Human practices behind the aquatic and terrestrial ecological decoupling to climate change in the tropical Andes

Running title: novel agropastoralism driven lake system

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Abstract

Anthropogenic climate change and landscape alteration are two of the most important threats to the terrestrial and aquatic ecosystems of the tropical Americas, thus jeopardizing water and soil resources for millions of people in the Andean nations. Understanding how aquatic ecosystems will respond to anthropogenic stressors and accelerated warming requires shifting from short-term and static to long-term, dynamic characterizations of human-terrestrial-aquatic relationships. Here we use sediment records from Lake Llaviucu, a tropical mountain Andean lake long accessed by Indigenous and post-European societies, and hypothesize that under natural historical conditions (i.e., low human pressure) vegetation and aquatic ecosystems' responses to change are coupled through indirect climate influences—that is, past climate-driven vegetation changes dictated limnological trajectories. We used a multi-proxy paleoecological approach including drivers of terrestrial vegetation change (pollen), soil erosion (Titanium), human activity (agropastoralism indicators), and aquatic responses (diatoms) to estimate assemblage-wide rates of change and model their synchronous and asynchronous (lagged) relationships using Generalized Additive Models. Assemblage-wide rate of change results showed that between *ca*. 3000-400 cal years BP terrestrial vegetation, agropastoralism and diatoms fluctuated along their mean regimes of rate of change without consistent periods of synchronous rapid change. In contrast, positive lagged relationships (i.e., asynchrony) between climate-driven terrestrial pollen changes and diatom responses (i.e., asynchrony) were in operation until *ca.* 750 cal years BP. Thereafter, positive lagged relationships between agropastoralism and diatom rates of changes dictated the lake trajectory, reflecting the primary control of human practices over the aquatic ecosystem prior European occupation. We interpret that shifts in Indigenous practices (e.g., valley terracing) curtailed nutrient inputs into the lake decoupling the links between climate-driven vegetation changes and the aquatic community. Our results demonstrate how rates of change of anthropogenic and climatic influences can guide dynamic ecological baselines for managing water ecosystem services in the Andes.

Keywords: tropical lakes, diatoms, pollen, paleolimnology, asynchrony, rate of change

1. Introduction

In the tropical Andes, climate warming is accelerating twice the global average (Vuille et al., 2003), and overprints the threats from multiple human stressors such as agriculture, grazing, urban expansion, and mining. The attendant effects of anthropogenic climate change on lakes which act as sensors of global change impacts such as pollution, warming, and biochemical cycle alteration (Fritz et al., 2019) requires the understanding of: i) the complex ecological influences on the dynamics of terrestrial and aquatic ecosystems, ii) the time-varying (dynamic) human impacts on aquatic and terrestrial ecosystems, and iii) the sensitivity of coupled human-environmental systems to climate change (Dearing et al., 2015). A standing challenge in paleoenvironmental reconstructions is shifting from static, reference historical characterizations of ecosystems to dynamic, rate of change-centered approaches (Williams et al., 2020). In this vein, the concept of ecological coupling, or how different abiotic and biotic components are connected in an ordered fashion across space or time (Ochoa-Hueso et al., 2021), has received little attention in paleolimnology, thus limiting our predictive capacity of ecological impacts under changing environments. By studying a long-term paleolimnological record of the Andean Lake Llaviucu (Ecuador), our study shows how the temporal dependencies between terrestrial and aquatic components were sensitive to varied rates of human impacts over the last *ca* 3000 years and provides new insights of the multiple impacts inducing lake transitions at centennial and millennial time scales.

Most mountain tropical research is focused on the overriding effect of climate as the sole driver of aquatic change at centennial (Michelutti et al., 2015) and millennial time scales (Bird et al., 2018; McGlynn et al., 2019). Growing evidence indicates that Indigenous (e.g., Incan Empire; 480-420 cal years BP, 1480-1532 CE) and post-European (i.e., following the 1492 CE Columbus arrival; 523 cal years before present; hereafter cal years BP) people had also attendant ecological effects on Andean lakes via agropastoralism practices (e.g. cultivation, fires, camelid domestication) (Nascimento et al., 2020). For instance, land-use change, and fish stocking were widespread in many parts of the high Andes leading to excess nutrient loads (cultural eutrophication, oxygen depletion), and phytoplankton community composition changes (e.g. shift from low to high-nutrient sensitive algal communities) (Van Colen et al., 2018). In Amazonian landscapes, cycles of deforestation and recovery followed waves of heterogeneous occupational human histories, depending on social and economic contexts (Hamilton et al., 2021). Unlike the lowlands, a fully environmental retrospective assessment is only available for a small suite of mountain tropical lakes (Vélez et al., 2021) despite their crucial role in water ecosystem services for millions of people (Buytaert et al., 2006). Therefore, there is a need to investigate rates and magnitudes of shared climate and human influences, and the dependencies between the two, on lake ecosystems if we are to predict how coupled terrestrial-aquatic ecosystems respond to the abrupt climate change the tropical regions will be experiencing in the next decades (Trisos et al., 2020).

