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

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The extinction of iconic species such as the dodo and the defor-estation of Easter Island are emblematic of the transformative impact of human colonization of many oceanic islands, especially those in the tropics and subtropics. Yet, the interaction of prehis-toric and colonial-era colonists with the forests and forest resources they encountered can be complex, varies between islands, and re-mains 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 postcolonization. Here we analyze paleoecological archives in forested landscapes of the Canary Islands and Cabo Verde, first colonized approximately 2,400 to 2,000 and 490 y ago, respectively. We demonstrate sensi-tivity to regional climate change prior to human colonization, fol-lowed 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 agri-cultural land, yet relictual subtropical laurel forests persisted with limited incursion of nonnative 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 ecosys-tems, information that will be critically important for current and future forest restoration and conservation management practices in these two biodiversity hotspots.

anthropogenic impacts | islands | Macaronesia | subtropical forests

Human colonization of virtually the entirety of the tropics and subtropics 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 prehistoric times (approximately in the last 3,000 y) or in the colonial era (post-1400 CE) (2). Humans have since transformed these systems, via habitat conversion, resource exploitation, hunting, and the intro-duction of nonnative species. Cases such as Easter Island exemplify a complete loss of preexisting forest cover (3), but often ecological cascades have had profound impacts within persisting forest com-munities. The loss of the dodo on Mauritius (4) and most of the land birds of Guam (5) (following the introduction of the brown tree snake) are emblematic. Moreover, the response of island for-ests to anthropogenic drivers varies greatly among islands: whereas forested areas on Hawaii contain many nonnative species (6), Canarian laurel forests are composed almost entirely of native species of trees and shrubs (7). Understanding the legacy of human impacts on these remote oceanic islands, and particularly on their forests, requires a combination of paleoecological and archaeo-logical studies over timelines that incorporate both pre- and posthuman dynamics (8).

For prehistoric 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 agri-cultural conversion. While prehistoric island societies typically interacted and traded with other islands or regions, most land-use decisions were made locally (8, 9). Island forests were subjected to clearance by fire (9), increasing agricultural activities, accelerated soil erosion (10), and the introduction of species such as goats, pigs, and rats (11), which are often implicated in extinctions of native vertebrates (11, 12). Colonial-era first colonists, in contrast, fre-quently made land-use decisions focused on colonial trading net-works, leading to aggressive, rapid acts of deforestation and land-use change, and generally involving accelerated rates of nonnative species introduction (13).

Here we present comparative paleoecological analyses of two oceanic archipelagos from the biogeographical region of Macaronesia (which comprises Cabo Verde, Canaries, Selvagens, Madeira, and Azores), namely 1) Cabo Verde, settled by the Portuguese in 1462 CE and the first tropical European colony, and 2) the subtropical Canary Islands, first settled by people from North Africa around 2,400 to

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Significance

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 paleoecological data (e.g. fossil pollen) to show that prehuman 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 thermoph-ilous 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 which tree species to restore and conserve in thermophilous woodlands within these biodiversity hotspots.

2,000 cal BP (14) 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 tropics (13) (*SI Appendix*). 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, 17–19).

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 ~100 to 600 meters above sea level (masl) in the Canaries and found from 500 to 1,500 masl in Cabo Verde, and second, laurel forest, which occurs from 500 to 600 m to 1,000 to 1,200 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 paleoecological 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 change, 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

Paleoecological 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 posthuman colonization landscape dynamics. Proxies for erosion, burning, and grazing show particularly prominent changes.

