The vanishing and the establishment of a new ecosystem on an oceanic island – Anthropogenic impacts with no return ticket

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HIGHLIGHTS

- Long-term perspectives from a multiproxy analysis of Lake Funda (Flores, Azores).
- Climate change and catchment processes drove lake dynamics before human arrival.
- Human disturbance triggered a state shift from mesotrophic to eutrophic conditions.
- Human disturbance, climate and in-lake processes caused a tipping point mid-16th C.
- Positive feedback of phosphorus cycling hampers the return to a mesotrophic state.

GRAPHICAL ABSTRACT
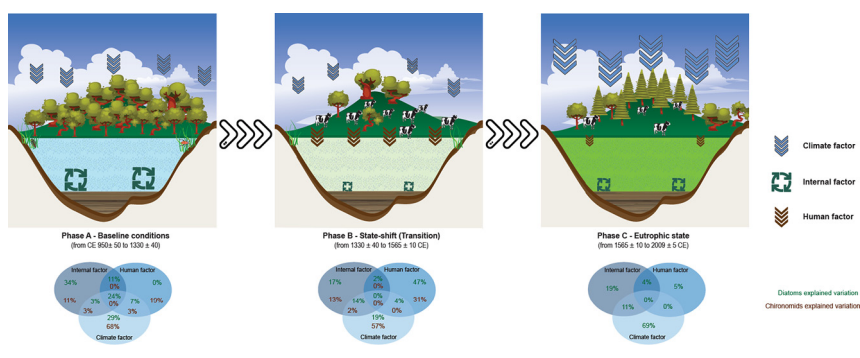
ABSTRACT

A multiproxy approach was applied to a sediment core retrieved from the deep crater Lake Funda, located in the middle of the North Atlantic Ocean on Flores Island, Azores archipelago (Portugal). The purpose of this study was to determine how this ecosystem responded to natural and anthropogenic forces over the last millennium. We distinguished three main phases in lake evolution using multiproxy reconstructions and documentary sources. (A) Climate and lake catchment processes, as well as internal ones, were the main drivers of ecosystem variability before 1335 CE, when human disturbances were absent in the Lake Funda catchment. (B) The second phase is marked by unprecedented changes in all studied proxies between 1335 and 1560 CE, including abrupt changes in the composition and diversity of diatom and chironomid assemblages. Synergistic effects from high climate variability and the onset of

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human disturbances in the catchment (e.g., introduction of livestock) during the Medieval Climate Anomaly-Little Ice Age transition, led to an increase in lake trophic state from mesotrophic to eutrophic conditions. (C) In the last phase (1560 CE to the present), the eutrophic conditions in Lake Funda were maintained through a positive feedback loop between lake productivity and in-lake phosphorous recycling. Variability within the lake ecosystem was mainly associated with climate variability and internal lake dynamics (e.g., phosphorus remobilization). Our results show that a paleoecological approach is crucial to understanding lake ecological states in the present-day in order to develop locally adapted management and restoration strategies. A long-term perspective enables us to understand the harmful consequences of ongoing climate change and human disturbances on lake ecosystems.

1. Introduction

Lakes are fundamental to the environment and the biosphere, supporting a global heritage of biodiversity (McIntyre et al., 2016; Vadeboncoeur et al., 2011). These ecosystems are highly sensitive to anthropogenic disturbances and climatic changes (Dubois et al., 2017; Woolway et al., 2020), and the combined effects of these changes are profoundly altering the chemical and biological processes potentially with irreversible modifications in lakes (Catalan et al., 2013; Szabó et al., 2020). Widespread changes within lakes include eutrophication (Pla-Rabés et al., 2005; Vázquez-Loureiro et al., 2019), acidification (Solomon et al., 2015), changes in water mixing regimes (Bao et al., 2015; Woolway and Merchant, 2019) and surface water temperatures (Zhong et al., 2016), morphological alterations (Saulnier-Talbot and Lavoie, 2018), invasive species (Raposeiro et al., 2017), and water budgets (Haddeland et al., 2014). These changes in lake ecosystems frequently result from a complex interplay among human disturbance and climate variability and ecosystem structure and functioning (Catalan et al., 2013; Dubois et al., 2017; Jaiswal et al., 2021). Understanding these complex interactions are essential for developing plans for ecosystem restoration and to protect lake ecosystems and their services.

Oceanic islands, particularly in the North Atlantic, are considered model systems for ecological studies (Vitousek, 2002) as humans only recently (<1500 years ago) occupied these islands (Nogué et al., 2021). Remote islands are an ideal location to disentangle the complex interactions between human disturbances and climate changes and how they affect lake ecosystems. Humans have encountered pristine environmental systems highly vulnerable to novel impacts as is the case of Azores islands (Nogué et al., 2021; Raposeiro et al., 2021b). Before the arrival of humans, the main drivers of lake ecosystems included natural forcings such as volcanic eruptions, climate variability and surficial processes in the catchment (e.g. Connor et al., 2012; Nogué et al., 2021). Humans, however, quickly transformed island environments to make them habitable (Castilla-Beltrán et al., 2019; Nogué et al., 2021; Rull et al., 2017). These effects often become apparent early in the colonization process by disturbances in lake catchment areas through agricultural and pastoral activities and the introduction of non-indigenous species (Connor et al., 2012; Nogué et al., 2021; Raposeiro et al., 2017; Rull et al., 2017). Later, population increases and technological advances have invariably resulted in widespread ecological transformations (Buchaca et al., 2011; Costa et al., 2021; Skov et al., 2010; Vázquez-Loureiro et al., 2019) that contributed to irreversible changes in lake ecosystems.

Lake sediments are archives for past climate and environmental conditions, which allows us to establish a range and rate of natural variability, and therefore quantify the magnitude of human impacts (Bennion et al., 2011; Dubois et al., 2017). Multiproxy paleolimnological records offer the opportunity to understand the reference baseline conditions before human-environment interactions and cause-effect linkages took place (Larocque-Tobler, 2016), providing insight into past lake disturbances and overall changes in the landscape as well as provide lake-based restoration actions (e.g. Larocque-Tobler and Pla-Rabés, 2015). For example, pollen assemblages, charcoal and sediment influx are frequently used to detect early human disturbances (Smol et al., 2001). However, these are not necessarily accompanied by evidence of a simultaneous aquatic transition depending on the magnitude of disturbance (see Dubois et al., 2017). On the other hand, biological remains of diatoms and chironomids, organisms

with short generation times, can provide evidence of a first detectable human impact on aquatic ecosystems through shifts in community composition and structure (McWethy et al., 2010).

Human-induced eutrophication or "cultural eutrophication" is one of the critical threats to freshwater ecosystems as it can lead to potential loss of biodiversity and other associated ecosystems services (Jilbert et al., 2020; Schindler, 2012). Accelerated cultural eutrophication has been explored in several studies as a response to intensified modern agricultural practices, urbanization and industrialization in recent centuries (e.g. Anderson et al., 2014; Zhang et al., 2018). In contrast, few studies have focused on the first human disturbance that leads to early cultural eutrophication on insular systems (McWethy et al., 2010; Vázquez-Loureiro et al., 2019). Furthermore, the lack of long-term monitoring information to support effective management and restoration activities is missing, leading to major knowledge gaps of how lakes respond to natural and/or anthropogenic changes and whether this has led to an irreversible change in the environment. According to Carpenter et al. (1999), theoretically, an irreversible change in a lake's environment does not exclude a return to the original state. Recent climate change and human disturbances might result in unprecedented and possibly irreversible modifications to lake catchments and their ecosystems (Genkai-Kato and Carpenter, 2005; Lotter and Birks, 2003; Messerli et al., 2000). The United Nations Decade of Restoration 2021–2030 (www.decadeonrestoration.org) has put restoration ecology and conservation management prominent on the political agenda, providing a timely statement to advocate for the inclusion of long-term natural variability studies before implementing restoration and conservation activities.

This study focuses on Lake Funda, a deep crater lake located on Flores Island (Azores Archipelago) in the middle of the North Atlantic. The sediment record presents the environmental history of the last 1000 years without the influence of active volcanism (Andrade et al., 2021), meaning that the lake was only impacted by human activities and climate change. Even though shallow lakes have long been archetypal systems for testing regime shift theories, such as alternative stable states (Scheffer et al., 2001; Scheffer and van Nes, 2007), recent studies provided evidence for alternative stable states in deep lakes (Bruel et al., 2018; Wang et al., 2012). We hypothesize that the lake has been increasingly affected by human pressure since the first signs of human disturbance, and combined with always present climate variability, the ecosystem entered a new eutrophic state that will be difficult to revert. Thus, our multiproxy reconstruction of Lake Funda provides an important perspective to understanding contemporary lake status and a quantitative, evidence-based guide to lake restoration, as they are at the core point of the future health of the lake environment.

