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Original plant diversity and ecosystems of a small, remote oceanic island (Corvo, Azores): Implications for biodiversity conservation

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ABSTRACT

Remote islands harbour many endemic species and unique ecosystems. They are also some of the world's most human-impacted systems. It is essential to understand how island species and ecosystems behaved prior to major anthropogenic disruption as a basis for their conservation. This research aims to reconstruct the original, pre-colonial biodiversity of a remote oceanic island to understand the scale of past extinctions, vegetation changes and biodiversity knowledge gaps.

We studied fossil remains from the North Atlantic island of Corvo (Azores), including pollen, charcoal, plant macrofossils, diatoms and geochemistry of wetland sediments from the central crater of the island, Caldeirão. A comprehensive list of current vascular plant species was compiled, along with a translation table comparing fossilized pollen to plant species and a framework for identifying extinctions and misclassifications.

Pollen and macrofossils provide evidence for eight local extinctions from the island's flora and show that four species listed as 'introduced' are native. Up to 23 % of the pollen taxa represent extinct/misclassified species. Corvo's past environment was dynamic, shifting from glacial-era open vegetation to various Holocene forest communities, then almost completely deforested by fires, erosion and grazing following Portuguese colonisation. Historical human impacts explain high ecological turnover, several unrecorded extinctions and the present-day abundance of vegetation types like *Sphagnum* blanket mire.

We use Corvo as a case study on how fossil inventories can address the Wallacean and Hookerian biodiversity knowledge gaps on remote islands. Accurate baselines allow stakeholders to make informed conservation decisions using limited financial and human resources, particularly on islands where profound anthropogenic disruption occurred before comprehensive ecological research.

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1. Introduction

Biodiversity loss is linked to declining ecosystem resilience, with knock-on effects for economies and societies (Cardinale et al., 2012). Humanity's ability to maintain biodiversity depends on access to accurate and comprehensive biodiversity knowledge (Meyer et al., 2015; Heaney et al., 2016). In this paper, we analyse multi-proxy palaeoecological data from a small, remote oceanic island to improve biodiversity baseline information. This work is relevant because the most influential theories on biodiversity and its evolution have come from the foundational studies of ecosystems on these oceanic islands (Darwin, 1859; MacArthur and Wilson, 1967; Whittaker and Fernández-Palacios, 2007). Biodiversity baselines determine whether species are included in macroecological analyses (e.g. species-area relationships, niche models and invasion potential; Price et al., 2018) and guide conservation and restoration efforts.

Oceanic islands have never been part of a continent and have developed distinctive, often ‘disharmonic’ biotic communities (Whittaker and Fernández-Palacios, 2007). They are also highly vulnerable to disturbances, among which human activity in the past millennium has had particularly severe ecological consequences (Russell and Kueffer, 2019; Nogué et al., 2021; Rull, 2023a). Historical extinction rates on islands have outstripped those of all the continents (Fernández-Palacios et al., 2021), leaving islands with both impoverished ecosystems (Brook et al., 2003) and extinction debts to be repaid by further extinctions (Otto et al., 2017). The extent of unrecorded extinctions and past human disturbances remain unclear for many island ecosystems (the ‘Hookerian shortfall’: Hooker, 1867; Carine and Menezes de Sequeira, 2020).

Fossil evidence remains the best indicator of species' occurrence in the original ecosystems (Webb, 1985; Pyšek et al., 2004). This evidence may include classic palaeobotanical or palynological remains or newer indicators such as leaf waxes and sedimentary ancient DNA (*sed*aDNA), as long as adequate preservation conditions and reference libraries exist. There is great potential for carefully designed research to address the problem of misclassified species, unrecorded extinctions and extirpations on islands to improve their conservation (Góis-Marques et al., 2019). For example, in Hawaii, fossil plant remains have informed ecological restoration, leading to the replanting of locally extinct taxa and contributing to overall ecological function and resilience (Burney and Burney, 2016). The same fossil deposits have yielded evidence of several insect extinctions and extirpations following human arrival (Porch, 2020; Liebherr and Porch, 2015). Insect and plant extirpations and extinctions have also been suggested by fossil records from the Marquesas Islands (Allen et al., 2022). Other examples include the unrecorded extinction of forest communities in New Zealand (Wood et al., 2017), Rapa Nui and other Pacific islands (Prebble and Dowe, 2008), and the loss of *Prunus lusitanica* subsp. *azorica*-dominated forests on the Azores (Góis-Marques et al., 2020). Instances where native species have been misclassified as ‘introduced’ have been identified using plant fossils on several archipelagos, including the Azores (van Leeuwen et al., 2005; Connor et al., 2012) and Galápagos (van Leeuwen et al., 2008; Coffey et al., 2011).

In this paper, we use multi-proxy data to reconstruct the original biodiversity of Corvo (Azores) as a case study for improving biodiversity baselines on remote islands more generally. We use the term ‘original’ in preference to ‘pristine’ or ‘natural’ as it better conveys the idea of ecosystems before major extractive human impacts and does not exclude other human interactions. Plant diversity patterns on the Azores have been described as enigmatic (Carine and Schaefer, 2010), given a scarcity of single-island endemics and the homogeneity of the flora on different islands. It has been hypothesised that island age, habitat similarity, climate stability and recent human impact could explain this pattern (Carine and Schaefer, 2010; Triantis et al., 2012; Price et al., 2018). Using fossil data, we aim to identify biodiversity knowledge shortfalls and address their implications for ecological theory and biodiversity management on islands.

1.1. Corvo Island

Corvo lends itself to this analysis because of its isolation (>1800 km from the nearest continent), small size, relatively low species richness and its lacustrine deposits, which preserve abundant, dateable fossils.

Along with Flores, Corvo is part of the Western Group of the Azores archipelago (Fig. 1) and is situated on the American tectonic plate. The Western Group experiences a maritime climate (Köppen classification Cfb), with an average temperature of 17.2 °C and 1642 mm annual rainfall at sea level, with higher rainfall at altitude (IPMA, 1971–2000). Corvo is the smallest and least populous of the nine inhabited islands of the Azores, having some 384 inhabitants (FFMS, 2021). Corvo's landscape is dominated by a central caldera, Caldeirão, which formed 0.43 ± 0.34 Mya ago on top of older subaerial and submarine volcanic deposits (Pacheco et al., 2023). The last major eruptions ended about 80–100 kya and cliff erosion has been the main geomorphic process since then (Bossis et al., 2023). The island's current area is 17.1 km^2, with a past maximum extent of 45 km^2 (Bossis et al., 2023) and approx. 38 km^2 during low sea levels of the last glacial period (Rijsdijk et al., 2014). Corvo's geology consists of alkaline basalts, scoria and pyroclastic deposits (Zbyszewski et al., 1967).

Corvo's vegetation is characterised by strong anthropogenic impact, having an extensively overgrazed landscape and a high proportion of exotic plant species (Fig. 2A). Treeless grasslands and *Sphagnum* blanket bog dominate and only a few patches of native forest remain on steep cliffs (Sjögren, 1979). Despite this, there are no recorded plant extinctions from the island. Forests are considered the potential natural vegetation of the island: *Picconia-Morella* forest along the coast, laurisilva at mid elevations, and *Juniperus-Ilex* communities on the caldera rim (Fig. 1; Elias et al., 2016). Forest disturbance began around 1450 CE, coinciding with Portuguese arrival (Connor et al., 2016; Raposeiro et al., 2021). Indications of earlier human impacts on Azorean vegetation remain controversial (Raposeiro et al., 2021; Elias et al., 2022; Rull, 2023a, 2023b).

An early historical report on Corvo, written between 1586 and 1590 by a priest, describes dense vegetation and large *Juniperus, Picconia, Laurus, Myrsine* and *Ilex* trees (Frutuoso, 1590). Biologists, however, did not visit Corvo before the late 19th century and no early species lists or specimens exist. The first comprehensive list of Azorean plant species was only published about 400 years after the arrival of the Portuguese colonizers (Seubert, 1844). Because of this, unrecorded extinctions could be a major driver of current diversity patterns (Cardoso et al., 2010; Góis-Marques et al., 2019).

