification recognised at a global scale, and has been linked to the reduction of resilience, this is, the ability of ecological communities to withstand disturbances (Gámez-Virués et al., 2015). Canonical Correspondence Analysis of the integrated pollen datasets was conducted to explore the influence of five environmental variables in the change of local vegetation: erosion (median grain size), herbivores (obligate coprophilous fungi), local and regional fire (micro- and macro-charcoal abundances), and organic matter (LOI percentage) (Figure 7.6). Samples dating to the human period (represented by stars) plot mainly in the top-left side of the graph, with the variables local fire, herbivores and erosion, while some samples from SA and SN plot in the bottom left side, as they are more influenced by organic matter and regional fire variables (represented by blue arrows). CCA results show that record samples representative of human-dominated landscapes tend to plot in tight clusters, indicating a trend towards landscape homogenization at the archipelago level (Fig. 7.6). The identification of increasing proportions of introduced species (represented by yellow triangles) through the post-human arrival sections of the records (between 500 cal yr BP and the present-day), likely is the main driver of this process. This can be also observed as an increase of rarefied palynological diversity in modern samples of the records, especially in Cova de Paúl (SA) (Fig. 7.2). The most common cultivars detected in the pollen records were *Zea mays* and Cerealia, likely due to higher pollen production of these cultivated grass taxa in comparison to cultivars such as *Ipomoea batatas* and *Persea americana*. Other common introduced herbaceous taxa were *Lantana camara*, *Commelina benghalensis*, *Asystasia*, *Portulaca*, Rosaceae, *Centaurea*, Agavoidea and *Opuntia.* Woody species were also introduced to the islands for afforestation and timber production (e.g. *Pinus*, *Eucalyptus*). Increases in erosion, local and regional fires and peaks in abundance of coprophilous fungi accompanied species introductions, and are related to different phases of land use; a new regime of compounded natural and human-driven disturbances. The introduction of grazers (e.g. goats, cows) was a main driver of the loss of natural vegetation cover and erosion (soil degradation) (Fig. 7.5), which likely led to a positive feedback loop between loss of vegetation cover and soil loss and infertility. In summary, the CCA results show how having experienced similar histories of human impacts and species introductions, a trend of biotic homogenisation is taking place in Cabo Verdean islands. This implies that individual islands may be undergoing decreases in the singularity of their biodiversity, therefore loosing landscape authenticity.

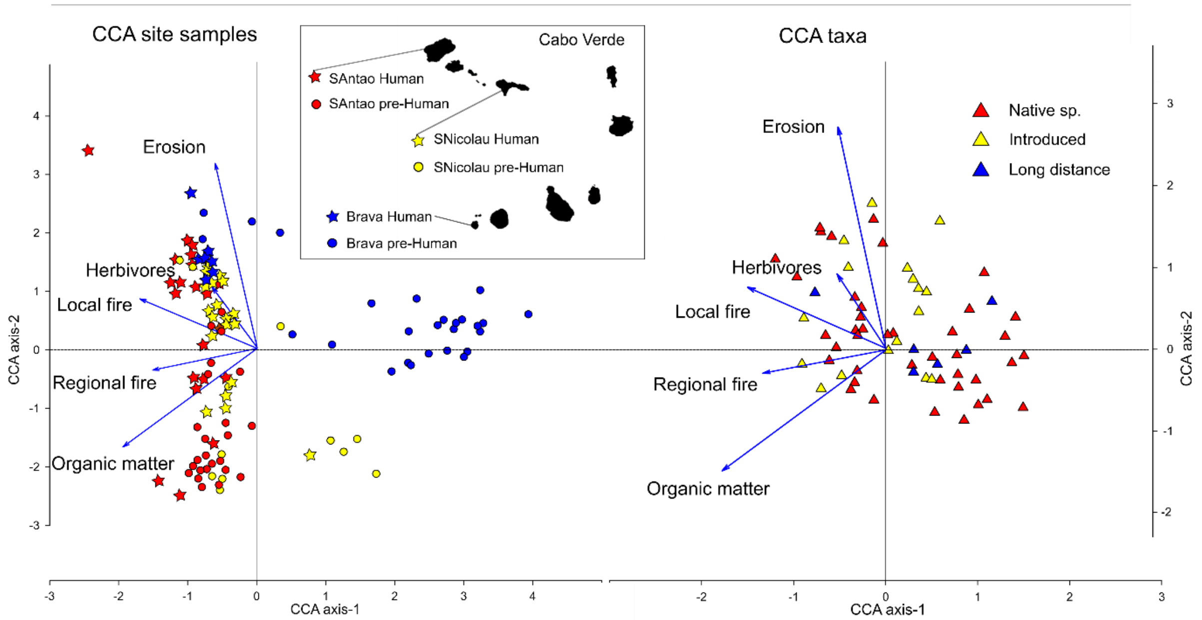


Figure 7.6: Plots showing Canonical Correspondence Analysis results of pollen percentages of three studied sites in Cabo Verde: Cova de Paúl (SA), Calderinha (SN) and Cova Galinha (Brava). Eigenvlaues: CCA axis-1, 0.28, CCA axis-2, 0.12. Proportion of variance explained: CCA axis-1, 51%, CCA axis-2, 22%. Most influential environmental variables per axes were local fire (axis-1 correlation score: -0.67), regional fire (axis-1

correlation score: -0.60), organic matter (axis-1 correlation score: -0.78), Erosion (axis-2 correlation score 0.88).

7.3.2.3 The socio-ecological consequences of landscape degradation

The pronounced biophysical impacts of the first centuries of human settlement of Cabo Verde could partially explain the lack of development of sustainable socio-ecological systems during the 17th, 18th, 19th and first half of 20th centuries. Disturbances that became chronic in this archipelago, such as soil degradation and loss of vegetation cover likely rendered island socio-ecological systems more vulnerable to extreme natural phenomena such as drought, and this impacted food security by affecting agricultural productivity. Extreme natural phenomena took the form of droughts, Saharan dust storms (that decimated crops), tropical storms and volcanic eruptions, and they played a prominent role in crop failure and the occurrence of famines and epidemics that unleashed between 1700 and 1945 CE (Figure 3.2; Patterson, 1988). For instance, phases of land-use change identified in the Cova de Paúl record (SA) between ca. 200–100 cal yr BP, consisted of the abandonment of grazing activities (absence of coprophilous fungal spores) and the spread of invasive species of the Verbenaceae family (e.g. *Lantana camara*). This phase is potentially linked to land-abandonment in periods of socio-economic and demographic stress such as droughts.

The main documented change in land management in Cabo Verde took place after the last great famine in 1945 CE, through government policies that aimed to put in place policies to enhance food security (Baptista et al., 2015). Stabilization and protection of soils and creating a sustainable agricultural system have become major priorities, especially after the independence of Cabo Verde in 1975 CE (MAA-DGA, 2008). A variety of methods to protect soils and avoid desertification have been put in place in the last seven decades, most notably terracing, reforestation with drought-resistant species and water retention systems (Baptista et al., 2015). More research into the historical land management strategies in different islands of Cabo Verde is needed to understand the complexity and nuances of socio-ecological interactions in different islands and settings. The development of Cabo Verdean cultures should also be taken into consideration when discussion socio-ecological systems in Cabo Verde. For instance, the preference for *Zea mays* as a staple food in Cabo Verde is thought to have played a role in episodes of crop failure and in generating soil erosion, as its cultivation was not performed with adequate soil protecting measures (Baptista et al., 2015).

7.3.3 What insights can palaeoecological research offer to guide biological conservation and ecological management in Cabo Verde?

Palaeoecological reconstructions are essential to set evidence-based conservation and restoration goals by defining ecological baselines, that is, the long-term composition and natural variability of ecosystems (Froyd & Willis, 2008; Nogué et al., 2017). Centennial or millennial views of island ecological change offer new narratives about the magnitude of human impacts on islands. To restore Cabo Verdean ecosystems, it is necessary to reflect on the insights offered by different lines of evidence, and to adopt an adequate ecological baseline. Due to the occurrence of a no-analogue climate during the AHP, 4,000 cal yr BP (end of the AHP) is the most logical starting point of the ecological baseline to be taken as a guideline for ecological restoration in Cabo Verde. As 500 cal yr BP is the approximate date of Portuguese settlement in the archipelago, this date could be taken as its end-point.

Fossil pollen data, notwithstanding its spatial biases and taxonomical limitations, can be used as a central source of information to guide ecological restoration. The majority of pollen records were dominated by a variety of herbaceous and shrubby taxa belonging to the families Asteraceae, Poaceae, Cyperaceae, Amaranthaceae, Urticaceae, Lamiaceae, Apiaceae and Brassicaceae. The restoration and conservation of herbaceous and shrubby taxa could be guided by giving priority to species belonging to the dominant families represented in pre-human pollen assemblages, yet it should be noted that the biases of pollen analysis are preventing the detection of ‘silent taxa’, this is, taxa that do not produce enough pollen grains to be detected in the records.

Woody taxa recorded in the three records are candidates for reforestation efforts in Cabo Verde, and include *Ficus sur* and *Ficus Sycomorus* subsp. (SA, SN, BR), *Euphorbia tuckeyana* (SN, BR), *Dracaena draco* subsp. *Caboverdeana* (SA, SN, BR), *Faidherbia albida* (SA, SN, BR), *Tamarix senegalensis* (SN), *Dodonaea viscosa* (SA, BR), *Dichrostachys cinerea* subsp. *Platycarpa* (SA, identified under Fabaceae), and *Phoenix atlantica* (phytoliths: SA, BR). These taxa belong to diverse plant communities typical of different altitudinal belts in the islands as defined by Neto et al., (2020), such as ‘*Ficus* and *Sideroxylon* Woodlands’ (highlands), ‘*Faidherbia* savannahs’ (mid-elevantion), and ‘other arborescent communities’, formed by *Dracaena caboverdeana* (mid-elevations)*, Phoenix atlantica, Tamarix senegalensis* (lower elevations) and ‘shrub vegetation’ (highlands and mid-elevations). Vegetation restoration actions will likely be beneficial for soil protection, by enhancing organic matter, soil fertility and preventing soil loss. While different combinations of pollen from these taxa were identified in our sites, it is difficult to ascertain what their abundance in the landscape in the past, partly due to different pollen production and dispersibility. For instance, pollen data from the Calderinha record (SN) suggests that *Ficus* species, *Dracaena draco* and *Euphorbia tuckeyana* were all part of highland vegetation mosaics, while in Cova de Paúl (SA) *Ficus*, *Sideroxylon* and *Faidherbia* were present in the caldera. Future research using landscape reconstruction modelling based on pollen data can help explore the configuration of pre-human vegetation mosaics in Cabo Verde.

Palaeoecological evidence suggests that introduced herbivores had a prominent role as drivers of landscape degradation after human settlement. The control of free herding and the eradication of feral introduced mammals will most likely protect native species (avoiding direct consumption and the dispersal of seeds of invasive species), and reduce soil erosion. For instance, research in the Auckland islands archipelago suggests that native species that had been heavily impacted recovered very rapidly after the removal of introduced herbivores from the islands (Wood et al., 2016). With increased control over herbivore populations, the capacity of recovery of native vegetation of Cabo Verde could be tested in the near-future, adding new insights to the resilience of these ecosystems.

Introduced species are a growing proportion of vegetation cover in Cabo Verde, and some of these taxa may now be an integral part of the cultural landscapes of the archipelago, while others hold no cultural value. The identification of introduced taxa in the pollen records can be useful to document processes of species expansion linked to different environmental drivers. Taxa such as *Opuntia*, *Furcraea foetida*, *Asystasia*, *Commelina benghalensis*, and *Lantana camara* were identified in association with land-use activities in our records. Managers and conservation institutions of Cabo Verde are already alert and attempting to control the spread of the most invasive ones, such *as Furcraea foetida* and *Lantana camara* (MAA-DGA, 2008). In addition, charcoal data suggest that the frequency and intensity of fires at a local and regional scale increased after human settlement, a process potentially linked to the extra fuel added by introduced plant species (MAA-DGA, 2008). Monitoring the spread of these and other taxa considered invasive, or with potential to become so, is central to the conservation of threatened species in Cabo Verde. While total restoration of pre-human ecosystems in Cabo Verde may be unrealistic, managers could aim to achieve more biodiverse ecosystems in which native and certain desired introduced species coexist, taking into account the value of the landscape for the culture and livelihoods of the human population.

Finally, disseminating the knowledge created by palaeoecological and other scientific evidence is vital to inform the public, managers and institutions about the legacy of centuries of human impacts (Nogué et al., 2017). This can help strengthen a ‘sense of place’ that links past and present in areas of special relevance for conservation (Burney & Burney, 2007). Future work is needed to convey scientific findings in a way that can be incorporated in outreach participatory activities and education programs to convey the message that biological heritage as an asset worth fighting for in Cabo Verde and beyond.

7.4 Conclusions

Understanding how island ecosystems have changed in response to natural and human-driven disturbances in the past is critical to conserve their unique biodiversity and plan for the sustainable management of future landscapes. The objective of this thesis was to investigate how human settlement impacted the ecosystems of the Cabo Verde archipelago. By using multiple palaeoecological methods, we provide a first overview of Holocene landscape change in the highlands of three island of Cabo Verde. It is a significant step to gain a deeper understanding of the natural variability of island ecosystems and the degree of their transformation since human settlement. The key findings are summarised bellow:

1- Palaeoecological research in Cabo Verde volcanic calderas is useful for the assessment of changes in highland vegetation, fungal communities, the occurrence of fires and erosion regimes.

The analysis of micro-fossils, combined with charcoal, sedimentological and geochemical analyses shows that natural sediment archives in the island of Cabo Verde can be used to investigate environmental change and socio-ecological interactions from a long-term perspective. The investigation of caldera soil sequences within other islands (e.g. Santiago, Fogo) and the application of innovative techniques (e.g. OSL dating, *seda*-DNA, hydrogen isotopic methods) has the potential to further improve palaeoecological reconstructions in this archipelago.

2- There is no clear evidence of ancient presence of laurel or Mediterranean woodlands in Cabo Verde during the Holocene.

Due to the presence of long-distance transported pollen in the studied assemblages, it is not possible to categorically rule out or confirm the presence of some Macaronesian or Mediterranean taxa in the past (*e.g. Pinus, Juniperus, Clethra*). However, the prevalence of open landscapes or native scrublands in the three studied records suggests that no significant laurel or Mediterranean forest formations existed in these islands through the time periods investigated.

3- Pre-human landscapes underwent phases of increased erosion and fire potentially linked to episodes of intensified monsoonal activity (e.g. during the AHP) and increasing aridity or changing seasonality after the African Humid Period.

Highland ecosystems in Cabo Verde exhibited a variety of responses to naturally occurring disturbances, such as wildfires and erosion pulses. However, they showed a higher degree of resilience to natural disturbances compared with post-settlement compounded natural and anthropogenic disturbances.

4- Phases characterised by the abundance of coprophilous fungal spores documented during the early, middle and late Holocene in different islands suggests the presence of significant pre-human native faunal communities in the archipelago.

Ascertaining the composition of these pre-human faunal communities could be done by studying the relationship between coprophilous fungal spores and the native fauna of Cabo Verde, as well as by applying alternative methods (e.g. sedaDNA) and by studying further macro-fossil evidence in the archipelago.

5- Phases of volcanic ash deposition were likely a driver of ecological change in the southern islands of Cabo Verde.