2. Study area

2.1. Geologic, climate and vegetation setting

The Azores Archipelago is comprised of nine islands of volcanic origin located near the triple junction of the North American, Eurasian and African plates (latitudes 37°-40° N and longitude 25°-31° W), with the Mid-Atlantic Ridge (MAR) dividing Flores and Corvo Islands, to the West, from the remaining islands located to the East. Terceira, Pico Faial, São Jorge and Graciosa, constitute the Central Group, while São Miguel and Santa Maria Islands belong to the Eastern Group of islands (Fig. 1). With an area of 143 km^2, Flores Island is only approx. 2.15 million years old,
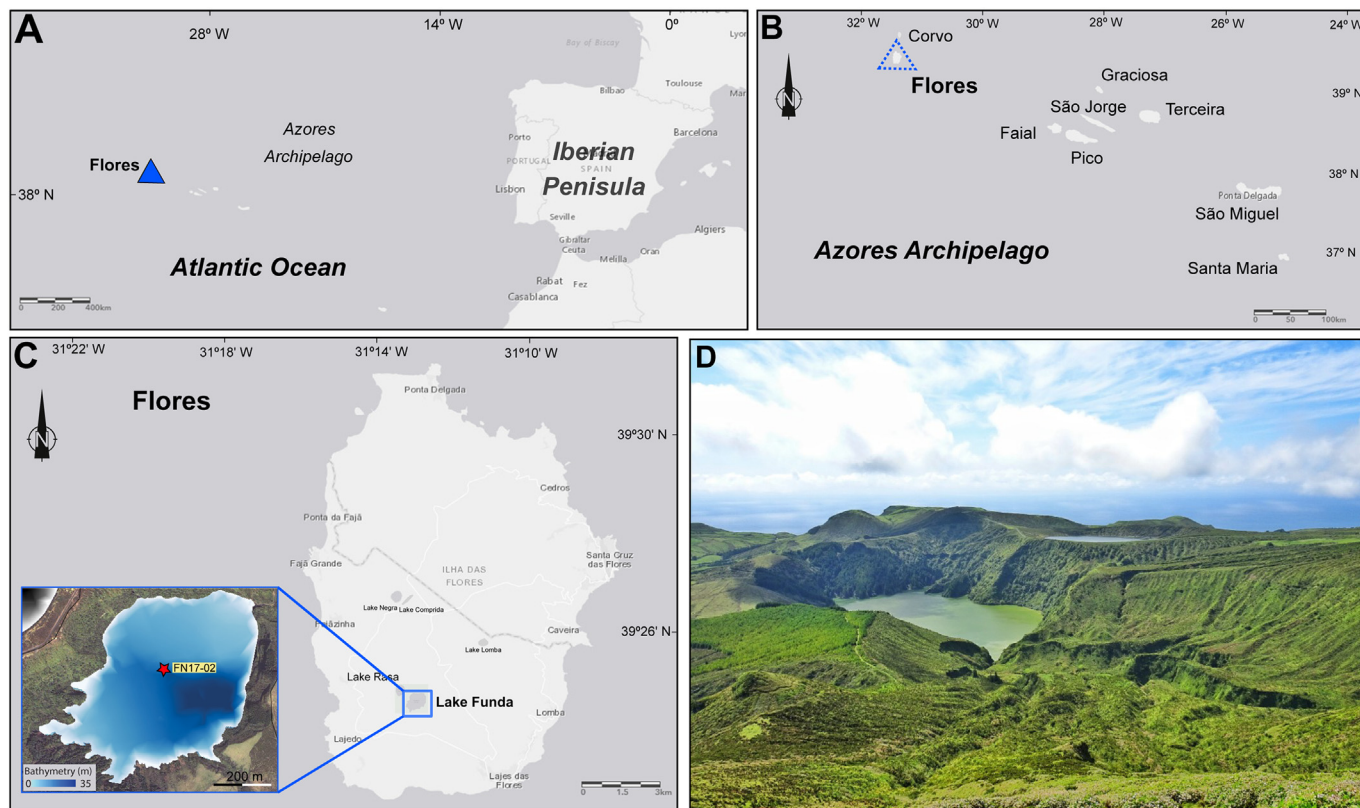
Fig. 1. A) Location of the Azores Archipelago on the North-eastern Atlantic region; B) Azores Archipelago – triangle indicates the location of Flores Island; C) Flores Island with aerial image of Lake Funda and its bathymetry. Dark blues indicate deep areas while light blues mark shallow ones. The red star shows the location of the studied core. D) Image of Lake Funda (left) and Lake Rasa (top and right), photo by Vítor Gonçalves in 2017.

and its volcanic activity ceased at around 2400 years CE (Andrade et al., 2021).

The climate in the Azores is classified as temperate oceanic, marked by low thermal amplitude, high humidity and persistent winds, and significant seasonal and interannual variability in precipitation (Hernández et al., 2016). In addition, factors such as altitude, proximity to the sea influence the local climate (DROTRH/INAG, 2001). The average rainfall in Flores Island is 1716 mm (data from 1970 to 1990), with average temperatures varying between 10.5 °C in February and 25.1 °C in August (CLIMAAT Project, 2007). The climatic conditions are determined by the strength and position of the Azores Current and a semi-permanent high-pressure system known as the Azores Anticyclone (Volkov and Fu, 2010). Most of its winter climate variability is determined by the NAO (North Atlantic Oscillation), with the southern dipole centered over the Azores Archipelago (Hernández et al., 2020a; Hurrell et al., 2003). However, when the NAO influence becomes weaker, the effects of other large-scale climate modes such as the East Atlantic (EA) variability increase, highlighting the non-stationary influence of the NAO on the Azorean climate (Hernández et al., 2016). Thus, NAO and EA combinations control seasonal climate variability on a regional scale (Comas-Bru and Hernández, 2018; Mellado-Cano et al., 2019; Hernández et al., 2020b). These atmospheric modes have affected the climate of the western Europe sector (Comas-Bru and McDermott, 2014; Mellado-Cano et al., 2019), however their role on the central North Atlantic is less-known, pointing to a winter precipitation and summer temperatures partly controlled by the NAO and EA, respectively (Hernández et al., 2015, 2016).

The most commonly accepted date of the colonization of Flores Island is 1452 CE by Portuguese sailors; however, a recent environmental reconstruction that covers the last 1500 years of the Azores archipelago shows that the colonization of these islands took place around 700–850 CE, approximately 700 years prior to the official historically documented

occupation (see Raposeiro et al., 2021b). Officially, the island was populated in 1475 CE when sheep were introduced, and human settlement was only established in 1510 CE (Frutuoso, 1978). Before the Portuguese colonization, the landscape in the highlands was dominated by dense laurisilva's forest and short-stature *Juniperus brevifolia* (Seub.) Antoine and *Morella faya* (Ait.) Wilbur (Connor et al., 2012; van Leeuwen et al., 2005). However, in the present-day about 95% of the native vegetation on the Azores has been destroyed (Triantis et al., 2010). Nowadays, the vegetation of Flores is highly degraded; lowland laurel forests are scarce and coastal woodlands are significantly reduced, and in most cases, invaded by *Pittosporum undulatum* Vent. (Elias et al., 2016).

2.2. Lake Funda

Lake Funda is located in the southern sector of the central plateau of Flores Island at 351 m altitude and occupies the bottom of a maar-explosion crater, 875 m in length and 625 m in width (Fig. 1). The lake occupies 0.37 km² and its total basin area is 3.14 km² (Andrade et al., 2019). Lake Funda is a deep monomictic lake (max. depth of 35.7 m), with temperatures ranging from 11.5 °C in January to 26.6 °C in August (continuous temperature records from October 2015 to June 2017) (Gonçalves et al., 2009). Stratification starts approximately in May/June and lasts until November. The residence time is 2.7 years (Andrade et al., 2019). Lake Funda has a high bathymetric gradient, and is hydrologically closed with reduced shallow littoral zones (Fig. 1).

During the summer months the hypolimnion develops below ca. 15 m depth and is characterized by a decrease in pH and oxygen, sometimes becoming fully anoxic, and an increase in total CO_2 (Antunes et al., 2006). The lake water belongs to the chlorinated sodium type but with a bicarbonate sodium tendency at the lake's bottom (Cruz et al., 2006). Marine salts mainly influence its chemical composition through atmospheric transport

and precipitation chemical composition (Cruz et al., 2006). Water pH varies from 6.71 to 9.94 (mean = 7.54 and median = 7.4). The electrical conductivity varies between 76 and 148 μS·cm^{-1} (mean = 106.4 μS·cm^{-1}, median = 123 μS·cm^{-1}), which reveals the reduced mineralization of this water (Antunes et al., 2006). The total CO_2 content along the water column ranges from 24.76 to 38.32 mg·L^{-1} (mean = 30.45 mg·L^{-1}). The seasonal effect on the total amount of CO_2 emitted into the atmosphere is present in the studied lake, and during summer is 0.36 t·d^{-1}, and through winter, the emissions should be higher due to the full mixing (Andrade et al., 2019).

3. Materials and methods

3.1. Coring, age model, organic and inorganic proxies

In June 2017, a 994-cm long sediment core (Core FN17-02) was retrieved from the deepest area of Lake Funda (Fig. 1; 39°24′23.1; "N, 31°13′03.2"W) using a UWITEC® piston corer installed in a UWITEC® platform (UWITEC Ltd., Mondsee, Austria). The core was sealed, transported to the laboratory and kept in a cold room at +4 °C until its opening at the Geosciences Barcelona (GEO3BCN-CSIC, Spain). The recovered lacustrine sedimentary sequence is described in detail by Raposeiro et al. (2021b). The age model was developed using ^{210}Pb and ^{137}Cs concentration profiles and 10 AMS ^{14}C dates measured on pollen concentrates extracted from sediment samples as described by Raposeiro et al. (2021; Fig. S1). Samples for bulk organic geochemistry of 1 cm thick were collected at 5 cm intervals (methodology described in supplemental material of Raposeiro et al. (2021b), and data available in Raposeiro et al. (2021a)). The better-preserved half of each section of the core was analyzed using X-ray fluorescence (XRF) with the AVAATECH XRF II core scanner at the Universitat de Barcelona (Spain). The XRF measurements were performed every 2 mm, where the material was well preserved (methodology described in supplemental material of Raposeiro et al., 2021b, and data available in Raposeiro et al. (2021a). Analyses of biogenic silica (BSi) contents (%) in 1 cm thick layers at 5 cm intervals from the Lake Funda sediment core were performed in the Marine Research Institute (IIM-CSIC, Spain) (data available in Richter et al. (2022)). BSi was dissolved following the wet-alkaline leaching procedure and dissolved silicate measured by the molybdate blue spectrophotometric method (Bernárdez et al., 2005).

3.2. Biological proxies

3.2.1. Pollen

Pollen samples of 0.5 cm^3 were analyzed at intervals of 16–64 cm, depending on the sedimentation rate, to obtain a regular age resolution between the samples. After spiking with Lycopodium clavatum, samples were digested with KOH, HCl, HF, and acetolysis. The residues were suspended in glycerin, and the microscopic slides were mounted in the same medium (Bennett and Willis, 2001). Samples were processed and analyzed at CSIC. Identification of pollen, spores and non-pollen palynomorphs (NPPs) was done at 400× magnification following Beug (2004), Demske et al. (2013) and Reille (1999), and supported by the growing library of the Azorean modern collection curated by the Freshwater Ecology Research Group of CIBIO-Açores at the University of the Azores in Ponta Delgada, São Miguel. Non-pollen palynomorphs (NPP) were identified according to Cugny et al. (2010), van Geel et al. (2003, 2011) and van Geel and Aptroot (2006). The pollen sum included all identified pollen and spore types with an ecological role in the landscape, except those from aquatic and semi-aquatic taxa (Cyperaceae, Myriophyllum and Potamogeton). Micro-charcoal particles were counted in the palynological slides considering >20 μm, to reflect fires on a regional scale (Whitlock and Larsen, 2001).