2. Materials and methods

Sediment cores were collected from Corvo's central crater, Caldeirão (Figs. 1, 2), in June 2014 with a Russian peat corer (39.7095°, −31.1085°, 410 m a.s.l.). A small (150 × 50 m) *Sphagnum–Eleocharis palustris* bog was selected for coring, because fossils in small wetlands tend to represent local flora and fauna better than fossils preserved in lake sediments (Sugita, 1994). The crater slopes are, like most of Corvo island, covered primarily in heavily-grazed herb-rich grassland. There are few woody species apart from hedgerows and clumps of introduced *Hydrangea macrophylla* and a small *Cryptomeria japonica* plantation on an island in the lake (species list in Supporting Information).

Current plant diversity knowledge on Corvo is based on historical botanical data and recent surveys. During 20 short visits to Corvo between 2000 and 2023, we compiled a comprehensive list of vascular plant species. Using the iNaturalist platform, we set up a project “Flora of the Azores” (https://www.inaturalist.org/projects/flora-of-the-azores), which allowed citizen scientists to upload photographs of plants they observe in the archipelago. Observations were identified with the artificial intelligence algorithm of iNaturalist and regularly confirmed or corrected by one of us (Hanno Schaefer). Representative herbarium specimens have been deposited in the TUM herbarium and

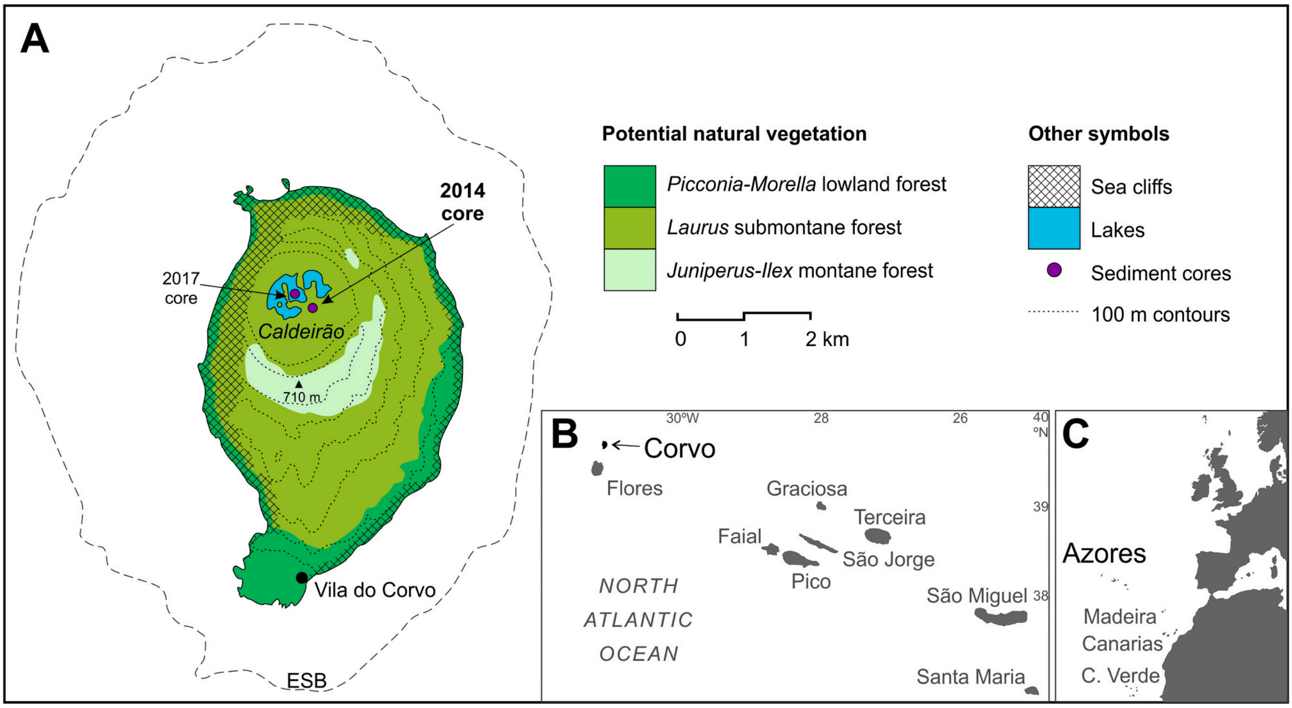

Fig. 1. A) Map of Corvo Island and the study site, Caldeirão, denoting the locations of the 2014 core (this study) and 2017 core (Raposeiro et al., 2021). The island's past maximum extent (ESB: erosional shelf break; Bossis et al., 2023) is shown, along with contour lines and potential natural vegetation under current climate conditions (Elias et al., 2016); B) Location of Corvo in the Azores Archipelago; C) Azores in relation to nearby archipelagos and continents.

DNA sequence data produced from Corvo material during taxonomic studies is available on Genbank (www.ncbi.nlm.nih.gov/genbank/).

We integrated various fossil indicators to reconstruct past biodiversity. Fossilized pollen (Fig. 2) was extracted using a standard procedure involving treatments with $Na_4P_2O_7$, KOH, HCl, acetolysis and HF (Moore et al., 1991). *Lycopodium* spore tablets were added to estimate pollen concentrations. Pollen identifications were made using published resources (Reille 1992, 1995, 1998; Morgado et al., 2018) and a reference collection compiled by the authors.

Plant macrofossils (Fig. 3) were sieved from 15 to 70 ml samples through a > 250 μm mesh and hand-picked under a stereo microscope. Identification was based on various resources, including Seubert (1844), Martin and Barkley (2000), Schaefer (2021), Cappers et al. (2012), a seed/fruit collection assembled specifically for the present study and the reference collection of one of the authors (TL). Determination of some remains to lower taxonomic levels was limited due to poor preservation.

Diatoms, an indicator of aquatic environmental conditions, were extracted using $Na_4P_2O_7$ and H_2O_2 treatments (Battarbee et al., 2001) and identified with Krammer and Lange-Bertalot (1986–1991) and Lange-Bertalot (2000–2003). Diatoms were assigned to groups representing alkaline, circumneutral and acidic environments (pH) using the same sources and Denys (1991).

Macroscopic charcoal, a fire proxy, was extracted by bleaching samples in domestic NaClO overnight and sieving through a 125-μm mesh (Whitlock and Larsen, 2001). All biological proxy specimens are archived in the Natural History Collection at the ANU.

To contextualise the biological proxies, geochemical indicators were estimated by continuous X-ray fluorescence (ITRAX) core scanning at 1.0 mm resolution (Croudace and Rothwell, 2015). Sediment organic content was approximated via loss-on-ignition of dried samples for five hours at 550 °C.

Ten radiocarbon dates were obtained from short-lived plant macrofossils (twigs, seeds, coarse organics) and a chronology constructed using Bayesian age–depth modelling (Bacon R package: Blaauw et al., 2021).

Plant macrofossils and diatoms are often identifiable to species level, but the same is not necessarily true of pollen. Some plant families, such as the Cyperaceae and Poaceae, have many species represented by a single pollen morphotype (Faegri et al., 1989). A key requirement when studying past diversity from pollen is a 'translation table' that assigns pollen morphotypes to all the potential source plants in a regional flora (Birks et al., 2016). We matched pollen types to extant plants following Walentowitz et al. (2023) and extended their approach of assigning native/non-native status to include additional categories (i.e. endemic, long-distance transported and extinct or incorrectly classified taxa). This produced a translation table for the flora of Corvo, showing how the island's plant diversity is reflected in pollen diversity (Supporting Information). The table is based on decades of collective experience in pollen morphological work and incorporates information on each taxon's morphological distinctiveness and its potential for long-distance pollen dispersal. Naming of pollen taxa follows the European Pollen Database convention (i.e. use of local plant species equivalents).