Under increasing human activities in the catchment (e.g. terraces for agriculture, fire) biogeochemical fluxes from terrestrial to aquatic systems can increase or decrease the input of detrital sediments, nutrients, and organic matter with attendant indirect, and often lagged effects, on the aquatic community (Beck et al., 2018b). Human effects can also indirectly amplify the sensitivity of lakes to record climatic changes in the catchment that otherwise would be buffered by natural vegetation (Bush et al., 2017). Moreover, lakes can respond directly to climate via changes in water temperature and stratification (Fritz, 2008), and aquatic changes can be either independent of (Leavitt et al., 2009) or synchronous with those in the catchment (Bracht-Flyears & Fritz, 2012). Factors explaining synchronous responses include a shared climatic and geological template (Riera et al., 2000), whereas intrinsic sensitivities to external forcing (Schneider et al., 2018) or varied signs of human activities (Bush et al., 2021) can explain the decoupling of terrestrial-lake interactions to climate change.

In tropical mountain ecosystems, abundant literature revolving around the “ecological resilience” concept have associated the lack of human activities as the main factor for ecosystems to remain stable, even with documented climatic changes such as the Medieval Climate Anomaly (900-1100 cal years BP) or the Little Ice Age (270–670 cal years BP) (Lüning et al., 2019). This notion has been supported by study cases documenting forest and aquatic structure recovery after the cessation of deforestation (Norden et al., 2009). However, existing analytical approaches prevent quantification of the relative strength of such variable climate-lake-human interactions. Our study uses a combination of advanced time-series methods to shed light on the long-term trajectories of vegetation, humans, and aquatic communities in Lake Llaviucu (Ecuador), part of an important ancient 80 km-long Amazonia-Andean trade route connecting the highlands in the Paramo (Tomebamba, today Cuenca) with the Amazon lowlands, in Paredones. The humid environment of the Paramo and Andean moist forest catchments develop thick organic soils, resulting in a tight coupling between vegetation and water chemistry (Catalan and Rondón, 2016). We hypothesize that such terrestrial-aquatic dynamics are an intrinsic feature of Lake Llaviucu conferring ecological resilience at long temporal scales and under certain climate regimes. Under natural conditions (i.e., low human pressure), past vegetation rate of change would predict diatom rate of change–that is, terrestrial vegetation and lake dynamics would have been temporally coupled. Alternatively, when humans began impacting the lake-catchment system, agropastoralism indicators (i.e. crop and disturbance pollen taxa, cattle grazing, and charcoal) would have had a greater predictive power on diatom changes over climate–that is, the terrestrial-aquatic dynamics would have become uncoupled.

2. Methods

2.1 Study site

Lake Llaviucu is located at 3150 m asl. in the Cajas National Park, in Ecuador: it lies below the Paramo, and is surrounded by moist montane forest (Fig. 1). Lake Llaviucu is of special economic and ecological interest for the city of Cuenca (old Tomebamba) because it provides 30% of the drinking water supply (Mosquera et al., 2017). The lake housed a fish hatchery and a brewery from 1978 to 1998, which resulted in lake eutrophication during this time (Barros et al., 2015). In the 1960s, a small weir was constructed, which raised the lake level ca. 2 m (Raczka et al., 2019). Once the fish farm was closed with the creation of Cajas National Park (1996), the lake recovered to the meso-oligotrophic conditions of today, showing nutrient concentrations comparable to other lakes in the region (Van Colen et al., 2017). An ancient road close to the Lake Llaviucu indicates that this catchment was long accessed for the trade by pre-Incan (Cañari) (*ca.* 3700-470 cal years BP) and Inca societies (480-420 cal years BP) (Prado Mogrovejo, 2009).