The identification of vegetation changes after tephra deposition in Brava suggests that volcanism could have triggered ecological changes in the southern islands of Cabo Verde. Comparing the direct and indirect effects of volcanic eruptions in Brava, Fogo and Santiago through time will yield new information on the socio-ecological dimension of current volcanic hazards.

6- Human transformation of the environment in Cabo Verde led to multiple disturbances including erosion of soils, increase in fires, and loss of native vegetation and introduction of exogenous species.

Documented anthropization processes involved the establishment of agricultural lands and the associated introduction of livestock, which caused soil erosion and vegetation change. With unprotected soils, the occurrence of extreme climatic phenomena such as droughts, *Harmattan* winds and tropical storms likely contributed to erosion, which became a chronic disturbance in Cabo Verde. Future investigations of the interaction of anthropogenic disturbances and extreme natural phenomena since human settlement are key to develop management strategies in the face of future crises.

7- Palaeoecological results can guide conservation/restoration goals, providing a long-term view on landscape degradation.

The sequences of ecological change can be used to provide historically contextualised management goals and should be used as auxiliary resources to guide conservation efforts already in place. The islands of Cabo Verde can serve as model systems for the study of human impacts on tropical dry islands, which is useful to call attention to the pressing socio-ecological challenges that the future will bring to southern Macaronesia and beyond.

Supplementary Figures

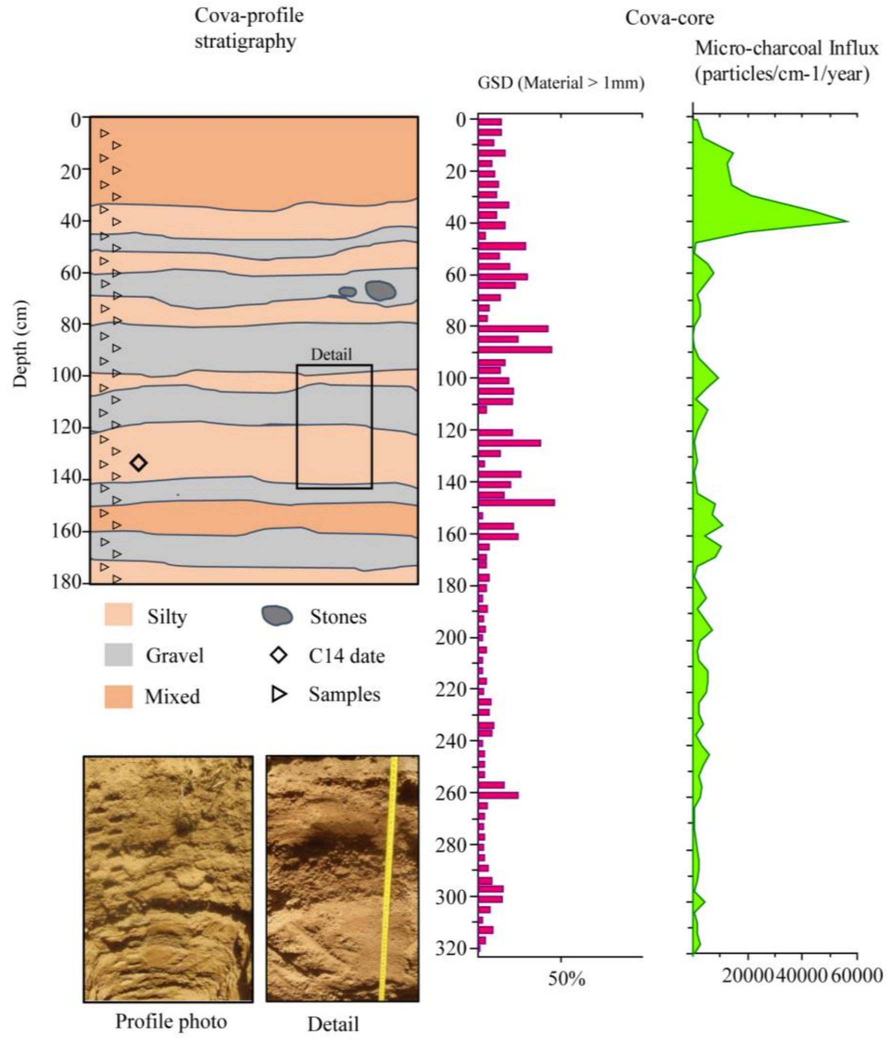
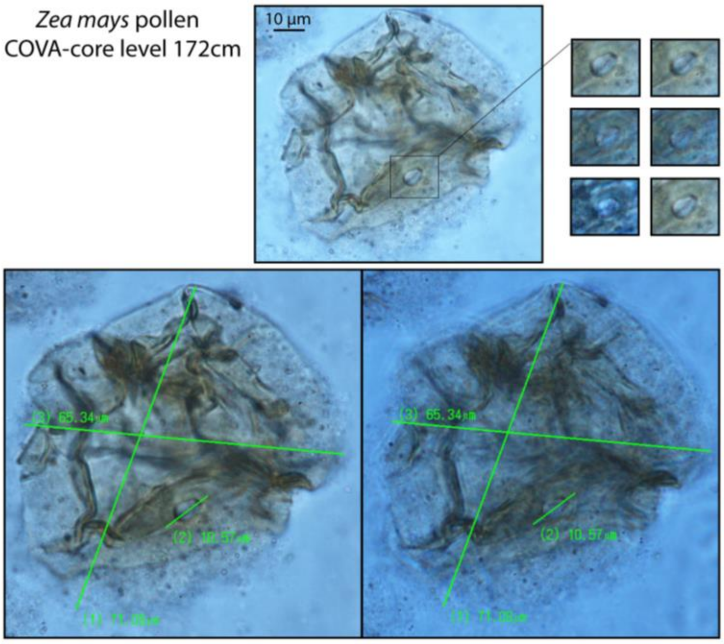
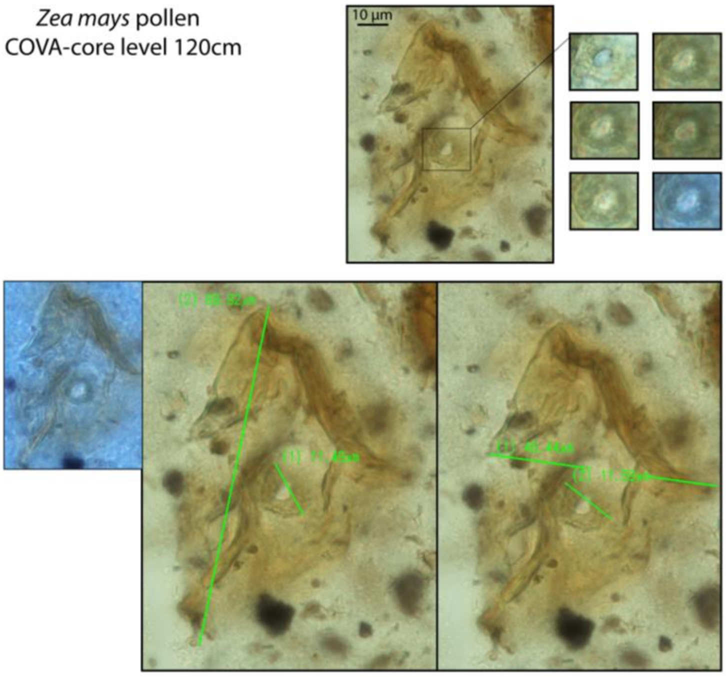


Figure S1: Stratigraphic diagrams of the soil profile (Cova-profile) and the core (Cova-core) of Cova de Paúl, Santo Antão. Right panels show the stratigraphy of the soil profile, including sediment descriptions, the sampling strategy (one sample every 5cm), and the sample taken for radiocarbon dating. Right panels show the Grain size distribution of Cova-core (bars) and micro-charcoal influx (curve).



Zea mays pollen
COVA-core level 172cm



Zea mays pollen
COVA-core level 120cm

Figure S2: 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).

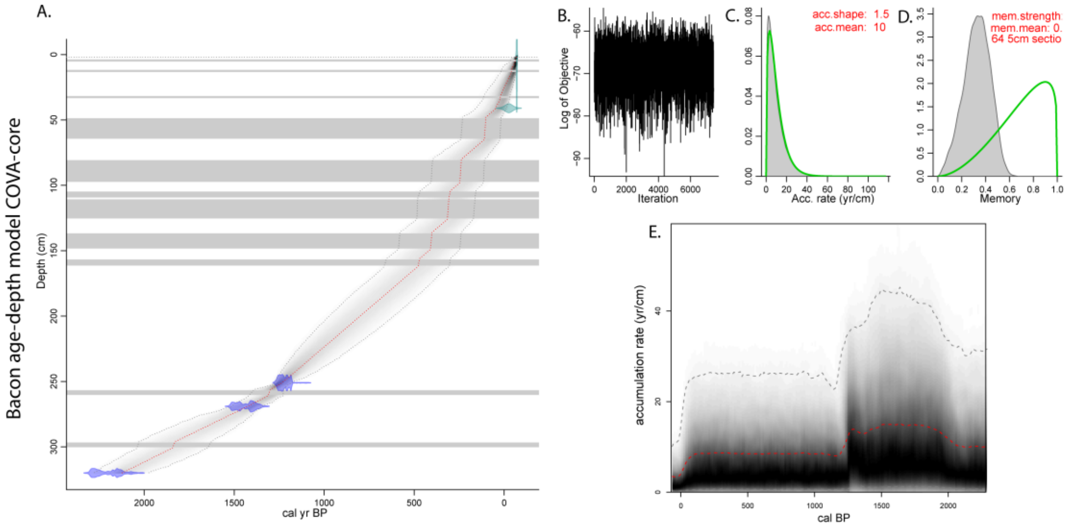


Figure S3: A: Bacon age–depth model for COVA-core, Cova de Paúl, Santo Antão. Grey area shows 95% confidence intervals based on calibrated C14 dates. Horizontal grey bands indicate sections of fast sediment deposition (‘slumps’) based on sedimentology data (>30% material > 1 mm). B: Markov Chain Monte 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.

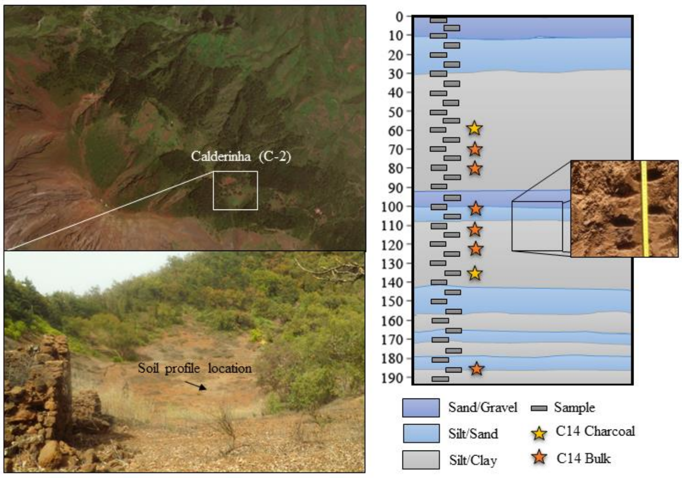


Figure S4: Calderinha site, São Nicolau Island with soil profile description and sampling method.

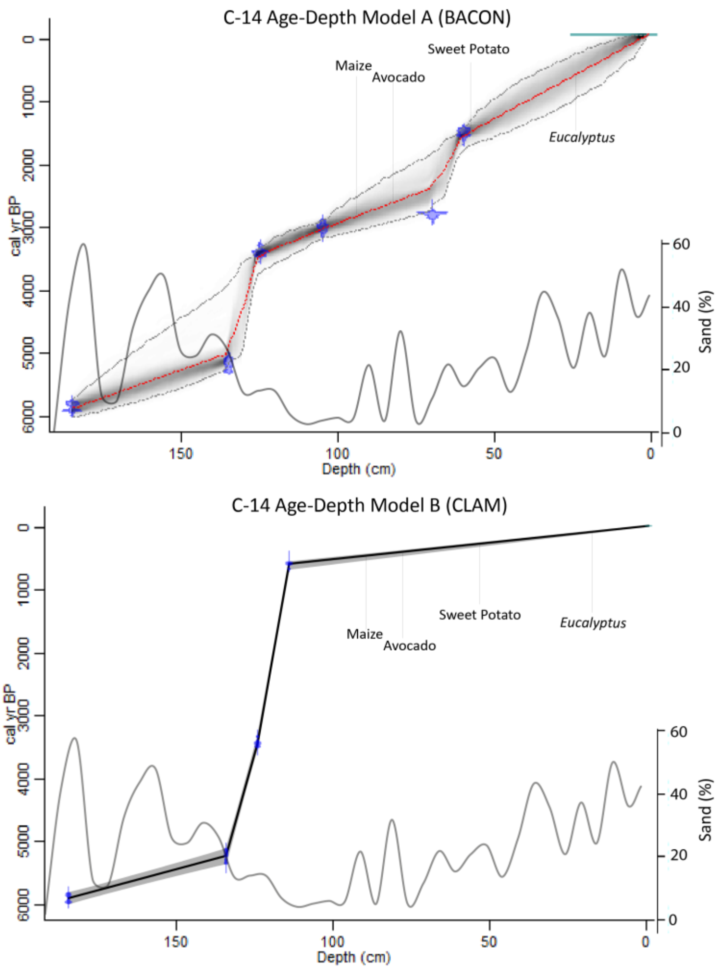


Figure S5: Alternative C-14 Age–depth models of the Calderinha record, São Nicolau Island, and their validation against granulometric data (sand content percentage, curve) and first occurrence of pollen from introduced species (silhouettes).

Radionuclide plots of ^{210}Pb and ^{137}Cs analyses, Calderinha record

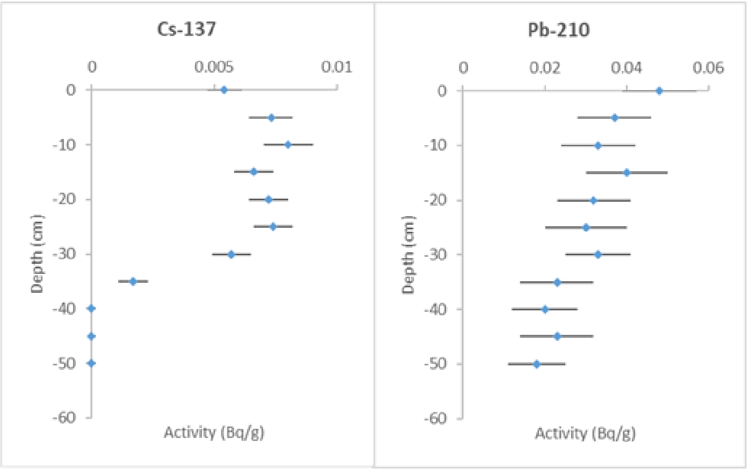


Figure S6: Radionuclide activity plots for Pb-210 and Cs-137 for the first 50cm of Calderinha record, São Nicolau Island.

