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3 Anthropogenic transitions from forested to human-dominated
4 landscapes in southern Macaronesia

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Abstract

The extinction of iconic species such as the Dodo and the deforestation of Easter Island are emblematic of the transformative impact of human colonization of many oceanic islands, especially those in the tropics and sub-tropics. Yet, the interaction of pre-historic and colonial-era colonists with the forests and forest resources they encountered can be complex, varies between islands and remains poorly understood. Long-term ecological records (e.g. fossil pollen) provide the means to understand these human impacts in relation to natural change and variability pre- and post-colonization. Here we analyze palaeoecological archives in forested landscapes of the Canary Islands and Cabo Verde, first colonized c. 2400–2000 and 490 years ago respectively. We demonstrate sensitivity to regional climate change prior to human colonization, followed by divergent but gradual impacts of early human settlement. These contrast with more rapid transformation in the colonial era, associated with significant increases in anthropogenic pressures. In the Canary Islands, at least two native tree taxa became extinct and lowland thermophilous woodlands were largely converted to agricultural land, yet relictual sub-tropical laurel forests persisted with limited incursion of non-native species. In Cabo Verde, in contrast, thermophilous woodlands were depleted and substituted by open landscapes and introduced woodlands. Differences between these two archipelagos reflect the changing cultural practices and societal interactions with forests and illustrate the importance of long-term data series in understanding the human footprint on island ecosystems; information that will be critically important for current and future forest restoration and conservation management practices in these two biodiversity hotspots

Significance Statement

Assessing the ecological consequences of human settlement can help preserve island forests and their ecosystem services, but to understand the legacy of these interactions requires datasets that span centuries. We used palaeoecological data (e.g. fossil pollen) to show that pre-human Holocene forests were dynamic in response to climatic changes, and that human colonization led to increased incidence of fire, soil erosion and grazing impacts in the Canary Islands and Cabo Verde. Humans have driven compositional convergence within the thermophilous woodland zone of Cabo Verde but in the Canary Islands relictual fragments of laurel forests persist. Our long-term view highlights the legacy of past human impacts, and what tree species to restore and conserve in thermophilous woodlands within these biodiversity hotspots.

Main Text

Introduction

Human colonization of virtually the entirety of the tropics and sub-tropics was accomplished by the start of the Holocene^{1, 2}. However, remote oceanic islands provide the exceptions to this generalization, many having been first colonized in late pre-historic times (c. last 3000 years) or in the colonial era (post 1400 CE)². Humans have since transformed these systems, via habitat conversion, resource exploitation, hunting, and the introduction of non-native species. Cases such as Easter Island exemplify a complete loss of pre-existing forest cover³, but often ecological cascades have had profound impacts within persisting forest communities. The loss of the Dodo on Mauritius⁴ and most of the land birds of Guam⁵ (following the introduction of the brown tree snake) are emblematic. Moreover, the response of island forests to anthropogenic drivers varies greatly among islands: whereas many forested areas on Hawaii contain many non-native species⁶, Canarian laurel forests are composed almost entirely of native species of trees and shrubs⁷. Understanding the legacy of human impacts on these remote oceanic islands, and

particularly on their forests, requires a combination of palaeoecological and archaeological studies over timelines that incorporate both pre- and post-human dynamics⁸.

For pre-historic settlers, island forests provided vital ecosystem services such as food (fruits, animal prey), medicines, shelter, tools, timber, wood for hearths and regulatory services including water flow regulation and soil erosion protection. The forested landscapes also provided growing conditions suitable for agricultural conversion. While pre-historic island societies typically interacted and traded with other islands or regions, most land-use decisions were made locally⁸.⁹. Island forests were subjected to clearance by fire⁹, increasing agricultural activities, accelerated soil erosion¹⁰, and the introduction of species such as goats, pigs and rats¹¹, which are often implicated in extinctions of native vertebrates^{11, 12}. Colonial-era first colonists, in contrast, frequently took land-use decisions focused on colonial trading networks, leading to aggressive, rapid acts of deforestation and land-use change, and generally involving accelerated rates of non-native species introduction¹³.

Here we present comparative palaeoecological analyses of two oceanic archipelagos from the biogeographical region of Macaronesia (which comprises Cabo Verde, Canaries, Selvagens, Madeira, and Azores), namely: (i) Cabo Verde, settled by the Portuguese in 1462 CE and the first tropical European colony, and (ii) the sub-tropical Canary Islands, first settled by people from North Africa around 2400–2000 BP¹⁴ and subsequently conquered by the Castilians over the course of the 15th Century. In the early colonial period, both archipelagos were inextricably connected to the development and spread of agricultural, economic and societal practices in the colonialization of the New World tropics¹³ (see Supporting Information). They thus provide ideal model systems^{15, 16} through which to understand how humans have impacted forested landscapes through diverse stages of technological and cultural development^{8, 17, 18, 19}.

Our analyses are based on five sequences from natural sediment deposits (volcanic calderas), representing two major ecosystem types (Fig. 1): first, thermophilous woodlands, thought to have originally spanned approximately 100–700 m asl in the Canaries and found from 500–1500 m asl in Cabo Verde, and second, laurel forest, which occurs from 500–600 m to 1000–1200 m in the Canary Islands but is absent from Cabo Verde (Fig. 2). To provide a comparative synthesis of the natural dynamics of these forested landscapes over time and how humans have changed them, we use multivariate analyses (ordination) to integrate palaeoecological datasets of forest composition (fossil pollen), fire regimes (charcoal), erosion (sediment elemental composition and median grain size), soil organic content (loss-on-ignition), and herbivore introductions (spores of coprophilous fungi). Prior to human colonization, forest variability within the last 10 ka showed evidence of the ecosystems responding to regional climate sensitivity, whereas after human colonization there is evidence for increased incidence of fire, soil erosion, and the arrival of domesticated animals (goats, pigs). These latter changes are associated with a reduction in the forest cover in both archipelagos and compositional convergence within the thermophilous woodland zone of the Cabo Verde islands.

Results

Palaeoecological analyses of sediment deposits from five volcanic calderas from: La Gomera, Gran Canaria (Canary Islands), Santo Antão, São Nicolau, and Brava (Cabo Verde), within the past 10 ka reveal distinct differences in pre- and post-human colonization landscape dynamics. Proxies for erosion, burning and grazing show particularly prominent changes.

Canary Islands: Sediment geochemistry for Laguna Grande (La Gomera, 1250 m asl) shows consistent values of SiO₂, Fe₂O₃, Al₂O₃, and TiO₂ from the base of the core (c. 9600 cal yr BP, 95% confidence interval, CI, 10,900–8700 cal yr BP; Fig. S1), then slight declines coincident with the regional drying trend of the End of the African Humid Period, c. 5500 cal yr BP (Fig. S2) until human colonization of the archipelago. Subsequently, values of Al₂O₃ and TiO₂ decline further,

yet SiO₂ and Al₂O₃ values abruptly rise c. 600 cal yr BP before declining again towards the present (Fig. S3). A peak in *Sporormiella* coprophilous spores also occurs c. 600 cal yr BP (Fig. 3). Macro-charcoal concentrations reach maximum values c. 1296 cal yr BP (95% CI 1926–940 cal yr BP, Fig. 3, Fig. S3). At Valleseco (Gran Canaria, 870 m asl), sediments show stable Fe₂O₃, Al₂O₃ and TiO₂ content from 5000 to 2500 cal yr BP, and enrichment in SiO₂ coinciding with peaks in macro-charcoal 2260 cal yr BP (95% CI 2517–2063 cal yr BP) followed by the highest concentrations of *Sporormiella* spores in the record, c. 2031 cal yr BP (95% CI 2364–1951 cal yr BP). Due to soil removal for agricultural purposes the record has a top date of c. 1208 cal yr BP.