2.2 Core collection and sediment indicator analyses

Two sediment cores were retrieved from the deepest basin of the lake (~15m depth): Llav-2009 is 11.5 m length and was collected using a Colinvaux-Vohnout piston corer; and Llav-2014, 1.95 m long, collected with a UWITEC gravity corer. Both cores were previously studied to decipher terrestrial vegetation (Llav-2009; Nascimento et al., 2020), and limnology (Llav-2014; Benito et al., 2021) histories of Lake Llaviucu over the last 12,000 years. Here, the Llav-2019 core was analyzed for the pollen dataset (thereafter 'native pollen'), while indicators of human activity were extracted as single data set– 'agropastoralism dataset'– including: *Sporiormella* spores (presence of herbivors), charcoal (fire) and *Hedyosmum*, *Rumex*, *Begoniaceae*, *Alnus*, *Cyperaceae*, *Cecropia*, *Asteracea*, *Zea mays*, *Phaseolus*, *Ipomoea* (disturbance and crops such as maize, common sorrel, beans, or sweet potato) (Flantua et al., 2016). Samples were processed following standard methods (Faegri and Iversen, 1989) by counting 300 terrestrial pollen grains for each sample and identified using the pollen database from Florida Institute of Technology (Bush and Weng, 2007). *Sporiormella* spores were counted until a total of 300 pollen grains was reached and are expressed as a percentage of the pollen sum. Charcoal fragments were based on macro fragment counts (>100 μm) hence indicating local fires (Whitlock and Larsen, 2001). See Nascimento et al. (2020) for additional pollen information. The Llav-2014 core was processed for diatom analysis following standard procedures (Battarbee et al., 2002). See Benito et al. (2021) for further information on diatom data processing and species identification. Diatom, pollen, and agropastoralism taxa were included in all the analyses if they occurred in more than 2 samples with a relative abundance greater than 1%. The Llav-2009 was analyzed for µXRF using a ITRAX core scanner at 1 mm resolution (Nascimento et al., 2020). Of the µXRF data, Titanium (Ti) was used to represent changes in terrigenous erosion. The diatom core (LLav-2014) was further analyzed for Si/Ti (silica to titanium ratio) and Mn/Fe (iron to magnesium) (Benito et al., 2021). These elemental ratios are commonly used as indicators of aquatic paleo-productivity and paleo-redox conditions, respectively (Davies et al., 2015).

2.3 Core chronologies

See supplementary figures 1 and 2 for the original Bayesian age-depth models and Table S1 for summary of radiocarbon and ^{210}Pb data (Arcusa et al., 2020; Benito et al., 2021; Nascimento et al., 2020). The entire inventory of unsupported ^{210}Pb was contained in the top 20 cm of the two cores. ^{14}C ages were calibrated with the IntCal13 calibration curve (Reimer et al., 2013). Here, we compared the original IntCal13 calibrated ages with the IntCal20 calibration curve (Reimer et al., 2020) using R *Bchron* package (Haslett and Parnell 2008) (Fig. S3-4). Results showed no differences between the two sets of calibrated ages. Thereby we refer the numerical analyses to the original age-depth models to allow for comparison with the present study.

2.4 Statistical analyses

Each dataset (native pollen, agropastoralism indicators, and diatoms) was Hellinger-transformed to meet normality assumptions. Sub-samples for diatom and pollen analyses were extracted at ca. 25-year and 40-year resolution, respectively. To overcome discrepancy between 2009 and 2014 cores related to temporal resolution, we applied two complementary approaches. First, we estimated a Principal Curve (PrC) on relative abundance data of diatoms, native pollen, agropastoralism indicators, and Ti datasets separately using the R analogue's *prcurve* function (Simpson and Oksanen, 2016). PrC is a nonlinear ordination technique that extracts a single gradient of variation from multivariate data. Subsequently, we modelled temporal trends of PrCs with a Generalized Additive Model (GAM) with a smoothing basis of cubic regression splines, and simulated GAM-inferred values to obtain a multiproxy dataset in a common time series for the response variable (diatoms) using the *mgcv* package (Wood, 2017). Second, we linearly interpolated the PrCs of diatoms to the pollen sample ages using the R's base function *approx*. The rationale was to infer values from the finer (diatoms) to the coarser (pollen) temporal resolution dataset.