We then developed a framework for deciding whether a fossil taxon may represent an extinct species or a native species that has been misclassified as 'introduced'. This framework was built and tested around our multi-proxy dataset from Corvo and provides an indication of the uncertainty associated with each classification (Fig. 4). This framework takes into account the morphological distinctiveness of the pollen, its pollen production/dispersal characteristics, the date of its occurrence, and sources of additional empirical support. Extinct taxa are those where no source plant for the fossil is found in the current flora. Local extinction (extirpation) occurs when the species survives elsewhere, even if survivor populations are genetically distinct, while global extinction involves worldwide loss of the species and all its populations. Mislabelled 'introduced' taxa are those that occur in the current flora but have reliable fossil occurrences dating back before colonisation.

Ecosystem-level turnover was assessed using Detrended Correspondence Analysis (DCA) of biological proxies with square-root transformation. Following Nogué et al. (2021), we compared absolute differences in DCA scores from before and after human colonisation on

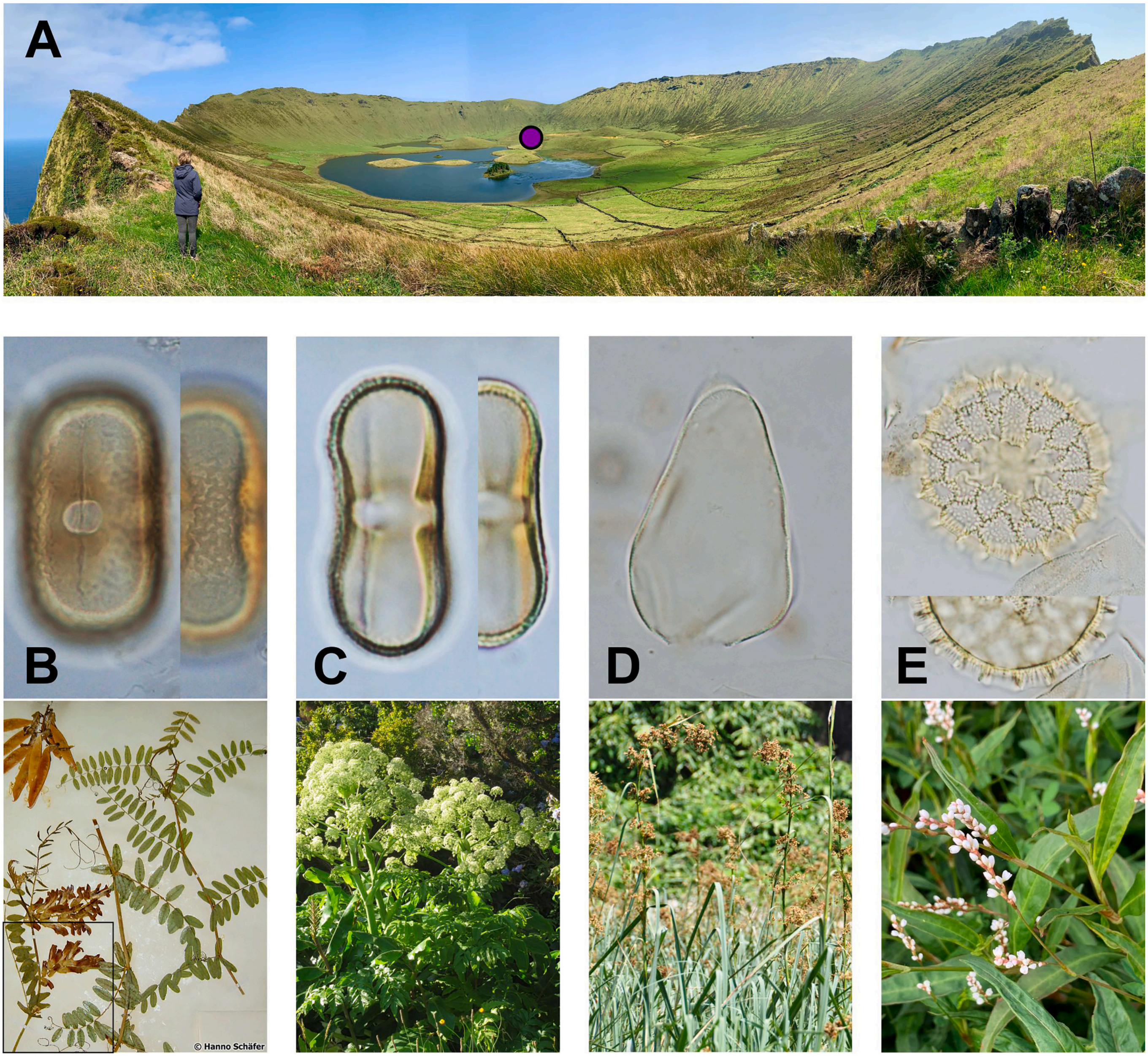

Fig. 2. The Caldeirão study site on Corvo Island, Azores, and selected fossilized pollen from pre-colonisation sediments (Early-Mid Holocene) from Caldeirão 2014 core. A) Panorama of the Caldeirão do Corvo, with a dot marking the coring location (Fig. 1); B) Fossil pollen and herbarium specimen of *Vicia dennesiana*; C) *Angelica lignescens*; D) *Cladium mariscus*; E) *Persicaria hydropiperoides*. Pollen sample depths: B) 297 cm; C) 280 cm; D) 240 cm; E) 260 cm. Photo credits: Hanno Schaefer and Simon Connor.

different Azores islands. Principal Components Analysis (PCA) was used to summarise the geochemical data.

3. Results

3.1. Plant census

The vascular plant species list for Corvo includes 136 native species, of which 50 are endemic (Supporting Information). The iNaturalist survey resulted in a total of 805 vascular plant observations for 220 species (including non-native species) by January 2024. Current observations are available at: https://www.inaturalist.org/observations?place_id=18266&project_id=flora-of-the-azores. Corvo's 136 native species are represented by 85 pollen types (Supporting Information).

3.2. Sediment core analyses

The 3-m sediment sequence covers the period from 12,400 cal. yr BP until the present, with a probable hiatus in sedimentation from approximately 2720 to 550 cal. yr BP (see age-depth model in Supporting Information). A slow-down in sedimentation rates is also seen in the neighbouring lake record from 1000 to 600 cal. yr BP (Raposeiro et al., 2021). In our core, the hiatus is indicated by a change from organic to more minerogenic sediment. Because the hiatus introduces uncertainty into the age-depth model, our analysis focuses on features that are least influenced by sedimentation rates. Fig. 5 provides a synthesis of environmental changes recorded in geochemistry, charcoal and diatoms, and compares these to the main trends in the composition of plant communities represented by pollen and macrofossil assemblages.

Environmental changes around Caldeirão since 12,400 cal. yr BP can

Fig. 3. Selected plant macrofossils in pre-colonisation sediments found in the Caldeirão 2014 core from Corvo Island, Azores. A) *Cladium mariscus* achene; B) *Persicaria hydropiperoides* achene; C) *Selaginella kraussiana* megaspore; D) *Euphorbia stygiana* seed; E) *Juniperus brevifolia* leaves (adaxial view). Scale Bars: D, E, 1 mm; A, B, 0.5 mm; C, 0.25 mm. . Sample depths: A, D) 247.5–252.5 cm, B, C) 197.5–202.5 cm, E) 167.5–172.5 cm. Photo credits: Nick Porch and Tara Lewis.

be summarised into five phases based on the terrestrial pollen zones (Fig. 5). The record begins with a *Juniperus-Angelica-Hypericum*-Poaceae association (*Juniperus* wooded grassland) growing on the crater slopes (Fig. 6). During this phase, *Eleocharis* was dominant in the wetland itself (probably an *Eleocharis* fen).

The next phase of terrestrial vegetation, from approximately 11,400 until 5400 cal. yr BP, has *Frangula*- and *Picconia*-dominated assemblages with diverse herbaceous taxa (open vegetation zone). Geochemical indicators, including ITRAX and sediment organic content (loss-on-ignition), suggest increased soil instability through this second phase.