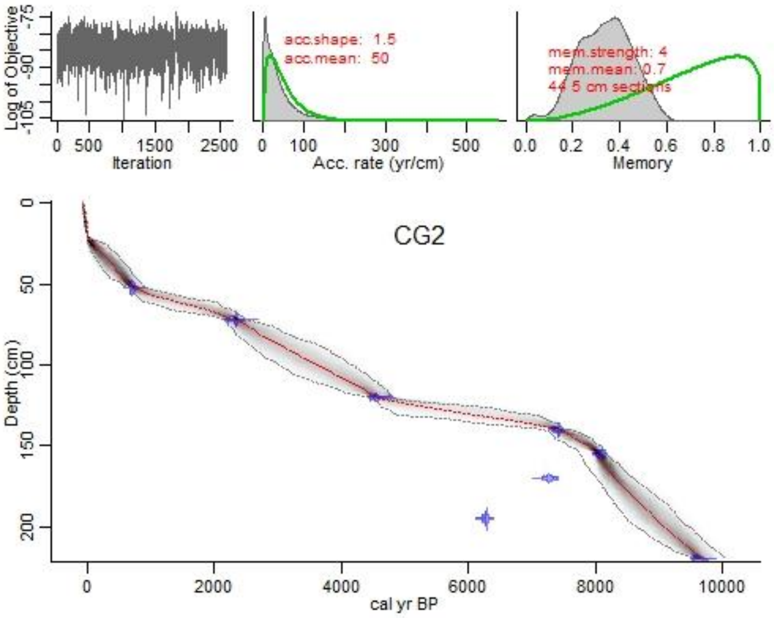


Figure S7: Age–depth model of Cova Galinha record, Brava Island, Cabo Verde, produced with Bacon. Label 'CG2' refers to the model version, and upper left panel shows Markov Chain Monte Carlo iterations of the model run. Upper central and right panel show accumulation rates and memory of rate distributions, respectively. Main panel shows calibrated ^{14}C dates in blue, and the grey shaded area represents a 95% confidence intervals based on calibrated ^{14}C dates age-depth model.

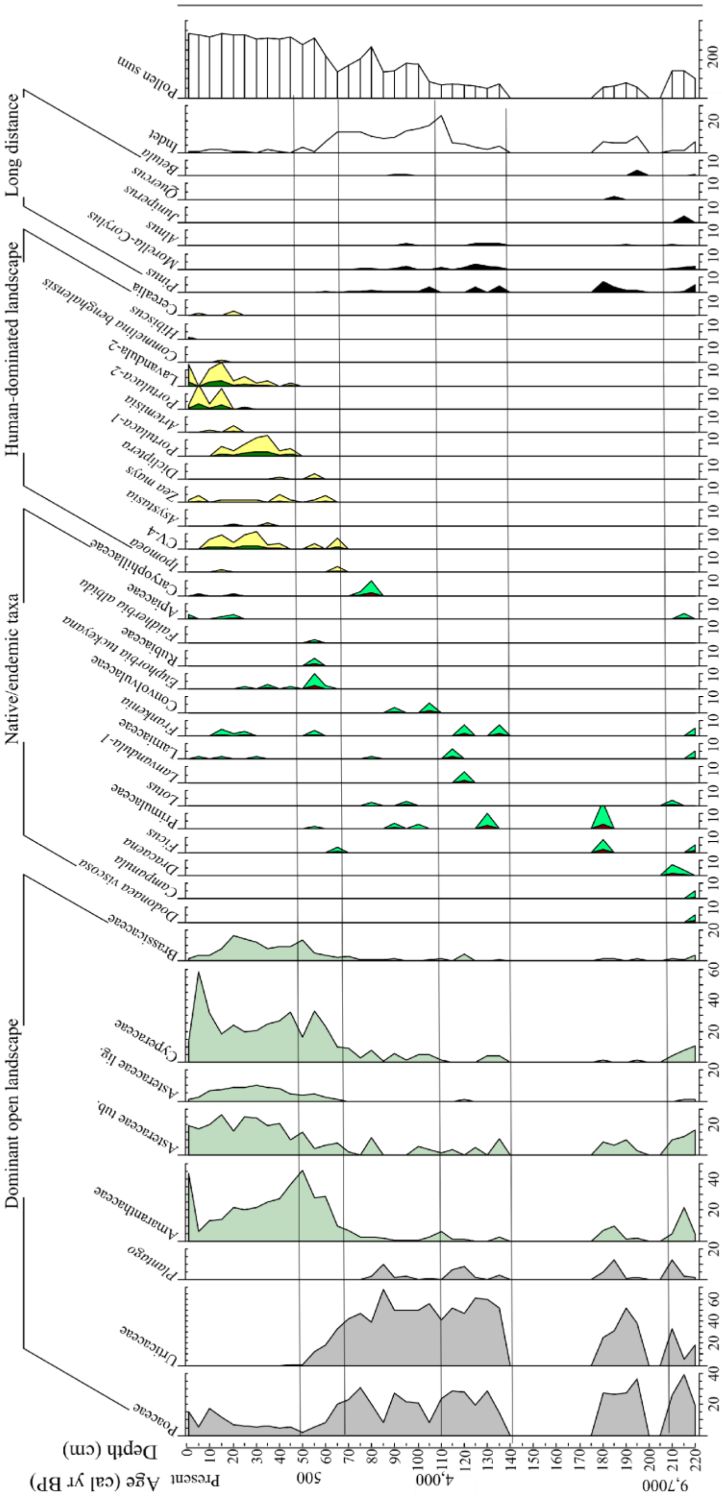


Figure S8: Pollen diagram (percentages) of the Cova Galinha record, Brava Island, Cabo Verde, produced with Tilia. Coloured exaggeration curves x5.

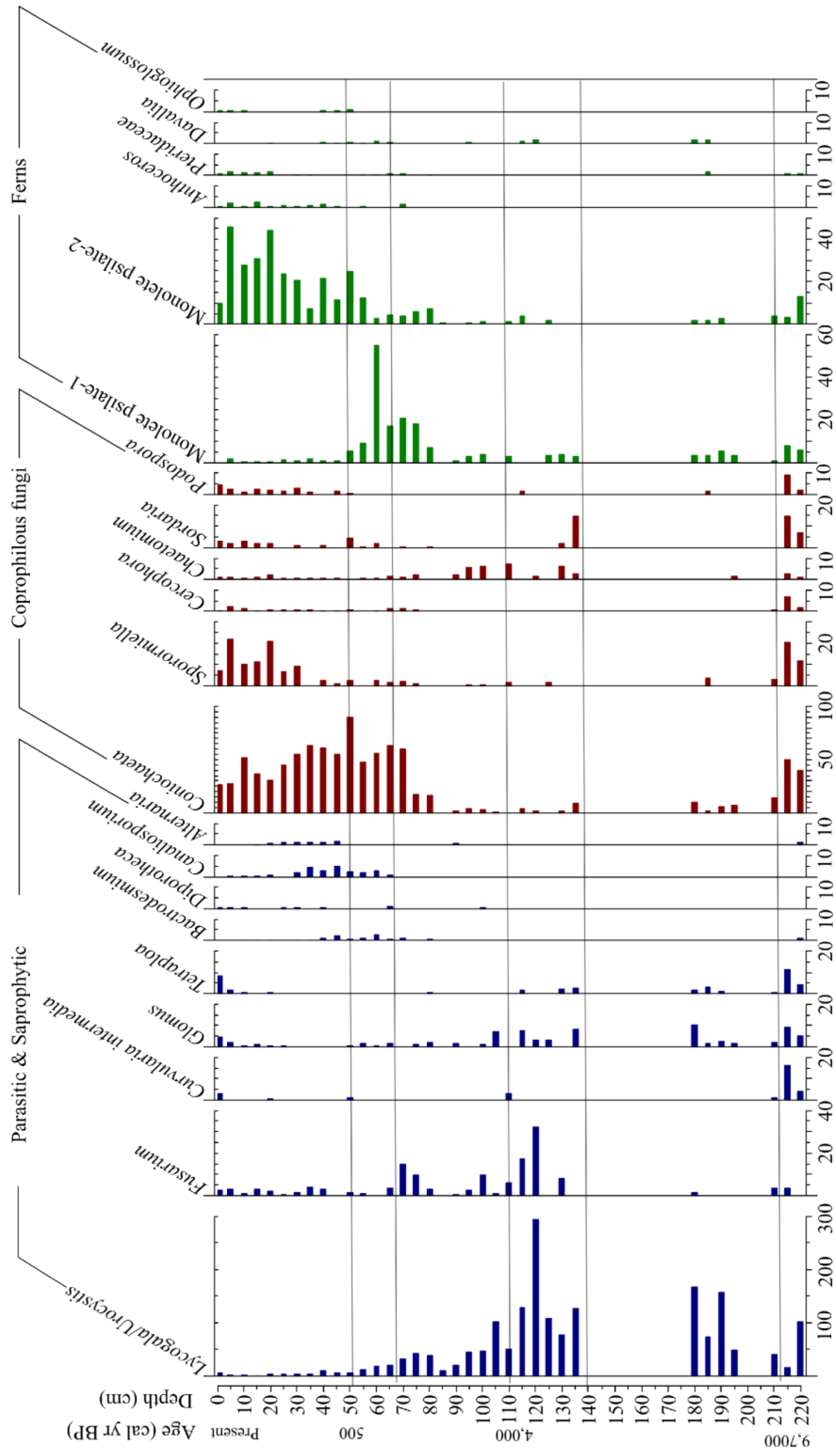


Figure S9: Non-pollen palynomorphs diagram (percentage over the pollen sum) of the Cova Galinha record, Brava Island, Cabo Verde, produced with Tilia.

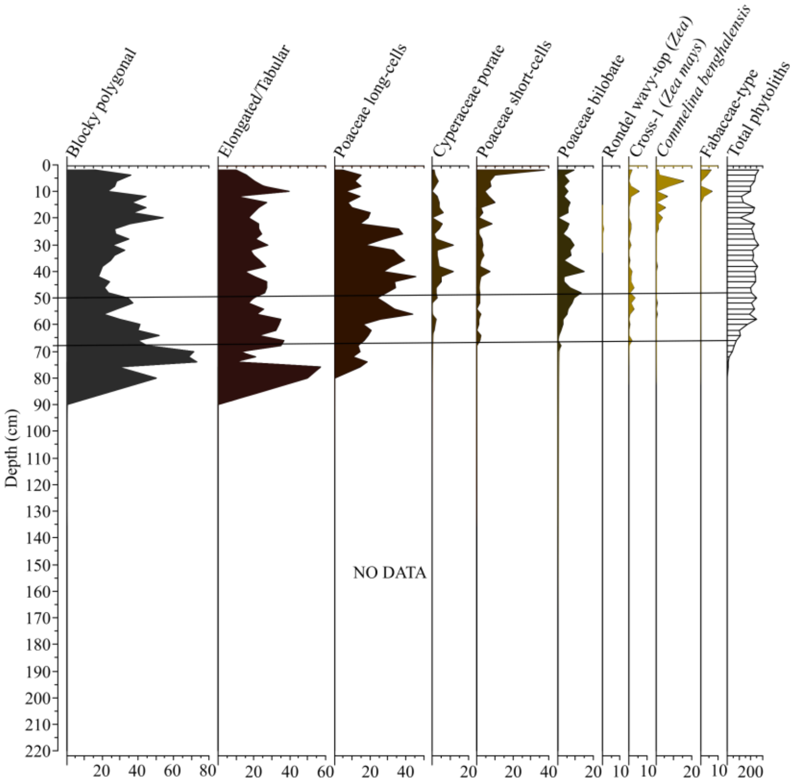


Figure S10: Phytolith percentage diagram of the Cova Galinha record, Brava Island, produced with Tilia.

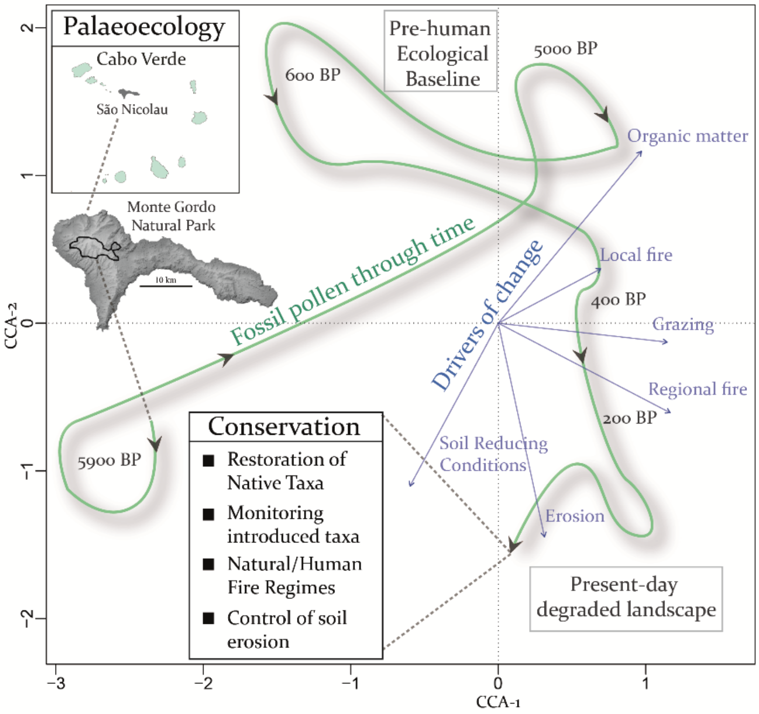


Figure S11: Graphical abstract Castilla-Beltrán et al., 2020.

Supplementary Tables

Table S1: List of taxa of our Cabo Verde reference collection and those used from the Canary Islands reference collection

Species or Genus	Family	Archipelago
Campylanthus glober	Plantaginaceae	Cabo Verde
Polycarpaea gayi	Caryophyllaceae	Cabo Verde
Phagnalon melanoleucum	Asteraceae	Cabo Verde
Echium hypertropicum	Boraginaceae	Cabo Verde
Asteriscus	Asteraceae	Cabo Verde
Euphorbia tuckeyana	Euphorbiaceae	Cabo Verde
Conyza feae	Asteraceae	Cabo Verde
Campanula jacobaea	Campanulaceae	Cabo Verde
Frankenia ericifolia	Frankeniaceae	Cabo Verde
Limonium braunii	Plumbaginaceae	Cabo Verde
Campylanthus glober	Plantaginaceae	Cabo Verde
Artemisia gorgonum	Asteraceae	Cabo Verde
Tornabenea	Apiaceae	Cabo Verde
Lavandula rotundifolia	Lamiaceae	Cabo Verde
Globularia amygdalifolia	Plantaginaceae	Cabo Verde
Diplotaxis	Brassicaceae	Cabo Verde
Asteriscus	Asteraceae	Cabo Verde
Erysimum	Brassicaceae	Cabo Verde
Coniza pannosa	Asteraceae	Cabo Verde
Lavandula	Lamiaceae	Cabo Verde
Sonchus	Asteraceae	Cabo Verde
Aeonium	Crassulaceae	Cabo Verde
Launaea picridioides	Asteraceae	Cabo Verde
Dracaena draco	Asparagaceae	Canary Islands
Sideroxylon	Sapotaceae	Canary Islands
Davallia canariensis	Polypodiaceae	Canary Islands

Table S2: Pollen and NPP sums per sample of the Calderinha record, São Nicolau Island.

Sample (cm)	Total NPPs counted	Total Pollen counted
1	384	256
5	480	325
10	610	306
15	442	317
20	460	311
25	274	331
30	322	307
35	302	316
40	413	354
45	503	321
50	940	314
55	1120	165
60	1307	171
65	1154	188
70	1089	161
75	1515	157

80	2549	150
85	1091	134
90	1017	137
95	1078	96
100	1394	108
105	1189	109
110	1764	99
115	962	160
120	853	105
125	782	114
130	369	75
135	326	85
175	273	82
180	197	55
185	213	30
190	272	48

Table S3: Record zonation derived from CONISS analysis of pollen data, and zone specific information of the Calderinha record, São Nicolau Island.