Cabo Verde: sites recording pollen from thermophilous woodland taxa are located in Cova Galinha (Brava, 810 m asl), Calderinha (São Nicolau, 1000 m asl), and Cova de Paúl (Santo Antão, 1150 m asl). The Brava site shows episodes of increased Al and SiO₂ between 8000 and 7000 cal yr BP, and increases in median grain size c. 4000 cal yr BP (95% CI 4326–3838 cal yr BP; Fig. 3, Fig. S3). Increased charcoal concentrations and peaks in *Sporormiella* spores occurred after c. 400 cal yr BP (95% CI 613–207 cal yr BP; Fig. 3). The São Nicolau site records increased median grain sizes and Ti % between 6000 and 5000 cal yr BP (Fig S2), and these erosion indicators steadily increased after 468 cal yr BP (95% CI 634–343 cal yr BP). The charcoal increases after c. 600 cal yr BP in this site and is abundant until the present (Fig. S3). On Santo Antão the sediments show steady increases in Si, Al, Ti % and median grain size between c. 470 cal yr BP (95% CI 640–320 cal yr BP) and the present, also coinciding with increased macro-charcoal concentrations and peaks of coprophilous fungal spores (Fig. 3, Fig. S2, Fig. S3).

Detrended Correspondence Analysis (DCA) of the fossil pollen records of the five sites revealed a gradient in the first axis from La Gomera laurel forest (right) to recent samples from the Cabo Verde thermophilous zone (left), with the second axis describing a gradient from pre-human colonization samples from Brava (low) to recent Gran Canaria samples (high) (Fig. 4a). In compositional terms, taxa from Canarian laurel forests such as Lauraceae, *Morella*, and Ericaceae have positive scores within DCA axis-1, while introduced taxa in Cabo Verde plot with negative scores (e.g. *Eucalyptus*, *Opuntia*, *Persea americana*, *Zea mays*; Fig. S4). DCA axis-2 positive values feature taxa typical for Canarian open landscapes (*Kleinia*, Fabaceae, *Rumex*) and thermophilous woodland taxa (Rhamnaceae, *Juniperus*), while negative scores correspond to taxa typical of humid environments (*Salix*, Juncaceae) and native taxa from Cabo Verdean thermophilous woodlands (*Dracaena draco*, Urticaceae, *Lotus*) (Fig. S4). The two Canarian data series show generally increasing values in axis-2 over time, whereas the Cabo Verde series converge within the left quadrant of the DCA plot (low values in both axes).

CCA analyses for each archipelago separately permit testing of the associations between proxies of vegetation change and environmental change (Fig. 4b, Table S1). For the Canary Islands, CCA axis-1 is negatively correlated with herbivores and soil organic matter and positively correlated with erosion variables, while axis-2 is negatively correlated with local fires. Samples dated between 2500 cal yr BP and the present representing the thermophilous woodland of Gran Canaria, plot with fire and erosion. Samples dated between 800 cal yr BP and present in the laurel forest of La Gomera have higher organic matter content (LOI) and herbivore presence (Fig. 4b, Table S1). Conversely, the Cabo Verde plot shows correlation between CCA axis-1 and soil organic matter and herbivores, and axis-2 with erosion, and samples dated between 500 cal yr BP are associated with herbivore presence, erosion, and local fires. Finally, samples from pre-human periods from São Nicolau and Santo Antão are associated with higher levels of organic matter (Fig. 4b, Table S1).

Discussion

A Holocene view of forest natural variability in southern Macaronesia

The Canarian laurel forests and Canarian/Cabo Verdean thermophilous woodlands were compositionally dynamic before human arrival. Changing environmental conditions are associated with shifts in species abundance and probably in altitudinal distribution. For example, the environmental changes consequent upon the shift in the monsoonal circulation at the end of the African Humid Period (c. 5500 cal yr BP)^{20, 21} illustrate the ecological effects of relatively abrupt regional change in Macaronesian forests. During this humid period, the continuous 10,000-yr record of Laguna Grande (La Gomera) geochemical values are generally stable, indicating a lack of abrupt erosion events, but pollen data shows changes in composition in response to the advent of drier climatic conditions²². Around 5500 years ago, decreases in the arboreal pollen from hygrophilous species such as the palm *Phoenix canariensis* and the willow *Salix canariensis* are evident, while pollen from the more drought-tolerant and xerophilous *Morella* and *Erica*, taxa of woody heath, increases. These taxa characterize a landscape that has endured until the present day²². The change also coincides with an acceleration in sediment accumulation rate and the occurrence of local fires, shown by an increase in macro-charcoal concentrations. Similarly, at Laguna de Valleseco (Gran Canaria) thermophilous woodland (*Juniperus* and *Phoenix canariensis*) was dominant at c. 4500 cal yr BP²³. Subsequently, charcoal concentrations increased between c. 4000 and 3000 cal yr BP, indicating great fire incidence prior to human colonization. This shift in fire regime, likely due to increasing aridity, drove a decline in thermophilous elements and increases in herbaceous taxa.

Before human arrival in Cabo Verde 560 years ago, pollen data from São Nicolau indicate a landscape dominated by woodlands on the upper slopes of Monte Gordo, the highest peak of the island (1200 m asl). This woodland included *Ficus* (fig) trees, *Dracaena draco* (dragon tree) and the shrub *Euphorbia tuckeyana*, with occasional acacia trees (*Faidherbia albida*)²⁴. These thermophilous woodlands were likely restricted to the highlands²⁵. In contrast, in Cova de Paúl (Santo Antão), pollen data suggest a more open landscape, with tree species represented by *Ficus*, *Faidherbia albida*, *Dichrostachys cinerea* and Sapotaceae (genus *Sideroxylon*). This is similar to Cova Galinha (Brava), which records the presence of the shrub *Dodonaea viscosa*, plus the trees *Ficus* and *Dracaena draco*^{26, 27}. During the period before human arrival in Cabo Verde, soil geochemistry indicates episodes of sediment erosion related to intense precipitation episodes during the African Humid Period on São Nicolau (c. 6000–5000 cal yr BP)²⁴ and Brava (c. 8000–7000 cal yr BP). Cabo Verdean pre-human landscapes also experienced fire events, as evidenced by discrete charcoal peaks in Santo Antão c. 2000 cal yr BP; and a prominent charcoal peak in São Nicolau c. 600 cal yr BP (95% CI 790–480 cal yr BP) that may be natural or anthropogenic. Prior to human disturbance, natural fires, probably resulting from regionally drier conditions, may have been linked to scrub encroachment²⁴.

Cumulative effects of first human colonization

Laurel forests and thermophilous woodlands of the Canary Islands and Cabo Verde have undergone radically different regimes of human impact: two waves of human colonization in the Canary Islands, a pre-colonial indigenous settlement c. 2400–2000 cal yr BP, followed by Castilian conquest after 1402 CE, and colonial settlement in Cabo Verde after 1460 CE. We found strong evidence of an increase in anthropogenic pressures (soil erosion, local fires, and grazing activity) linked to human arrival in all studied sites. Forests in both archipelagos displayed heterogeneous ecological responses to initial anthropogenic pressures (Fig. 3), as shown by two different trajectories over time within the multivariate analyses (Fig. 4): divergence for the Canarian laurel and thermophilous woodlands due mainly to differences in forest type, and convergence in Cabo Verde due to reduction of woodland cover and plant community homogenisation related to the introduction of cultivars and invasive species.

The first use of Canarian forests by aboriginal settlers was probably related to livestock keeping (e.g. pigs), and the gathering of useful species for food (*Arbutus*, *Visnea*, *Canarina*), wood (*Pinus*, *Apollonias*, *Juniperus*, *Olea*, *Persea*) or fodder (*Chamaecytisus*, *Teline*)⁷. These activities

appeared to have had little impact on the forest. In La Gomera's laurel forest, for example, c. 1800 years ago, local fires and organic matter flux within the basin only showed discrete increases, and the laurel forest composition did not change significantly (Figs 3 and 4). This may reflect initially small local human populations whose permanent dwellings were at lower elevation²⁸. Later, at c. 750 cal yr BP (95% CI 830–700) sharp increases occur in indicators of herbivore presence (coprophilous fungi) probably representing introduced ovicaprids (*Capra hircus*, *Ovis aries*) and pigs (*Sus domestica*), followed by higher organic matter flux. These two environmental variables, which are potentially linked, are identified as the main drivers of recent subtle laurel forest change.