The third phase was a *Juniperus-Myrsine* phase (forest zone) in which erosion indicators declined as tree cover expanded. Plant macrofossils and pollen indicate that the wetland was overtaken by *Cladium mariscus* at the first half of this zone (Fig. 6). This third phase is interrupted by the hiatus around 2720 cal. yr BP. Pollen assemblages from the neighbouring lake indicate the *Juniperus-Myrsine* phase continued until a *Juniperus* decline dated to approximately 725–500 cal. yr BP (Raposeiro et al., 2021).

From 550 to 180 cal. yr BP (1400–1800 CE), *Juniperus* declined in both macrofossil and pollen records, and *Myrsine* became dominant in the terrestrial pollen record (Fig. 6). Fire and erosion indicators increased rapidly (initial impact zone) and Poaceae and *Sphagnum* began to expand. Mean sedimentation rates in this zone (0.29 cm y^{-1}) were ten times higher than in the previous one (0.029 cm y^{-1}). Plant macrofossils suggest several rapid shifts in dominance in wetland vegetation. Diatoms were more abundant after the hiatus and point to increasing acidification as *Sphagnum* expanded (Fig. 5).

The fifth and final vegetation phase is dominated by Poaceae, indicating the spread of pastures and loss of tree cover (complete deforestation zone). Rapid ecological turnover has continued through this phase despite a decline in burning and erosion (Fig. 5).

3.3. *Biodiversity indicators*

Using the framework in Fig. 4, we were able to identify 12 pollen taxa that are not listed in the current flora of Corvo or are incorrectly

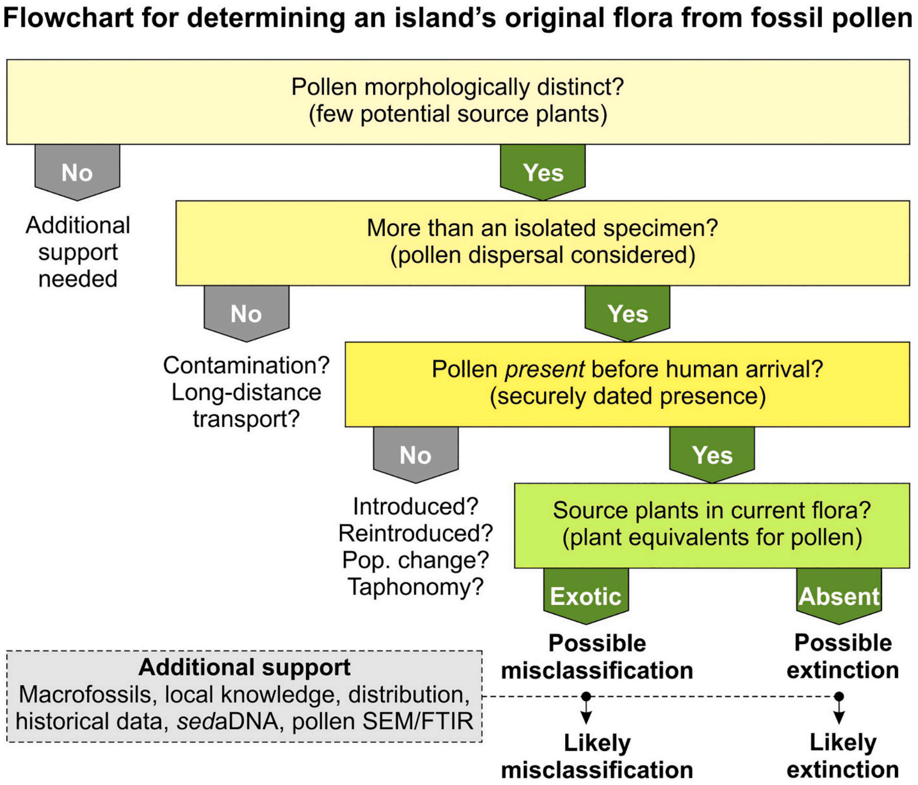

Fig. 4. Proposed framework for using fossilized pollen to help determine the original flora of an island. Whether a pollen occurrence constitutes an 'isolated specimen' depends on pollen production and dispersal. A single grain of some taxa (e.g. *Viola*) can indicate local presence, whereas most other taxa cannot be interpreted in this way, particularly wind-pollinated taxa (e.g. *Pinus* or *Quercus*). Abbreviations: pop. Change – population change; *seda*DNA – sedimentary ancient DNA; pollen SEM/FTIR – Scanning Electron Microscopy or Fourier Transformed Infrared Spectroscopy of single pollen grains.

listed as 'introduced', with two of the taxa found as abundant macrofossils (Fig. 6; Table 1). The 12 taxa can be divided in two groups: the first group consists of eight species which appear have become extinct/extirpated after human arrival on Corvo, including the rare endemic species *Angelica lignescens* (Fig. 2) and *Chaerophyllum azoricum* (Apiaceae). Both have a scattered distribution across the archipelago, with *Chaerophyllum azoricum* found locally on the neighbouring island Flores and more common in the highland of São Jorge (extinct on Faial island since the 1970s). *Angelica lignescens* is also found on neighbouring Flores, and other islands in the archipelago (Faial, Pico, São Jorge, Terceira, and São Miguel) and is always restricted to very limited areas, especially volcanic craters. It is very likely that both species originally grew in the Caldeirão crater of Corvo but were extirpated due to overgrazing. In addition, six non-endemic species seem to have disappeared from Corvo: three ferns (*Ophioglossum lusitanicum*, *Botrychium lunaria*, *Adiantum capillus-veneris*), and the herbs *Cladium mariscus* (a wetland species from the Cyperaceae family that locally forms large stands on Flores), *Viola* cf. *palustris* and a species of *Vicia* (likely the globally extinct *V. dennesiana*).

The second group includes three species still existing on Corvo but currently misclassified as "introduced": the American wetland species *Persicaria hydropiperoides* (Polygonaceae) could be identified to species level using macrofossils (Fig. 3B). It occurred abundantly prior to European colonisation and is almost certainly native to Corvo and probably other islands of the Azores. *Solanum nigrum, Scrophularia* cf. *auriculata* and a species of *Urtica*, probably *U. membranacea*, which had been listed as introduced species, are also suggested as native (Fig. 6). Finally, an abundance of *Selaginella kraussiana* megaspores confirms – to species level – that this plant is native to the Azores (Fig. 3C). This reaffirms less taxonomically-resolved palynological evidence for *Selaginella*'s native status (van Leeuwen et al., 2005).

The number of extinctions and extirpations equates to 15 % and mislabelled 'introduced' taxa to 8 % of the 53 native/endemic pollen taxa identified in wetland sediments from Caldeirão (23 % total). There are major biodiversity implications if this is representative of extinction and misclassification levels on Corvo generally. There is also a large discrepancy between taxa in the strictly 'introduced' category and those in the mixed category that includes both native and introduced taxa (Fig. 7).

Compared to other available pollen records from the Azores with high taxonomic resolution, Corvo exhibits the highest turnover (Fig. 8A). Endemic taxa declined at all sites and almost disappeared from low-elevation records (Fig. 8B).

4. Discussion

4.1. Determining an island's original flora using pollen

The accurate classification of species according to native or introduced status is important for ecological theory, applied research and biodiversity management as currently practised. Knowledge of the original biota of islands, prior to major disruption, is also key to understanding the functioning and assembly of individual island ecosystems. Of all the sources of fossil evidence, pollen data are the most ubiquitous and abundant, yet can also be the most difficult to interpret (Faegri et al., 1989).