Zone code	Section	Age interval (cal yr BP)	Pollen Samples (N)
Cld-4	95-1cm	410–present day	20
Cld-3	135-95cm	4900–410	8
Cld-2	174-136cm	5700–5000	1
Cld-1	190-175cm	5900–5700	4

Table S4: Recorded volcanic eruptions in Cabo Verde (Fogo Island) and their characteristics (after Ribeiro, 1960).

Date	Source of eruption	Duration	Tephra output	Other remarks
1500 CE	Central cone and two side-vents	Very prolonged	Ashfall	
1564 CE	Central cone	Prolonged		
1596 CE	Central cone	Prolonged		
1604 CE	Central cone and side-vent	Prolonged	Ashfall	
1664 CE	Central cone and two side-vents			
1675 CE				
1680 CE			Smoke	Earthquake, land sterility, migration of many families to Brava
1689 CE	Central cone		Smoke, ashfall	
1693 CE				
1695 CE	Central cone	Prolonged		
1697 CE			Smoke, ashfall	
1699 CE	Central cone			
1712-13 CE	Central cone		Smoke clouds	

1721-25 CE			Smoke, ash-fall	
1761 CE				
1774 CE	Central cone lower vents			Famine in Fogo
1785 CE	Central cone, northern side-vents	32 days		
1799 CE	Central cone, northern side-vents	26 days	Ashfall	
1816 CE	Vent north of Chã das Caldeiras			
1847 CE	Central cone SW vents	< 1 month	Ashfall	
1852 CE	Central cone SW vents			
1857 CE	Central cone SW vents			
1951 CE	Central cone SW vents	> 2 months	Ashfall	
1995 CE	Central cone SW vents			
2014-15 CE	Central cone SW vents	> 2 months	Ashfall	

Table S5: Pollen zones of the Cova Galinha record, Cabo Verde, conducted using stratigraphically constrained CONISS analysis with Tilia software (Grimm, 1993).

Record zone	**Age (cal yr BP)**	**Sample depths (cm)**
Zone CG-1	9,700–9,500	220–215
Zone CG-2	9,500–6,800	210–140
Zone CG-3	6,800–4,100	135–115
Zone CG-4	4,100–1,800	110–70
Zone CG-5	1,800–650	65–55
Zone CG-6	650– present-day	50–1

Appendix A An exploratory analysis of pollen assemblages in surface soils on the highland slopes of Santo Antão island, Cabo Verde

In this appendix the results of the analysis of soil surface samples collected on the 2018 fieldwork expedition to Santo Antão Island are briefly described. The objective of this exercise was to explore the variability of pollen assemblages in the study area. I obtained a set of surface soil samples throughout an altitudinal gradient of Rivera de Paúl basin, from Pico de la Cruz (1450m amsl) to the Rivera de Paúl village (700m amsl) (Figure S12). I gathered soil samples along a trekking path, at two or more meters distance from the trail when the slope permitted it. Samples were taken every 100m (50m in the highest point of the island), and gathered ca. 5 cm^3 of sediment from more than four points in a square meter, plus a moss pollster if moss was present. I recorded the coordinates of each location and elaborated a brief description of the surrounding landscape (Table S6, Figure S13).

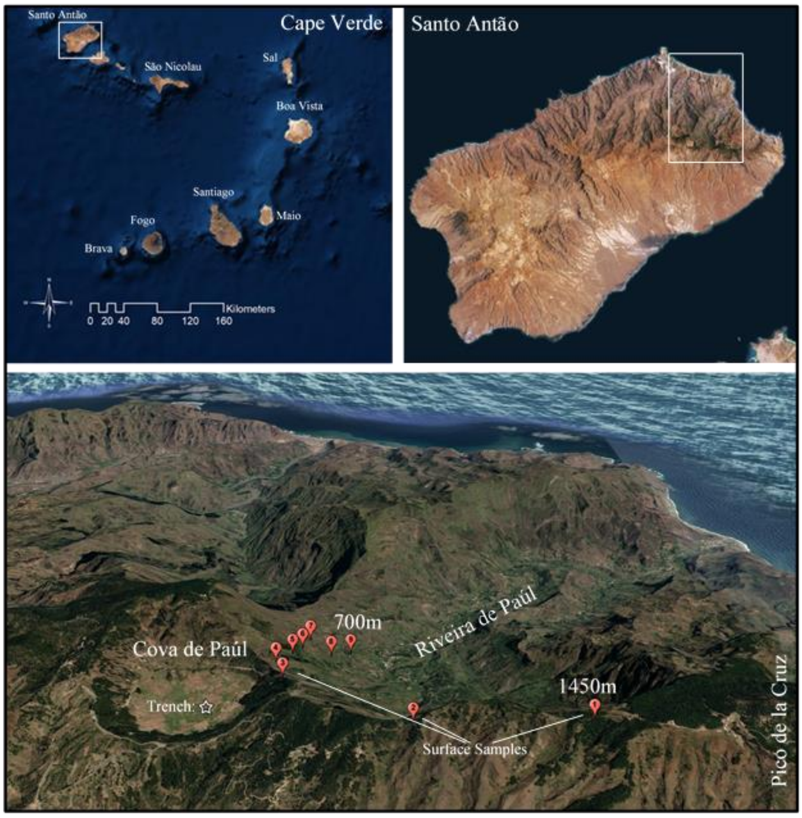


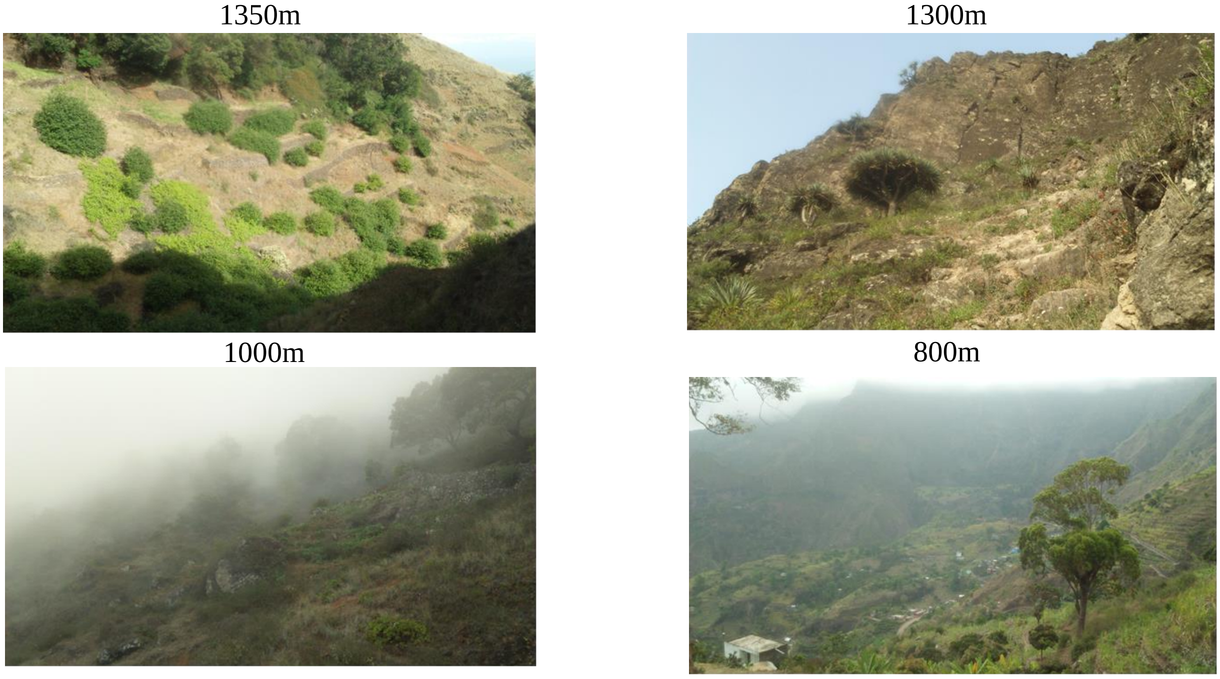
Figure S12: Maps showing the Cabo Verde archipelago, the island of Santo Antão and the Cova de Paúl dataset including the elevation transect and the Cova the Paúl palaeoenvironmental site (trench).

Soil samples were collected on an altitudinal transept between 1450 and 700m asl from Pico de la Cruz to Rivera de Paúl. During the months of September and November of 2018 I processed and analysed nine surface samples of for pollen analysis in the Palaeoecological Laboratory of the University of Southampton. Here I report the results of the laboratory analyses carried out in the Southampton Palaeoecological Laboratory, showing the recorded stratigraphy of Cova de Paúl and the modern pollen data. These findings can aid interpret sedimentary fossil pollen assemblages from the highlands of Santo Antão.

For pollen extraction, I followed standard protocol involving acid treatment to deflocculate the sediments and remove carbonates and silicates (Erdtman, 2013). I added tables of a *Lycopodium* marker to allow for the calculation of pollen concentration. Finally, I mounted the samples in microscope slides using glycerine oil, and counted pollen grains under the microscope at 400x magnification. I counted a minimum of 300 pollen grains per sample in all levels except sample 8 (800 meters), in which I counted 170 pollen grains due to low pollen concentration.

Table S6: Landscape descriptions at different altitudes.

Altitude	**Description of local landscape**
1450–1350 m	Dry vegetation (southern slope of the Pico de la Cruz mountain): mostly introduced and planted sp. (*cupressus sp., pinus sp.*), rocky wall plants, savannah-type vegetation
1300–1200m	Northern slope of Cova de Paúl: Ferns, presence of *Dracaena draco*, rock vegetation including *Aeonium sp*.
1100–1000 m	Abundant Poaceae (including bamboo) patches, some cultivation: specially fruit trees
1000–900 m	Cultivation in terraces, abundance of invasive species (*e.g*. *Lantana camara*), introduced tree species (*Eucaliptus,* Proteaceae).
900–800 m	First natural springs and canalizations (abundance of introduced Cyperaceae species in these areas), cultivation of sugar cane and banana
800–700 m	Economic landscape with heavy cultivation of fruit trees, sugar cane, and abundance of introduced Cyperaceae in water springs.


1350m

1300m

1000m

800m

Figure S13: Photographs of landscape change at diverse altitudes in Pico de la Cruz and Rivera de Paúl, taken by Alvaro Castilla-Beltrán, 2018.

Pollen analysis of nine surface samples at altitudes ranging from 1450m and 700m amsl revealed a strong variability in pollen assemblages (Figure S14). The majority of the recorded taxa are locally present in the island, except in two cases: *Alnus* (sample 2: 1350m) and *Morella* (sample 5: 1100 m). Based on CONISS analysis of the pollen percentages using Tilia, I distinguished three main zones in the altitudinal gradient: zone 1 (1450–1250m), zone 2 (1250–900m) and zone 3 (900–700m):

Zone-1 is characterized by the dominance of *Acacia* pollen (ranging between 10 and 50%), and the presence *of Pinus canariensis* and *Cupressus* sp., which are introduced trees in the highlands. The most abundant herbaceous pollen was Brassicaceae (up to 20%), followed by Poaceae and Cyperaceae. Presence of wall taxa such as echium and Campanulaceae, and the presence of long-distance transported *Alnus*.

Zone-2 showed the highest levels of Pocaceae pollen, as well as peaks of Apiaceae, Scrophulariaceae-type and Amaranthaceae, produced by vegetation in the Barranco, usually covered in the cloud belt. *Lotus* sp. and *Euphorbia tuckeyana* pollen reflect the presence of endemic species in the mountain steep walls. Long-distance transported *Morella* was present, and of taxa associated with economic landscapes such as *Ficus* sp. and *Psidium guayaba*.

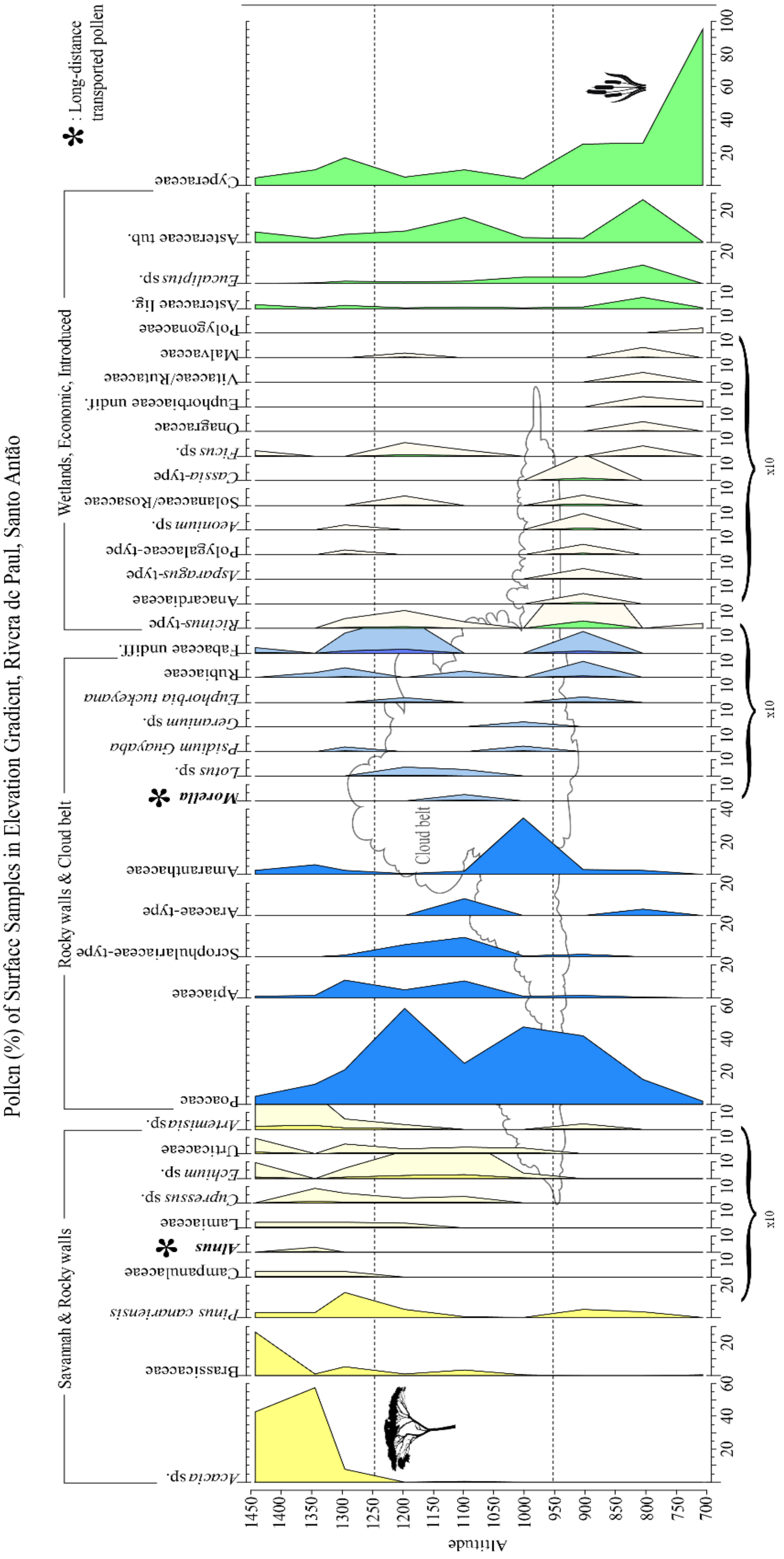


Figure S14: Pollen diagram showing the percentage of taxa per altitude. Different colours are used to group pollen types that occur at similar altitudes. Cloud silhouette indicates the positioning of the cloud belt on the time of sampling.