Canary Islands. Sediment geochemistry for Laguna Grande (La Gomera, 1,250 masl) shows consistent values of SiO_2, Fe_2O_3, Al_2O_3, and TiO_2 from the base of the core (approximately 9,600 cal BP, [calibrated years before present], 95% CI [confidence interval], 10,900 to 8,700 cal BP; *SI Appendix*, Fig. S1), then slight declines coincide with the regional drying trend of the end of the African humid period, approximately 5,500 cal BP (*SI Appendix*, Fig. S2) until human colonization of the archipelago. Subsequently, values of Al_2O_3 and TiO_2 decline further, yet SiO_2 and Al_2O_3 values abruptly rise approximately 600 cal BP before declining again toward the present (*SI Appendix*, Fig. S2). A peak in *Sporormiella* coprophilous spores also occurs approximately 600 cal BP (Fig. 3). Macrocharcoal concentrations reach maximum values approximately 1,296 cal BP (95% CI 1,926 to 940 cal BP, Fig. 3 and *SI Appendix*, Fig. S3). At Valleseco (Gran Canaria, 870 masl), sediments show stable Fe_2O_3, Al_2O_3, and TiO_2 content from 5,000 to 2,500 cal BP, and enrichment in SiO_2 coinciding with peaks in macrocharcoal 2,260 cal BP (95% CI 2,517 to 2,063 cal BP) followed by the highest concentrations of *Sporormiella* spores in the record, approximately 2,031 cal BP (95% CI 2,364 to 1,951 cal BP). Due to soil removal for agricultural purposes the record has a top date of approximately 1,208 cal BP.

Cabo Verde. Sites recording pollen from thermophilous woodland taxa are located in Cova Galinha (Brava, 810 masl), Calderinha (São Nicolau, 1,000 masl), and Cova de Paúl (Santo Antão, 1,150 masl). The Brava site shows episodes of increased Al and Si between 8,000 and 7,000 cal BP, and increases in median grain size approximately 4,000 cal BP (95% CI 4,326 to 3,838 cal BP; Fig. 3 and *SI Appendix*, Fig. S2). Increased charcoal concentrations and peaks in *Sporormiella* spores occurred after approximately 400 cal
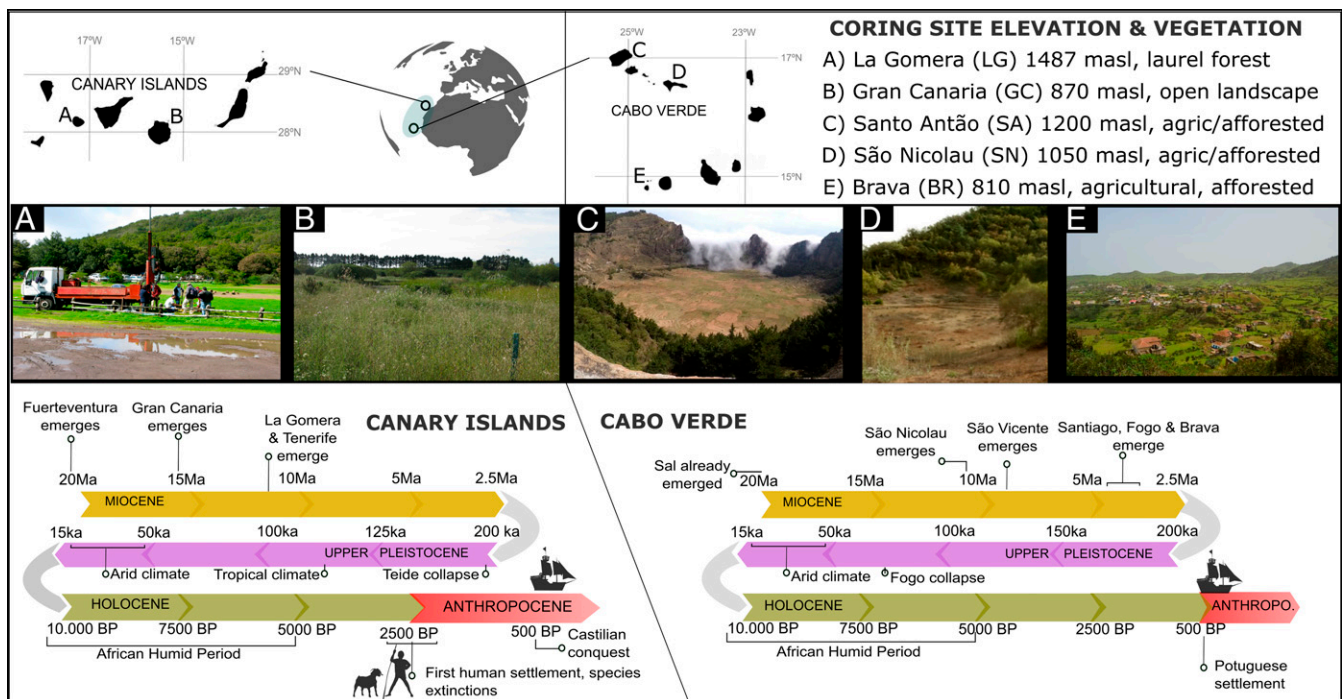