In establishing *Selaginella kraussiana* as a native plant on the Azores from fossil spores, van Leeuwen et al. (2005) used the spores' abundant occurrence in various samples prior to human colonisation, as well as biogeographical factors, to argue for local presence. This approach was developed further on the Galápagos, where six 'introduced' species were identified as native plants from their frequent occurrence in pollen assemblages prior to human arrival (van Leeuwen et al., 2008). Subsequent work on the Azores found *Illecebrum verticillatum* and a *Persicaria*

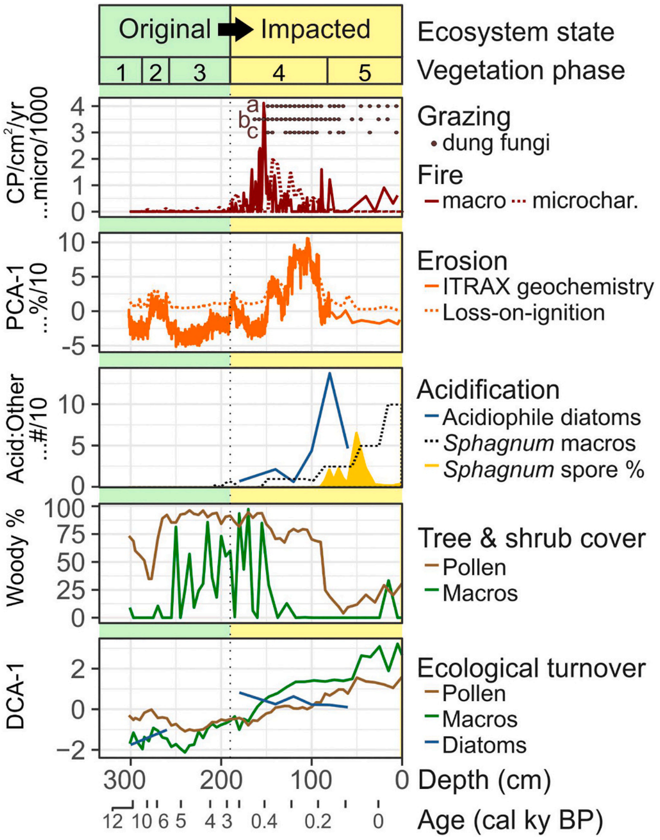

Fig. 5. Major proxies from the Caldeirão 2014 core, split into original (pre-hiatus) and impacted (post-hiatus) ecosystem states. Vegetation phases correspond to pollen zones. Grazing: fungal spore occurrence of a – *Sporormiella*, b – *Podospora* and c – *Cercophora*. Fire: macroscopic charred particle (CP) accumulation rates; dotted line indicates microscopic charcoal accumulation rates (divided by 1000). Erosion: ITRAX geochemical indicators (Principal Components Analysis axis 1) and loss-on-ignition. Acidification and *Sphagnum*: ratio of acidophile diatoms to other taxa, *Sphagnum* macrofossil abundance (No./10, dotted) and *Sphagnum* spore abundance (%, filled curve). Trees and shrub cover: woody taxa percentage. Ecological turnover: compositional change in biological proxies from Detrended Correspondence Analysis axis 1.

species to be native (Connor et al., 2012).

The framework provided here (Fig. 4) builds on that approach to provide an appropriate classification tool where historical records are data-deficient (Essl et al., 2018). The framework is ostensibly simple, but its application is complicated by its requirements for: a) excellent pollen-taxonomic information; b) good preservation of abundant fossil pollen with no potential contamination; c) unequivocal information about when human impacts began on the island; d) robust dating of the pollen-bearing sediments; and e) knowledge of the dispersal characteristics and pollen productivity of the taxa in question. It is desirable to seek additional support, such as historical records, *sed*aDNA, macrofossils or biogeographic clues, to corroborate the pollen evidence and establish a clearer picture of original island ecosystems (Fig. 4).

Our framework only addresses the likely presence of species and does not consider other aspects of the original ecosystem. Palaeoecological data can also contribute valuable information about past vegetation cover, floristic richness, turnover and disturbance regimes through carefully designed modelling and calibration studies (Abraham et al., 2016; Adeleye et al., 2021).

4.2. *Corvo's original ecosystems and potential drivers of extinction*

The occurrence of several unexpected pollen and macrofossil taxa in sediments prior to permanent human colonisation of the island leads to the conclusion that these taxa were part of the island's original ecosystem. Corroborating evidence helps to reduce levels of uncertainty (Table 1).

In compiling Table 1, we have made the simplifying assumption that the fossil remains are most likely to represent plants still extant on nearby islands or archipelagos (in the case of locally extinct taxa) or represent plants in the current flora of the island (in the case of mislabelled ‘introduced’ taxa). This assumption is necessary given the taxonomic limitations of fossil evidence. For *Vicia*, an example of probable extinction, fossil evidence could indicate: a) the historically recorded *Vicia dennesiana* went extinct; or b) one or more species of closely related *Vicia* went extinct, as no current *Vicia* species on the Azores produce the pollen type encountered in the Caldeirão sediments (Fig. 2). The same uncertainty applies to all the identified extinct/extirpated taxa to varying degrees. Molecular sequence data have proven useful in determining the provenance of certain Azorean plants (Schaefer, 2015) and show that a single species can include both native and introduced populations (Baumgarten et al., 2023). Single grains of fossilized pollen may also be studied using a combination of light and electron microscopy (e.g. SEM; Vieira et al., 2022) or chemical analysis using Raman or Fourier Transformed Infrared Spectrometry (FTIR) to untangle these issues (Kenđel and Zimmermann, 2020).

The long-term record of environmental change from Caldeirão (Fig. 5) helps shed light on the reasons behind some of the inferred extinctions and extirpations. The record dates back thousands of years earlier than previous records from the Azores archipelago and reveals much greater dynamism in Holocene environments (cf. Connor et al., 2012; Raposeiro et al., 2021). The crater's late-glacial and early-mid Holocene vegetation was relatively open, judging from the abundance of grasses and especially of herbs. Geochemical indicators like Titanium suggest enhanced soil instability, which perhaps favoured juniper dominance (Elias and Dias, 2009b). Open landscapes provided more suitable conditions for light-demanding species like *Azorina vidalii*, *Angelica lignescens* and extinct *Vicia dennesiana* than the denser forests of the mid-late Holocene.

Frangula azorica and *Picconia azorica* were also prevalent during this open vegetation phase and were later replaced by dense *Juniperus brevifolia* and *Myrsine retusa* forest communities around 5500 cal. yr BP. The timing of this replacement coincides with the end of the African Humid Period and pronounced drying on the Canary Islands (Nogué et al., 2013). In agreement with our data, historical reports of Corvo from the 16th century noted that the dominant woody species were *Juniperus, Picconia, Laurus, Myrsine* and *Ilex* and, within Caldeirão's crater, many juniper trees were harvested for timber (Frutuoso, 1590: 153). It is important to note that *Laurus azorica* pollen is rarely preserved (Connor et al., 2013) and *Laurus* leaf cuticles with stomata imprints (Rull et al., 2017) were not found, so past *Laurus azorica* abundance can only be inferred from other laurisilva elements like *Picconia azorica* and *Frangula azorica*. Likewise, charcoalified forests of *Prunus lusitanica* subsp. *azorica* indicate this tree was once dominant in Azorean laurisilva, but its entomophilous pollen is rarely detected in lake sediments (Góis-Marques et al., 2020).

It seems that habitat niches for many of the now-extinct or extirpated taxa, particularly the light-demanding herbs, were declining even before European transformation of the island's ecosystems. Climatic changes promoting dense tree cover and sea-level rise reducing island area are possible drivers (Rijsdijk et al., 2014). Coastal erosion could be another important factor, with an estimated 5000 to 100,000 m^3 of material eroded each year since the island's formation (Bossis et al., 2023). The dynamic Holocene environment is reflected in dynamic vegetation, particularly as sea levels rose in the early Holocene, forcing coastal vegetation to migrate inland and upslope.