Zone-3 is dominated by sedges (Cyperaceae, around 30%, increasing up to 90% close to wetland areas in water springs) and Asteraceae pollen. Increase in percentages of *Eucalyptus* sp. and a variety of species from the Euphorbiaceae, Fabaceae and Solanaceae families reflect a wet human/dominated landscape. It must be noted that Cyperaceae pollen in these areas was likely produced by introduced *Cyperus* species.

Comparing the most abundant pollen types in surface samples with the dominant vegetation per altitudinal zone is a first step to assess which taxa are preferentially represented in local palynological assemblages (see de Nascimento et al., 2015 for a study of pollen traps in the Canary Islands). In zone 1 (1450–1250m) arboreal taxa such as *Acacia* and *Pinus* pollen reach the highest percentage values. Most of these samples were taken in the summit and south-facing dryer façade of the mountain, where Savannah vegetation and planted forest formations are abundant. This is reflected in the palynological record. Zone 2 (1250–950m) comprised the north-facing slopes of the mountain, which were covered by a cloud belt. In this altitudinal zone herbaceous pollen dominates, especially from the Poaceae and Amaranthaceae families. It is worth noting that introduced plants such as *Lantanta camara* (present along the path) were not abundantly represented in the pollen record, meaning that wind-pollinated herbaceous species are preferentially represented in this area. Also, endemic species such as *Euphobia tuckeyana* and *Dracaena draco* were not present in the pollen record, suggesting that they were not abundant enough in this area to be evident in the palynological assemblage. Finally, in the lower altitudinal zone studied (950–700m), taxa characteristic from wetland environments (Cyperaceae) and of open landscapes (Asteraceae) were preferentially represented, with a higher presence of economic species such as Solanaceae and *Eucalyptus.* This pollen assemblage represents a human-driven economic landscape, yet abundant economic species such as Banana (*Musa*) and other fruit trees (*Prunus*) were not represented in the palynological assemblage.

This analysis of pollen assemblages from soil samples in an altitudinal gradient has provided a first spatial view of how diverse taxa are represented in the pollen record depending on elevation and local plant communities. The presence of long-distance pollen types such as *Alnus* and *Morella* reinforce our hypothesis that part of the pollen assemblage of highlands in Cabo Verde originates from the Mediterranean, the Canary Islands, or Mainland Africa (see Hooghiemstra et al., 2006). In lack of more precise quantitative analyses including standardised botanical surveys, this pilot study represents a first attempt to explore how modern pollen signals can help interpret fossil pollen assemblages in this archipelago, an effort that will continue in the future.

Appendix B Full *n*-alkane methodology

To avoid contamination of organic compounds, all laboratory material was heated at 450 °C for 10 hours. We followed a modified protocol of Bhattacharya et al. (2017) for lipid extraction: we placed ca. 2 g of freeze-dried sediment on an ultrasonic bath (3x30 min, at less than 30°C) with 20 ml of dichloromethane/methanol (DCM:MeOH, 9:1, v:v), centrifuged the samples (3 x 10 min) at 4700 rpm, and filtered them through annealed glass wool (Rushdi et al., 2018).

We separated the total lipid extract in two fractions: Fraction 1 (F1: *n*-alkanes) and fractions 2-6 (polar fractions). For it, we used a 2 mL solid phase column filled with glass wool, 0.1 g of pure sand (50-70 mesh) and 1g of silica (70-230 mesh) that had been burned at 450 °C for 10 hours. We used hexane corresponding to the dead volume (DV, 1.5mL) to precondition the column. Fraction 1 eluted with 3/8 of DV in Hexane (ca. 600 µL), and fraction 2-6 with four times the DV in methanol. Both fractions were dried using an N_2 flow in an Organomation evaporator, and we added internal standard (IS) 5alpha-androstane (2000 mg/L in DCM, purity ≥99.9%, Sigma-Aldrich) 4 mg/L, and the volume was topped with 50 µL of DCM. Samples were analyzed with a gas chromatography equipped with an HP-5MS capillary column (30 m length x 0.25 mm i.d., 0.25 µm film thickness) and coupled to a mass-selective detector (GC-Agilent 7890B, MSD Agilent 5977A) with an electron impact interface

The GC started the analysis at a temperature of 70 °C for 2 min, then heated to 140 °C (heating rate 12 °C/min) and to 320 °C (heating rate of 3 °C/min) for 15 min, using helium as carrier gas (2 ml/min). To avoid interferences with other compounds the total run time was set at 82.83 min. The multimode injection (split ratio 5:1) was set at an initial temperature of 70 °C during 0.85 min and heated to 300 °C (heating rate of 720 °C/min). Measurements were repeated twice. We operated the MS in full scan mode (*m/z* 40-580, 70 eV of electron ionization energy), with ion source and quadruple set at 230 °C and 150 °C. Quantification of *n*-alkanes of the most intense fragment ions (m/z 43, 57, 71 and 85, and m/z 67, 95, 81 and 245 for IS) was taken.

We identified *n*-alkane compounds by comparing their retention times and mass spectra to those of reference compounds (mix C_8-C_{40}, 500 mg/L of each *n*-alkane in DCM, purity ≥90.1%, Sigma-Aldrich), $C_{26:0}$ (purity ≥95%, Sigma-Aldrich), $C_{28:0}$ (purity ≥98%, Sigma-Aldrich). We obtained calibration curves by plotting the area/area$_{IS}$ ratio vs the concentration of each reference compound and used them for quantification of *n*-alkanes, calculating concentrations by normalizing values to sample dry weight (expressed µg of compound per g).

Appendix C Calderinha record chronological models and their validation (São Nicolau)

Radiocarbon assays from Calderinha support two main histories of sediment deposition though time in the volcanic caldera. Thus, to develop a chronological model for the record, we first calculated two alternative models: model A using the BACON calibration model (Blaauw & Christen, 2013), and model B using the CLAM calibration model (Blaauw, 2010) (Fig. S5). For model A, we used six Radiocarbon dates (depths: 185, 135, 125, 105, 70, 60cm) and excluded two (depths: 115, 80cm), as BACON restricts the inclusion of dates that would result in highly disparate accumulation rates. Model A was the best fit possible, with only two dates excluded. For model B we used the first four dates starting from the bottom of the profile (depths: 185, 135, 125, 115), and excluded the four higher ones (depths: 105, 80, 70, 60cm) (Figure 4). Because of the above-stated limitations of BACON, we used a linear interpolation model in CLAM. Model B suggests a period of very slow sedimentation from ca. 5000 to ca. 1000 BP, and/or a hiatus.

To assess how reasonable these models are, we first plotted them against sand content data to test their fit with erosion trends in the record. Model A showed slow sedimentation in sections of increased erosion (e.g. between 70 and 100 yr/cm in section 80–70 cm). In contrast, model B yielded rapid accumulation rates in zones of erosion (5.5 yr/cm in section 80–70 cm), and slower sedimentation rates in zones with lowest sand content (between 170 and 280 yr/cm in section 135–115cm). When plotting the occurrence of pollen from taxa introduced by the Portuguese to Cabo Verde against model estimated ages, Model A predictably yielded dates that were too old: 3000 cal yr BP for *Zea mays*, 2900 cal yr BP for *Persea americana*, 1400 cal yr BP for *Ipomoea batatas*, 550 cal yr BP for *Eucalyptus*). Model B yielded more reasonable dates for the introduction of these taxa: 400 cal yr BP for *Zea mays*, 350 cal yr BP for *Persea americana*, 210 cal yr BP for *Ipomoea batatas*, 60 cal yr BP for *Eucalyptus*).

Pb-210 and Cs-137 dating were used to verify the chronology in the uppermost (0-50cm), most recently deposited, section of the Calderinha record. The successful use of these techniques is not dependent on the presence of in situ organic or carbonate material, and has been demonstrated previously in mixed alluvial and colluvial sediment sequences (e.g. Cundy & Stewart, 2004). Pb-210 and Cs-137 specific activities in the upper sediment profile are relatively low, due to the relatively coarse mean sediment grain size (Figure 3), but both show activity-depth profiles typical of accumulating sediment columns (e.g. Cundy et al., 2003) (Fig, S5). Pb-210 activity shows a general decline with depth to near-constant specific activities below 40 cm depth, and indicates (based on the CF:CS or simple model of Pb-210 dating, Appleby & Oldfield, 1992) an average sediment accumulation rate of ca. 1.5 yr/cm (2σ range = 1.2 – 1.8 yr/cm). Cs-137 shows a broad activity maximum between 5 and 30 cm depth. Assuming that the lower part of this maximum represents the increase in Cs-137 fallout due to the “spike” in deposition from above-ground nuclear weapons testing in 1963 (Ritchie & McHenry, 1990), this indicates a sediment accumulation rate of ca. 2 yr/cm in this upper profile section.

Sediment accumulation rates based on Pb-210 and Cs-137 dating support the validity of applying Model B as the preferred dating model for this sequence (Figure 3), particularly in the more recent period of direct human landscape modification (zone Cld-4). Despite the omission of more RC dates, we conclude that model B is the more plausible chronology for the Calderinha record. The presence of scrambled RC dates in sections of the record that are within or adjacent to sediments affected by human action indicates that erosion processes were active. This is not unprecedented in the archipelago; a similar dating problem was present in the record of Cova de Paúl, Santo Antão (Castilla-Beltrán et al., 2019). Uninterpretable dates are due to two factors: erosion processes that bring old carbon deposits into the records, and the practice of in-situ agriculture that, while not altering the general stratigraphy, can create interfaces of mixed sediments through the pulling up of old roots and the infiltration of new ones. In the Calderinha record, these processes would explain the scrambling of RC dates in the section 105–60 cm.

List of References

Albani, S., Mahowald, N., Winckler, G., Anderson, R., Bradtmiller, L., Delmonte, B., François, R., Goman, M., Heavens, N. & Hesse, P. (2015) Twelve thousand years of dust: the Holocene global dust cycle constrained by natural archives. *Climate of the Past*, **11**, 869-903.

Alexandré, A., Meunier, J.-D., Lezine, A.-M., Vincens, A., & Schwartz, D. (1997) Phytoliths: indicators of grassland dynamics during the late Holocene in intertropical Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **136**, 213-229.

Andersen, T., Carstensen, J., Hernandez-Garcia, E. & Duarte, C.M. (2009) Ecological thresholds and regime shifts: approaches to identification. *Trends in Ecology and Evolution*, **24**, 49-57.

Arechavaleta Hernández, M., Pérez, N.Z., Gómez, M.C.M., & Esquivel, J.M. (2005) *Lista preliminar de especies silvestres de Cabo Verde. Hongos, Plantas y Animales Terrestres*. Gobierno de Canarias. Consejería de Medio Ambiente y Ordenación Territorial.

Azzoug, M., Carré, M., Chase, B.M., Deme, A., Lazar, A., Lazareth, C.E., Schauer, A.J., Mandeng-Yogo, M., Simier, M., & Thierno-Gaye, A. (2012) Positive precipitation–evaporation budget from AD 460 to 1090 in the Saloum Delta (Senegal) indicated by mollusk oxygen isotopes. *Global and Planetary Change*, **98**, 54-62.

Baldacchino, G., Niles, D. (2011) *Island futures: Conservation and development across the Asia-Pacific region*. Springer Science & Business Media.

Balée, W. (2006) The research program of historical ecology. *Annual Review of Anthropology*, **35**, 75-98.

Baptista, I., Ritsema, C. & Geissen, V. (2015) Effect of integrated water-nutrient management strategies on soil erosion mediated nutrient loss and crop productivity in Cabo Verde drylands. *PloS one*, **10**, e0134244.

Barnosky, A.D., Hadly, E.A., Gonzalez, P., Head, J., Polly, P.D., Lawing, A.M., Eronen, J.T., Ackerly, D.D., Alex, K. & Biber, E. (2017). Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science*, **355**, eaah4787.

Barone Tosco, R. (2005) La flora endémica de Cabo Verde, un tesoro a conservar. *Rincones del Atlántico*, 126-130.

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F. & Nyström, M. (2003) Reserves, resilience and dynamic landscapes. *AMBIO*, **32**, 389-396.

Benton, S.W. (2013) *Forestry on the island of Santo Antão, Cabo Verde, West Africa*. Sioux Falls, SœD, USA.

Berendse, F., van Ruijven, J., Jongejans, E. & Keesstra, S. (2015) Loss of plant species diversity reduces soil erosion resistance. *Ecosystems*, **18**, 881-888.

Berkes, F. &Turner, N.J. (2006) Knowledge, learning and the evolution of conservation practice for social-ecological system resilience. *Human Ecology*, **34**, 479.

Beug, H.-J. (2004) *Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete*. Verlag Friedrich Pfeil, Munich.

Bhattacharya, S., Dutta, S. & Summons, R.E. (2017) A distinctive biomarker assemblage in an Infracambrian oil and source rock from western India: Molecular signatures of eukaryotic sterols and prokaryotic carotenoids. *Precambrian Research*, **290**, 101-112.

Birks, H.J.B. & Birks, H.H. (1980) *Quaternary palaeoecology*. Edward Arnold, London.

Birks, H.J.B. & Line, J.M. (1992) The use of rarefaction analysis for estimating palynological richness from Quaternary pollen-analytical data. *The Holocene*, **2**, 1-10.

Blaauw, M. (2010) Methods and code for 'classical'age-modelling of radiocarbon sequences. *Quaternary Geochronology*, **5**, 512-518.

Blaauw, M. & Christen, J.A. (2013) Bacon Manual e v2. 3.5, 387-394.

Boessenkool, S., Mcglynn, G., Epp, L.S., Taylor, D., Pimentel, M., Gizaw, A., Nemomissa, S., Brochmann, C. & Popp, M. (2013) Use of ancient sedimentary DNA as a novel conservation tool for high-altitude tropical biodiversity. *Conservation Biology*, **28**, 446-455.

Bouimetarhan, I., Dupont, L., Schefuß, E., Mollenhauer, G., Mulitza, S. & Zonneveld, K. (2009) Palynological evidence for climatic and oceanic variability off NW Africa during the late Holocene. *Quaternary Research*, **72**, 188-197.

Brunelle, A., Minckley, T.A., Shinker, J.J. & Heyer, J. (2018) Filling a Geographical Gap: New Paleoecological Reconstructions From the Desert Southwest, US. *Frontiers in Earth Science*, **6**, 1-17.

Buggle, B., Wiesenberg, G.L. & Glaser, B. (2010) Is there a possibility to correct fossil n-alkane data for postsedimentary alteration effects? *Applied Geochemistry*, **25**, 947-957.

Burney, D.A. & Burney, L.P. (2007) Paleoecology and "inter-situ" restoration on Kaua'i, Hawai'i. *Frontiers in Ecology and the Environment*, **5**, 483-490.

Burney, D.A. & Burney, L.P. (2016) Monitoring results from a decade of native plant translocations at Makauwahi Cave Reserve, Kauai. *Plant Ecology*, **217**, 139-153.

Burney, D.A. & Flannery, T.F. (2005) Fifty millennia of catastrophic extinctions after human contact. *Trends in Ecology & Evolution*, **20**, 395-401.

Cadd, H., Fletcher, M.S., Mariani, M., Heijnis, H. & Gadd, P.S. (2019) The influence of fine-scale topography on the impacts of Holocene fire in a Tasmanian montane landscape. *Journal of Quaternary Science*, **34**, 491-498.