In Gran Canaria's thermophilous woodlands, significant local fires and soil erosion are the first evidence for the impact of aboriginal people. Between 2640 and 2250 cal yr BP, peaks in charcoal suggests that the first people colonizing the island used fires for land clearing; at this time there was an associated decline in trees and an expansion of herbaceous plants²³. Shortly after, soil erosion increased, possibly reflecting a change in sediment source and amount associated with the opening of the landscape (Fig. 3). CCA results support this scenario, linking fire and erosion as the most significant environmental drivers in the degradation of the thermophilous forests of Gran Canaria (Fig. 4). The presence of herbivores (evidenced by spores of coprophilous fungi) also increased sharply c. 2130 cal yr BP (95% CI 2360–1950 cal yr BP). This finding aligns with another palaeoecological record from La Laguna (Tenerife), which shows the rapid decline of at least two tree taxa, oak (*Quercus* spp.) and hornbeam (*Carpinus* cf. *betulus*), most likely reflecting human transformation of the landscape on a large scale through burning and grazing²⁹. The Castilian arrival in the XV century brought new impacts on vegetation related to tree-felling technology, wood demand and the translocation of forest soils for improving agricultural land¹⁹.

Within the thermophilous woodlands and open landscapes of Cabo Verde, the onset of anthropogenic pressures occurred after 1462 CE and the arrival of European settlers (Fig. 3). In the studied woodlands and open landscapes, several drivers –fire, herbivory, and consequent soil erosion– were simultaneously associated with land-use change, as shown in the CCA (Fig. 4). Soil organic matter decreased after human settlement, indicating that soils lost some organic content, likely due to increased soil erosion, which diluted organic inputs into the sediment. Anthropogenic pressures, namely the exploitation of fig trees for wood and of dragon trees for medicine³⁰, are historically documented in the in São Nicolau and Santo Antão (the northern islands); these practices appear to have severely depleted the thermophilous woodlands of Cabo Verde and led to a decrease in extent of woody taxa²⁴. These compounded human-driven impacts likely played a role in the socio-ecological crises that affected the archipelago between the 16th and early 20th centuries^{31, 32}, and consequent land abandonment could have created epicentres for the spread of introduced species. The pollen records show an increasing presence of pollen from introduced species after 500 cal yr BP, including herbaceous taxa such as *Asystasia*, *Portulaca*, Rosaceae, *Centaurea*, *Commelina benghalensis*, and taxa currently considered invasive species (or with potential of invasiveness) such as *Lantana camara*, Agavoidea and *Opuntia*, as well as pollen from cultivated species such as *Zea mays*, Cerealia, *Ipomoea batatas* and *Persea americana*^{26, 2424}. *Lantana camara* is currently being targeted for action as its substantial and increasing biomass is flammable and generates a high wildfire risk³³. Thus, our analyses suggest that vegetation differences between islands have been diminished due to the impact of colonial activities such as woodland clearance and also by species introductions (Fig. 4). In sum, the legacy of 500 years of land-use in Cabo Verde appears to be a trend towards biotic homogenization and the loss of landscape authenticity. If remaining woodland differences are not maintained and protected, then the biodiverse landscapes of the archipelago could decline even further.

From knowledge to management: the future of southern Macaronesian forests

Given that 2021 is the launch year of the UN's International Decade of Restoration and Conservation³⁴, the question of understanding past tree coverage and composition before initiating forest restoration projects is moving rapidly up the political agenda. To understand the former composition of forests requires datasets that span centuries due to the time it takes trees to reach maturity. Our integrated palaeoecological analyses provide an important comparative perspective to understanding contemporary (sub)tropical island forest status, and a quantitative evidence-based to guide forest restoration³⁵. The evidence suggests that in the Canary Islands thermophilous woodlands were heavily impacted since the first human settlement, while continued exploitation during the historical period has resulted in extreme reduction of its natural distribution and in poor condition for recovery, currently being the most threatened ecosystem of the Canaries³⁶. The laurel forest was comparatively less affected by first contact and subsequent anthropogenic pressures (indeed they have experienced a significant natural recovery in the last three decades⁷). In Cabo Verde, the story is different. Our analysis suggests that the degradation of the thermophilous woodlands through human pressures greatly surpassed their ability to recover naturally, especially in a context of rapid land use changes (agriculture, livestock, wood provisioning), soil erosion, fire occurrence, and the introduction of invasive species (e.g. *Furcraea foetida*, *Lantana camara*, *Leucaena*), all heightened by episodes of socio-ecological stress between 1550 and 1750 CE³². Importantly, our findings show loss of biotic distinctiveness of the thermophilous woodlands of Cabo Verde, through a combination of decreasing endemics and the introduction of generalist species, generating 'biotic homogenization'³⁷. This trend of forest convergence during the past 500 years suggests a generalized loss of landscape authenticity at archipelago level that may have had an impact on overall island forest biodiversity and resources. The most likely explanation for why thermophilous woodlands rather than laurel forests were more heavily impacted by human activities may be related to their geographical location. The thermophilous woodlands occupy the mid-elevations of the Canaries and the highlands in Cabo Verde. These are areas that were probably more suitable for human land use in each archipelago, as they feature fertile soils and water resources.

There is growing global interest in the restoration of degraded, damaged or destroyed forest ecosystems to provide the goods and services that people value and benefit from (including sequestration of atmospheric CO₂, water flow regulation, soil erosion protection and important habitats for native forest biodiversity^{38, 39}), and in this context the questions of which tree species to plant and where, are a pressing issue. To answer this question requires understanding how and why forests changed from their pre-anthropogenic baselines⁸. In biodiversity hotspots such as the Canary Islands and Cabo Verde, understanding legacies of past human impacts becomes even more critical, because planting fast growing non-native species can lead to serious environmental degradation and biodiversity loss. This is a situation that is now common in many biodiverse areas of the world, often representing an attempt to sequester atmospheric CO₂. Conservation managers may face a trade-off between rapid reforestation to provide particular ecosystem goods (e.g., to fight soil erosion) and the spread of invasive species that may ultimately endanger the endemic flora.

In both Cabo Verde and the Canary Islands, legislation and afforestation practices to address land degradation were put in place during the early mid-20th century^{36, 40}. In the Canaries, efforts were first focused on the recovery of pine forests, partly planting Canarian pine but also using non-native fast growing tree species, including *Pinus radiata* and *Eucalyptus*. Early pine forest plantations pursued provision (source of wood) and regulation (soil erosion control) goals. Only in the last two decades active restoration, focused on conservation aims, has taken place in the laurel forest (e.g. Gran Canaria⁷) and thermophilous woodlands (e.g. Teno, Tenerife³⁶). In Cabo Verde, plantations of fast-growing drought-resistant plant species were established, such as *Prosopis juliflora*, *Eucalyptus*, and *Pinus canariensis*. The result is that, currently, only a small fraction of the forested territory supports endemic and native woodlands that include woody species inhabiting the highlands such as *Dracaena draco*, *Ficus sycomorus*, *Ficus sur*, *Dodonaea viscosa*, *Sideroxylon marginata*, *Faidherbia albida* and *Dichrostachys*

cinerea in the midlands, and *Tamarix senegalensis* and *Phoenix atlantica* in the coastal areas²⁵. These native trees could be included in reforestation efforts, together with fruit-producing taxa such as Cabo Verdean native *Ficus* that could be beneficial for the local fauna. In addition, further research on the use of timber plantation development may help ascertain if the undesirable effects, such as inhibiting forest understory growth⁴⁰, can be outweighed by the potential benefits, such as soil protection.

Our results also show the importance of applying targeted restoring efforts towards the remaining thermophilous forest. In this context, where habitat loss and fragmentation are dominating the island's landscape and in the event of anthropogenic climate change¹⁹, restoration practices may be especially challenging and conservationists might be required to implement complementary *ex-situ* measures such as safe warding thermophilous plant species in seed banks to preserve the genetic diversity⁴¹. Therefore, enhancing seed banks in both the Canary Islands (e.g. the Canarian Botanical Garden "Viera y Clavijo") and in Cabo Verde (e.g. Cape Verde National Agricultural Research and Development Institute, INIDA) should also be considered as a conservation priority. This long-term view has highlighted the amount of change that these island forests have undergone and the urgent need to preserve and restore the existing forest remnants, when possible, with extra efforts dedicated to the more seriously diminished communities of thermophilous woodlands in both archipelagos.

Materials and Methods

Sedimentary sequences: Our analyses comprise sediment records previously published and obtained within highland and mid-elevation volcanic calderas in five islands: La Gomera and Gran Canaria (Canary Islands) and Santo Antão, São Nicolau and Brava (Cabo Verde). Sample collection was carried out through coring techniques of the former lakes and calderas of Laguna Grande (La Gomera), Laguna de Valleseco (Gran Canaria) and Cova de Paúl (Santo Antão), and direct sampling from soil profiles was done in Calderinha (São Nicolau) and Cova Galinha (Brava) sites (Fig. 1).