3.2.2. Diatoms

Diatom samples of 0.5 cm^3 were analyzed at intervals of 5–10 cm, depending on the sedimentation rate. Fossil diatoms in each sample were analyzed following standard methods (Battarbee et al., 2001b). At least 600

valves were counted and identified along transects at 1000× magnification using a light microscope (Leica DM 1000) equipped with a brightfield 100× C Plan objective (Leica) with a numerical aperture of 1.25 with oil immersion. Diatom taxonomy followed general floras (Krammer and Lange-Bertalot, 1991; Lange-Bertalot et al., 2017), complemented with other literature (Morales et al., 2015; Novais, 2011). Diatom nomenclature has been updated according to the most recent publications as indicated in the OMNIDIA v.6.0 database (Lecointe et al., 1993). The fossil diatom data were expressed as relative abundance (in percent).

3.2.3. Chironomids

Chironomid samples were prepared at every 10 cm interval throughout the sediment core, following the protocol described in Brooks et al. (2007). Samples of wet sediment (2–4 g) were deflocculated in a warm (c. 70 °C) water bath with 10% solution of potassium hydroxide (KOH) for 30 min and subsequently sieved with a 100 μm mesh-size sieve. Sieved residues were stored in 70% ethanol, and chironomid head capsules were hand-picked under a stereoscope (Olympus SZX7). All head capsules were mounted in slides with a solution of Entellan® after a minimum of 50 counts was reached. Taxonomic identifications were made at 400× magnification using a Leica DM 2500 microscope, and chironomid species were then identified following mainly Brooks et al. (2007) and Rieradevall and Brooks (2001).

3.3. Numerical methods

Biological data were Hellinger transformed (Legendre and Gallagher, 2001) prior to the identification of biostratigraphic zones. Zonation of the pollen, diatom and chironomid taxonomic profile is based on stratigraphically constrained cluster analysis (CONISS). Statistically significant stages were selected using the broken-stick model (Bennett, 1996) using R software for Windows (R version R-3.5.2) with the statistical package Rioja 0.9-9 (Juggins, 2015).

The species information was plotted using C2 software version 1.7.7. (Juggins, 2007). For the diatom and chironomid diagram, species with less than 5% relative abundance were not included in the visual representation. For display purposes in the diatom diagram, several taxa were grouped into complexes if they shared similar trends through time. Groupings include Ulnaria complex (Ulnaria acus, U. delicatissima, U. danica). Taxa were arranged according to their life-forms (benthic, tychoplanktonic or planktonic) following Denys (1992), Van Dam et al. (1994), Vos and De Wolf (1993) and Witkowski et al. (2000).

3.3.1. Ordination analysis

Patterns of change in diatom and chironomid communities were summarized using detrended corresponded analysis (DCA). DCA resulted in a gradient length of 2.7 D units for both diatom and chironomid assemblage data, indicating that linear methods (i.e., principal component analysis – PCA) were appropriate for subsequent ordination analyses (Birks, 1995).

To determine how human impacts and climate changes have affected the lake ecosystem, the direct relationship between diatoms and chironomids assemblages and the predictor data was explored by redundancy analysis (RDA) using biplot centered on interspecies distances. The δ^{15}N was used as an indicator of in-lake dynamics variability. A rise of nutrients (mainly phosphorus) availability increase lake trophic status and N_2-fixing cyanobacteria blooms in Azorean lakes (Cordeiro et al., 2020; Santos et al., 2005) and elsewhere (Taranu et al., 2015), resulting in a lower isotopic signal (Struck et al., 2000). Internal-lake P recycling in dimictic and monomictic lakes, as Lake Funda, is related to the hypolimnetic oxygen depletion during summer stratification, leading to a sharp increase in P and ammonia during the overturn period (Cruz et al., 2015; Richter et al., submitted). Therefore, hypolimnetic oxygen depletion during summer stratification increased lake P availability and the rise in N-fixing cyanobacteria. However, we are aware that the isotopic record could also be related to climate and anthropogenic impacts in the lake catchment (e.g. Catalan and Fee, 1994). Consequently, we should consider that during

pre-anthropogenic periods with low cyanobacterial blooms and low phosphorus availability the $\delta^{15}N$ signal would be mainly related to climate variability and changes in the lake-catchment vegetation. The pollen record is sensitive to landscape changes due to climate variability but is also highly sensitive to land-use changes caused by humans including deforestation (Delcourt et al., 1986). Hence, we can expect some degree of shared variance between climate and anthropogenic impacts. Still, anthropogenic land-use changes have been the main cause of long-term changes in Lake Funda and in the Azores Archipelago during the last millennia (Raposeiro et al., 2021b). Abrupt climate fluctuations could also cause a change in the pollen record, but previous results show a rapid vegetation recovery to previous conditions after these abrupt climate fluctuations or volcanic disruptions (Connor et al., 2012; Raposeiro et al., 2021b). For the climate factors, the variables used were the annual NAO and EA index, temperature, and precipitation from climate model simulations described in Raposeiro et al. (2021b). RDA analyses were used to calculate the independent effect of each factor that can explain the main patterns of diatom and chironomid variations among phases. The statistical significance of the relationship between the assemblages and the whole set of predictor variables in a constrained ordination model was evaluated using the Monte Carlo permutation test (499 permutations), which allowed us to judge the statistical significance of each selected variable in a regression model for a model selection to discern the distribution of unique, shared and unexplained variance for each biological assemblage in each ecological phases. PCA and RDA were implemented using the software CANOCO 5.01 (Ter Braak and Smilauer, 2002).

4. Results & interpretations

4.1. Sedimentary facies and age-depth model

The lower part of the studied core (994–368 cm) consists of brown to black organic-rich mud with plant remains, interbedded with sands and erosive gravel layers containing trunk fragments. The uppermost 368 cm of the core are laminated facies, composed of brown mud and yellow diatom oozes. The age-depth model is also published by Raposeiro et al. (2021b). The uppermost 798 cm reveals that the recovered sedimentary sequence displays the climate and environmental evolution of the lake over the last ca. 720 years (Fig. S1). The lower coarse grain-size deposits in the

bottom have an average sedimentation rate of ca. 7.3 mm.yr^{-1}, whereas the sedimentation rate decreases in the uppermost 368 cm muddy laminated deposits to ca. 5.2 mm.yr^{-1}. The overall high sedimentation rate of Funda deposits is related to the high topographic gradient of the lake catchment, and a well-developed alluvial system in the lake's north margin.

4.2. Detrital inputs, organic content, and sediment chemistry

The detrital inputs, organic content and sediment chemistry results of Lake Funda are already published, described and available (Raposeiro et al., 2021a, 2021b). Here, we present a summed description of the results that will be used to interpret the diatoms and chironomids changes of the present work (Fig. 2).

The total organic carbon (TOC) content ranged from 3.43 to 20.20% wt (total dry weight). The mean TOC values were the highest (12.45 ± 0.6% wt) between the depths 706–323 cm (GC1) when compared to the depths 323–151 cm (GC2) (8.46 ± 0.62% wt) and depths 151–9 cm (GC3) (7.02 ± 0.27% wt). The total nitrogen (TN) content ranged from 0.19 to 1.20% wt. The mean TN values were also the highest (0.69 ± 0.04% wt) in GC1, but the lowest in GC2 (0.67 ± 0.03% wt). The mean values remained on the lower spectrum in zone GC3 (0.68 ± 0.02% wt) (Fig. 2). The TOC/TN ratio fluctuated between 8.92 and 26.96 (Raposeiro et al., 2021b), and the highest mean values were documented in GC1 (18.58 ± 0.44), the intermediate mean values in GC2 (12.16 ± 0.35), and finally, the lower values in GC3 (10.35 ± 0.11). The $\delta^{13}C$ isotopic signature ranged from −29.32 to −19.95‰. The lower mean values were recorded in GC3 (−27.29 ± 0.14‰), while the higher mean values were in GC2 (−26.12 ± 0.04‰). GC1 maintained the lower mean values recorded in the previous zone (−26.35 ± 0.14‰); however, values presented higher variability. As for the $\delta^{15}N$, the isotopic signature varied between 0.95 and 6.25‰ and followed the TOC/TN mean values trend with the highest mean values being documented in GC1 (3.89 ± 0.09‰), and the lowest in GC3 (1.84 ± 0.09‰). GC2 recorded in-between mean values of 2.91 ± 0.10‰. Biogenic Silica (BSi) ranged from 0.5% to 11.0% at its maximum. The highest, more variable, mean BSi values were recorded in GC3 (6.74 ± 0.39%), and higher values were also documented in GC3 (5.31 ± 0.26%). GC1 presented the lowest BSi mean values for the core (1.99 ± 0.15%) (Fig. 2).
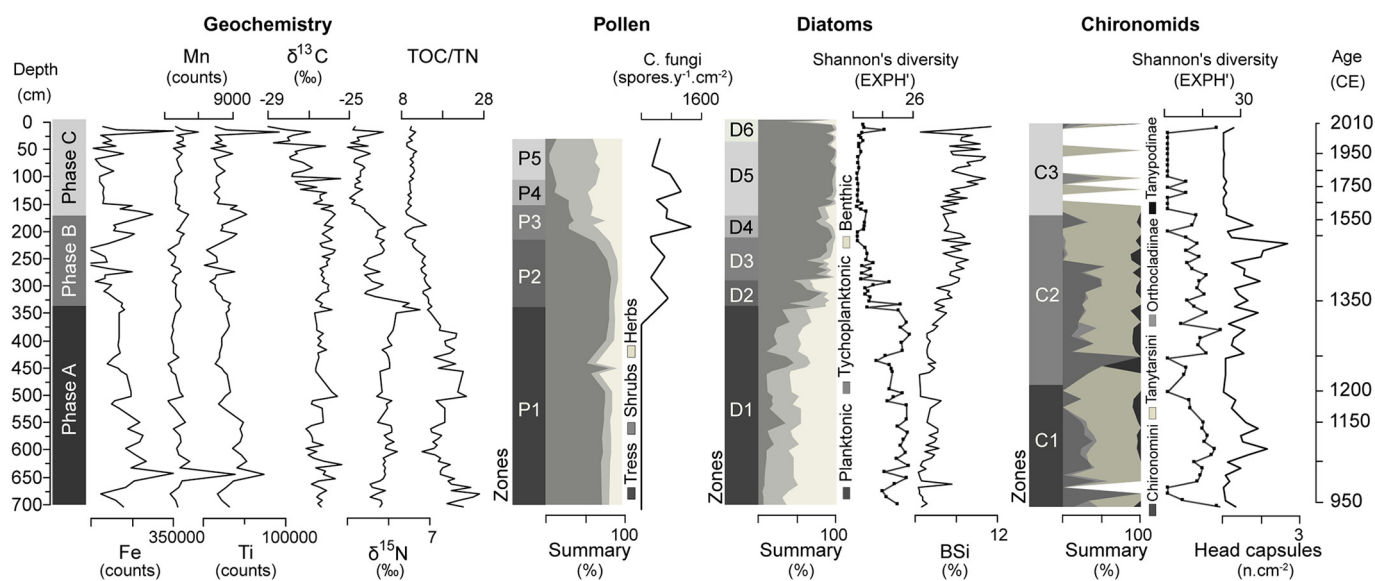

Fig. 2. Stratigraphic profiles of geochemical and biological data from Lake Funda, Flores Island. From left to right: geochemistry stratigraphic zones, Fe, Mn, Ti, $\delta^{13}C$, $\delta^{15}N$ and TOC/TN profiles, pollen stratigraphic zones, summary of major pollen groups, % of fungi profile, diatom stratigraphic zones, summary of major diatom groups, diatom diversity profile, biogenic silica profile, chironomid stratigraphic zones, chironomid diversity and head capsules profiles.