Fig. 1. Maps of the Cabo Verde and the Canary Islands and photographs and elevation of the studied volcanic calderas. We use Anthropocene in an informal sense to indicate the period since human colonization, which differs island to island. (*Lower*) Chronological axes showing geological, climatic, and human milestones of the last 20 My in southern Macaronesia. See *SI Appendix, Supplementary Text* for references.
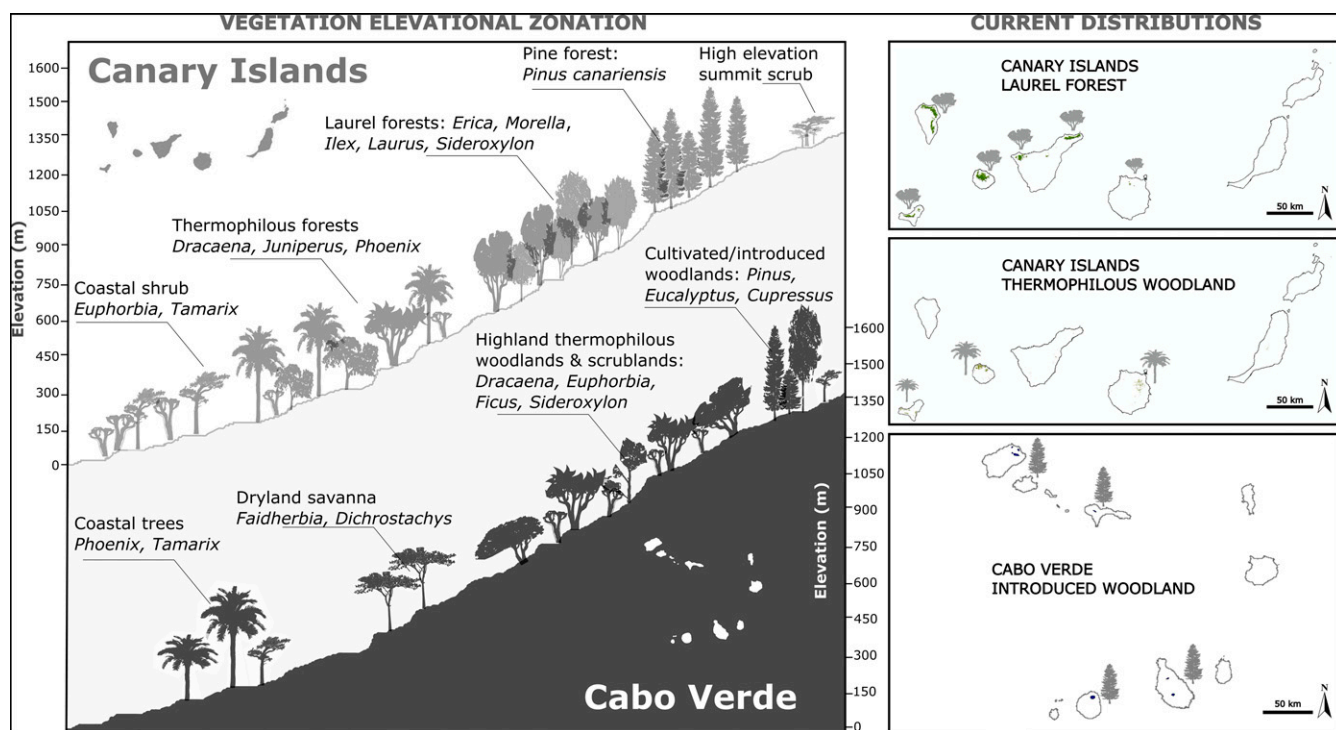
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Fig. 2. Distribution of woodland vegetation types in southern Macaronesia. (*Left*) Schematic elevational zonation. (*Right*) Remaining distribution of laurel forest and thermophilous woodlands in the Canary Islands based on ref. 43 and of introduced woodland in Cabo Verde based on ref. 44.