Chronology: We constructed age-depth models using the recently updated calibration curves (IntCal20) to convert radiocarbon dates into calibrated ages for all the island sequences using the R package *rbacon*⁴². We used model 'boundaries' in the Gran Canaria, Santo Antão and São Nicolau records to allow for differential sedimentation rates in records with pronounced changes in accumulation of sediment (Fig. S1). Bacon outputs are reported as cal yr BP; with 1950 CE as zero by definition, and a confidence interval of 95% is used for interpretation (Fig. S1, Fig. S4).

Palaeoecological datasets: We studied multiple indicators of plant biodiversity and environmental change in each site, including biotic proxies (fossil pollen, fungal spores, and charcoal particles) and abiotic proxies (granulometry and/or soil elemental composition). Proxy-specific information and details of coring sites, laboratory methods and pollen sums are provided as follows: Laguna Grande²², Laguna de Valleseco²³ and Cova de Paúl^{26,26}, Calderinha²⁴ and Cova Galinha²⁷. Rock FUS-X-Ray Fluorescence was used for the analysis of sediment geochemistry in the Canarian sites, providing oxide percentages (e.g. TiO₂) and organic matter percentage values, and pXRF was used for analysis of Cabo Verde sites, providing elemental percentage data (e.g. Ti).

Ordination analysis: For statistical analyses, percentage values of Non-Pollen Palynomorphs over pollen sum (including unidentifiable grains in Cabo Verde sites), concentration values of macro-charcoal particles, size measurements of granulometry and percentage values of XRF were normalised (values range between 0 and 1). We carried out Detrended Correspondence Analysis (DCA) with the *Vegan* package in RStudio (R core team) using pollen percentage values to quantify palynological turnover⁴³. For Canonical Correspondence Analysis (CCA), we used the same software and used normalised values of selected environmental variables. We chose samples from every environmental variable that shared depth values used in pollen analyses, and

when sampling depth values did not coincide, we selected the closest neighbouring samples. Thus, environmental variables represent roughly synchronous phenomena. We used 1) percentages of the spores of coprophilous fungi *Sporormiella* to represent herbivore abundance in the local catchment, 2) loss of ignition percentage (Cabo Verde) and organic matter percentage (Canary Islands) as a proxy of soil organic content and organic matter flux within the basins, 3) macro-charcoal particle concentrations to represent local fire occurrence, and 4) median grain size (microns) in the Cabo Verde sites and SiO₂ percentages in the Canary Island sites as proxies for erosion (sediment run-off from caldera margins).

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Figures

Figure 1.

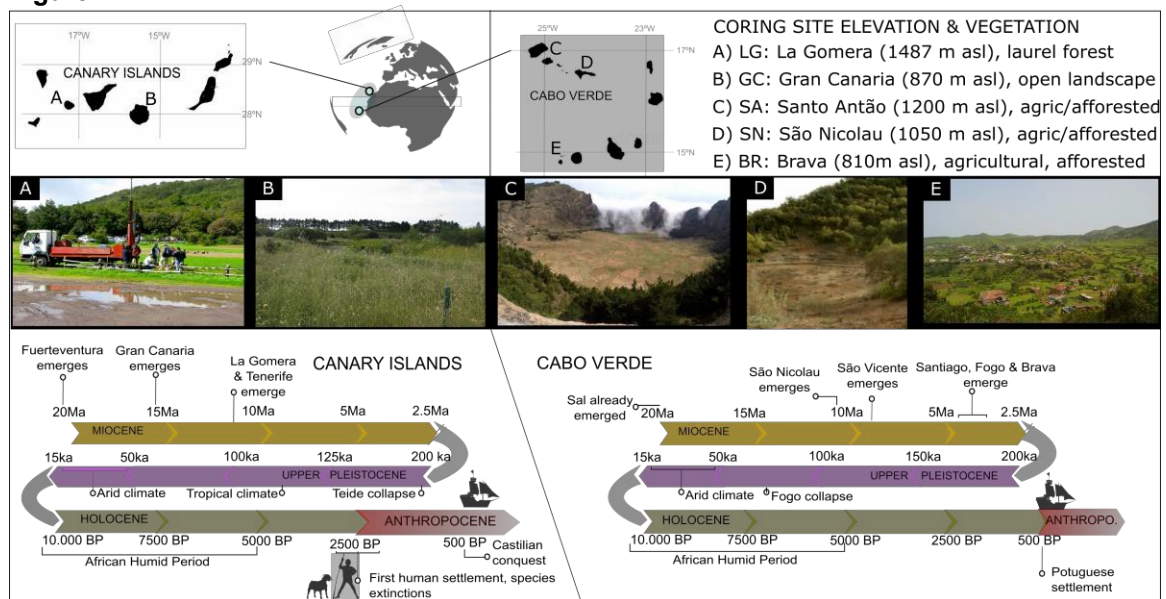


Figure 1: Maps of the Cabo Verde and the Canary Islands and photographs and elevation of the studied volcanic calderas. We use Anthropocene in an informal sense to indicate the period since human colonization, which differs island to island. In the lower panels, chronological axes showing geological, climatic and human milestones of the last 20 Myr in Southern Macaronesia. See Supporting Information text for references.

Figure 2.

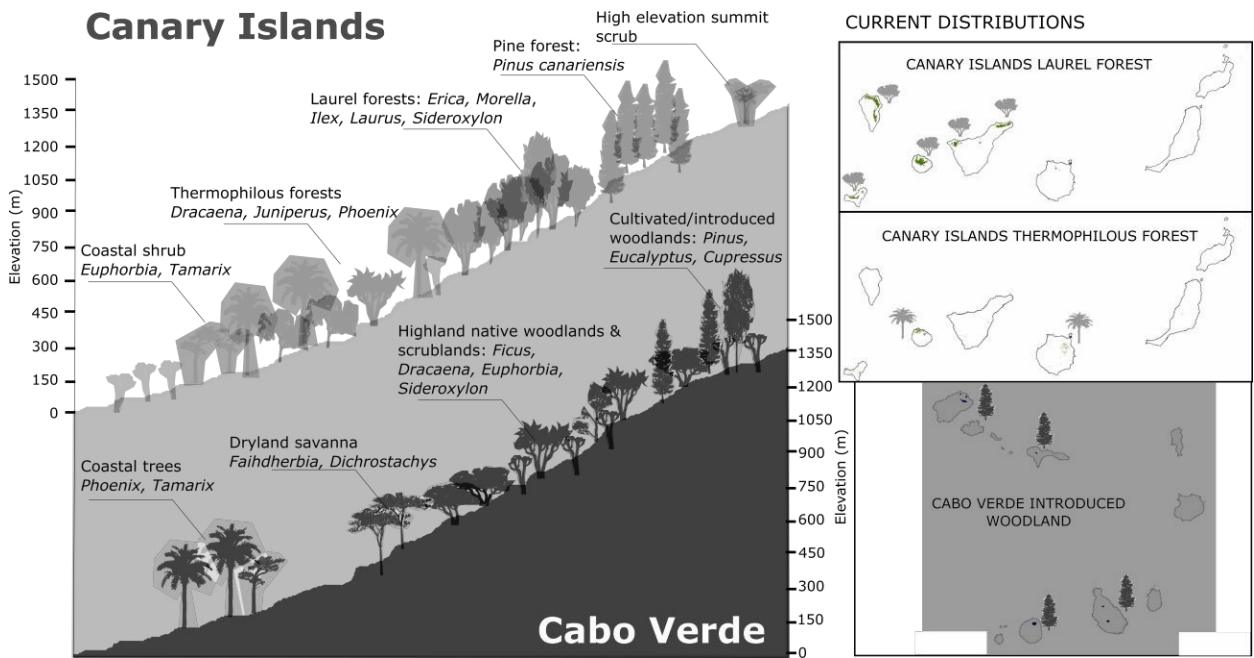


Figure 2: Distribution of woodland vegetation types in southern Macaronesia. Left: schematic elevational zonation. Right: Remaining distribution of laurel and thermophilous forest types in the Canary Islands based on del Arco et al. 2006 and of introduced woodland in Cabo Verde based on USGS 2013 data (<https://eros.usgs.gov/westafrica/land-use-land-cover-map>).