European impacts are evident in unprecedented burning of vegetation (charcoal), almost complete deforestation (pollen), multiple species introductions (macro/pollen), livestock grazing (NPPs), soil instability

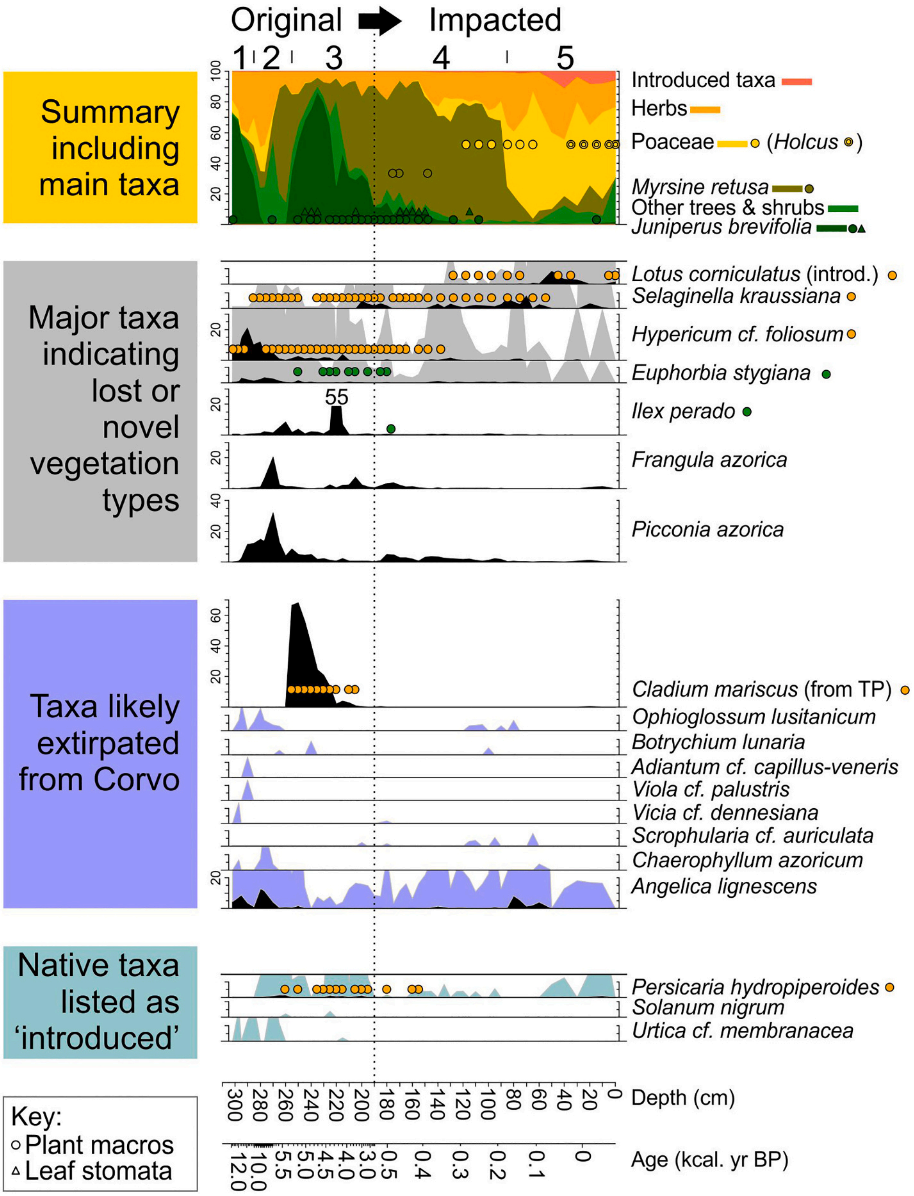

Fig. 6. Plant macrofossils (dots) and pollen/spores (curves) from the Caldeirão 2014 core, indicating changes in plant diversity on Corvo. Pollen percentages calculated from terrestrial pollen sum (except *Cladium mariscus*, from total pollen (TP)). Shaded curves are exaggerated 50 times.

Table 1
Pollen taxa without equivalents in the current flora of Corvo island. Status: Intro –introduced/naturalised. Refer to Fig. 4 for other criteria.

Taxon	Current status Corvo	Distinct pollen?	Before human?	Abundant?	Revised status	Additional support
Angelica lignescens	Absent	Y	Y	Y	Extirpated	Endemic to Azores islands
Adiantum cf. *capillus-veneris*	Absent	Y	Y	Y	Extirpated	*A. capillus-veneris* native
Botrychium lunaria	Absent	Y	Y	Y	Extirpated	Native on Pico island
Chaerophyllum azoricum	Absent	Y	Y	Y	Extirpated	Endemic to Azores islands
Cladium mariscus	Absent	Y	Y	Y	Extirpated	Macrofossils abundant
Ophioglossum lusitanicum	Absent	Y	Y	Y	Extirpated	Extant on Flores; pre-human on Pico
Persicaria hydropiperoides	Intro	Y	Y	Y	Native	Macrofossils; other Az sites
Scrophularia cf. *auriculata*	Intro	Y	Y	Y	Native	*S. auriculata* native to Azores
Solanum nigrum	Intro	Y	Y	Y	Native	Pollen poorly dispersed
Urtica cf. *membranacea*	Intro	Y	Y	Y	Native	Association with bird colonies
Vicia cf. *dennesiana*	Absent	Y	Y	Y	Extinct	*V. dennesiana* listed extinct on São Miguel
Viola cf. *palustris*	Absent	Y	Y	Y	Extirpated	*V. palustris* native on Flores

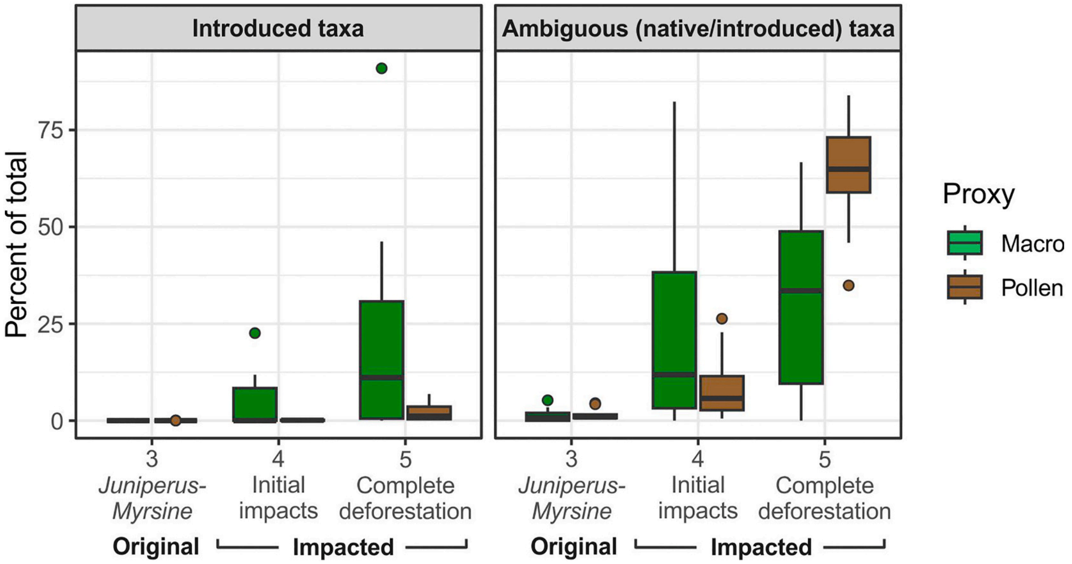

Fig. 7. Changes in the prevalence of introduced taxa and mixed or ambiguous taxa (native/introduced) in Corvo's Holocene vegetation, from original (zone 3) to impacted ecosystems (4 & 5). Introduced taxa alone may underestimate the extent of introduced vegetation.