4.3. Biological proxies

4.3.1. Pollen assemblages

A total of 64 pollen and spore types were identified in the pollen record (Fig. S2). Trees are highly abundant but display low diversity. Herbaceous plant species, grasses and ferns are highly diverse, with most taxa present in low percentages. In addition, 16 recognized NPP types were recorded, including stomata of *Juniperus brevifolia* and *Laurus*, coprophilous fungal ascospore types, algae, and erosion indicators (Fig. S2).

4.3.1.1. Pollen zone P1: 797–346 cm (724 ± 50–1330 ± 40 yr CE). In the bottom part of the sequence, the terrestrial pollen assemblages show a *Juniperus*-dominated forest, with *Picconia* trees, *Myrsine* shrubs, and *Ilex perado* trees' co-dominance indicating a highly wet high-altitude forest (Fig. S2).

Presence of *Juniperus* stomata indicate the local presence of *Juniperus* trees, and stomata of *Laurus* show that these trees were locally present in the landscape as well. *Erica*, *Euphorbia* and *Morella faya*, are present as canopy trees or shrubs. The vegetation was thick, and mosses would cover branches of trees and shrubs and dominate the understory (Fig. 2). A diverse and abundant herbaceous layer was mainly constituted by the larger ferns *Culcita* and *Pteris incompleta*, and to a lesser extent *Dryopteris azorica*, *Athyrium filix-femina*, *Selaginella* and *Trichomanes*. Common herbs found are *Angelica*, *Ammi*, *Hypericum*, *Tolpis* and Poaceae. No indicators of human or cattle presence have been recognized in this zone (Fig. S2).

4.3.1.2. Pollen zone P2: 346–233 cm (1330 ± 40–1415 ± 20 yr CE). Pollen taxa diversity remains comparable to the previous zone (Fig. S2). The zone change seems predominantly driven by a rapid increase of *Picconia*, and a more gradual increase of *Myrsine* shrubs, while *Juniperus* slowly decreases, accelerating towards the top of this zone. The stomata of *Laurus* become rare, and the herbs *Angelica*, *Lactuca*, *Hypericum* and *Potentilla*, and the ferns *Dryoteris azorica* and *Athyrium filix-femina* abruptly disappear from the record. Increasing values of *Poaceae* and *Trichomanes* replace these lower understory species. Coprophilous dung fungal spores of *Sporormiella* are present for the first time in the record at the start of this zone, indicating the presence of larger vertebrates (Fig. S2, Fig. 2 and Fig. 3).

4.3.1.3. Pollen zone P3: 233–152 cm (1415 ± 20–1650 ± 10 yr CE). The onset of this zone is typified by significant composition turnover (Fig. S2). Already starting to decrease in the previous zone, the abundance of *Juniperus* becomes very low. The stomata of *Juniperus* and *Laurus* almost disappear, supporting the local decrease in tree cover. *Picconia* also rapidly loses its foothold in the current vegetation composition. Instead, there is an increase in *Myrsine* and *Erica* shrubs/trees and Poaceae, indicating an abrupt change towards a more open landscape and less dense forest vegetation. To a lesser extent, this zone also sees increases in *Vaccinium*, *Morella faya*, *Potentilla*, and ferns *Pteridium* and *Selaginella*. These latter taxa indicate the turnover that also happened in the lower and understory vegetation. Many human indicators are present: coprophilous fungal spores *Podospora*, *Sordaria*, and *Sporormiella* indicate the arrival of more introduced animals on the island and closer to the lake. The occasional presence of *Diporotheca* indicates erosion events on high sectors of the lake bottom (Fig. S2). *Potamogeton* also suggests changing water properties, potentially towards higher nutrient levels. Furthermore, a continuous occurrence of *Neurospora crassa* spores and higher charcoal inputs indicate frequent induced human fires in the landscape (Jacobson et al., 2004; Stivrins et al., 2019).

4.3.1.4. Pollen zone P4: 152–112 cm (1650 ± 10–1780 ± 10 yr CE). After two centuries of relative stability in the vegetation composition and cover, the record indicates a rapid shift of several exotic species (Fig. S2). Most obvious is the introduction of *Hydrangea* to the island, which propagates via streams, expanding rapidly. *Spergula* type also becomes a relatively abundant herb. Values of trees further decline as *Juniperus*, *Picconia* and *Myrsine* decrease in abundance, while the proportion of grasses remains high. In this zone, *Lotus* starts appearing, an introduced herb commonly

found in agricultural fields, evidence that the area around Lake Funda is used for pastoral activities (Fig. S2). A sharp peak of *Coelastrum reticulatum* green algae suggests a blooming event indicating rapid aquatic changes.

4.3.1.5. Pollen zone P5: 112–32 cm (1780 ± 10–1990 ± 5 cal yr CE). The last zone records the lowest tree abundance (Fig. S2, Fig. 2). The introduction of Cryptomeria to Flores was relatively late, and this is reflected in the pollen record (Fig. S2). Cryptomeria is currently planted on the west side of Lake Funda. No significant differences are recorded between P4 and P5, except for exceptionally high values of *Hydrangea*, and to a lesser extent, high values of *Spergula* type.

4.3.2. Diatom assemblages

In total, 216 species of diatoms belonging to 57 genera were identified in the 77 Lake Funda sediment core samples. However, only 18 taxa reached relative abundances ≥5% and appeared in more than seven samples (Fig. S3). The species that fulfilled these criteria include six taxa of planktonic diatoms such as *Aulacoseira ambigua*, *Cyclotella meneghiniana*, *Fragilaria tenera* and species belonging to the *Ulnaria* complex, which includes *U. danica*, *U. acus*, *U. delicatissima* and *U. delicatissima* var. *angustissima*. The seven tychoplanktonic species were all small *Fragilaria s. l.*, which included *Staurosira subsalina*, *Staurosirella pinnata*, *Pseudostaurosira elliptica*. The five benthic species, *Achnanthidium minutissimum*, *U. ulna* and *Navicula cryptocephala* were the most frequent and abundant. Benthic and tychoplanktonic species dominated diatom assemblages until 1330 yr CE, and since then, planktonic species have dominated the lake (Fig. 2). CONISS analysis revealed six diatom stratigraphic zones (Fig. S3). These groups were also evident along the PCA sample trajectories, where sample assemblages were close together within groups (Fig. 2 and Fig. 4, Fig. S5).

4.3.2.1. Diatom zone D1: 705–346 cm (950 ± 50–1330 ± 40 yr CE). Diatom assemblages were dominated mainly by alkaliphilous tychoplanktonic and benthic species, revealing a diverse (12.7 < Exponential of Shannon Index (ESI) < 24.7) and rich (mean richness = 49.2) (Fig. S3), mesotrophic system. This trophic level is further revealed by the first ordination axis (PC1) that accounts for 41.2% of the diatom assemblage's variability (Fig. S5). This variability relates to the high benthic taxa contribution (e.g., *A. minutissimum*, *N. crytocephala*, *Fistulifera saprophila*, *Cocconeis lineata*, *Planothidium lanceolatum*) during this zone. Although the most considerable contribution was from the small benthic species, the dominant ones were tychoplanktonic *P. elliptica* and *S. pinnata*. *Staurosirella pinnata* starts to decrease around 1210 yr CE, giving place to the planktonic *Fragilaria tenera* (up to 40.1% abundances) and later, upon transition to D2, *Cyclotella meneghiniana* (Fig. S3). Aquatic to aerophilic species (e.g., *Nitzschia amphibia*, *Gomphonema parvulum*, *Humidophila brekkaensis*, *Humidophila perpusilla*) were also present.

4.3.2.2. Diatom zone D2: 346–295 cm (1330 ± 40–1380 ± 50 yr CE). Acidophilic *F. tenera* and planktonic *C. meneghiniana* dominated diatom assemblages in this zone and become rare for the rest of the core (Fig. S3). Along with these planktonic species, *Ulnaria* complex and *S. pinnata* (which underwent a drastic decrease at the beginning of this zone) increased their relative abundances up to 47% and 25% at around 1360 yr CE, respectively (Fig. S3). However, total diatom assemblages decreased diversity (5.3 < ESI < 20.5) and richness (m = 36.3 spp.) in this 50 cm zone, the planktonic:benthic ratio increased, yet the trophic level was maintained and this is clearly seen in the PC1 (Fig. 4, Fig. S5).