Figure 3.

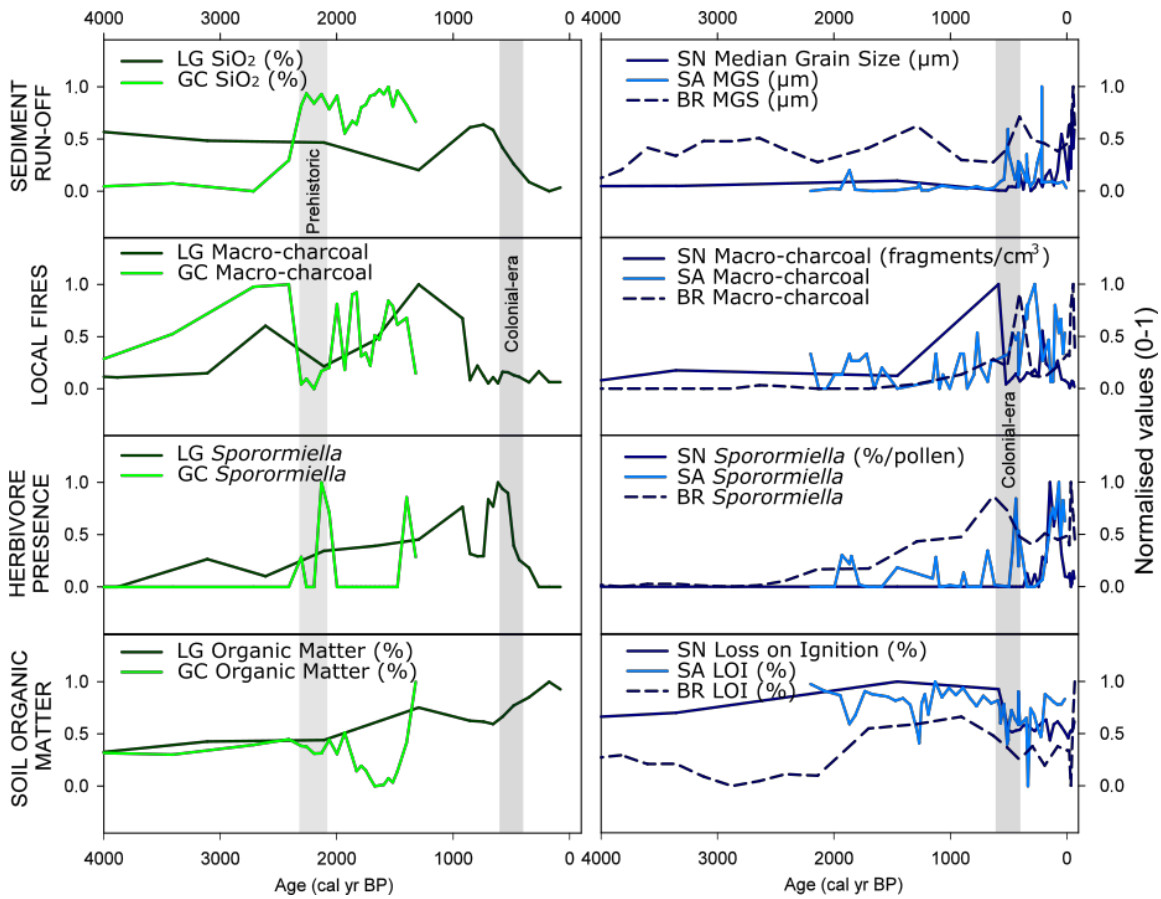


Figure 3: Longitudinal data series for key environmental proxies (normalised values 0-1) from five cores from the **Canary** (left) and **Cabo Verde islands** (right). SiO₂ content and median grain size (MGS) are indicators of rates of erosion within the catchment. Charcoal refers to macro-charcoal concentration (number of fragments per cm³) a proxy for local fires, *Sporormiella* refers to spores of these coprophilous fungi, which are indicators of presence of herbivores. Loss on Ignition (LOI) is an indicator of soil organic matter. The green vertical band indicates best estimates of data of human colonization of the Canary Islands¹⁴. Vertical bands indicate the timing of Prehistoric and European colonial settlement¹⁹.

Figure 4.

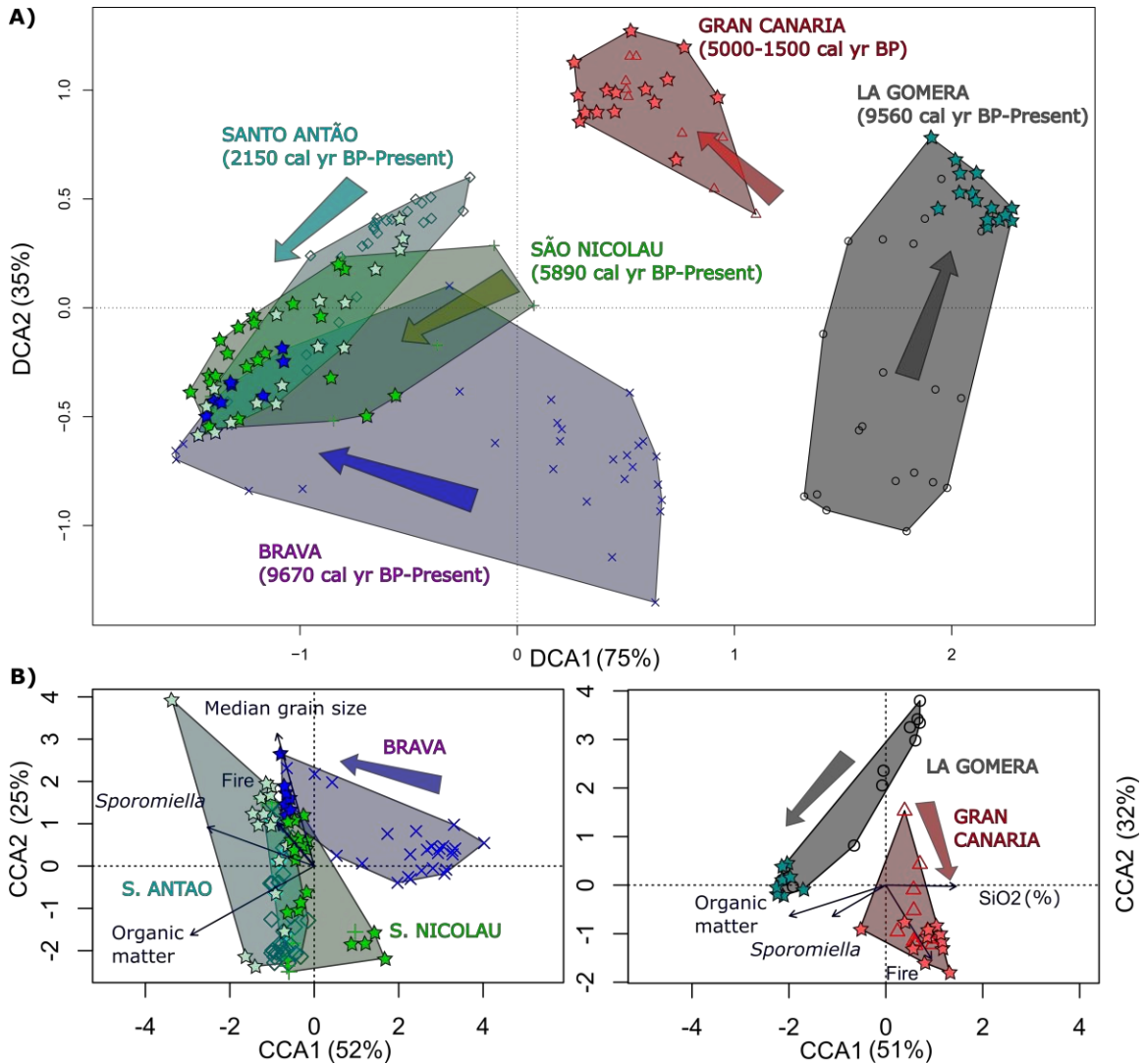


Figure 4: Ordination plots of fossil pollen data from southern Macaronesia. Colored polygons differentiate samples from different islands. Arrows show the main trend of change from older to younger samples. Upper panel: Detrended Correspondence Analysis, DCA. Stars show samples dated after human settlement, other symbols pre-human settlement. Lower panels: Canonical Correspondence Analyses, CCA for three Cape Verde islands (left) and two Canarian islands (right). CCA shows associations between pollen percentages and four proxies of environmental change (thin blue arrows): see Table S1 in Supporting Information for correlation scores with axes 1 and 2. Coring site elevations as per Fig. 1. Proxies as per Fig. 3 and Methods.