BP (95% CI 613 to 207 cal BP; Fig. 3). The São Nicolau site records increased median grain sizes and Ti % between 6,000 and 5,000 cal BP (*SI Appendix*, Fig. S2), and these erosion indicators steadily increased after 468 cal BP (95% CI 634 to 343 cal BP). The charcoal increases after approximately 600 cal BP in this site and is abundant until the present (Fig. 3). On Santo Antão the sediments show steady increases in Si, Al, Fe%, and median grain size between approximately 470 cal BP (95% CI 640 to 320 cal BP) and the present, also coinciding with increased macro-charcoal concentrations and peaks of coprophilous fungal spores (Fig. 3 and *SI Appendix*, 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 prehuman colonization samples from Brava (low) to recent Gran Canaria samples (high) (Fig. 4*A*). 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*; *SI Appendix*, 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*) (*SI Appendix*, 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).

Canonical correspondence analysis (CCA) for each archipelago separately permits testing of the associations between proxies of vegetation change and environmental change (Fig. 4*B* and *SI Appendix*, 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 2,500 cal BP and the present representing the thermophilous woodland of Gran Canaria, plot with fire and erosion. Samples dated between 800 cal BP and the present in the laurel forest of La Gomera have higher organic matter content (loss on ignition [LOI]) and herbivore presence (Fig. 4*B* and *SI Appendix*, 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 BP and the present are associated with herbivore presence, erosion, and local fires. Finally, samples from prehuman periods from São Nicolau and Santo Antão are associated with higher levels of organic matter (Fig. 4*B* and *SI Appendix*, 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 elevational distribution. For example, the environmental changes consequent upon the shift in the monsoonal circulation at the end of the African Humid Period (approximately 5,500 cal BP) (20, 21), illustrate the ecological effects of relatively abrupt regional change in Macaronesian forests. During this humid period, the continuous 10,000-y record of Laguna Grande (La Gomera) geochemical values are generally stable, indicating a lack of abrupt erosion events, but pollen data show changes in composition in response to the advent of drier climatic conditions (22). Around 5,500 y 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 day (22). The change
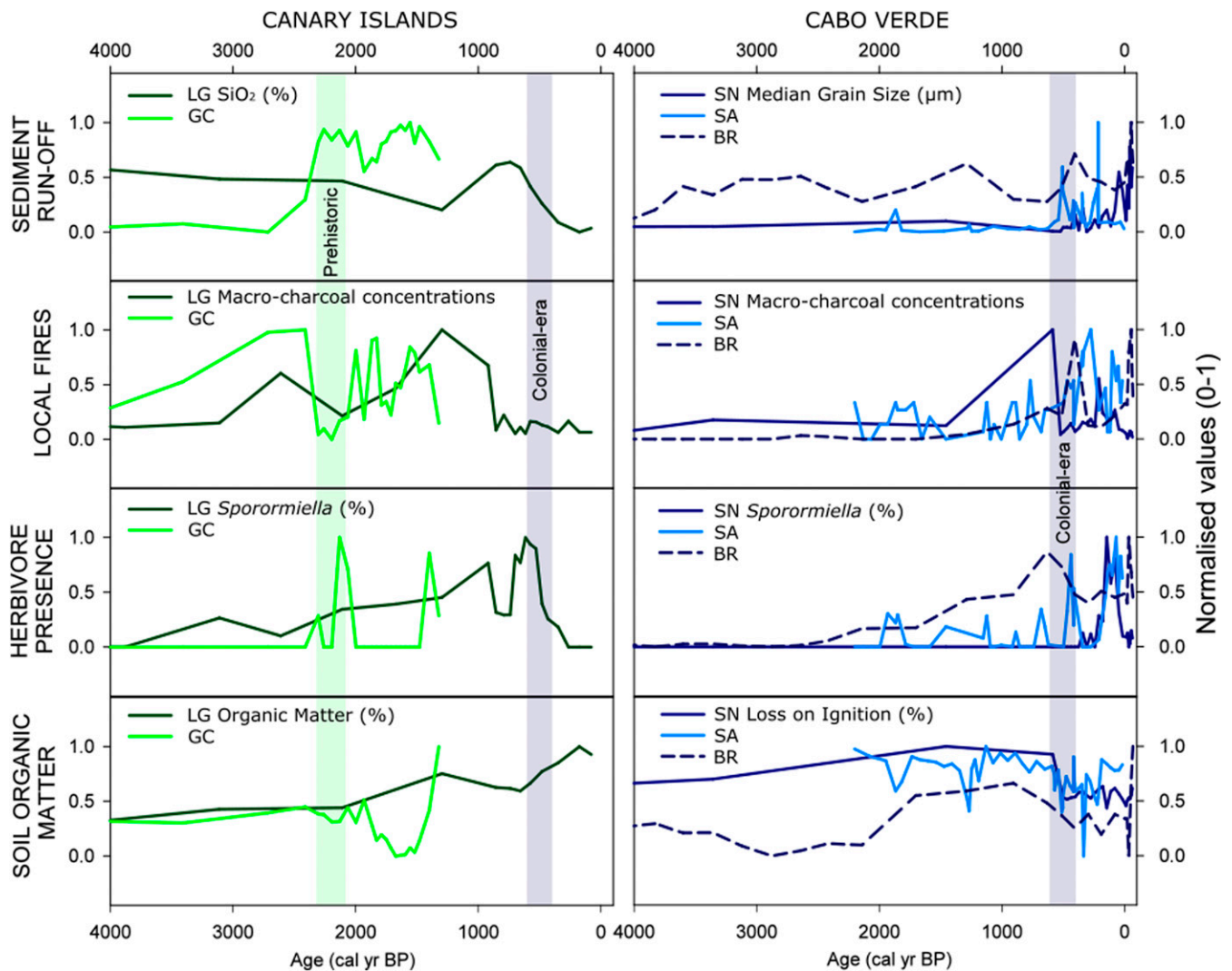
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Fig. 3. Longitudinal data series for key environmental proxies (normalized values 0 to 1) from five cores from the Canary Islands (*Left*) and Cabo Verde islands (*Right*). SiO₂ (%) content and median grain size (MGS, in micrograms) are indicators of rates of erosion within the catchment. Charcoal refers to macrocharcoal concentration (number of fragments per cubic centimeter), a proxy for local fires; *Sporormiella* (% over pollen sum) refers to spores of these coprophilous fungi, which are indicators of the presence of herbivores. Loss on ignition (%) and organic matter content (%) are indicators of soil organic matter. Vertical bands indicate the best estimates of the timing of Prehistoric (green) and European colonial (gray) settlement (14, 19).