4.3.2.3. Diatom zone D3: 295–216 cm (1380 ± 50–1440 ± 20 yr CE). According to the CONISS analysis, the most significant differences occurred between zones D2 and D3 (Fig. S3) and it's also evident in the diatoms PC1 (Fig. 4, Fig. S5). D3 features an abrupt decrease in the previous dominant planktonic species and an increase in *Aulacoseira* species for the first time in the record. Planktonic eutrophic species *A. ambigua* and *A. granulata* dominate the diatom assemblage and represent 80% of the total diatom assemblage. *Ulnaria* complex follows the same trend as in D2
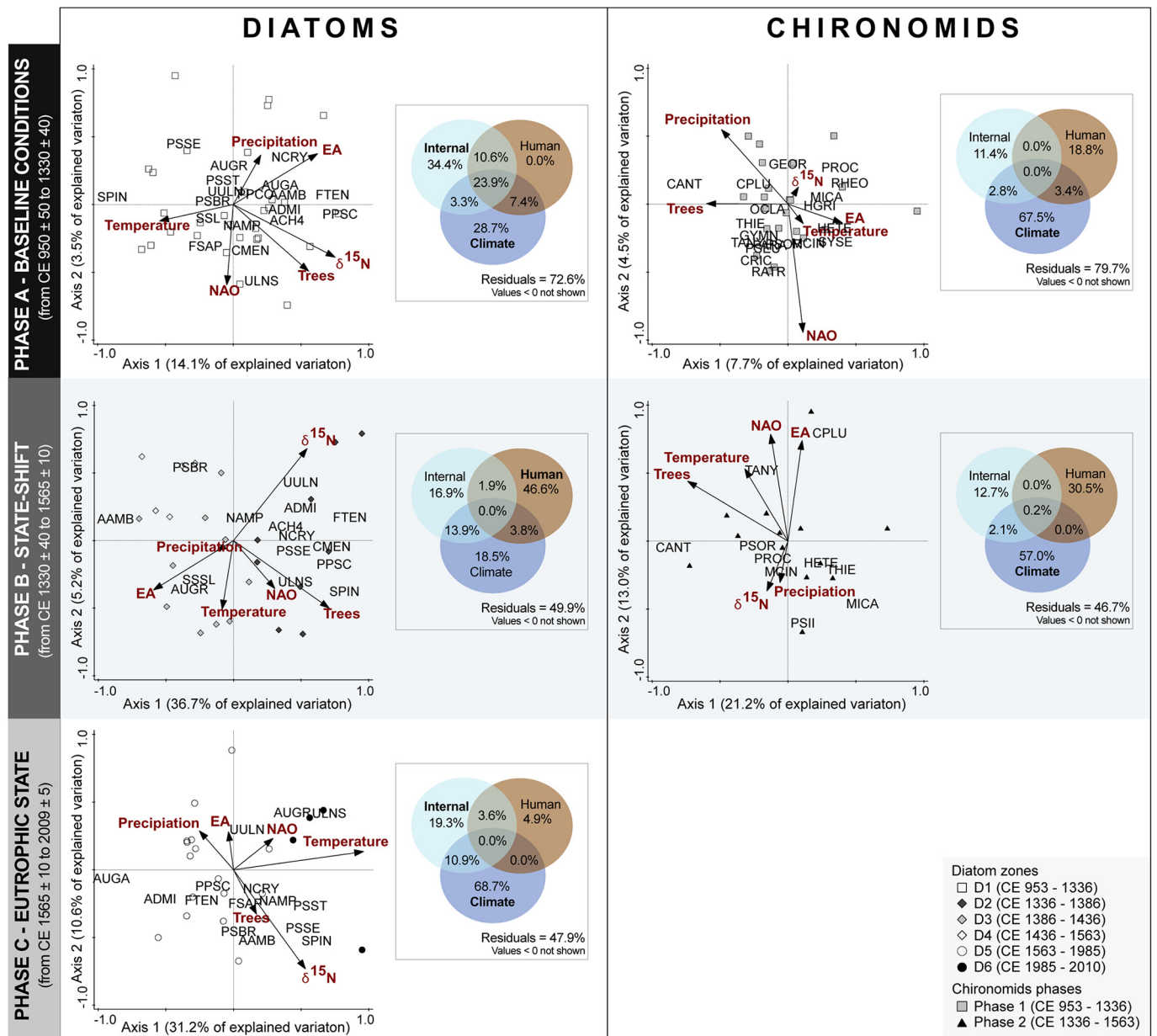
Fig. 3. Partial redundancy analysis (RDA) ordination diagram showing the relative contributions of explanatory variables as vectors and samples ages (CE) as symbols. Variation partitioning derived from each partial RDA using internal-lake factor (δ^{15}N), human impact factor (percentage of trees) and climatic variables (North Atlantic Oscillation (NAO), Eastern Atlantic (EA), Temperature and Precipitation anomalies computed for 850–1950 CE) as explaining variables. The amount of explained variance was calculated from the sum of all eigenvalues in each analysis. The circles are not drawn to scale. The complete variation explained table for each partial RDA is given in the Supplementary Material (Table S1). A list of the acronyms is provided in the Supplementary material (Table S2).

and pulses around 1415 yr CE. The drastic drop of diversity (1.8 < ESI < 8.6) and richness (m = 26.6 spp.), together with the dominance of *Aulacoseira* spp., revealed increased lake productivity and trophic state (Fig. 2 and Fig. 4; Fig. S3, Fig. S5,).

4.3.2.4. Diatom zone D4: 216–178 cm (1440 ± 20–1565 ± 10 yr CE). This zone does not account for major changes, except for the dominance of *A. ambigua* adding up to 90% of the total diatom assemblage, and therefore, decrease in *A. granulata* (Fig. S3). This increase might have been triggered by colder conditions in comparison to the previous zone. Some benthic species and *P. elliptica* reappeared with low abundances which increased richness (m = 27.5 spp.), yet this zone presented the lowest diversity of the record (1.8 < ESI < 5.0) (Fig. S3).

4.3.2.5. Diatom zone D5: 178–36 cm (1565 ± 10–1985 ± 5 yr CE). Previously dominant *A. ambigua* disappears completely in D5, and this zone is overtaken by cosmopolitan *A. granulata var. angustissima*. This species alone contributes to 85% of the total diatom assemblage, co-dominating with a species of the same genus, *A. granulata* (Fig. S3). Both planktonic species represent 95% of the assemblage, overruling any benthic or tychoplanktonic species contributions. Diversity continues to be low (1.5 < ESI < 5.7), and richness reaches its minimum value (m = 20.7 spp.) (Fig. S3). The lake becomes highly productive, increasing its trophic level as revealed by the increased values in PC1 (Fig. S5) and for the high values of BSi (Fig. 2).

4.3.2.6. Diatom zone D6: 36–9 cm (1985 ± 5–2009 ± 5 yr CE). The last and most recent diatom stratigraphic zone is dominated by *A. granulata* (45%),
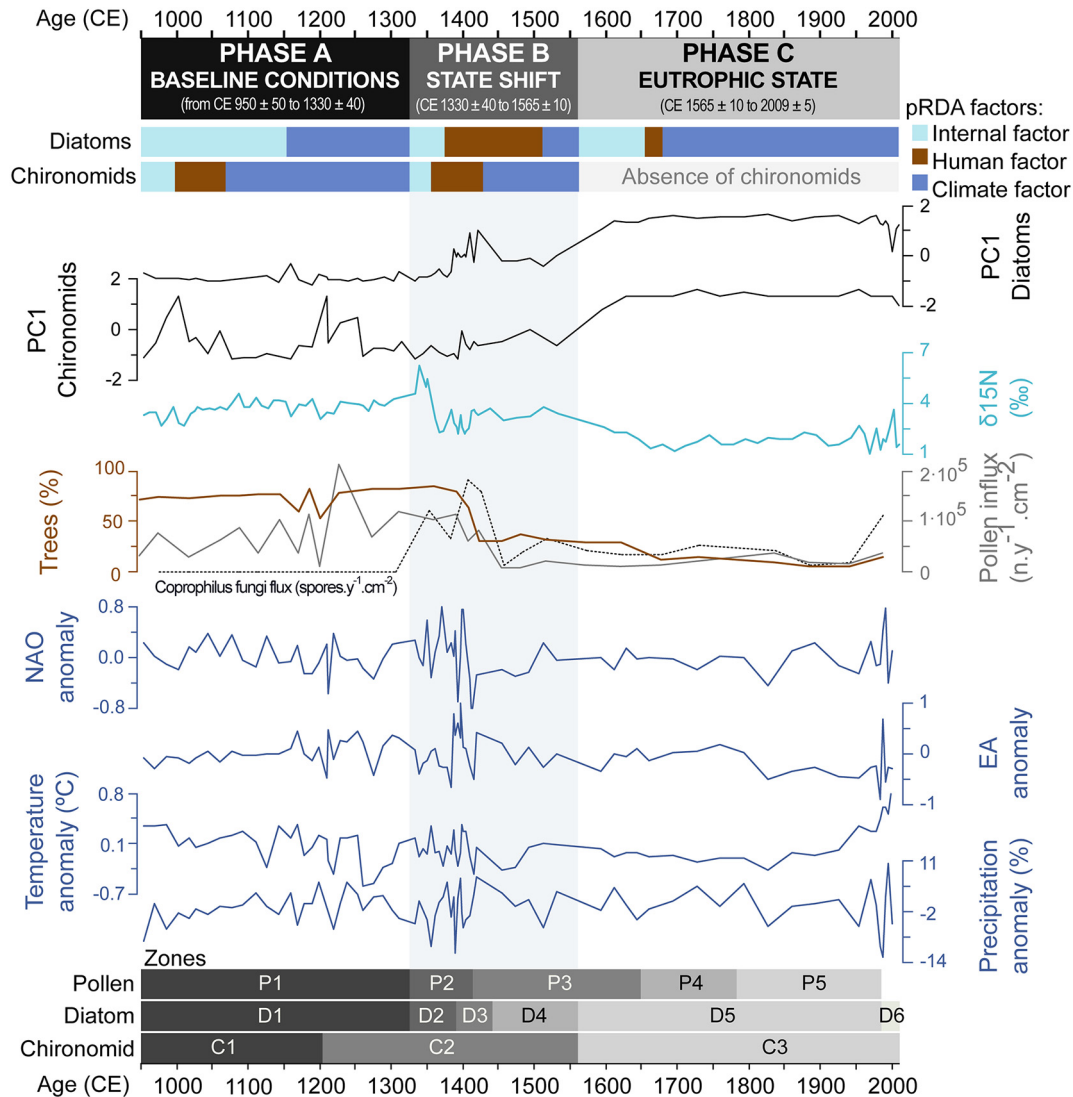
Fig. 4. From top to bottom: three main phases of Lake Funda, percentage of explained variance from the RDA ordination diagram, data profiles from the first PCA eigenvector (PC1) for diatoms and chironomids, all factors included in the RDA models – internal-lake factor (δ^{15}N), human impact factor (percentage of trees) and climatic variables (North Atlantic Oscillation (NAO), Eastern Atlantic (EA), Temperature and Precipitation anomalies computed for 850–1950 CE), and stratigraphic zones defined for each biological proxy (pollen, diatoms and chironomids).

co-occurring with the previous largely dominating diatom, *A. granulata* var. *angustissima* (Fig. S3). This species does not present such large relative abundances in D6 as in D5, but is still relevant, with 34% of the total contribution. The last species making 96% of the cumulative contribution is *Ulnaria* complex, reaching abundances of 23%. The abrupt input of sediment at 19 cm, clearly marked by the sudden decrease in the ^{210}Pb profile, and probably caused by climatic instability is worth mentioning, as *S. pinnata* and other tychoplanktonic species appeared and increased their contributions (Fig. 4, Fig. S3). This event led to an increase in diversity (2.6 < ESI < 13.5) and richness (m = 24.9 spp.), however the high trophic level is maintained despite the rapid event (Fig. S5).