Cai, W., Borlace, S., Lengaigne, M., Van Rensch, P., Collins, M., Vecchi, G., Timmermann, A., Santoso, A., McPhaden, M.J. & Wu, L. (2014) Increasing frequency of extreme El Niño events due to greenhouse warming. *Nature Climate Change*, **4**, 111.

Campbell-Hunt, D. (2014) Ecotourism and sustainability in community-driven ecological restoration: case studies from New Zealand. *WIT Transactions on Ecology and the Environment*, **115**, 13-22.

Cardoso, J.L. & Monge Soares, A.M. (2010) A estação arqueológica de Salamansa (ilha de São Vicente, República de Cabo Verde). *Revista Portuguesa de Arqueologia*, **13**, 167-214.

Carrión, J.S., González-Sampériz, P., López Sáez, J.A., López García, P. & Dupré, M. (2009) Quaternary pollen analysis in the Iberian Peninsula: the value of negative results. *Internet Archaeology*, **25**, 1-53.

Castilla-Beltrán, A., Hooghiemstra, H., Hoogland, M.L.P., Pagán-Jiménez, J., van Geel, B., Field, M.H., Prins, M., Donders, T., Herrera Malatesta, E., Ulloa Hung, J., McMichael, C.H., Gosling, W.D. & Hofman, C.L. (2018) Columbus' footprint in Hispaniola: A paleoenvironmental record of indigenous and colonial impacts on the landscape of the central Cibao Valley, northern Dominican Republic. *Anthropocene*, **22**, 66-80.

Castilla-Beltrán, A., de Nascimento, L., Fernández-Palacios, J.M., Fonville, T., Whittaker, R.J., Edwards, M. & Nogué, S. (2019) Late Holocene environmental change and the anthropization of the highlands of Santo Antão Island, Cabo Verde. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **524**, 101-117.

Castilla-Beltrán, A., Duarte, I., de Nascimento, L., Fernández-Palacios, J.M., Romeiras, M., Whittaker, R.J., Jambrina-Enríquez, M., Mallol, C., Cundy, A.B., Edwards, M. & Nogué, S. (2020) Using multiple palaeoecological indicators to guide biodiversity conservation in tropical dry islands: The case of São Nicolau, Cabo Verde. *Biological Conservation*, **242**, 108397.

Coffey, E.E., Froyd, C.A. & Willis, K.J. (2011) When is an invasive not an invasive? Macrofossil evidence of doubtful native plant species in the Galápagos Islands. *Ecology*, **92**, 805-812.

Cole, L.E., Bhagwat, S.A. & Willis, K.J. (2014) Recovery and resilience of tropical forests after disturbance. *Nature communications*, **5**, 3906.

Connor, S.E., van Leeuwen, J.F., Rittenour, T.M., van der Knaap, W.O., Ammann, B. & Björck, S. (2012) The ecological impact of oceanic island colonization–a palaeoecological perspective from the Azores. *Journal of Biogeography*, **39**, 1007-1023.

Corella, J.P., Brauer, A., Mangili, C., Rull, V., Vegas-Vilarrúbia, T., Morellón, M., Valero-Garcés, B.L., (2012) The 1.5-ka varved record of Lake Montcortès (southern Pyrenees, NE Spain). *Quaternary Research*, **78**, 323-332.

Correia, E.L.T. (1996) Contribuições para o conhecimento do clima de Cabo Verde. *Série de Geografia*, **15**, 81-107.

Correia, E.L.T. (2000) A propósito da ideia de ‘anos bons’ após as erupções na ilha do Fogo. *Série de Geografia*, **17**, 47-60.

Crisafulli, C.M., Swanson, F.J., Halvorson, J.J. & Clarkson, B.D. (2015) *Volcano ecology: Disturbance characteristics and assembly of biological communities*, in: Sigurdsson, H., Houghton, B., McNutt, S., Rymer, H. & Stix, J. (Eds.) *The encyclopedia of volcanoes*. Academic Press, London, pp. 1265-1284.

Cropper, T. (2013) The weather and climate of Macaronesia: past, present and future. *Weather*, **68**, 300-307.

Croudace, I.W. & Rothwell, R.G. (2015) *Micro-XRF Studies of Sediment Cores: Applications of a non-destructive tool for the environmental sciences*. Springer, Doldrecht, Heidelberg, New York, London.

Crutzen, P.J. & Stoermer, E.F. (2000) The Anthropocene. *Global change newsletter*, **41**, 17-18. International Geosphere–Biosphere Programme (IGBP).

Cugny, C., Mazier, F. & Galop, D. (2010) Modern and fossil non-pollen palynomorphs from the Basque mountains (western Pyrenees, France): the use of coprophilous fungi to reconstruct pastoral activity. *Vegetation History and Archaeobotany*, **19**, 391-408.

Cundy, A., Sprague, D., Hopkinson, L., Maroukian, H., Gaki-Papanastassiou, K., Papanastassiou, D. & Frogley, M. (2006) Geochemical and stratigraphic indicators of late Holocene coastal evolution in the Gythio area, southern Peloponnese, Greece. *Marine Geology*, **230**, 161-177.

Cundy, A.B., Croudace, I.W., Cearreta, A. & Irabien, M.a.J. (2003) Reconstructing historical trends in metal input in heavily-disturbed, contaminated estuaries: studies from Bilbao, Southampton Water and Sicily. *Applied Geochemistry*, **18**, 311-325.

Cundy, A.B. & Stewart, I.S. (2004) Dating recent colluvial sequences with 210Pb and 137Cs along an active fault scarp, the Eliki Fault, Gulf of Corinth, Greece. *Tectonophysics*, **386**, 147-156.

Danielson, J.J. & Gesch, D.B. (2011) *Global multi-resolution terrain elevation data 2010 (GMTED2010)*. U.S. Geological Survey Open-File Report 2011–1073, 26 p

Darwin, C. (2011, originally published 1891) *Geological Observations on the Volcanic Islands, Visited During the Voyage of H.M.S. Beagle, together with some brief notices on the geology of Australia and the Cape of Good Hope*. Cambridge University Press, Cambridge.

de Boer, E. (2014) *Mauritius since the last ice age: paleoecology and climate of an oceanic island*. PhD Thesis, University of Amsterdam, The Netherlands.

de Boer, E.J., Slaikovska, M., Hooghiemstra, H., Rijsdijk, K.F., Vélez, M.I., Prins, M., Baider, C. & Florens, F.V. (2013) Multi-proxy reconstruction of environmental dynamics and colonization impacts in the Mauritian uplands. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **383**, 42-51.

de Lima, T.M., Weindorf, D.C., Curi, N., Guilherme, L.R., Lana, R.M. & Ribeiro, B.T. (2019) Elemental analysis of Cerrado agricultural soils via portable X-ray fluorescence spectrometry: Inferences for soil fertility assessment. *Geoderma*, **353**, 264-272.

de Nascimento, L., Nogué, S., Criado, C., Ravazzi, C., Whittaker, R.J., Willis, K.J. & Fernández-Palacios, J.M. (2016) Reconstructing Holocene vegetation on the island of Gran Canaria before and after human colonization. *The Holocene*, **26**, 113-125.

de Nascimento, L., Nogué, S., Fernández-Lugo, S., Méndez, J., Otto, R., Whittaker, R.J., Willis, K.J. & Fernández-Palacios, J.M. (2015) Modern pollen rain in Canary Island ecosystems and its implications for the interpretation of fossil records. *Review of Palaeobotany and Palynology*, **214**, 27-39.

de Nascimento, L., Nogué, S., Naranjo-Cigala, A., Criado, C., McGlone, M., Fernández-Palacios, E. & Fernández-Palacios, J.M. (2020) Human impact and ecological changes during prehistoric settlement on the Canary Islands. *Quaternary Science Reviews*, **239**, 106332.

de Nascimento, L., Willis, K.J., Fernández-Palacios, J.M., Criado, C. & Whittaker, R.J. (2009) The long-term ecology of the lost forests of La Laguna, Tenerife (Canary Islands). *Journal of Biogeography*, **36**, 499-514.

Dean Jr, W.E. (1974) Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. *Sedimentary Research*, **44**, 242-248.

Dearing, J., Acma, B., Bub, S., Chambers, F.M., Chen, X., Cooper, J., Crook, D., Dong, X., Dotterweich, M., Edwards, M., Foster, H.T., Gaillard, M.-J., Galop, D., Gell, P., Gil, A., Jeffers, E., Jones, R., Krishnamurthy, A., Langdon, P.G., Marchant, R., Mazier, F., McLean, C., Nunes, L., Raman, S., Suryaprakash, I., Umer, M., Yang, X., Wang, R. & Zhang, K. (2015) Social-Ecological Systems in the Anthropocene : The Need for Integrating Social and Biophysical Records at Regional Scales. *Anthropocene Review*, **2**, 1-27.

Dearing, J., Battarbee, R., Dikau, R., Larocque, I. & Oldfield, F. (2006) Human–environment interactions: learning from the past. *Regional Environmental Change*, **6**, 1-16.

Dearing, J.A., Bullock, S., Costanza, R., Dawson, T.P., Edwards, M.E., Poppy, G.M. & Smith, G.M. (2012) Navigating the perfect storm: research strategies for socialecological systems in a rapidly evolving world. *Environmental Management*, **49**, 767-775.

deMenocal, P., Ortiz, J., Guilderson, T., Adkins, J., Sarnthein, M., Baker, L. & Yarusinsky, M. (2000) Abrupt onset and termination of the African Humid Period: rapid climate responses to gradual insolation forcing. *Quaternary Science Reviews*, **19**, 347-361.

Duarte, M.C., Rego, F., Romeiras, M.M. & Moreira, I. (2008) Plant species richness in the Cape Verde Islands: eco-geographical determinants. *Biodiversity and Conservation*, **17**, 453-466.

Duarte, M.C. & Romeiras, M.M. (2009) *Cape Verde Islands*, in: Gillespie, R.G. & Clague, D.A. (Eds.), *Encyclopedia of islands*. University of California Press, Berkeley, Los Angeles, London, pp. 143-148.

Duarte, M.C., Romeiras, M.M., Santos-Guerra, A., Nepi, C. & Francisco-Ortega, J. (2017) Joseph D. Hooker's 1839 Cabo Verde collections. *Curtis' Botanical Magazine*, **34**, 146-168.

Dzikiti, S., Ntshidi, Z., Le Maitre, D.C., Bugan, R.D., Mazvimavi, D., Schachtschneider, K., Jovanovic, N.Z. & Pienaar, H.H. (2017) Assessing water use by Prosopis invasions and Vachellia karroo trees: Implications for groundwater recovery following alien plant removal in an arid catchment in South Africa. *Forest Ecology and Management*, **398**, 153-163.

Eichhorn, B., Neumann, K. & Garnier, A. (2010) Seed phytoliths in West African Commelinaceae and their potential for palaeoecological studies. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **298**, 300-310.

Ejarque, A., Anderson, R.S., Simms, A.R. & Gentry, B.J. (2015) Prehistoric fires and the shaping of colonial transported landscapes in southern California: A paleoenvironmental study at Dune Pond, Santa Barbara County. *Quaternary Science Reviews*, **112**, 181-196.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B. & Norberg, J. (2003) Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, **1**, 488-494.

Erdtman, G. (2013) *An introduction to pollen analysis*. Read Books Ltd, Redditch, UK.

Evans, C., Sørensen, M.L.S., Allen, M.J., Appleby, J., Casimiro, T.M., French, S.I., Lima, J., Newman, R., Richter, K. & Scaife, R. (2017) Finding Alcatrazes and early Luso-African settlement on Santiago Island, Cape Verde. *Antiquity*, **91**, 1-9.

Evans, C., Sorensen, M.L.S. & Richter, K. (2012) *Excavation of one of the earliest Christian churches in the tropics: Na. Sa. da Conceicao, Cidade Velha, Cape Verde*, in: Green, T. (Ed.), *Brokers of Change: Atlantic Commerce and Cultures in Pre-Colonial Guinea of Cape Verde*. Oxford UniversityPress/British Academy, London.

FAO (2005) *FAO Forestry Paper 147: Global Forest Resources Assessment 2005. Progress towards sustainable forest management*. Food and Agriculture Organization of the United Nations, Rome.

Fei, S., Phillips, J. & Shouse, M. (2014) Biogeomorphic impacts of invasive species. *Annual Review of Ecology, Evolution, and Systematics*, **45**, 69-87.

Fernández-Palacios, J.M., de Nascimento, L., Otto, R., Delgado, J.D., García-del-Rey, E., Arévalo, J.R. & Whittaker, R.J. (2011) A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. *Journal of Biogeography*, **38**, 226-246.

Fernández-Palacios, J.M., Nogué, S., Criado, C., Connor, S., Góis-Marques, C., Sequeira, M. & de Nascimento, L. (2016) Climate change and human impact in Macaronesia. *PAGES Magazine*, **24**, 68-69.

Fiantis, D., Ginting, F.I., Nelson, M. & Minasny, B. (2019) Volcanic Ash, Insecurity for the People but Securing Fertile Soil for the Future. *Sustainability*, **11**, 3072.

Ficetola, G.F., Poulenard, J., Sabatier, P., Messager, E., Gielly, L., Leloup, A., Etienne, D., Bakke, J., Malet, E. & Fanget, B. (2018) DNA from lake sediments reveals long-term ecosystem changes after a biological invasion. *Science Advances*, **4**, eaar4292.

Finsinger, W. & Tinner, W. (2005) Minimum count sums for charcoal concentration estimates in pollen slides: accuracy and potential errors. *The Holocene*, **15**, 293-297.

Fitzhugh, B., Butler, V.L., Bovy, K.M. & Etnier, M.A. (2019) Human ecodynamics: A perspective for the study of long-term change in socioecological systems. *Journal of Archaeological Science: Reports*, **23**, 1077-1094.

Fitzpatrick, S.M. & Keegan, W.F. (2007) Human impacts and adaptations in the Caribbean Islands: an historical ecology approach. *Earth and Environmental Science Transactions of the Royal Science of Edinburgh*, **98**, 29-45.

Folke, C. (2006) Resilience: The emergence of a perspective for social–ecological systems analyses. *Global Environmental Change*, **16**, 253-267.

Folke, C., Carpenter, S., Elmqvist, T., Gunderson, L., Holling, C.S. & Walker, B. (2002) Resilience and Sustainable Development: Building Adaptive Capacity in a World of Transformations. *BIOONE*, **31**, 437-440.

Freitas, R., Romeiras, M., Silva, L., Cordeiro, R., Madeira, P., González, J.A., Wirtz, P., Falcón, J.M., Brito, A. & Floeter, S.R. (2019) Restructuring of the 'Macaronesia'biogeographic unit: A marine multi-taxon biogeographical approach. *Scientific Reports*, **9**, 1-18.

Froyd, C.A. & Willis, K.J. (2008) Emerging issues in biodiversity & conservation management: the need for a palaeoecological perspective. *Quaternary Science Reviews*, **27**, 1723-1732.

Gaillard, M.-J., Dutoit, T., Hjelle, K., Koff, T. & O'Connell, M. (2009) *European cultural landscapes: insights into origins and development*. In Krzywinski, K., O'Connell, M. & Küster, H. (Eds.) *Cultural Landscapes of Europe*. Aschenbeck Media, Bremen, 35-46.

Gaki-Papanastassiou, K., Cundy, A.B. & Maroukian, H. (2011) Fluvial versus tectonic controls on the late Holocene geomorphic and sedimentary evolution of a small Mediterranean fan delta system. *The Journal of Geology*, **119**, 221-234.