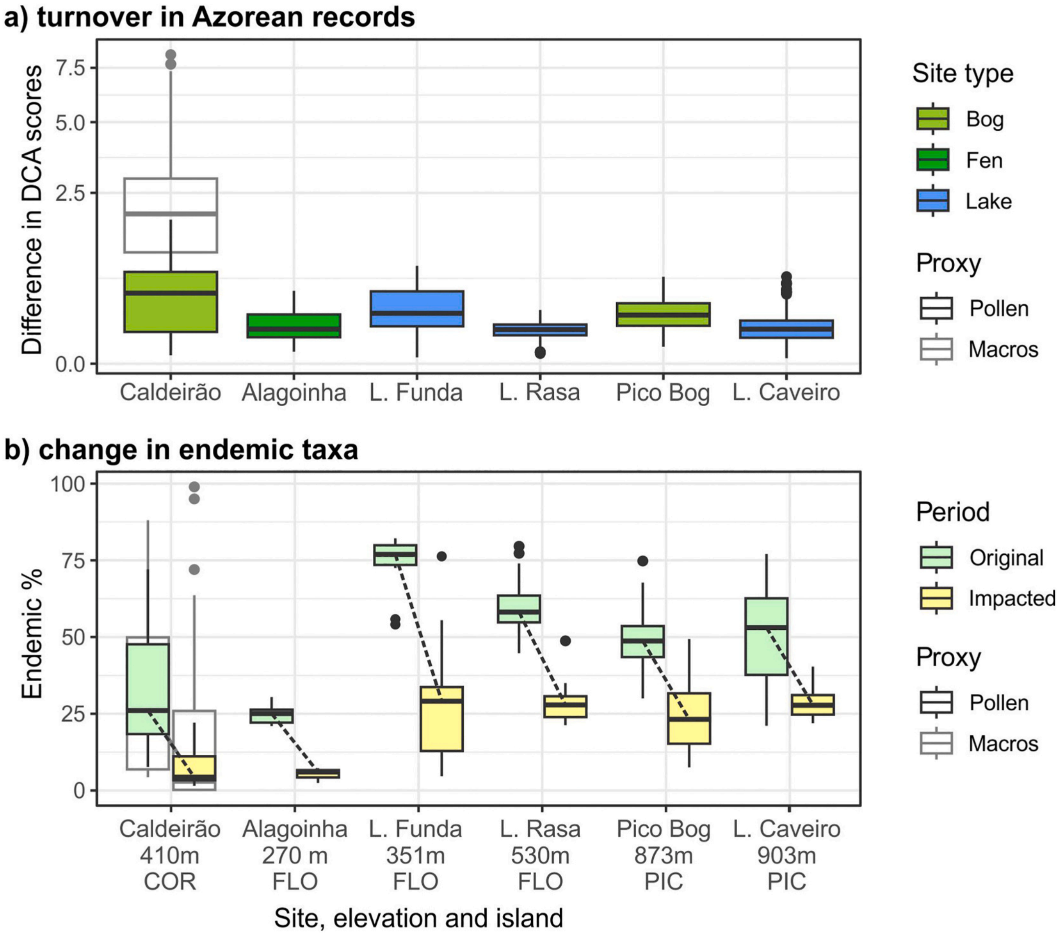

Fig. 8. A) Turnover differences between pre-colonial and post-colonial periods in various Azorean pollen records (Connor et al., 2012, 2013; Raposeiro et al., 2021; Ritter et al., 2022) compared to pollen and plant macrofossils from Caldeirão (this study). Boxplots are shaded according to site type. Square-root scaling used on y-axis for clarity. B) Change in the percentage of endemic taxa in the same records. Sites are ordered by island and elevation. COR – Corvo, FLO – Flores, PIC – Pico.

(ITRAX, loss-on-ignition) and wetland acidification (diatoms – Fig. 5). Human impacts of this nature caused extinctions on islands worldwide (Fernández-Palacios et al., 2021; Nogué et al., 2021) and Corvo is no exception to the global pattern.

In our data and given dating uncertainties, the timing of the impacts is clearly linked to 15th-century Portuguese colonisation (Fig. 5).

Raposeiro et al. (2021) argued for earlier colonisation of the Azores, possibly by Vikings, involving extensive settlements and profound ecological disturbance. This hypothesis was later disputed (Elias et al., 2022; Rull, 2023a, 2023b). The long hiatus in our record, perhaps caused by a dry climatic episode around 575 cal. yr BP (Richter et al., 2022), means we cannot exclude pre-Portuguese impacts. However, the persistence of forest cover and limited turnover until Portuguese colonisation point to continuity rather than disruption. This is consistent with the hypothesis that animals were released on the Azores prior to colonisation (Dias, 1996; Ritter et al., 2022). The magnitude and progression of Portuguese colonisation's ecological impact is clearly seen in unprecedented turnover within Corvo's plant communities (Fig. 5). Despite the most severe phases of erosion and fire having ended >200 years ago, the island's plant communities continue to follow a trajectory away from pre-colonisation baselines.

4.3. *Ecological changes at the community level*

Species extinction/extirpation is only one aspect of biodiversity loss. At the level of plant communities, the Corvo data indicate the loss of distinct vegetation types that dominated at various times before human impact (Fig. 6), consistent with previous studies (Connor et al., 2012; Raposeiro et al., 2021; Ritter et al., 2022). These include forest communities dominated by *Juniperus brevifolia, Ilex perado, Picconia azorica, Euphorbia stygiana* and *Frangula azorica*. All these species are rare in Corvo's current vegetation. *Frangula azorica* is nowadays reduced to two isolated plants on Corvo, whereas in the past it must have been widespread and abundant, given its low pollen production. Likewise, open vegetation communities with dominant *Hypericum foliosum* (also insect pollinated) and wetlands dominated by *Cladium mariscus* have disappeared from the contemporary landscape of Corvo. However, not all declines were anthropogenic. For example, the shift from *Juniperus brevifolia* to *Ilex perado* dominance on Corvo around 4000 cal. yr BP (Fig. 6) may relate to natural senescence of *Juniperus brevifolia* forest (Elias and Dias, 2009a), changes in regional climate (Björck et al., 2006) or the reconfiguration of Corvo through sea-level rise and coastal erosion.

Sphagnum expanded on Corvo following human disturbances associated with human colonisation, as indicated by abundant *Sphagnum* macrofossils and spores accompanied by indicators of fire, erosion and grazing. Post-colonisation *Sphagnum* spore increases are also seen in palaeoecological records from Flores and Pico (Connor et al., 2012) and other remote islands globally (e.g. Lawson et al., 2007; Coffey et al., 2012). While some *Sphagnum*-dominated communities on the Azores are associated with landslides (Elias and Dias, 2009b) and there is no suggestion that these are novel, the data from Corvo reinforce the hypothesis that blanket mire communities (Mendes and Dias, 2013) have greatly expanded following cutting of juniper/laurisilva forests and widespread burning of vegetation (Sjögren, 1973). These communities now play a key role in controlling erosion and providing habitat for rare epiphytic ferns and bryophytes but may not be suitable as restoration targets because of their likely anthropogenic origin.

4.4. *Implications for island biogeography and conservation*

Corvo is an excellent location to make a fossil-based assessment of original island ecosystems because, for a small remote island, it has a distinctive flora that has relatively few species. As such it can act as a model for other islands with greater diversity and habitat complexity where the task of linking fossil remains to extant or extinct species is more complicated.

4.4.1. *Extinctions and colonisation status*

The number of species in Corvo's original flora has been underestimated for two reasons: extinction/extirpation and incorrect colonisation status. The eight extinct species include one globally extinct and two locally extinct endemics. Compared to the endemic flora of neighbouring Flores Island, all other endemics are still present on Corvo, making it one of the Azorean islands with the highest percentage of endemics (almost 38 %). The low extirpation rate of endemics despite the deep anthropogenic impact on Corvo shows that extinction debts can accumulate over centuries. However, the populations of several endemic plants on Corvo are now so small (<50 individuals) that there is a risk of their extinction in the coming decades.