4.3.3. Chironomid assemblages

In total, 25 Chironomidae taxa distributed among 18 genera and 3 sub-families were identified from head capsules (HC) present in the 57 core sediment samples (Fig. S4). The Orthocladiinae showed the greatest richness (15 taxa), followed by Chironominae (8 taxa) and Tanypodinae (2 taxa). *Micropsectra*-type A (occurred in 61% of samples), *Chironomus anthracinus*-type (53%) and *Micropsectra insignilobus*-type (51%) were the dominant taxa in the studied core. Subdominant taxa included *Procladius*-

type, *Psectrocladius sordidellus*-type and *Tanytarsus pallidicornis*-type. The abundance of chironomid HC showed large variations along with the core, ranging from 0 to 30 HC per cubic centimeter (HC·cm^{-3}) of sediment (mean of 5.1 HC·cm^{-3}). The CONISS analysis identifies three main stratigraphic zones (Fig. S4). The first two PCA axes explained 52.7% of total variation (Fig. S5). The first axis of the ordination (35.9% of total variation) is related to the decrease of diversity and increase of detritivore/grazers, hypoxia-tolerant, eutrophic species like *Chironomus plumosus*-type and *Paramerina* sp. The second axis of the ordination (16.8% of total variation) is related to the increase in the opportunistic taxon (i.e., *C. anthracinus*-type).

4.3.3.1. Chironomid zone C1: 705–463 cm (950 ± 50–1210 ± 30 yr CE). C1 is the richest and most diverse zone, recording an average of 6.0 HC·cm^{-3}, dominated by oligo/mesotrophic, oxyphilous species, such as *Micropsectra*-type A and *M. insignilobus*-type. Assemblages also included the mesotrophic, free-living *Procladius* sp. (Fig. S4). All these taxa are typical inhabitants of profundal zones of lakes. *Chironomus anthracinus*-type and *Psectrocladius sordinellus*-type were frequent and often associated with lakes' littoral zones (Raposeiro et al., 2018).

4.3.3.2. Chironomid zone C2: 463–178 cm (1210 ± 30–1565 ± 10 yr CE). In this zone, a slight increase in HC concentration was observed (11.3 HC·cm^{-3}). *Microspectra*-type A, *M. insignilobus*-type increase their dominance, while most of the littoral species decline, leading to a drastic decrease in richness and diversity (Fig. S4) probably related to increased lake productivity. The increase in the opportunistic taxon (i.e., *C. anthracinus*-type) indicated its adaptation to weak light conditions resulting from the increase of the trophic state.

4.3.3.3. Chironomid zone C3: 178–9 cm (1565 ± 10–2009 ± 5 yr CE). Several and abrupt changes occur in this zone. First, a drastic decrease in HC concentration was observed, where the HC's almost disappeared. Second, only the most common taxa from the previous zone were sporadically detected, such as *Microspectra*-type A and *M. insignilobus*-type (Fig. S4). However, in the last sample (9 cm), a slight increase in HC concentration, richness and diversity was observed.

5. Discussion

5.1. Main ecological phases in Lake Funda

Climate and local volcanism were the main factors affecting ecosystems before the arrival of humans on the North Atlantic Islands, however, this did not lead to any lasting changes in terrestrial and aquatic ecosystems (Björck et al., 2006; Connor et al., 2012; Raposeiro et al., 2021b). However, human disturbances (i.e. deforestation) had a longer-lasting impact on the pristine vegetation on islands than climatic changes and volcanic activity (Castilla-Beltrán et al., 2021; Nogué et al., 2021). This is particularly relevant for Flores Island during the last millennium (Andrade et al., 2021; Connor et al., 2012; Raposeiro et al., 2021b).

To distinguish the relevance of climate, anthropogenic and internal lake dynamics in the lake ecosystems across the last millennia, we have defined three main ecological phases in Lake Funda according to our biotic and geochemical results. The absence of anthropogenic biomarkers (fecal sterol biomarkers, 5β-cholestan-3β-ol and 5β-stigmastanol (Raposeiro et al., 2021b), as well as coprophilous fungal spores, *Sporormiella*-type and *Sordaria*-type) define the pre-anthropogenic phase. Abrupt changes in biotic assemblages and sediment geochemistry set the limit between phases two and three. These three phases denote two alternative stable states: phase A, the mesotrophic state; phase B, the transition phase between both stable states; phase C, the eutrophic state. However, a synchronized response by the three analyzed biological proxy-based indicators was not observed. Differential sensitivity to climate, human disturbance, and in-lake dynamics could be the underlying cause. Although the pollen record is sensitive to landscape changes due to climate variability, it is also highly sensitive to land-use changes caused by humans (Delcourt et al., 1986). Chironomids are affected by water temperature, dissolved oxygen and trophic state in deep lakes, primarily responding to climate conditions or changes in the lake functioning (Lotter et al., 1999; Raposeiro et al., 2018). Diatoms (primary producers with short generation times) are highly sensitive to habitat and resources availability such as light, nutrients and temperature (Battarbee et al., 2001a; Gonçalves et al., 2015; Pla-Rabés et al., 2005;). Hence, climate, land-use and atmospheric composition variability and their effect in lake dynamics drive changes in diatoms assemblages (Catalan et al., 2013; Pereira et al., 2014; Pla-Rabés et al., 2005).

5.1.1. Phase A (from 950 ± 50 to 1330 ± 40 CE) - baseline conditions (mesotrophic state)

Phase A predates the extensive human disturbance period. This phase is characterized by the absence of coprophilous fungi (Fig. 2) and presence of a dense forest-cover around the Lake Funda catchment (Fig. S2; Raposeiro et al., 2021b). As expected, the pollen record consists of approx. 75% arboreal pollen indicating *Juniperus*-dominated the forests at higher altitudes and a submontane *Laurus* forest in the lower areas of the Lake Funda catchment (Fig. S2). The Lake Funda pollen spectra are similar to Lake Rasa on Flores Island, Lake Caveiro on Pico Island (Connor et al., 2012) and Lake

Azul on São Miguel Island (Rull et al., 2017) during the same period. The high TOC/TN ratios (around 18) and δ^{15}N signatures (ranging from 2.6 to 6.3‰) (Fig. 2) indicate that lake organic matter was mainly from allochthonous sources (Meyers, 2003).

During this pre-colonization impact phase, RDA results revealed how climate explains a higher variability of chironomid and diatom assemblages (67.5%; 28.7%, respectively) than deforestation (18.8%; 0%, respectively) and internal lake dynamics (11.4%; 34.4%, respectively) (Fig. 3). However, the human disturbance on chironomid assemblages described in the above sentence as deforestation is linked to climate change effects on Flores island vegetation instead of human-induced deforestation (see Section 3.3.1 for further explication) (Fig. 4, Fig. S2). Diatom assemblages further reveal how all factors (climate, vegetation, and in-lake nutrients recycling) are related since their shared variability is significant (23.9%) (Fig. 3). Therefore, the δ^{15}N signature, our internal lake dynamics indicator, is related to climate-induced changes in the vegetation and, thus, in the sources of lake organic matter. Additionally, climate-driven changes in lake water level (as a hydrologically closed lake via precipitation-evapotranspiration balance) and long-term changes in the intensity and duration of overturn and stratification periods are more significant in high bathymetric gradient deep lakes with reduced zones of shallow water littoral zones, like Lake Funda (e.g., Woolway et al., 2021). Both factors are relevant for lake biota assemblages through changes in habitat and resources availability (light and nutrients), and the lake physicochemical environment (Adrian et al., 2009; Catalan and Fee, 1994; Raposeiro et al., 2018).

As described above, climate variability was the main force of variability for Lake Funda aquatic biological assemblages during this phase, which corresponds to the Medieval Climate Anomaly (MCA; 900–1450 CE). According to simulated precipitation (Raposeiro et al., 2021b), drier conditions occur in the Azores over two short periods ca. 940–960 CE and 1070–1080 CE, and wetter conditions between 1350 and 1450 CE. During the MCA period, diatom and chironomid assemblages were co-dominated by small mesotrophic tychoplanktonic diatom taxa (i.e., *Pseudostaurosira* spp. and *Staurosirella* spp.) and by mesotrophic, oxyphilous chironomid taxa (i.e. *Micropsectra* spp.) indicating that Lake Funda was both mesotrophic and deep (Fig. S3, Fig. S4). The presence of oxyphilous taxa supports low in-lake phosphorus cycling, also indicated by the low values of BSi (1.99 ± 0.15%) and high TOC/TN ratio (Fig. 2). In fact, Lake Azul (São Miguel Island), another mesotrophic deep Azorean Lake, displays very similar diatom and chironomid assemblages above 20 m depth, supporting this interpretation (Raposeiro et al., 2018; Vázquez-Loureiro et al., 2019). The stable climate conditions present in this period led to lake stability, reflected by diverse and steady biological assemblages and expected stable internal lake processes (Adrian et al., 2009).

Around 1200 CE, changes in the diatom and chironomid assemblages were observed (Fig. 2, Fig. S3 and Fig. S4), suggesting water level oscillations due to frequent intense runoff episodes. First, an increase of allochthonous aerophilic diatoms (e.g. *Nitzschia amphibia*, *Humidophila brekkaensis*, *Humidophila perpusilla*) indicates runoff enhancement (Lange-Bertalot et al., 2017; Van Dam et al., 1994), resulting in the delivery of new nutrients from the catchment. This evidence is supported by i) the increase in Fe, Mn and Ti values (Fig. 2), indicating an increase of detrital input (Croudace et al., 2006; Davies et al., 2015); ii) the replacement of tychoplanktonic *S. pinnata* by the planktonic *Fragilaria tenera* (up to 40.1% abundances) (Fig. S3) due to increased habitat availability (expanded water column in the limnetic zone) and nutrients inputs from the lake catchment (rise in the TOC/TN ratio) (Fig. 2); iii) the decrease of *P. sordidellus*-type (Fig. S4), a sensitive taxon to hypoxia (Luoto, 2009); iv) the increase of *Chironomus* spp. and *Procladius* spp. (Fig. S4), two profundal taxa well adapted to low oxygen conditions (Little et al., 2000) reinforcing our point on the increase of lake depth; and v) the presence of a coarse grain-size deposits rich in terrestrial plant remains, an increase of allochthonous aerophilic diatoms. Furthermore, climate model simulations suggest enhanced rainfall conditions around 1190–1210 CE and 1240–1250 CE (Raposeiro et al., 2021b).