also coincides with an acceleration in sediment accumulation rate and the occurrence of local fires, shown by an increase in macrocharcoal concentrations. Similarly, at Laguna de Valleseco (Gran Canaria) thermophilous woodland (*Juniperus* and *P. canariensis*) was dominant at approximately 4,500 cal BP (23). Subsequently, charcoal concentrations increased between approximately 4,000 and 3,000 cal BP, indicating increased 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 y 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 (1,200 masl). This woodland included *Ficus* (fig) trees, *D. draco* (dragon tree), and the shrub *Euphorbia tuckeyana*, with occasional acacia trees (*Faidherbia albida*) (24). These thermophilous woodlands were likely restricted to the highlands (25). In contrast, in Cova de Paúl (Santo Antão), pollen data suggest a more open landscape, with tree species represented by *Ficus*, *F. 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 *D. 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 (approximately 6,000 to 5,000 cal BP) (24) and Brava (approximately 8,000 to 7,000 cal BP) (27). Cabo Verdean prehuman landscapes also experienced fire events, as evidenced by discrete charcoal peaks in Santo Antão approximately 2,000 cal BP, and a prominent charcoal peak in São Nicolau approximately 600 cal BP (95% CI 790 to 480 cal 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 encroachment (24).

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 precolonial indigenous settlement approximately 2,400 to 2,000 cal BP, followed
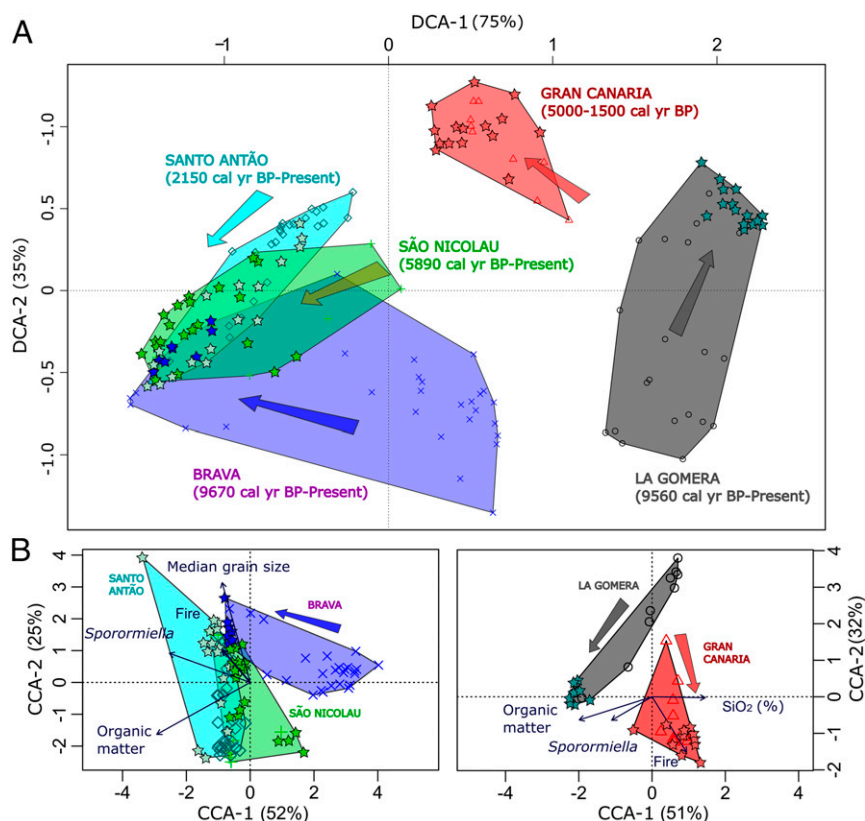
Fig. 4. Ordination plots of fossil pollen data from southern Macaronesia. Colored polygons differentiate samples from different islands. Arrows show the main trend of change from older to younger samples. (*A*) DCA. Stars show samples dated after human settlement; other symbols show prehuman settlement. (*B*) CCA for three Cabo Verde islands (*Left*) and two Canarian islands (*Right*). CCA shows associations between pollen percentages and four proxies of environmental change (thin blue arrows). See *SI Appendix*, Table S1 for correlation scores with axes 1 and 2. Coring site elevations are as per Fig. 1. Proxies are as per Fig. 3 and *Materials and Methods*.

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 homogenization 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*, *Canarina*, *Visnea*), wood (*Apollonias*, *Juniperus*, *Olea*, *Persea, Pinus*), or fodder (*Chamaecytisus*, *Teline*) (7). These activities appeared to have had little impact on the forest. In La Gomera's laurel forest, for example, approximately 1,800 y 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 elevation (28). Later, at approximately 750 cal BP (95% CI 830 to 700) sharp increases occur in indicators of herbivore presence (coprophilous fungi) probably representing introduced ovicaprids (*Capra hircus*, *Ovis aries*) and pigs (*Sus domestica*) (14) 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 2,640 and 2,250 cal BP, peaks in charcoal suggest 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 plants (23). 