Different tie-points (n=8) between the 2009 and 2014 cores were visually identified using Ti data, and correlation was calculated to determine strength of tie-points (r Pearson=0.81) to support the linear interpolation of datasets (Fig. S5). To visually explore relationships among aquatic and terrestrial variables, the PrCs of diatom, pollen, and agropastoralism indicators, and titanium were analyzed using an indirect gradient analysis (Detrended Correspondence Analysis; DCA). This plot shows the main temporal trajectories of change in aquatic and terrestrial assemblages, representing the lake-catchment links through time.

We applied a three-step analytical procedure to test for the relationship between Lake Llaviucu's terrestrial and aquatic ecosystem trajectories (Fig. 2). First, a multivariate GAM was fitted to the diatom PrCs using the mgcv's *gam* function, with pollen and agropastoralism PrCs, and Ti as covariates. This allowed to identify the important trends in the aquatic ecosystem as it responds to changes in the catchment by extracting the contributions of the individual model covariates (pollen, agropastoralism, Ti) to the fitted values of the response variable (diatom PrCs) (*Covariates model* in Fig. 2). By including both agropastoralism PrC and Ti in the model, we are partially factoring out the additive effect of climate (i.e., soil erosion, Ti plus native pollen) from human practices (i.e., agropastoralism) destabilizing the soil surrounding Lake Llaviucu. *Age* was also included as covariate in the model to control against spurious temporal correlation. We would expect covariates to have a significant effect on the response after considering the passage of time alone. The number of years accumulated per sample (i.e., time difference between two consecutive samples) from the coarser dataset was included in gam's *weights* argument as a measure to account for change in variance over time.

Second, we modelled assemblage-wide and estimated average rate of change among species using Hierarchical GAMs to quantify the extent to which different lake-catchment components (pollen, agropastoralism, diatoms) exhibit synchronous fluctuations over time (*Synchronous model* in Fig. 2). We applied a HGAM type that consists of fitting separate temporal models for each species of the assemblages (i.e. diatoms, natural pollen, agropastoralism) while allowing each group-specific smoother (i.e., species) have its own shape and complexity (model I in Pedersen et al., 2019). Because of the likely differences in sensitivities between pollen and diatoms time series detecting local and regional changes, we allowed smoothing functions of covariates to freely capture temporal variance in these time series. In practice, this is achieved via the use of the *by* argument within the smooth term in the function *gam* of the *mgcv* package. Models were fitted with a negative binomial distribution to guard against overdispersion of the data and including lake years per sample to account for changes in variance due to sediment compaction. We used Restricted Maximum Likelihood (REML) for parameter estimation fitted with a thin plate smoother and k = 20-30 basis functions depending on each assemblage (Table 1) and after checking if k is too low with *gam.check* function. To account for detectability across samples, we added an offset equal to the log of the total count of diatom valves and pollen grains in each sample. We estimated species-specific rates of change for each species of the assemblages in each year from the model posterior distribution by simulating 250 estimates of counts for each species and aggregating across simulations, using the methods detailed in Pedersen et al. (2020). We then calculated the average rate of change of relative log-abundances (mean richness) and associated 95% confidence intervals for 25-years evenly spaced time series to match with the median temporal resolution of the diatom record, following Pedersen et al. (2020). Finally, we compared the rate of change among all assemblage-wide time series. The observed mutual information value “shared” (representing the amount of information between two time series) was compared against a null expectation, using the *muti* R package (Scheuerell, 2017).

Third, we generated 100 lagged predictor time series of assemblage-wide rate of change of pollen and agropastoralism indicators to test for asynchrony relationships between time-delayed samples of pollen and agropastoralism indicators (predictors) and diatoms (response) (*Asynchronous model* in Fig. 2). Titanium time series was not included in the asynchronous model because it is a single variable. Replicating the recent analytical approach by Gil-Romera et al. (2019), we fitted generalized least squares on diatom rate of change and predictors once per *lag* (100 x 25 'years' sample age = 2500 years) using the *gls* function of the R package *nlme*. To test for the goodness of fit of the asynchronous models, pseudo R^2 and standardized coefficient with associated 95% confidence intervals were extracted. All numerical analyses were performed using the R software version 3.3.1 (R Core Team, 2020)