Gámez-Virués, S., Perović, D.J., Gossner, M.M., Börschig, C., Blüthgen, N., De Jong, H., Simons, N.K., Klein, A.-M., Krauss, J. & Maier, G. (2015) Landscape simplification filters species traits and drives biotic homogenization. *Nature Communications*, **6**, 1-8.

Garfield, R. (2015) Three islands of the Portuguese Atlantic: Their economic rise, fall and (sometimes) rerise. *Shima*, **9**, 47-59.

GEF/UNEP (2015) *Fifth National Report on the Status of Biodiversity in Cabo Verde*. National Directorate for the Environment.

Gelorini, V., Verbeken, A., van Geel, B., Cocquyt, C. & Verschuren, D. (2011) Modern nonpollen palynomorphs from East African lake sediments. *Review of Palaeobotany and Palynology*, 164, 143-173.

Gillson, L. (2015) *Biodiversity conservation and environmental change: using palaeoecology to manage dynamic landscapes in the Anthropocene*. Oxford University Press, Oxford, UK.

González, J., Montes, C., Rodríguez, J. & Tapia, W. (2008) Rethinking the Galapagos Islands as a complex social-ecological system: implications for conservation and management. *Ecology and Society*, **13**, online.

Gosling, W.D., De Kruif, J., Norder, S.J., De Boer, E.J., Hooghiemstra, H., Rijsdijk, K.F. & McMichael, C. (2017) Mauritius on fire. *Biotropica*, **49**, 778-783.

Gosling, W.D., Miller, C.S. & Livingstone, D.A. (2013) Atlas of the tropical West African pollen flora. *Review of Palaeobotany and Palynology*, **199**, 1-135.

Green, T. (2012) *The rise of the trans-Atlantic slave trade in Western Africa, 1300–1589*. Cambridge University Press, Cambridge.

Grimm, E. (1993) TILIA: a pollen program for analysis and display. Retrieved from Springfield. Illinois State Museum.

Grimm, E.C., Maher, L.J. & Nelson, D.M. (2009) The magnitude of error in conventional bulk-sediment radiocarbon dates from central North America. *Quaternary Research*, **72**, 301-308.

Hamann, O. (2004) Vegetation change over three decades on Santa Fe Island, Galapagos, Ecuador. *Nordic Journal of Botany*, **23**, 143-152.

Havinga, A.J. (1967) Palynology and pollen preservation. *Review of Palaeobotany and Palynology*, **2**, 81-98.

Heckman, J. (1985) Culture and the environment on the Cape Verde islands. *Environmnetal management*, **9**, 141-150.

Heilweil, V.M., Gingerich, S.B., Plummer, L.N. & Verstraeten, I.M. (2010) *Groundwater Resources of Ribeira Paúl Basin, Island of Santo Antão, Cape Verde, Africa*. Report for U.S. Department of the Interior, U.S. Geological Survey, p. 4.

Heiri, O., Lotter, A.F. & Lemcke, G. (2001) Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of Paleolimnology*, **25**, 101-110.

Hély, C., Braconnot, P., Watrin, J. & Zheng, W. (2009) Climate and vegetation: simulating the African humid period. *Comptes Rendus Geoscience*, **341**, 671-688.

Herbert, D.A., Fownes, J.H. & Vitousek, P.M. (1999) Hurricane damage to a Hawaiian forest: nutrient supply rate affects resistance and resilience. *Ecology*, **80**, 908-920.

Hodgson, D., McDonald, J.L. & Hosken, D.J. (2015) What do you mean,'resilient'? *Trends in Ecology & Evolution*, **30**, 503-506.

Hoefs, M.J., Rijpstra, W.I.C. & Damsté, J.S.S. (2002) The influence of oxic degradation on the sedimentary biomarker record I: Evidence from Madeira Abyssal Plain turbidites. *Geochimica et Cosmochimica Acta*, **66**, 2719-2735.

Hofman, C., Mol, A., Hoogland, M., & Valcárcel Rojas, R. (2014) Stage of encounters: migration, mobility and interaction in the pre-colonial and early colonial Caribbean. *World Archaeology*, **46**, 590-609.

Holling, C.S. (2001) Understanding the complexity of economic, ecological, and social systems. *Ecosystems*, **4**, 390-405.

Holmgren, M., Stapp, P., Dickman, C.R., Gracia, C., Graham, S., Gutiérrez, J.R., Hice, C., Jaksic, F., Kelt, D.A. & Letnic, M. (2006) Extreme climatic events shape arid and semiarid ecosystems. *Frontiers in Ecology and the Environment*, **4**, 87-95.

Hooghiemstra, H. (1988) Changes of major wind belts and vegetation zones in NW Africa 20,000-5000 yr BP as deduced from a marine pollen record near Cap Blanc. *Review of Palaeobotany and Palynology*, **55**, 101-140.

Hooghiemstra, H. & Agwu, C.O. (1986) Distribution of palynomorphs in marine sediments: a record for seasonal wind patterns over NW Africa and adjacent Atlantic. *Geologische Rundschau*, **75**, 81-95.

Hooghiemstra, H., Agwu, C.O.C. & Beug, H.-J. (1986) Pollen and spore distribution in recent marine sediments: a record of NW-African seasonal wind patterns and vegetation belts. *Meteor' Forschungs Ergebnisse Reihe C*, **40**, 87-135.

Hooghiemstra, H., Lézine, A.M., Leroy, S.A., Dupont, L. & Marret, F. (2006) Late Quaternary palynology in marine sediments: a synthesis of the understanding of pollen distribution patterns in the NW African setting. *Quaternary International*, **148**, 29-44.

Hooghiemstra, H., Stalling, H., Agwu, C.O.C. & Dupont, L.M. (1992) Upper Pleistocene vegetational and climatic changes at the northern fringe of the Sahara: evidence from 4 marine pollen records located between Portugal and the Canary Islands. *Review of Palaeobotany and Palynology*, **74**, 1-53.

Horrocks, M., & D'Costa, D.M. (2003) Stratigraphic palynology in porous soils in humid climates: An example from Pouerua, northern New Zealand. *Palynology*, **27**, 27-37.

Hunt, T.L. (2007) Rethinking Easter Island's ecological catastrophe. *Journal of Archaeological Science*, **34**, 485-502.

Imbert, D. & Portecop, J. (2008) Hurricane disturbance and forest resilience: assessing structural vs. functional changes in a Caribbean dry forest. *Forest Ecology and Management*, **255**, 3494-3501.

Jenkins, G.S., Brito, E., Soares, E., Chiao, S., Lima, J.P., Tavares, B., Cardoso, A., Evora, F. & Monteiro, M. (2017) Hurricane Fred (2015): Cape Verde’s first hurricane in modern times: Observations, impacts, and lessons learned. *Bulletin of the American Meteorological Society*, **98**, 2603-2618.

Johannes, R.E. (2002) Did indigenous conservation ethics exist. *SPC Traditional Marine Resource Management and Knowledge Information Bulletin*, **14**, 3-7.

Kirch, P.V. (2017) *On the road of the winds: an archaeological history of the Pacific Islands before European contact*. University of California Press, California, USA.

Kirch, P.V. & Ellison, J. (1994) Palaeoenvironmental evidence for human colonization of remote Oceanic islands. *Antiquity*, **68**, 310-321.

Krammer, K. & Lange-Bertalot, H. (1999a). *Bacillariophyceae. 1. Teil: Naviculaceae. Süßwasserflora von Mitteleuropa, Band 2/1.* Gustav Fischer Verlag, Stuttgart.

Krammer, K. & Lange-Bertalot, H. (1999b). *Bacillariophyceae. 2. Teil: Bacillariaceae, Epithemiaceae, Surirellaceae. Süßwasserflora von Mitteleuropa, Band 2/2.* Gustav Fischer Verlag, Stuttgart.

Krammer, K. & Lange-Bertalot, H. (2000) *Bacillariophyceae. 3. Teil: Centrales, Fragilariaceae, Eunotiaceae. Süßwasserflora von Mitteleuropa, Band 2/3*. Gustav Fischer Verlag, Stuttgart.

Krammer, K. & Lange-Bertalot, H. (2004) *Bacillariophyceae. 4. Teil: Achnanthaceae. Kritische Ergänzungen zu Achnanthes s.l., Navicula s.str., Gomphonema*. *Süßwasserflora von Mitteleuropa, Band 2/3.* Gustav Fischer Verlag, Stuttgart.

Kröpelin, S., Verschuren, D., Lézine, A.-M., Eggermont, H., Cocquyt, C., Francus, P., Cazet, J.-P., Fagot, M., Rumes, B. & Russell, J. (2008) Climate-driven ecosystem succession in the Sahara: the past 6000 years. *Science*, **320**, 765-768.

Kuhlmann, H., Meggers, H., Freudenthal, T. & Wefer, G. (2004) The transition of the monsoonal and the N Atlantic climate system off NW Africa during the Holocene. *Geophysical Research Letters*, 31.

La Serna-Ramos, I.E. & Domínguez-Santana, M.D. (2003) *Pólenes y esporas aerovagantes en Canarias*. Servicio de Publicaciones de la Universidad de La Laguna, La Laguna, Tenerife.

Langworthy, M. & Finan, T.J. (1997) *Waiting for Rain: Agriculture and Ecological Imbalance in Cape Verde*. Lynne Rienner, Boulder, CO.

Lepape, M.C. (1980) *Browse in the Cape Verde Islands, a preliminary study*, in: Hourerou, N.H. (Ed.), *Browse in Africa: the current state of knowledge. International Livestock Centre for Africa*. Addis Ababa, Ethiopia, pp. 123-125.

Leppard, T.P. (2017) The biophysical effects of Neolithic island colonization: general dynamics and sociocultural implications. *Human Ecology*, **45**, 555-568.

Leroux, S. & Hall, N.M. (2009) On the relationship between African easterly waves and the African easterly jet. Journal of the *Atmospheric Sciences*, **66**, 2303-2316.

Levis, C., Costa, F.R.C., Bongers, F., Peña-Claros, M., Clement, C.R., Junqueira, A.B., Neves, E.G., (…) & ter Steege, H. (2017) Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science*, **355**, 925-931.

Lewis, S.L & Maslin, M.A. (2015) Defining the anthropocene. *Nature*, **519**, 171.

Lézine, A.M., Hély, C., Grenier, C., Braconnot, P. & Krinner, G. (2011) Sahara and Sahel vulnerability to climate changes, lessons from Holocene hydrological data. *Quaternary Science Reviews*, **30**, 3001-3012.

Lindskog, P. & Delaite, B. (1996) Degrading land: an environmental history perspective of the Cape Verde Islands. *Environment and History*, **2**, 271-290.

Lobban Jr, R.A. (1998) *Were the Portuguese the First To Visit Cape Verde? Cimboa*, **5**, 10.

Loughlin, N.J., Gosling, W.D., Coe, A.L., Gulliver, P., Mothes, P. & Montoya, E. (2018) Landscape-scale drivers of glacial ecosystem change in the montane forests of the eastern Andean flank, Ecuador. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **489**, 198-208.

MAA-DGA (2008) *Plano de gestão – Parque Natural Monte Gordo*. Monte Gordo, Cabo Verde, p. 222.

Mace, G., Masundire, H., Baillie, J., Ricketts, T., Brooks, T., Hoffmann, M., Stuart, S., Balmford, A., Purvis, A. & Reyers, B. (2005) *Biodiversity: millennium ecosystem assessment: current state and trends: findings of the condition and trends working group. Ecosystems and Human Well-being*. Island Press, Washington, DC.

Mack, M.C. & D'Antonio, C.M. (1998) Impacts of biological invasions on disturbance regimes. *Trends in Ecology & Evolution*, **13**, 195-198.

Madeira, J., Mata, J., Mourão, C., da Silveira, A.B., Martins, S., Ramalho, R. & Hoffmann, D.L. (2010) Volcano-stratigraphic and structural evolution of Brava Island (Cape Verde) based on 40Ar/39Ar, U–Th and field constraints. *Journal of Volcanology and Geothermal Research*, **196**, 219-235.

MAHOT (2014) *Estratégia Nacional e Plano de Ação para a Conservação da Biodiversidade 2015-2030*. Direção Geral do Ambiente, Praia, República de Cabo Verde, p. 100.

Maley, J. & Brenac, P. (1998) Vegetation dynamics, palaeoenvironments and climatic changes in the forests of western Cameroon during the last 28,000 years BP. *Review of Palaeobotany and Palynology*, **99**, 157-187.

McArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press Princeton. New Jersey.

McGlade, J. (1995) Archaeology and the ecodynamics of human-modified landscapes. *Antiquity*, **69**, 113-132.

McWethy, D.B., Whitlock, C., Wilmshurst, J.M., McGlone, M.S. & Li, X. (2009) Rapid deforestation of South Island, New Zealand, by early Polynesian fires. *The Holocene*, **19**, 883-897.

Menezes de Sequeira, M., Jardim, R. & Capelo, J. (2007) *A chegada dos Portugueses às ilhas—o antes eo depois*—Madeira. Árvores e Florestas de Portugal: Açores e Madeira—A Floresta das Ilhas Público, Comunicação Social SA, Fundação Luso Americana para o Desenvolvimento e Liga para a Protecção da Natureza, 165-196.

Miracle, M.P. (1965) The introduction and spread of maize in Africa. *The Journal of African History*, **6**, 39-55.

Mitchell, P. (2004) Towards a comparative archaeology of African Islands. *Journal of African Archaeology*, **2**, 229-250.

Mitchell-Thomè, R. (1981) Vulcanicity of historic times in the Middle Atlantic Islands. *Bulletin Volcanologique*, **44**, 57-69.

Møberg, J., Esu, I. & Malgwi, W. (1991) Characteristics and constituent composition of Harmattan dust falling in Northern Nigeria. *Geoderma*, **48**, 73-81.

Moran, E.F. (1982) The evolution of Cape Verde's agriculture. *African Economic History*, **11**, 63-86.

Mulitza, S., Heslop, D., Pittauerova, D., Fischer, H.W., Meyer, I., Stuut, J.-B., Zabel, M., Mollenhauer, G., Collins, J.A. & Kuhnert, H. (2010) Increase in African dust flux at the onset of commercial agriculture in the Sahel region. *Nature*, **466**, 226-228.

Musche, M., Adamescu, M., Angelstam, P., Bacher, S., Bäck, J., Buss, H.L., Duffy, C., Flaim, G., Gaillardet, J. & Giannakis, G.V. (2019) Research questions to facilitate the future development of European long-term ecosystem research infrastructures: A horizon scanning exercise. *Journal of Environmental Management*, **250**, 109479.

Neto, C., Costa, J.C., Figueiredo, A., Capelo, J., Gomes, I., Vitória, S., Semedo, J.M., Lopes, A., Dinis, H., Correia, E., Duarte, M.C. & Romeiras, M.M. (2020) The Role of Climate and Topography in Shaping the Diversity of Plant Communities in Cabo Verde Islands. *Diversity*, **12**, 80.

Nicosia, C. & Stoops, G. (Eds.) (2017) *Archaeological soil and sediment micromorphology*. John Wiley & Sons, NJ.

Nogué, S., de Nascimento, L., Fernández-Palacios, J.M., Whittaker, R.J. & Willis, K.J. (2013) The ancient forests of La Gomera, Canary Islands, and their sensitivity to environmental change. *Journal of Ecology*, **101**, 368-377.

Nogué, S., de Nascimento, L., Froyd, C.A., Wilmshurst, J.M., De Boer, E.J., Coffey, E.E.D., Whittaker, R.J., Fernández-Palacios, J.M. & Willis, K.J. (2017) Island biodiversity conservation needs palaeoecology. *Nature Ecology and Evolution*, **1**, 1-9.