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 approximately 2,130 cal BP (95% CI 2,360 to 1,950 cal BP). This finding aligns with another paleoecological 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 grazing (29). The Castilian arrival in the 15th century brought new impacts on vegetation related to tree-felling technology, wood demand, and the translocation of forest soils for improving agricultural land (19).

Within the thermophilous woodlands and open landscapes of Cabo Verde, the onset of anthropogenic pressures occurred after 1462 CE and the arrival of European Portuguese 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

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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 medicine, are historically documented in São Nicolau and Santo Antão (the northern islands) (30); these practices appear to have severely depleted the thermophilous woodlands of Cabo Verde and led to a decrease in extent of woody taxa (26). These compounded human-driven impacts likely played a role in the socioecological crises that affected the archipelago between the 16th and early 20th centuries (31, 32), and consequent land abandonment could have created epicenters for the spread of introduced species. The pollen records show an increasing presence of pollen from introduced species after 500 cal 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 *Z. mays*, Cerealia, *Ipomoea batatas*, and *P. americana* (24, 26, 27). *L. camara* is currently being targeted for action as its substantial and increasing biomass is flammable and generates a high wildfire risk (33). 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 y of land use in Cabo Verde appears to be a trend toward 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 United Nations International Decade of Restoration and Conservation (https://www.decadeonrestoration.org), 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 paleoecological analyses provide an important comparative perspective to understanding contemporary (sub) tropical island forest status and a quantitative evidence-based guide to forest restoration (34). 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 Canaries (35). 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 decades) (7). 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*, *L. camara*, *Leucaena*), all heightened by episodes of socioecological stress between 1550 and 1750 CE (32). 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" (36). This trend of forest convergence during the past 500 y 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