3. Results

Proxy trends and covariates model–The diatom PrC trend modelled against pollen and agropastoralism PrCs, and Ti using GAMs indicates that only agropastoralism indicators have an overall significant effect on the response (*Covariates model*, Fig. 3; Table 1). The covariates pollen PrC and Ti fitted to diatom PrC were not significant over the range of each smooth (i.e., within the 95% pointwise confidence intervals; Fig. 3). Similar results, i.e., agropastoralism as the solely significant covariable affecting diatom PrCs trend, are also found in the PrC-GAM inferred dataset, indicating that the interpolation method did not influence the results (Table 1). The fitted GAM captures two distinct phases of agropastoralism influences on diatom PrC with a shift from positive to negative contributions at *ca.* 1400 cal years BP (Fig. 3). This change is likely due to the disappearance of the diatom *Nupela* sp. following a marked increase in *Sporormiella* and charcoal and decrease in Si/Ti values (as a proxy of nutrient availability) (Fig. 4 and Fig. S7). Before *ca.* 1400 cal years BP there was a relationship between pollen taxa indicative of cultivation and crop-related herbs (e.g. *Zea mays*, *Rumex*) and the diatom species *Nupela*, sp. *Encyonopsis* sp., *Denticula kuetzingii*, *Gomphonema* sp. (up to 55% of the total assemblage; Fig. 4). This relationship between agropastoralism indicators and diatoms is indicated by the significant positive contributions in the fitted trend that occurred *ca.* 2000 cal years BP (Fig. 3), and it is coincident with low Mn/Fe ratio values (a proxy of hypoxia at the bottom waters), and high Si/Ti values (Fig. 4 and Fig. S7). Between 1400 and 200 cal years BP, agropastoralism effects were manifested with increase in abundance of diatom taxa *Achnanthidium minutissimum*, *Fragilaria* cf. *capucina,* and *Cymbella cymbiformis* (Fig. 4). Mn/Fe and Si/Ti exhibited increase and decrease trends, respectively (Fig. 4). A positive increasing trend, albeit not significant, in the fitted diatom PrC occurred in the most recent period (last 200 years; Fig. 3). The temporal sequence of PrCs and Ti within the DCA multivariate space shows that natural pollen and agropastoralism indicators are positively correlated and opposed to diatoms along the first axis, suggesting a lake-catchment gradient (Fig. S6). DCA axis 1 separates the samples in two groups: one *ca.* 200-3000 cal years BP and another one 200 cal years BP-present. DCA axis 2 is correlated with Ti (soil erosion).

Synchronous model–Average rates of change modelled using HGAMs indicate that there is no substantial period when the time-series of pollen and agropastoralism rates of change differed significantly from zero (at 95% level) between *ca.* 3000 and 1000 cal years BP (Fig. 5b, c). At *ca.* 1000 cal years BP an abrupt decrease in the three proxy's rate of change occurred and remained negative until present day (Fig. 5b, c). The average rate of change of diatoms fluctuated significantly between 3000 and 1400 cal years BP, yet the most rapid and persistent decline began *ca.* 500 cal years BP and continued until present day (Fig. 5a). Mutual information values—representing the amount of shared information—were statistically significant (p<0.05) at lag -4 only between past agropastoralism values and concurrent diatom rates of change (Table S3).

Asynchronous model–The asynchronous model fitted on past natural pollen rate of change predicting current diatom values shows a maximum effect at *ca.* 1000 cal years BP with a decreasing effect until 750 cal years BP, hence converging with the asynchronous model of agropastoralism indicators (Fig. 6a-b). The agropastoralism asynchronous model (i.e. the effect of time-delayed agropastoralism indicators on current rate of change of diatoms) shows two periods of statistically significant increasing influence of agropastoralism indicators on diatoms, one between 750-500 (R^2=0.3), and another one 250-200 cal years BP (R^2=0.15) (Fig. 6b). These two asynchronous peaks show opposite influences on diatoms, negative between 750-500 cal years BP, and positive between 250-200 cal years BP (Fig. 6b).