Supplementary Information for
Anthropogenic transitions from forested to human-dominated
landscapes in southern Macaronesia

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This PDF file includes:

Supplementary text
Figure S1
Figure S2
Table S1

Supplementary background information :
Biogeography of the laurel and thermophilous forests

The Canary Islands and Cabo Verde are the product of contemporaneous volcanic hotspots on the Eastern Atlantic margin of the African plate that have been active for around 60 Myr, most of the current islands emerging between 20 and 1 Maⁱ (Fig. 1). The Canaries show a subtropical-Mediterranean climate, characterized by mild temperatures, dry summers and wet winters, while Cabo Verde has a tropical monsoon climate with warm temperatures and a rainy season centred in late summer, but dry climate and scarce precipitation the rest of the yearⁱⁱ. Even with the vast distances between them (c. 1500 km) and the latitudinal north-south configuration of these archipelagos (15°), their closeness to the African continent and the sea currents and trade winds that connect them explain shared biological features as lineages have colonized and diversified across and within the archipelagos of Macaronesia^{iii, iv}.

Macaronesian islands have also acted as off-shore refuges for plant lineages and communities that became extinct on the adjacent mainland. The laurel forest native to the Azorean, Madeiran, and Canarian archipelagos is made up of some 20 tree species and is dominated by several Lauraceae genera (*Apollonias*, *Laurus*, *Ocotea*, *Persea*), some of which are relicts of the Palaeotropical Geoflora that was distributed along the margins of the Tethys Sea but mostly disappeared at the end of the Pliocene^{i, v}. In the Canaries, the survival of the laurel forest is dependent on the humidity of the cloud belt generated by trade winds on windward slopes (600-800 m asl) and is thus potentially sensitive to climate change^{vi}. The laurel forest is currently absent from the eastern Canary Islands (Lanzarote and Fuerteventura), which are too low in elevation, and from the Selvagens, which are too small and too low. In Cabo Verde, monsoon-type seasonal precipitation prevents full-year humid conditions needed to sustain laurel forests^{vii}. The higher incidence of the dust-carrying Saharan Air Layer in Cabo Verde^{viii} might have also contributed to creating harsher environmental conditions for their establishment and survival.

The thermophilous woodlands present in southern Macaronesia are typical from mid-elevations (100–300 m on windward slopes and 400–700 m on leeward slopes) in the Canaries and mid- to highland elevations (500–1500 m) in Cabo Verde, and are represented in Macaronesia by different communities that have two independent palaeogeographical origins. 1) A first floristic element is composed of old lineages (such as *Euphorbia*, *Gymnosporia*, *Hypericum*, *Sideroxylon*, etc.) stemming from the so-called African Rand-Flora^{ix}, widely distributed in the African continent during the Miocene period. After the Congo Basin tropicalization and the Sahara desertification,

these taxa found refugia in the continental African margins and the Macaronesian islands^{ix}. 2) A second element is the Plio-Pleistocene Mediterranean flora present in the Canaries, but not in Cabo Verde. Their main communities are dominated by trees such as *Juniperus*, *Olea* or *Pistacia*, which are widely distributed around the Mediterranean Basin. The assignment of *Phoenix* (the native palms of the Canaries and Cabo Verde) to the Rand Flora (itself a composite grouping described as an example of biogeographical pseudocongruence), or to the Mediterranean element, is still controversial. So too is the taxonomic adscription of the Cabo Verde palms (*P. atlantica*), which for some authors are just long-isolated populations of the date palm (*P. dactylifera*)^x. In Cabo Verde, native thermophilous forests are almost exclusively preserved in the highlands of mountainous islands, and little is known about their past distribution^{xi} (but see^{xii}). These include communities of arborescent taxa also present in lowlands, including a subspecies of dragon tree *Dracaena draco* subsp. *caboverdeana*^{xiii}, *Phoenix atlantica*, and *Tamarix senegalensis*. Tree taxa include *Ficus sur* and *Ficus sycomorus*, of Afrotropical origin, and *Sideroxylon*, of Macaronesian origin^{xiv, viii} (Fig. 2).

Historical context and culture–environment interactions

Whereas three Macaronesian archipelagos (Azores, Madeira, Cabo Verde) were first settled in the Middle Ages (Madeira 1420 CE, Azores 1439 CE after a possible early Viking settlement) by Europeans^{xv}, the Canary Islands underwent early settlement between 2400 and 2000 cal yr BP (or possibly earlier), which had profound ecological consequences^{xvi}. These first settlers of the Canary Islands, known as Canarian aborigines (and who appear to have had Libyan/Berber origins in North-West Africa), had a way of life heavily centred in animal (goat and sheep) husbandry, but also cultivated crops such as barley, wheat, beans, lentils, peas and figs and had a significant impact on the biodiversity of the islands^{xvii}. The first settlers introduced multiple species, including goats (*Capra hircus*), sheep (*Ovis aries*), pigs (*Sus domestica*), dogs (*Canis familiaris*), house mice (*Mus musculus*), and cereals (*Triticum* spp., *Hordeum vulgare*), legumes (*Lens culinaris*, *Pisum sativum*, *Vicia faba*) and fig trees (*Ficus carica*)^{xviii}. Palaeoecological evidence suggests that following human colonization, competition with introduced species, loss of habitats and hunting pressure led to the extinction of key animal species, including endemic birds, rodents and lizards prior to subsequent European conquest in the 15th Century^{xix, xx, xxi}. In the western Canary Islands, it is likely that in addition to clearance by fire, forest composition was altered by the presence of forest pigs and replacement of endemic rodents with non-native rodents, and by the gathering of useful species, either for food (*Arbutus*, *Visnea*, *Canarina*), wood (*Pinus*, *Apollonias*, *Juniperus*, *Olea*, *Persea*) or fodder (*Chamaecytisus*, *Teline*)^{vii}. Pollen data from La Laguna (560 m asl) on Tenerife indicate local

presence of *Quercus* and *Carpinus* as forest components, both of which had been lost by the time of Castilian conquest at the end of the 15th century: neither is now considered native to the Canaries^{xxii}.

The Macaronesian biogeographic region provided the setting of two main historical milestones of European colonial expansion all over the world. The Norman-Castilian conquest of the Canaries (1402–1496 CE) constituted an early precedent of European nations defeating indigenous populations and incorporating overseas territories into their kingdoms. This experience is considered as the onset of colonial domination and resource extraction strategies that characterized subsequent global colonial systems^{xxiii}. The European settlement was marked, as elsewhere, by the exposure of indigenous people to novel diseases, displacement and enslavement (for example, Canarians were taken to work in sugar plantations established after the settlement of Madeira). In the Canaries, it also involved an intensified exploitation of Canarian ecosystems and the introduction of crop plants (e.g. *Malus*, *Prunus*, *Saccharum officinarum*, *Solanum tuberosum*, *Vitis*, *Zea mays*, etc.) and animals (*Equus*, *Bos*, *Oryctolagus*)^{xv}. The Castilian arrival in the 15th century brought new impacts related to their more advanced technology, including logging the forests with iron axes and the intensified use of fire for obtaining agricultural land for cereals, vineyards and potatoes, cattle rangeland (mainly *Bos*, new varieties of *Capra* and *Ovis*, and *Equus* and *Camelus*) and the new aliens: cats, rats and rabbits. Forest impacts attributable to Castilians include the deforestation of the majority of Tenerife's thermophilous woodlands and Gran Canaria's laurel forest^{xxiv}, the fragmentation of the continuous distributions of the laurel forests in Tenerife, La Palma and El Hierro and of the thermophilous woodland in La Palma. Several sugar mills were installed soon after the conquest and their huge energetic demands constituted a key driver in the clearance of the closest forests^{vii}. Besides these more evident impacts, all the forests suffered intense degradation, acquiring lower canopies and thinner trees everywhere (except the summit region of La Gomera) and the alteration of their species composition, in favour of useful species, such as those producing good quality charcoal (*Erica* and *Morella*) or wood (*Pinus*, *Juniperus*) producers.