midelevations 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 CO_2, water flow regulation, soil erosion protection, and important habitats for native forest biodiversity) (37, 38), and in this context the questions of which tree species to plant and where, are pressing. To answer these questions requires understanding of how and why forests changed from their pre-anthropogenic baselines (8). 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 nonnative 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 CO_2. 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 (35, 39). In the Canaries, efforts were first focused on the recovery of pine forests, mainly planting Canarian pine but also using fast-growing nonnative 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 has active restoration, focused on conservation aims, taken place in the laurel forest (e.g., Gran Canaria) (7) and thermophilous woodlands (e.g., Teno, Tenerife) (35). 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 *D. draco*, *Ficus sycomorus*, *Ficus sur*, *D. viscosa*, *Sideroxylon marginata*, *F. albida*, and *D. cinerea* in the midlands, and *Tamarix senegalensis* and *Phoenix atlantica* in the coastal areas (25). 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 growth (39), can be outweighed by the potential benefits, such as soil protection.

Our results also show the importance of applying targeted restoration efforts toward the remaining thermophilous forest. In this context, where habitat loss and fragmentation are dominating the islands' landscape and in the event of anthropogenic climate change (17), restoration practices may be especially challenging and conservationists might be required to implement complementary ex situ measures such as safeguarding thermophilous plant species in seed banks to preserve the genetic diversity (40). Therefore, enhancing seed banks in both the Canary Islands (e.g., the Canarian Botanical Garden "Viera y Clavijo") and in Cabo Verde (e.g., Cabo 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 midelevation 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* (41). 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 (*SI Appendix*, Fig. S1). Bacon outputs are reported as calibrated years before present; with 1950 CE as zero by definition, and a confidence interval of 95% is used for interpretation (*SI Appendix*, Figs. S1 and S3).

Paleoecological Datasets. We studied multiple indicators of plant biodiversity and environmental change in each site, including biotic proxies (fossil pollen, *Sporormiella* fungal spore, 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 Grande (22), Laguna de Valleseco (23), Cova de Paúl (26), Calderinha (24), and Cova Galinha (27). Rock Fusion X-ray fluorescence was used for the analysis of sediment geochemistry in the Canarian sites, providing oxide percentages (e.g., TiO_2) and organic matter percentage values, and portable X-ray fluorescence (XRF) was used for analysis of Cabo Verde sites, providing elemental percentage data (e.g., Ti) (*SI Appendix*, Fig. S2).

Ordination Analysis. For statistical analyses, percentage values of non-pollen palynomorphs over pollen sum (including unidentifiable grains in Cabo Verde sites), concentration values of macrocharcoal particles, size measurements of granulometry, and percentage values of XRF were normalized (values range between 0 and 1). We carried out DCA with the *Vegan*

package in RStudio (R Core Team) using pollen percentage values to quantify palynological turnover (42). For CCA, we used the same software and normalized 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 neighboring samples. Thus, environmental variables represent roughly synchronous phenomena. We used 1) percentages of the spores of coprophilous fungi *Sporormiella* to represent herbivore presence in the local catchment, 2) loss-on-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) macrocharcoal particle concentrations to represent local fire occurrence, and 4) median grain size (in micrometers) in the Cabo Verde sites and SiO_2 percentages in the Canary Island sites as proxies for erosion (sediment run-off from caldera margins).

Data Availability. Pollen data for Laguna Grande (22), Laguna de Valleseco (23), Cova de Paúl (26), and Calderinha (24), sites islands can be downloaded from ref. 8. Pollen data of Cova Galinha site (27) have been deposited in Neotoma Paleoecology Database (https://apps.neotomadb.org/explorer/?datasetid=48891). The rest of the data used in the paper are provided within the *SI Appendix*.

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