4. Discussion

The historical role of humans and climate on aquatic and terrestrial ecosystems in the tropical Andes have been largely described in the literature, but independently in most cases (de Souza et al., 2019; Ekdahl et al., 2008; Flantua et al., 2016; Lombardo et al., 2020), including earlier publications from Lake Llaviucu. Here, we investigated when and how human activities could have disrupted the links between terrestrial and aquatic responses to climate change over the last three millennia. Our results supported the hypothesis of the reconstructed human activities via livestock grazing, cultivation, and burning (i.e. agropastoralism indicators) being stronger influences than climate-driven vegetation changes predicting post-disturbance diatom trajectory over the last three millennia. Diatom ecological change and human practices were in operation before the European contact through positive and negative feedbacks resulting in agropastoralism lagged effects at *ca.* 750 and 200 cal years BP. These results suggest that the aquatic ecosystem is also responding to the cycle of deforestation (Indigenous land-use), abandonment (European contact), and re-use (regained modern impacts), like documented in Pan-tropical terrestrial vegetation records (Hamilton et al., 2021). Our study advances the notion that shifts to novel diatom assemblages were driven by varied, historical rates of change of anthropogenic forcings even in remote areas (i.e., high-elevation lakes).

4.1 Terrestrial-aquatic dynamics and ecological decoupling

Titanium concentrations in lake sediments can be associated with catchment disturbances (e.g. deforestation) or climate (e.g. precipitation changes). For instance, Schneider (2018) found an increased precipitation frequency after 1300 AD (*ca.* 700 cal years BP) coinciding with Inca occupation of the Lake Llaviucu's catchment. In mountain and lowland tropical lakes, human activities amplified subtle climatic signal that otherwise could have been buffered by natural vegetation (Åkesson et al., 2020; Bush et al., 2017). In our study, the difficulty in teasing apart sources of natural and human factors on long-term limnological change has been partially resolved by two lines of independent evidence. First, our results indicated that agropastoralism effects are independent from climate change, here interpreted as the additive effects of soil erosion and native pollen in the GAM covariates model (Fig. 3). Second, the DCA analysis showed that terrestrial vegetation changes (i.e., pollen and agropastoralism PrCs) are highly correlated but independently associated with soil erosion (Ti) (Fig. S6). Taken together, we interpret that soil erosion is likely not sourced from precipitation changes but originated from human-driven catchment disturbances (i.e., agropastoralism). Here, we must acknowledge that the lack of statistically significant temporal contributions of native pollen and Ti on the diatom trajectory could well be because of the data origin (i.e., diatom and pollen proxies come from two different records), and data were interpolated. Nevertheless, our results are robust because we attempted two independent cross-core correlation methods yielding similar results (Table 1). Previous studies in South America in general, and in Lake Llaviucu in particular, also demonstrated the overriding effect of human practices on ecosystem dynamics (Nascimento et al., 2019). On longer time scales and despite harsh climate events for historical societies to thrive such as droughts during the Mid Holocene Dry Event (*ca*. 9000-4000 cal years BP), agropastoralism spread along with exponential human population growth (Goldberg et al., 2016; Riris and Arroyo-Kalin 2019).

Between ~3000 and 500 cal years BP, the diatom trajectory (PrC) suggests a complex ecological history due to varied contributions of terrestrial vegetation and agropastoralism indicators. The dominance of the benthic diatoms *Nupela* sp., *Encyonopsis* sp., *Denticula kuetzingii*, and *Gomphonema* sp. between *ca.* 3000-1400 cal years BP, suggest a stable benthic habitat characterized by light limitation, slightly acidic and mesotrophic waters (Wojtal, 2009). The coeval dominance of upper forest montane taxa and Poaceae (up to 90% of the total pollen assemblage) (Fig. 4 and Fig. S8) indicates a catchment covered with native forest and grasses and well-developed soils that potentially provided a large supply of nutrients and dissolved organic matter into the lake reducing light availability conditions while likely enhancing lake productivity and acidity (Beck et al., 2018a). These trends are supported by higher nutrient availability, as indicated by higher Si/Ti ratios (Fig. 4). Subsequently, prominent peaks in *Sporiormella* (proxy of herbivory presence) and charcoal (proxy of local fires) at *ca.* 1400 cal years BP were coincident with a diatom shift towards an assemblage of less acidophilus, disturbance tolerant and oligotrophic species (*Achnanthidium minutissimum, Fragilaria* cf. *capucina, Cymbella cymbiformis*)