On the other hand, the colonization in 1462 CE of Cabo Verde by Portuguese settlers and by the African slaves brought by them from the continent, constituted the very first tropical colony of Europeans^{xxv}. In 1460 CE, the Portuguese founded the first European tropical city, Cidade Velha, on the island of Santiago. The archipelago became an important node in the early trading networks of the Portuguese empire, providing a strategic spot for the provisioning of boats with animal products and manufactures^{xv}, and being a node of the early slave trade^{xxvi}. Historical sources suggest that New World crops had crossed the Atlantic and made it to this archipelago by 1535 CE^{xxvii}, and merchant

accounts already recorded concern about the impacts of changing land-use on these islands ca. 1550 CE^{xi}. Famines and epidemics linked to drought, coupled with such human-driven landscape degradation, caused progressive isolation of Cabo Verde from the colonial trading networks^{xxviii}, outcompeted by more successful colonies such as Brazil and the islands of the Guinean Gulf^{xxix}. The first European settlers found in Cabo Verde an uninhabited territory with a relictual thermophilous woodland (*Dracaena*, *Euphorbia*, *Phoenix*, *Sideroxylon*) subject to very harsh environmental conditions, such as reiterative drought events and frequent Sahara haze (*Harmattan*). Woodlands were soon logged and burnt at mid-elevations, to provide arable (including maize, recently arrived from America) and pastoral land. Fortunately, a few remnants of such woodlands, albeit very much transformed in density and species composition, were able to endure on the summits of the higher islands, where demand for agricultural use was limited^{viii}.

Fig. S1.

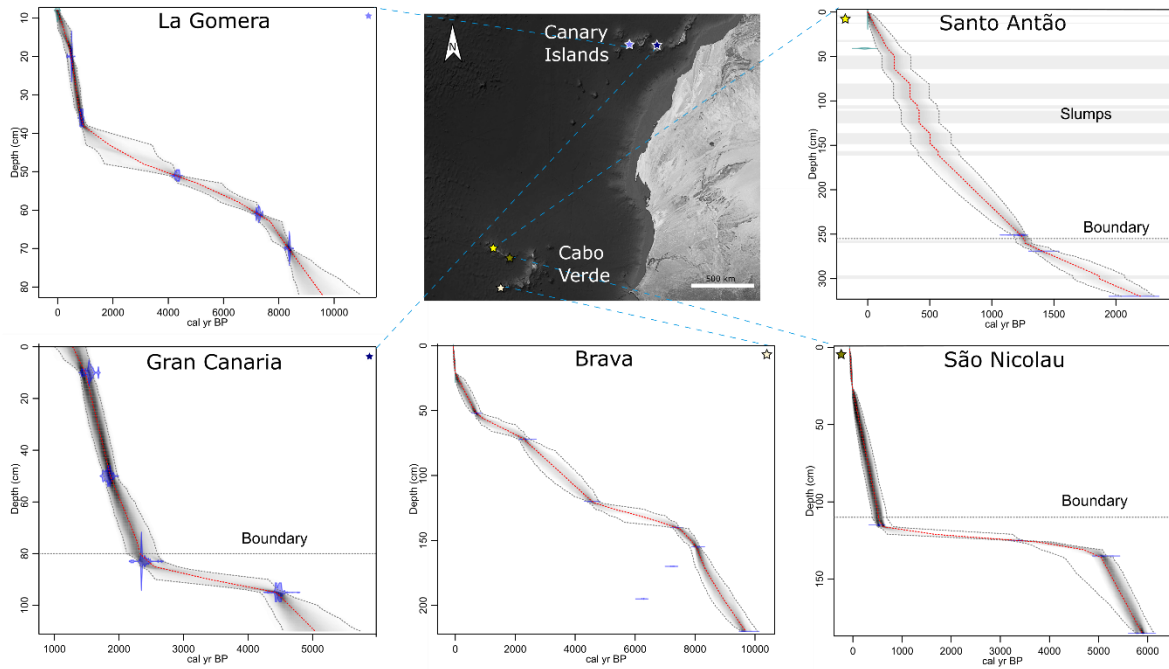


Fig. S1: Age–depth models of the five studied sites in the Canary Islands and Cabo Verde, produced with the rbacon package in Rstudio. Slumps (episodes of rapid sedimentation) were permitted in segments dominated by gravel, and boundaries were introduced to allow for abrupt changes in sedimentation rate in three sites.

Fig. S2.

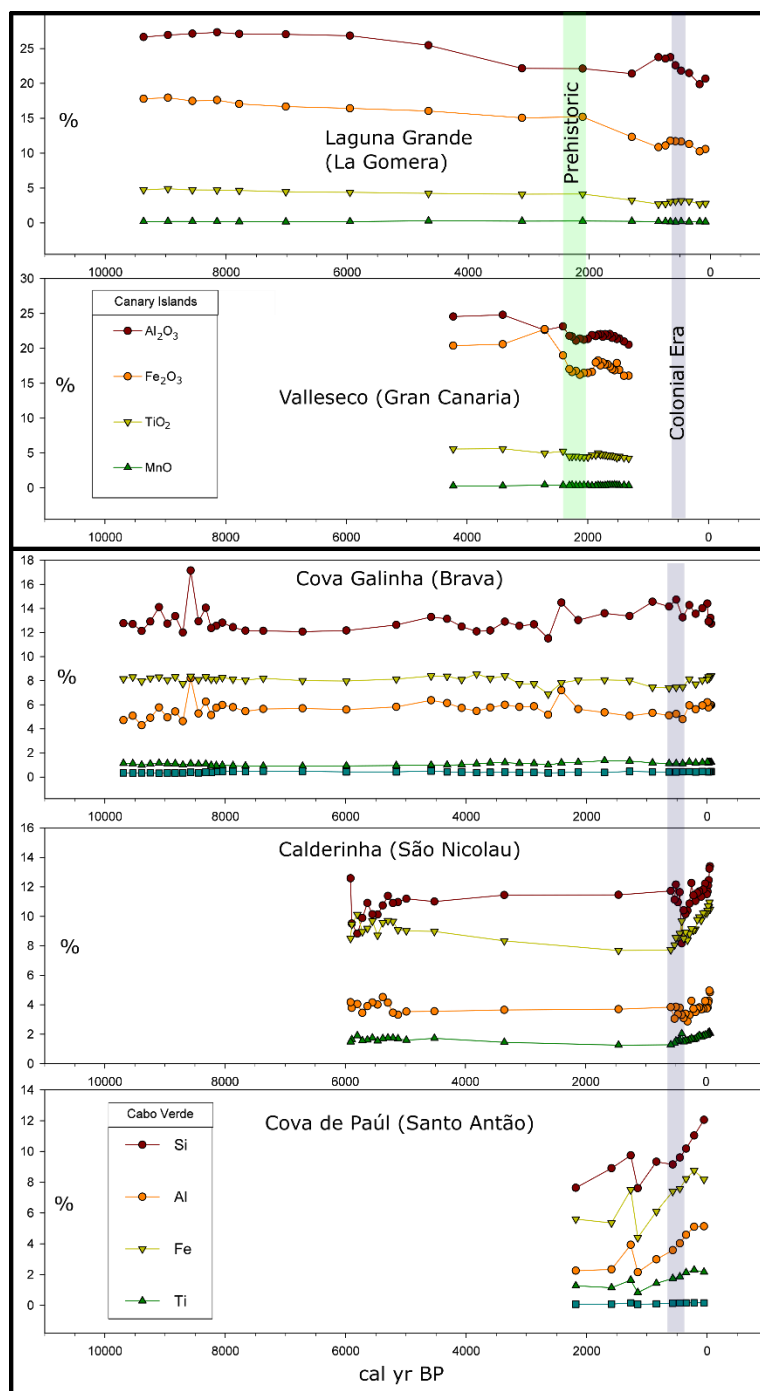


Fig. S2. Comparative soil elemental composition plots showing abundant elements, as obtained from XRF analyses from sites in the Canary Islands (top panels, FUS-XRF, oxides) and Cabo Verde (bottom panels, portable XRF, elements). Horizontal axes represent sample age (cal yr BP) and vertical axes percentages of elemental composition.

Fig. S3.