Norder, S.J., de Lima, R.F., de Nascimento, L., Lim, J.Y., Fernández-Palacios, J.M., Romeiras, M.M., Elias, R.B., Cabezas, F.J., Catarino, L., Ceríaco, L.M., Castilla-Beltrán, A., Gabriel, R., Menezes de Sequeira, M., Rijsdijk, K., Nogué, S., Kissling, D., van Loon, E., Hall, M., Matos, M. & Borges, P.A. (2020) Global change in microcosms: environmental and societal predictors of land cover change on the Atlantic Ocean Islands. *Anthropocene*, 30, 100242.

Earth Observatory, N.E. (2014) *Eruption at Fogo November 29 2014*. NASA.

Ortiz, J.E., Sánchez-Palencia, Y., Torres, T., Domingo, L., Mata, M.P., Vegas, J., España, J.S., Morellón, M. & Blanco, L. (2016) Lipid biomarkers in Lake Enol (Asturias, Northern Spain): coupled natural and human induced environmental history. *Organic Geochemistry*, **92**, 70-83.

Paine, R.T. (2012) *Ecological disturbance*. Enciclopaedia Britannica.

Paine, R.T., Tegner, M.J. & Johnson, E.A. (1998) Compounded perturbations yield ecological surprises. *Ecosystems*, **1**, 535-545.

Pancost, R.D., Baas, M., van Geel, B. & Damsté, J.S.S. (2002) Biomarkers as proxies for plant inputs to peats: an example from a sub-boreal ombrotrophic bog. *Organic Geochemistry*, **33**, 675-690.

Parr, J.F., Lentfer, C.J. & Boyd, W.E. (2001) A comparative analysis of wet and dry ashing techniques for the extraction of phytoliths from plant material. *Journal of Archaeological Science*, **28**, 875-886.

Patterson, K.D. (1988) Epidemics, famines, and population in the Cape Verde Islands, 1580-1900. *The International Journal of African Historical Studies*, **21**, 291-313.

Pausata, F.S., Gaetani, M., Messori, G., Berg, A., de Souza, D.M., Sage, R.F. & deMenocal, P.B. (2020) The Greening of the Sahara: Past Changes and Future Implications. *One Earth*, **2**, 235-250.

Payne, R.J. & Egan, J. (2019) Using palaeoecological techniques to understand the impacts of past volcanic eruptions. *Quaternary International*, **499**, 278-289.

Pezeshki, S. & DeLaune, R. (2012) Soil oxidation-reduction in wetlands and its impact on plant functioning. *Biology*, **1**, 196-221.

Piperno, D.R. (2006) *Phytoliths: a comprehensive guide for archaeologists and paleoecologists*. Lanham, Rowman Altamira, New York, USA.

Plesner, S., Holm, P.M. & Wilson, J.R. (2003) 40 Ar–39 Ar geochronology of Santo Antão, Cape Verde Islands. *Journal of Volcanology and Geothermal Research*, **120**, 103-121.

Pogue, S.J., Dearing, J.A., Edwards, M.E. & Poppy, G.M. (2015) Examining change in complex social-ecological systems using multiple long-term records: the New Forest–a case study. *WIT Transactions on The Built Environment*, **168**, 273-287.

Prins, M.A. & Weltje, G.J. (1999) *End-member modeling of siliciclastic grain-size distributions: the late Quaternary record of eolian and fluvial sediment supply to the Arabian Sea and its paleoclimatic significance*, in: Harbaugh, J. (Ed.), *Numerical Experiments in Stratigraphy: Recent Advances in Stratigraphic and Sedimentologic Computer Simulations*. SEPM (Society for Sedimentary Geology) Special Publication, pp. 91–111.

Ramalho, R.A. (2011) *Building the Cape Verde Islands*. Springer Science & Business Media.

Rando, J.C. (2003) Protagonistas de una catástrofe silenciosa. Los vertebrados extintos de Canarias. *El Indiferente*, **14**, 4-15.

Rando, J.C., Alcover, J.A., Navarro, J.F., García-Talavera, F., Hutterer, R. & Michaux, J. (2008) Chronology and causes of the extinction of the Lava Mouse, Malpaisomys insularis (Rodentia: Muridae) from the Canary Islands. *Quaternary Research*, **70**, 141-148.

Reaser, J.K., Meyerson, L.A., Cronk, Q., De Poorter, M., Eldrege, L., Green, E., Kairo, M., Latasi, P., Mack, R.N. & Mauremootoo, J. (2007) Ecological and socioeconomic impacts of invasive alien species in island ecosystems. *Environmental Conservation*, **34**, 98-111.

Ribeiro, O. (1960) *A ilha do Fogo e as suas erupções.* Junta de investigaçôes do ultramar, Ministerio do Ultramar, Lisbon, Portugal.

Rick, T.C., Kirch, P.V., Erlandson, J.M. & Fitzpatrick, S.M. (2013) Archeology, deep history, and the human transformation of island ecosystems. *Anthropocene*, **4**, 33-45.

Ritchie, J., Eyles, C. & Haynes, C.V. (1985) Sediment and pollen evidence for an early to mid-Holocene humid period in the eastern Sahara. *Nature*, **314**, 352-355.

Ritchie, J.C. & McHenry, J.R. (1990) Application of radioactive fallout cesium-137 for measuring soil erosion and sediment accumulation rates and patterns: a review. *Journal of Environmental Quality*, **19**, 215-233.

Rodrigues, N.M.L. (1997) Ca*pe Verde: site and archaeological heritage conservation at Cidade Velha*, in: Ardouin, C.D. (Ed.), *Museums and Archaeology in West Africa*. Smithsonian Institution Press, Oxford, James Currey and Washington, pp. 98-104.

Rognon, P., Coude-Gaussen, G., Revel, M., Grousset, F.E. & Pedemayl, P. (1996) Holocene Saharan dust deposition on the Cape Verde Islands: sedimentological and Nd-Sr isotopic evidence. *Sedimentology*, **43**, 359-366.

Romeiras, M.M., Catarino, L., Torrão, M.M. & Duarte, M.C. (2011) Diversity and origin of medicinal exotic flora in Cape Verde Islands. *Plant Ecology and Evolution*, **144**, 214-225.

Romeiras, M.M., Catarino, S., Gomes, I., Fernandes, C., Costa, J.C., Caujapé-Castells, J. & Duarte, M.C. (2016) IUCN Red List assessment of the Cape Verde endemic flora: towards a global strategy for plant conservation in Macaronesia. *Botanical Journal of the Linnean Society*, **180**, 413-425.

Romeiras, M.M., Duarte, M.C., Santos-Guerra, A., Carine, M. & Francisco-Ortega, J. (2014) Botanical exploration of the Cape Verde Islands: from the pre-Linnaean records and collections to late 18th century floristic accounts and expeditions. *Taxon*, **63**, 625-640.

Romeiras, M.M., Monteiro, F., Duarte, M.C., Schaefer, H. & Carine, M. (2015) Patterns of genetic diversity in three plant lineages endemic to the Cape Verde Islands. *AoB Plants*, **7**, plv051.

Romero, A., Chilbert, S. & Eisenhart, M.G. (1999) Cubagua's Pearl-Oyster beds: the first depletion of a natural resource caused by Europeans in the American Continent. *Journal of Political Ecology: Case Studies in History and Society*, **6**, 57-78.

Rostain, S. (2016) *Islands in the rainforest: landscape management in pre-Columbian Amazonia*. Routledge, Walnut Creek (CA).

Rull, V., Lara, A., Rubio-Inglés, M.J., Giralt, S., Gonçalves, V., Raposeiro, P., Hernández, A., Sánchez-López, G., Vázquez-Loureiro, D. & Bao, R. (2017) Vegetation and landscape dynamics under natural and anthropogenic forcing on the Azores Islands: A 700-year pollen record from the São Miguel Island. *Quaternary Science Reviews*, **159**, 155-168.

Rushdi, A.I., DouAbul, A.A., Al-Maarofi, S.S. & Simoneit, B.R. (2018) Impacts of Mesopotamian wetland re-flooding on the lipid biomarker distributions in sediments. *Journal of Hydrology*, **558**, 20-28.

Schaan, D. (2010) Long-term human induced impacts on Marajó Island landscapes, Amazon estuary. *Diversity*, **2**, 182-206.

Schäfer, H. (2003) Chorology and diversity of the Azorean flora. *Willdenowia*, **33**, 481-482.

Schlesinger, W.H., Bruijnzeel, L., Bush, M.B., Klein, E.M., Mace, K.A., Raikes, J.A. & Whittaker, R. (1998) The biogeochemistry of phosphorus after the first century of soil development on Rakata Island, Krakatau, Indonesia. *Biogeochemistry*, **40**, 37-55.

Schüler, L. & Hemp, A. (2016) Atlas of pollen and spores and their parent taxa of Mt Kilimanjaro and tropical East Africa. *Quaternary International*, **425**, 301-386.

Shabaka, L.H. (2013) *Transformation of "old" slavery into Atlantic slavery: Cape Verde Islands, C. 1500–1879*. Doctoral thesis, Michigan State University.

Shanahan, T.M., McKay, N.P., Hughen, K.A., Overpeck, J.T., Otto-Bliesner, B., Heil, C.W., King, J., Scholz, C.A. & Peck, J. (2015) The time-transgressive termination of the African Humid Period. *Nature Geoscience*, **8**, 140.

Siegel, P.E., Jones, J.G., Pearsall, D.M., Dunning, N.P., Farrell, P., Duncan, N.A., Curtis, J.H. & Singh, S.K. (2015) Paleoenvironmental evidence for first human colonization of the eastern Caribbean. *Quaternary Science Reviews*, **129**, 275-295.

Sluyter, A (1997) Analysis of maize (Zea mays subsp. mays) pollen: Normalizing the effects of microscope-slide mounting media on diameter determinations. *Palynology*, **21**, 35-39.

Steffen, W., Broadgate, W., Deutsch, L., Gaffney, O. & Ludwig, C. (2015) The trajectory of the Anthropocene: the great acceleration. *The Anthropocene Review*, **2**, 81-98.

Tershy, B.R., Shen, K.-W., Newton, K.M., Holmes, N.D. & Croll, D.A. (2015) The importance of islands for the protection of biological and linguistic diversity. *Bioscience*, **65**, 592-597.

Tierney, J.E., Pausata, F.S., deMenocal, P.B. (2017) Rainfall regimes of the Green Sahara. *Science Advances*, **3**, e1601503.

Troll, V.R., Deegan, F.M., Burchardt, S., Zaczek, K., Carracedo, J.C., Meade, F.C., Soler, V., Cachao, M., Ferreira, J., Barker, A.K. (2015) Nannofossils: the smoking gun for the Canarian hotspot. *Geology Today*, **31**, 137-145.

van Dam, H., Mertens, A. & Sinkeldam, J. (1994) A coded checklist and ecological indicator values of freshwater diatoms from the Netherlands. *Netherland Journal of Aquatic Ecology*, **28**, 117-133.

van Geel, B., Buurman, J., Brinkkemper, O., Schelvis, J., Aptroot, A., van Reenen, G. & Hakbijl, T. (2003) Environmental reconstruction of a Roman Period settlement site in Uitgeest (The Netherlands), with special reference to coprophilous fungi. *Journal of Archaeological Science*, **30**, 873-883.

van Geel, B., Gelorini, V., Lyaruu, A., Aptroot, A., Rucina, S., Marchant, R., Sinninghe Damsté, J.S. & Verschuren, D. (2011) Diversity and ecology of tropical African fungal spores from a 25,000-year palaeoenvironmental record in southeastern Kenya. *Review of Palaeobotany and Palynology*, **164**, 174-190.

van Langevelde, F., Van De Vijver, C.A., Kumar, L., Van De Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L. & Bond, W.J. (2003) Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology*, **84**, 337-350.

van Leeuwen, J.F., Froyd, C.A., van der Knaap, W.O., Coffey, E.E., Tye, A. & Willis, K.J. (2008) Fossil pollen as a guide to conservation in the Galápagos. *Science*, **322**, 1206-1206.

Vellend, M. (2017) The biodiversity conservation paradox. *American Scientist*, **105**, 94-101.

von Suchodoletz, H., Glaser, B., Thrippleton, T., Broder, T., Zang, U., Eigenmann, R., Kopp, B., Reichert, M. & Ludwig, Z. (2013) The influence of Saharan dust deposits on La Palma soil properties (Canary Islands, Spain). *Catena*, **103**, 44-52.

White, F. (1983) *The vegetation of Africa*. UNESCO, Paris.

Whittaker, R.J. & Fernández-Palacios, J.M. (2007) I*sland biogeography: ecology, evolution, and conservation*. Oxford University Press, Oxford, UK.

Whittaker, R.J., Fernández-Palacios, J.M., Matthews, T.J., Borregaard, M.K. & Triantis, K.A. (2017) Island biogeography: Taking the long view of nature's laboratories. *Science*, **357**, 8326.

Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2008) A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, **35**, 977-994.

Williams, D. (2015) Cape Verde at the End of Atlantic Slavery. *Slavery & Abolition*, **36**, 160-179.

Willis, K., Bailey, R., Bhagwat, S. & Birks, H. (2010) Biodiversity baselines, thresholds and resilience: testing predictions and assumptions using palaeoecological data. *Trends in Ecology & Evolution*, **25**, 583-591.

Willis, K.J., Araújo, M.B., Bennett, K.D., Figueroa-Rangel, B., Froyd, C.A. & Myers, N. (2007) How can a knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*, 175-187.

Willis, K.J., Gillson, L., Brncic, T.M. & Figueroa-Rangel, B.L. (2005) Providing baselines for biodiversity measurement. *Trends in Ecology & Evolution*, **20**, 107-108.

Wilmshurst, J.M. & McGlone, M.S. (1996) Forest disturbance in the central North Island, New Zealand, following the 1850 BP Taupo eruption. *The Holocene*, **6**, 399-411.

Wilmshurst, J.M., Moar, N.T., Wood, J.R., Bellingham, P.J., Findlater, A.M., Robinson, J.J. & Stone, C. (2013) Use of pollen and ancient DNA as conservation baselines for offshore islands in New Zealand. *Conservation Biology*, **28**, 202-212.

Wood, J.R., Alcover, J.A., Blackburn, T.M., Bover, P., Duncan, R.P., Hume, J.P. & Wilmshurst, J.M. (2017) Island extinctions: processes, patterns, and potential for ecosystem restoration. *Environmental Conservation*, **44**, 348-358.

Wood, J.R., Wilmshurst, J.M., Turney, C.S. & Fogwill, C.J. (2016) Palaeoecological signatures of vegetation change induced by herbivory regime shifts on subantarctic Enderby Island. *Quaternary Science Reviews*, **134**, 51-58.

Wood, J.R., Wilmshurst, J.M., Worthy, T.H. & Cooper, A. (2011) Sporormiella as a proxy for non-mammalian herbivores in island ecosystems. *Quaternary Science Reviews*, **30**, 915-920.

Wood, J.R., Wilmshurst, J.M., Worthy, T.H., Holzapfel, A.S. & Cooper, A. (2012) A lost link between a flightless parrot and a parasitic plant and the potential role of coprolites in conservation paleobiology. *Conservation Biology*, **26**, 1091-1099.

Zobel, D.B. & Antos, J.A. (2017) Community reorganization in forest understories buried by volcanic tephra. *Ecosphere*, **8**, e02045.