5.1.2. Phase B (from 1330 ± 40 to 1565 ± 10 CE) – state-shift (Transition)

Phase B develops during the MCA - Little Ice Age (LIA; 1450–1850 CE) transition. It is characterized by high climate variability that took place during this transition and the onset of the first anthropic disturbances in the catchment that led to an unprecedented and rapid response in the ecosystem of Lake Funda.

Climate instability characterizes the first ca. 150 years of the LIA with extraordinarily irregular precipitation and temperature (Mann et al., 2009; Hernández et al., 2017). This is evident in our record, which shows the highest levels of variability in all the studied proxies (Fig. 4). According to Azorean proxy-based reconstruction (Hernández et al., 2017) and climate model simulations (Raposeiro et al., 2021b) an overall humid with warmer-than-usual conditions dominated the end of the MCA, and colder temperatures between 1400 and 1500 CE. This transition is associated with weakened westerlies over the Azores Archipelago and enhanced northerly winds during NAO⁻/EA⁻ phases. The climate factor was the most important explanatory factor of chironomids (57.0%) and diatoms (18.5%), followed the human disturbance factor (30.5% and 46.6%, for chironomids and diatoms, respectively), and finally, internal lake dynamics (12.7% and 16.9%, respectively) (Fig. 3).

At 1330 CE the first occurrence of spores of coprophilous dung fungi (e.g. *Sporormiella*), characteristic of domestic livestock and wild herbivores (Davis, 1987), identifies the beginning of human-related disturbances in the lake basin (Fig. 2 and Fig. 4). The replacement of native forest (*Angelica, Lactuca* and *Hypericum* herbs, and the ferns *Drypoteris azorica* and *Athyrium filix-femina*) by exotic plants such as *Trichomanes* (Fig. S2) was followed by a second increase in dung fungal spores in ca. CE 1415 (1689 spores cm^2.yr^{-1}), which co-occurred with a drastic drop in arboreal pollen from 75.2 ± 2.1% to 54.9 ± 9.3% (Fig. 2). These changes are an unequivocal signal of animal husbandry in the Lake Funda catchment. Similar trends are found on other Azorean sedimentary records (Connor et al., 2012; Raposeiro et al., 2021b; Rull et al., 2017) and archipelagos (Castilla-Beltrán et al., 2021). The strong human impact combined with climate instability acted synergistically and transformed the Lake Funda ecosystem abruptly. In forested catchments, changes in vegetation affect the supply of dissolved organic carbon (DOC) and nutrients to the lake due to soil destabilization and erosion, influencing aquatic communities and biological productivity (Anderson et al., 2008; Mackay et al., 2012). The abrupt changes in diatoms and chironomid assemblages, and sediment geochemistry supports this idea (Fig. 2).

Rapid deforestation and fluctuating precipitation (Fig. 4) (see Raposeiro et al., 2021b) resulted in soil destabilization, increased wind exposure and enhanced soil erosion in the catchment of Lake Funda during this phase. The organic matter deposited in the lake bottom turns from allochthonous (TOC/TN 18.9 ± 0.4) to autochthonous source (12.8 ± 0.32), the sedimentation rate increase (from 9.4 ± 0.8 mm.yr^{-1} to 12.2 ± 1.0 mm.yr^{-1}) and peaks on Fe, Mn and Ti values support this scenario (Fig. 2). Furthermore, the initial increase in δ^{15}N values (max. 6.25‰ at 1340 ± 20 CE) and subsequent decrease to 3.08‰ at 1362 ± 10 CE, suggest an increase in N-fixing cyanobacteria, which combined with the rise in centric planktonic diatom taxa such as *C. meneghiniana* in the first 50 years of this phase (Fig. S3), and the abrupt increase in BSi (from 1.99 ± 0.15% to 5.32 ± 0.25%), indicate the consequent increase in lake trophic state brought by the anthropogenic pressure (e.g. Bannister et al., 2019; Catalan et al., 2013). In fact, the shift between *Cyclotella-Aulacoseira-Fragilaria* taxa in 1385 CE taxa (Fig. 2, Fig. S3) implies an ecosystem shift (e.g. Barnosky et al., 2012). Furthermore, the *Microseptra*-association in the chironomid assemblages (Fig. S4) is also typically found before the onset of an intense eutrophication phase in deep lakes (Lods-Crozet and Lachavanne, 1994).

Intensification of human activities at ca. 1500 CE is evident in the sedimentary record, and synchronic with the settlement of the Portuguese on Flores Island, which took place around 1508–1510 CE under the direction of the first colonizers (Lages, 2000). The first Portuguese settlements occurred on the southeastern coast of Flores Island at Lages (approx. 4 km south of Lake Funda). According to Frutuoso (1978, 1981), sheep were previously disembarked in 1475 CE, and after human settlement in 1510 CE, agriculture and livestock were the dominant economic activities.

This abrupt ecosystem change was revealed by a second drop in arboreal pollen observed, from to 37.5% to 29.6% and an increase in dung fungal spores (538 spores cm^2.yr^{-1}) (Fig. S2, Fig. 2). Consequently, a significant limnological change took place with the onset of the sedimentation of brown massive silty mud and the dominance of planktonic diatoms such as *Aulacoseira* spp. (Fig. S3). In addition, the increase in the abundance of chironomids head capsules, from 5.6 ± 1.0 to 9.9 ± 1.9 head capsules cm^2.yr^{-1}, and the reduction of the low oxygen tolerant taxa (*Chironomus* spp.) (Fig. S4), most probably related to a more extended period of hypolimnion anoxia (Raposeiro et al., 2018) indicate an eutrophication process (Fig. 2 and Fig. 4). Lake Funda response followed the most widespread form of immediate action to water nutrient enrichment (Vitousek et al., 1997). The increase in nutrient levels led to a loss of biological diversity (e.g., Liu et al., 2017; Lotter, 2001; Witak et al., 2017) and major alterations in the community structure, especially of primary producers (Sommer, 1989) (Fig. S3, Fig. S4 and Fig. 2).

5.1.3. Phase C (from 1565 ± 10 to 2009 ± 5 CE) – eutrophication (eutrophic state)

The effects of Portuguese colonizers after 1563 CE are apparent in Lake Funda during Phase C. Combined with the introduction of exotic plant species (e.g., *Hydrangea* and *Spergula*) during the 17th century and a second deforestation episode suggested by the 8% drop in arboreal pollen (Fig. S2), we reveal how human disturbances in the landscape had a constant impact on the lake functioning. Furthermore, the high influx of coprophilous fungi (467 spores cm^2 yr^{-1}) suggests that cattle were present in the lake catchment (Fig. 4).

A more extended period with low hypolimnetic oxygen characterizes this phase. The increase in TOC concentrations in the sediment promoted microbial respiration and consequent oxygen depletion (Jones et al., 2008) and the near absence of chironomids (Fig. 2, Fig. S4) support this change in lake dynamics. The abrupt observed decrease in diversity and abundance of head capsules was reported in another Azorean deep lake, Lake Azul, indicating low dissolved oxygen levels, high electrical conductivity, and increased organic matter concentrations (Raposeiro et al., 2018). According to Gonçalves (2008), Lake Funda displays, currently, severe anoxic stratification during the summer period below 20 m of water depth. The dominance (>85%) of planktonic eutrophic species (*Aulacoseira granulata* and *A. granulata v. angustissima*) (Fig. S3) suggests Lake Funda was a deep eutrophic lake at this point. High BSi (max. 10.99%, mean 6.75 ± 0.39%) and lower TOC/TN ratio (10.26 ± 0.11) clearly demonstrate how the algal-derived organic matter was higher than in previous phases (Fig. 2). The near atmospheric δ^{15}N values indicate a system dominated by N-fixing cyanobacteria (Fig. 2 and Fig. 4). The low impact of the anthropogenic factor during this phase would be related to the new trophic state of the lake. Once the lake has reached a eutrophic state, in-lake production due to phosphorus remobilization become a dominant factor in explaining lake productivity (e.g., Bao et al., 2015). Under these in-lake dominated conditions, anthropogenic deforestation or reforestation has a secondary effect, and consequently, climate and internal lake dynamics would be the primary source of variability (Fig. 3).

Our results show that climate was the most important factor (68.7%) controlling the biological assemblages in this period (Fig. 3 and Fig. 4). Between 1700 and 1800 CE, coinciding with the latest stages of the LIA, climate model simulations display colder-than-usual temperatures accompanied by wetter conditions and one dry event ca. 1770 CE. Temperature simulations show colder temperatures between 1700 and 1730 CE and 1750–1770 CE, increasing progressively afterwards (Fig. 4, Raposeiro et al., 2021b). Precipitation shows fluctuations, displaying one significant dry episode at 1670–1690 CE. However, climate related processes such as increased lake water depth could also contribute to the observed increase of the hypolimnetic waters and oxygen depletion which led to an increase in-lake recycling. Climate warming could also promote chemical weathering rates (Catalan et al., 2014), increasing solutes external loading.

Furthermore additional interactions between climate and other components of the current global change such as atmospheric pollution and its interaction with climate warming could change lake ecology and its biotic assemblages (Catalan et al., 2013; Pla-Rabés et al., 2005).

Internal lake processes also play a key role in Lake Funda dynamics, as $\delta^{15}N$ explained 19.3% of the variance observed on diatoms assemblages (Fig. 3). Changes in the carbon isotope signal of accumulated organic matter (Fig. 2) may also serve as an additional qualitative line of evidence for inferring past lake trophic status (Brenner et al., 1999). The low $\delta^{13}C$ values ($-27.12 \pm 0.16‰$) (Fig. 2) are typical of autochthonous microbial biomass (Ivanić et al., 2018). The low values of TOC/TN reinforce the decline of the allochthonous source of organic matter (Fig. 2). The further decrease in $\delta^{15}N$ values from $3.30 \pm 0.18‰$ to $1.89 \pm 0.09‰$ (Fig. 2 and Fig. 4) suggests enhanced atmospheric N-fixation by cyanobacteria in this highly productive system (Gu et al., 2006). This shift in the ecosystem productivity increased the associated biological oxygen demand in the hypolimnion, leaving a sediment layer with low potential redox, which shows the ongoing brown massive silty mud present and reducing conditions. The small changes in all proxy-based indicators illustrate the prevalence of limited oxygen conditions. The positive in-lake nutrient recycling feedback mechanism maintains these anoxic and high productivity conditions, which kept chironomids from surviving. Even though the eutrophication process already started in Phase B, it becomes more intense in this phase, resulting in an alternative state caused by P-remobilization and increased N-fixing cyanobacteria.