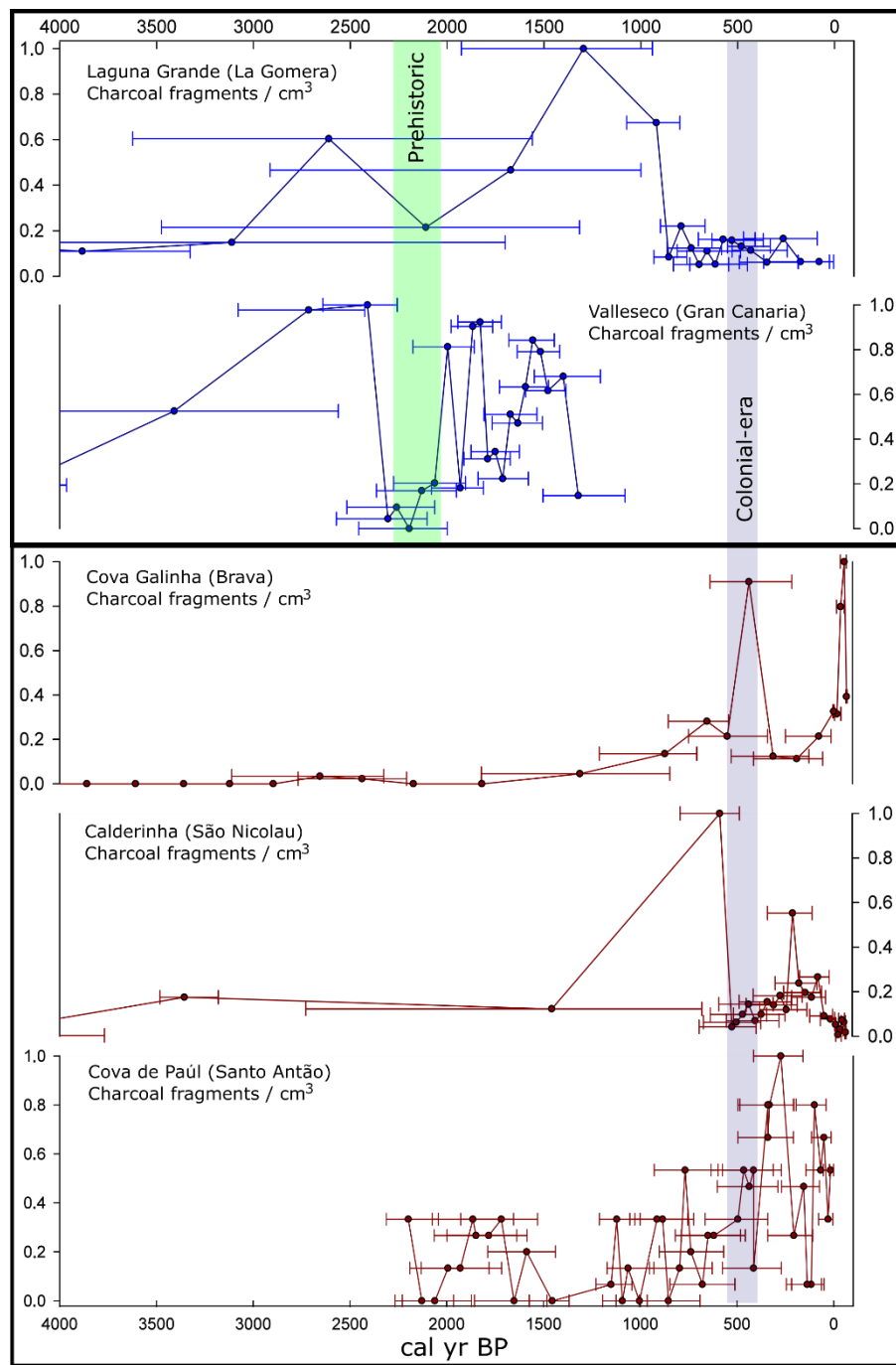


Fig. S3: Comparative macro-charcoal concentration plots during the last 4000 cal yr BP including age confidence interval. Horizontal axes represent sample age (cal yr BP), vertical axes normalized charcoal particle concentrations and error bars 95% age confidence interval obtained in age–depth models (Fig. S1)

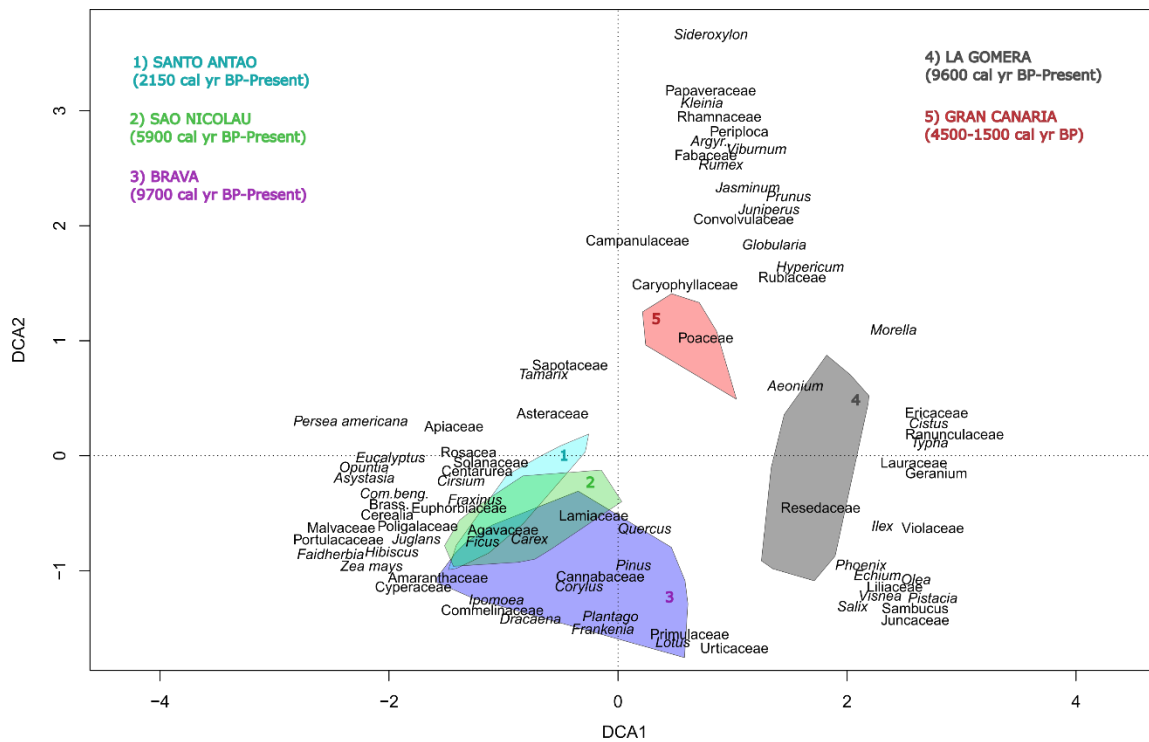


Fig. S4. Detrended Correspondence Analysis Ordination plot (equivalent to Fig. 4) showing species and polygons were samples from different islands plot. Analysis was carried out using pollen percentages from study sites of the Canary Islands and Cabo Verde, avoiding label overlapping by manually adjusting species labels. Abbreviations: Brass. (Brassicaceae), Argyr. (*Argyranthemum*), Com. Ben. (*Commelina Benghalensis*).

Table S1. Canonical Correspondence Analysis correlation scores and cumulative proportion explained per archipelago.

		Canary Islands		Cabo Verde	
		CCA axis-1	CCA axis-2	CCA axis-1	CCA axis-2
Environmental Driver	Proxy	Correlation scores			
Herbivores	<i>Sporormiella</i>	-0.5164	-0.30054	-0.2469	0.2897
Local fire	Macro-charcoal particles/cm ³	0.4408	-0.71019	-0.2469	0.2897
Soil organic matter	Loss on Ignition (%)	-	-	-0.8337	-0.4650
Soil organic matter	Organic matter (%)	-0.9320	-0.29635	-	-
Erosion	SiO ₂ (%)	0.6804	-0.01148	-	-
Erosion	Median Grain Size (microns)			-0.2506	0.8930
		Cumulative proportion explained			
		0.5178	0.3240	0.5271	0.2570

SI References

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