Four ‘introduced’ species were identified as being native to Corvo. This number may be higher if some fossil remains represent more than one species. Three of these species are listed as “native” for Madeira (Menezes de Sequeira et al., 2011) and their biology clearly fits to the remaining native Azores flora: *Solanum nigrum* is a bird-dispersed small herb associated with nitrogen-rich habitats like seabird colonies. *Urtica membranacea* occurs in similar habitats, though it is also possible that *Urtica* pollen represents an extinct species such as *U. morifolia* (endemic to the Canaries and Madeira). *Persicaria hydropiperoides* is a wetland specialist and was originally classified as “introduced” since it is a mainly North American species (Schaefer, 2003), but dispersal by waterbirds to the Azores thousands of years ago is possible. Since the fossil data represent only a subset of the total flora and a single sampling location, it is likely that more extinctions and misclassified species will be discovered in the future. There are several other plant species where status remains controversial and fossil or *sed*aDNA data are needed for a definitive classification. These include the iconic dragon tree (*Dracaena draco*), several grass species and herbs for which a status decision based on habitat, historical data and biology of the species is difficult (Schaefer, 2003).

4.4.2. *Biodiversity shortfalls*

Similar levels of extinction and misclassification may apply to many other islands and could be higher on large, complex islands (e.g. Hawaii, Burney and Burney, 2016). Gaps in biodiversity knowledge from extinctions can be considered a ‘Linnean shortfall’ if evidence for extinction of undescribed species is found. Misclassified species and previously-described extirpated species, by altering the known geographic range of species, constitute a ‘Wallacean shortfall’ (Hortal et al., 2015). Both have major implications for management and conservation. Firstly, the species-area relationships that underpin global analyses of island biodiversity (Whittaker and Fernández-Palacios, 2007; Price et al., 2018) could be skewed by unrecorded extinctions and misclassifications. If some of the species found as fossils later prove to be endemics, this could likewise skew patterns of endemicity across islands and archipelagos.

The drivers behind diversity patterns in Macaronesia, particularly the Azores, are much debated and include factors such as island age, size, geology, habitat similarity, climate stability and recent human impact (Carine and Schaefer, 2010; Schaefer et al., 2011b; Amorim et al., 2012; Triantis et al., 2012; Price et al., 2018). Our data indicate that incomplete biodiversity knowledge (Linnean and Wallacean shortfalls) is likely to be a more significant factor than previously considered (Schaefer et al., 2011a, 2011b) and we urge a degree of caution when relying on biodiversity checklists to develop generalisations about island biogeography, not just on the Azores, but on all remote islands.

By directly addressing uncertainties surrounding the degree to which biodiversity patterns have been shaped by anthropogenic vs natural processes, our data are relevant to the ‘Hookerian shortfall’ (Carine and Menezes de Sequeira, 2020). Our data prove that the first detailed botanical descriptions of Corvo in the mid-19th century occurred in a deforested landscape recovering from centuries of burning, erosion, grazing and exotic species introductions (i.e. phase 5, Fig. 5). Non-native pollen has been used to assess Hookerian shortfalls on remote islands globally (Walentowitz et al., 2023). Given that the percentage of misclassified species may be significant, one should be cautious when drawing conclusions about the timing and trajectory of species introductions. On the other hand, this approach perhaps underestimates the extent of habitat modification. On Corvo, for example, non-native pollen average only 2 % in phase 5, compared to 22 % for plant macrofossils (Fig. 7). This discrepancy is caused by ambiguous or 'mixed' pollen taxa (Walentowitz et al., 2023) that represent both native and non-native plant species (e.g. Poaceae), masking the extent of species introductions. When ambiguous taxa are considered (Fig. 7), it is possible that non-native species have dominated Corvo's vegetation for the last two centuries. This long-term perspective is critical for understanding rates of habitat transformation and species invasion on islands.

Corvo's status as one of the most anthropogenically transformed islands of the Azores is reflected in higher turnover (Fig. 8) compared to records from Flores and Pico, islands where relict woody vegetation is preserved. However, pollen turnover may also be influenced by site characteristics, such as basin size and steepness, given that adjacent sites like Lagoa Funda and Lagoa Rasa exhibit substantial differences (Fig. 8). Turnover metrics may underestimate habitat modification around sites with large pollen source-areas, such as lakes (Sugita, 1994). To overcome this possible limitation, it is desirable to couple turnover with additional information. In the Azores' case, changes in endemic taxa could be seen as a clearer indicator of the Hookerian shortfall (Fig. 8B), differentiating sites today surrounded by introduced vegetation (Alagoinha and Caldeirão) from sites with sizeable patches of relict vegetation.

4.4.3. *Habitat restoration*

Past island habitats may have been very different to today's habitats and may have harboured very different species assemblages (Bush et al., 2014). For example, species that today are most abundant in coastal lowlands (e.g. *Picconia azorica* and *Azorina vidallii*) apparently occurred inland at higher elevations on Corvo under different climatic conditions (cf. Fig. 1A). Relict populations suggest that this could be true of other islands as well (Schaefer, 1999). While previous palaeoecological research on the Azores has emphasised vegetation stability and post-disturbance recovery prior to human impact (Connor et al., 2012; Raposeiro et al., 2021), the longer-term evidence from Corvo reveals a much more dynamic situation, representing multiple possibilities for restoration baselines.

Restoration or rehabilitation of habitats is critical to prevent further extinctions on islands where substantial extinction debts have accumulated (Otto et al., 2017), but what restoration baseline is appropriate? Potential natural vegetation (PNV) is a useful tool for landscape management and conservation, providing a model of the spatial distribution of vegetation types under current climatic conditions (e.g. Elias et al., 2016). Fossil data and historical information complement these spatial models by adding a dynamic temporal dimension. On islands, fossil data are fundamental to updating biodiversity checklists, distinguishing original communities from those that have arisen through anthropogenic disruption, and for understanding vegetation dynamics under various disturbance regimes (Nogué et al., 2021; Walentowitz et al., 2023).

Fossil evidence remains a more robust method of investigating past extinctions than estimates that rely on inference (Lambdon and Cronk, 2020; Brook et al., 2003). Fossil evidence is more actionable than inferred extinctions, in that landscape management can act on direct evidence. For example, this evidence could be used to justify translocation of species whose remaining habitats on other islands are under threat. The capacity of fossil analyses to reveal gaps in biodiversity knowledge is clearly demonstrated by the potential extinctions/extirpations and mislabelled 'introduced' taxa described in this study. Despite this, fossil data have numerous blind spots and the analytical work can be extremely time consuming. Fossil-based research may be more difficult on islands with rich and diverse floras, in areas with few wetlands or other sedimentary deposits, on larger islands or those close to continents, in areas where taxonomic knowledge is lacking, or where human occupation history is more complex (i.e. archaeophytes: Preston et al., 2004). In such situations, *seda*DNA is an informative adjunct to fossils (Garcés-Pastor et al., 2022). Given how unique the biodiversity of remote islands is, investment in comprehensive palaeobotanical research could avoid costly mistakes in the future.

5. Conclusion

In this study, we demonstrate how fossil data can be analysed to develop a clearer picture of past island ecosystems. Using the small remote island of Corvo as a case study, we document several previously unrecognised extinctions or extirpations and expand the native geographic ranges of several plant species that were previously regarded as introductions. We show that human colonisation caused drastic ecosystem transformations that continue to affect ecological trajectories today, long after the eroded 'moonscapes' created by pervasive burning and grazing have been forgotten. In this way, the research addresses both the Wallacean and Hookerian biodiversity shortfalls. On many islands, our framework for interpreting pollen evidence with the aid of multi-proxy research opens up new possibilities for reconstructing the past diversity and dynamics of island ecosystems. Such research assists the development of biogeographic theory and sustainable management by contributing to a more complete picture of island biodiversity.

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Permissions

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CRediT authorship contribution statement

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Declaration of competing interest

The authors have no conflicts of interest to declare.

Data availability

All data are available in Supporting Information and will be uploaded to the Neotoma Palaeoecology Database on initial acceptance of the manuscript. Code is provided in Supporting Information.

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