Significant changes in diatom assemblages have been observed and related to recent climate warming across the globe (Rühland et al., 2008), and since 1985 CE, the diatom record of Lake Funda has also revealed some modifications. The co-occurrence of *A. granulata*, increase of *Ulnaria* complex (Fig. S3), and deposition of benthic and aerophilic taxa during extreme precipitation events is congruent with monitoring data from the last 20 years (Gonçalves et al., 2009, 2018b). Moreover, current phytoplankton communities are also dominated by N-fixing cyanobacteria, mainly *Aphanizomenon gracile*. Frequently, during summer and autumn, this species contribution reaches up to 70% of the total biomass, which would explain the low $\delta15N$ values from the sediment (Fig. 2 and Fig. 4). On the other hand, during winter and spring, diatoms can reach up to 76% of the total biomass (Gonçalves et al., 2013), which would explain the high BSi values (Fig. 2). According to the Secchi disc depth, the photic zone mean depth has been 1.7 m (ranging from 0.5 to 3.5 m) between 2015 and 2018 (Gonçalves et al., 2019), which also indicates an eutrophic lake (Carlson, 1977).

5.2. Possible recovery to the previous state?

In 2021 the United Nations launched the International Decade of Restoration and Conservation. All over the world, natural resources have irreplaceable value to maintain the health of the associated socio-economic system, hence managing these resources can help preserve ecosystems and socio-economic systems. In this restoration context, one of the biggest challenges environmental managers face addressing conservation problems is the lack of long term monitoring data, making million dollars questions, such as "Has this ecosystem changed from a natural or pre-disturbance state?" or "What was their natural variability?" (Willis and Birks, 2006).

Our results show that Lake Funda underwent severe ecological changes caused by human-induced land-use changes during the last millennium. As a result, its current conditions (excess loading of nutrients, cyanobacteria blooms, eutrophic state) are very different from the mesotrophic lake in 950 CE. While conservation efforts are being made to restore the ecosystems in the Azores, paleoecology studies are scarce but allow us to understand the pre-disturbance state of this lake. Therefore, we must ask several questions before defining restoration targets: Are the changes in Lake Funda reversible? Is it possible to recover Lake Funda from severe eutrophication to the previous mesotrophic pristine conditions?

Lakes are regulated by the tolerance ranges of their components and the threshold for change (Langdon et al., 2016). According to Szabó et al.

(2020), minor effects in lake ecosystems usually return the system to its original state. However, significant effects generate a whole new system that is quite different from the original. Our results showed a clear ecosystem shift from a mesotrophic lake to a eutrophic lake dominated by cyanobacteria blooms during late summer and autumn (Gonçalves, 2008; Gonçalves et al., 2009). This new state is stabilized by a positive feedback loop between lake productivity and in-lake P recycling. An additional source that increases P availability is the presence of fishes, which have affected Azorean lakes since their introduction upon the establishment of the first settlers on the Azorean Islands (Raposeiro et al., 2017). Nowadays, it is believed that carps (*Cyprinus carpio carpio* Linnaeus 1758) and roaches (*Rutilus rutilus* Linnaeus 1758) are the species that compose the fish community in Lake Funda (unpublished data). However, to our best knowledge, no data exist on the abundance, biomass, or fish affects internal lake dynamics (e.g., nutrients mobilization).

The current global warming context poses a new challenge for restoration efforts, particularly for a deep monomictic eutrophic lake (Genkai-Kato and Carpenter, 2005). Warmer temperatures increase the length and intensity of summer stratification and consequently reduce the oxygen content in the hypolimnion, which exacerbates the positive internal nutrient loading feedback. In Lake Funda, P release parallels oxygen depletion in the hypolimnion (Gonçalves et al., 2009; Richter et al., submitted). Indeed, both factors, higher temperatures and nutrient availability (i.e. internal and external loading), can lead to an increase in cyanobacterial blooms (Taranu et al., 2015). Furthermore, the endorheic condition of Lake Funda induces a relatively high water residence time (2.7 years; Andrade et al., 2019). Hence, reducing external nutrient inputs would not be enough to drive Lake Funda to a previous mesotrophic state. Consequently, external nutrient loading control would be inefficient, and eutrophication levels should be repaired via physical and bioremediation methods (Larocque-Tobler and Pla-Rabés, 2015; Zhao et al., 2020).

Nevertheless, the reduction of external nutrient loading is also a fundamental premise for lake restoration (Jeppesen et al., 2009). The primary external nutrient source in the catchment of Lake Funda is pastures, meadows, and other permanent grasslands under agricultural use. The role of catchment attributes greatly determined nutrient concentrations, and forested lakes are usually poorer in nutrients, phytoplankton, and primary production. The modification of the current agricultural land use to a semi-natural forested area that resembles Phase A, together with the establishment of buffers strips and erosion control measures, should be combined with in-lake techniques to reduce internal lake P recycling as biomanipulation typically works most effectively in combination with the reduction of external nutrient loading (Kasprzak et al., 2009). Thus, mitigation and conservation efforts should combine external nutrient removal and biomanipulation. Biomanipulation will likely yield the most favorable results when the total phosphorous concentration is below 20 $\mu g.l^{-1}$ in deep lakes (Jeppesen et al., 2009). Today lake Funda average concentration of total phosphorus is 57 $\mu g.l^{-1}$ (Gonçalves et al., 2018a).

The mitigation of nutrient recycling using macrophytes is not a feasible solution in a deep lake with a small photic zone due to algal blooms as Lake Funda. The lake littoral area available is small due to its high-gradient morphology and catchment features, such as water depth and high internal slopes. The absence of a littoral area inhibits the establishment of macrophytes and littoral macroinvertebrate communities. Another commonly used internal approach to restore and improve lake water quality is removing fish in an effort to enhance zooplankton (Jilbert et al., 2020). Fish greatly facilitate the resuspension of sediment transporting nutrients (Scheffer et al., 2003), and feed on the zooplankton community that is needed to control phytoplankton. Long term studies have proven the success of this method in reducing sediment resuspension and nutrient recycling in shallow lakes (Søndergaard et al., 2017). Although feasible, fish removal was already applied in the Azores, specifically in Furnas Lake, however this method was not enough to change lake conditions towards a lasting clear state dominated by macrophytes, since excessive nutrient loads in water and sediments prevailed (Bio et al., 2008). Furthermore, this method has been proved successful in shallow lakes (e.g. Meijer et al.,

1999; Søndergaard et al., 2017), but not viable in larger lakes and watersheds (e.g. Parker et al., 2001). A traditional restoration method for increasing water quality is suppressing cyanobacterial blooms using the aluminum sulphate treatment. This method would most likely work for Funda because when dosing methods are applied correctly (Kuster et al., 2020), results have proven to be the most effective, efficient, and with the highest longevity (over a century) to reduce P availability in lakes with the absence of surface inflows and small catchment areas (Huser et al., 2016; Rönicke et al., 2021). Other methods such as hypolimnetic aeration have shown positive long-term results in some historical cases (see review in Cooke et al., 2005); however many studies have questioned the efficacy of aeration itself (e.g. Chorus et al., 2020; Taipale et al., 2020). This method has also been implemented for more than a decade in Furnas Lake, with no improvement in its trophic status (Ribeiro et al., 2014).

Further research should aim to establish the current annual biogeochemical cycle on nutrients and dissolved and particulate organic matter in the lake, especially for quantifying natural and anthropogenic contributions to the lake's water column. With this basic understanding, the next steps would be to look for in-lake nutrient inactivation methods or different eutrophication recovery trajectories possible for Lake Funda, and at this stage, it is difficult to foresee the recovery time, cost and even possibility. In the case of Lake Funda, we agree with Duarte et al. (2009) in that the expectation that this ecosystem can be returned to an idealized past reference status by virtue of reducing direct human pressures is as likely as the existence of *Neverland*. However, ecosystem management must develop proper strategies to deal with shifting baselines and maintain ecosystem services at a sustainable level rather than trying to restore an ecosystem to a past state (Kemp et al., 2005).

6. Conclusions

This study clearly reveals how Lake Funda has been increasingly affected by human pressure since the first signs of human disturbance, and combined with climate variability, the ecosystem entered a new eutrophic state that will be difficult to revert.

Our results highlight the importance of using a multiproxy approach. Diatom and chironomid assemblages responded differently to climate, human disturbance, and internal lake dynamics, depending on the magnitude of each driver. The synergistic effect between high climate variability (MCA-LIA transition) and a strong first anthropic disturbance forced unprecedented changes in the Lake Funda ecosystem. First, an abrupt shift in biological assemblages and a drastic decline in diversity, led to a state shift from mesotrophic to eutrophic conditions in the lake ecosystem. Second, the positive feedback loop between lake productivity and in-lake P recycling hampers recovery in eutrophic deep stratified lakes. Thus, the recovery process has a long way to go, and probably the contemporary assemblages remain different from those observed in the baseline conditions. Restoring lakes to a particular past state in a constantly changing world is difficult, so this concept should be replaced by objectives that ensure the preservation of main ecosystem functions, and consequently, the maintenance of ecosystem services. Here the paleolimnological approach plays an important role in providing key insights into changes in lakes over centuries, establishing a benchmark to help managers develop sustainable adaptation and aquatic ecosystem management strategies. Close collaboration among the research community, managers and policymakers on these issues is urgently needed to lead to effective implementation strategies for better management, preservation, and restoration of aquatic freshwater ecosystems.

CRediT authorship contribution statement

Catarina Ritter: Conceptualization, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Vítor Gonçalves:** Investigation, Conceptualization, Resources, Writing – original draft, Writing – review & editing. **Sergi Pla-Rabes:** Investigation, Conceptualization, Writing – original draft, Writing – review & editing. **Erik J. de Boer:** Investigation, Writing – review & editing. **Roberto Bao:** Investigation, Resources, Writing – review & editing, Funding acquisition. **Alberto Sáez:** Investigation, Writing – review & editing. **Armand Hernández:** Investigation, Writing – review & editing. **Marta Sixto:** Investigation. **Nora Richter:** Investigation, Writing – review & editing. **Mario Benavente:** Investigation. **Ricardo Prego:** Resources, Writing – review & editing. **Santiago Giralt:** Resources, Writing – review & editing, Funding acquisition. **Pedro M. Raposeiro:** Conceptualization, Formal analysis, Investigation, Resources, Writing – original draft, Writing – review & editing, Visualization, Funding acquisition.

Declaration of competing interest

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

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Appendix A. Supplementary data

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