(Tapia et al., 2006; Vélez et al., 2011), which is interpreted as evidence for a reduced nutrient availability in the lake. Reduced nutrient inputs were likely driven by greater slope stability associated with human practices (i.e. terracing). These are consistent with changing land use practices across the tropical Andes at that time as seen in the Peruvian Andes (Matthews-Bird et al., 2017), highlands of Colombia (Vélez et al., 2021), and Bolivian Altiplano (Marsh, 2015). Fire could be another human-associated disrupting factor on terrestrial material inputs. Natural fires rarely occur in moist forest lake-catchments such as Llaviucu. Fires derive terrestrially derived organic compounds out of the combustion into the lake, leading to less penetration of light and ultimately a less productive system (Beck et al., 2018). This could also be the case here because of the high relative increase in *Achnanthidium minutissimum* as a characteristic disturbance, opportunistic taxon in the Ecuadorean Andes (Benito et al., 2019). Overall, our data suggest a strong link between terrestrial vegetation and aquatic systems likely driven by nutrient changes. Accurately interpreting such links require attention to factors that could influence lake nutrient status, which might include direct climate effects via thermal stratification, indirect climate-driven vegetation changes (as discussed above), or both.

Despite its deep waters, dominance of benthic diatoms between *ca.* 3000 and 500 cal years BP in Lake Llaviucu supports the view of an aquatic basin characterized by sunlit gradual slopes covered by macrophyte vegetation. Shifts in benthic vs planktic diatoms have been widely attributed to lake level changes resulting from precipitation variability under warm/dry climates (Weide et al., 2017). For instance, the Medieval Climate Anomaly (MCA) triggered lower lake levels and was recorded on many different tropical Andean paleolimnological records (Lüning et al., 2019). Although the signal of MCA on Lake Llaviucu's sediments is inconclusive (Benito et al., 2021), one consequence of potential warming/drying is an enhanced lake productivity promoted by less mixing within the water column, as seen in analogous moist forest Andean lakes (Loughlin et al., 2018). Lake Llaviucu's mesotrophic diatom assemblages between *ca.* 3000-1400 cal years BP were supported by low Mn/Fe ratio values, which could reflect reduced oxygenation because of a gradual trend towards a reduced mixing (Boyle, 2001) (Fig. 4).

Our data suggest that an increase in nutrient cycling towards mesotrophic conditions is a plausible alternative explanation to indirect climate-driven vegetation cover changes (Jenny et al., 2016). Nonetheless, either forcing is suggested to be in operation under natural conditions: climate-driven terrestrial vegetation change preceded change in diatom assemblages.

4.2 Time-varying aquatic responses to human impacts

The asynchronous model of pollen and agropastoralism indicators converged at 750-years lag, and time-delayed pollen effects on current rate of change of diatoms did not resume after, indicating a decoupling once Indigenous activities began to insensitively impact the catchment. It may seem counterintuitive that such a large time interval (750-years lag) characterized the time-delayed diatom responses, but for instance, Beck et al. (2018b) identified a 1600-year lag of aquatic (cladoceran) responses to pollen changes in a Tasmanian lake. Here, one potential explanation could be a non-analogue situation between the type of responses of diatoms and the disturbance regime: there are no equivalent current benthic dominated assemblages responding to cumulative human pressures in the catchment with slow processes and small variability (e.g., Williams and Jackson, 2007). Benthic diatoms respond in more complex ways to axes of trophic conditions (i.e., organic matter, acid-base conditions, cation exchanges) as opposed to planktic species that are more subjected to water column variability such as light regimes or mixing (Juggins et al., 2013; Rivera-Rondón and Catalan, 2020). Another explanation could be found in the variability of Indigenous land-use. Terracing practices may have begun earlier downstream than upstream because of more favorable terrain or different societal needs (Kendall, 2013). As consequence, agropastoralism effects on lake diatoms were delayed until a larger portion the Llaviucu's catchment was occupied with more sophisticated systems to control runoff and slope stabilization for cultivation (Chepstow-Lusty & Jonsson, 2000). We cannot discard the possibility that diatoms or pollen records were not accurately responding to forcing drivers in the catchment, and therefore, additional aquatic geochemical proxies (e.g., organic matter, nutrient isotopes, sedimentary pigments) could help to generate a stronger inference from multiproxy paleoenvironmental records.

Certain tropical Andean Lakes have suffered recent physical habitat changes coinciding with the onset of wind speed reductions and rising temperatures (Michelutti et al., 2016). Associated changes in thermal structure led to biotic regime shifts favoring proliferation of planktic assemblages (Giles et al., 2018; Labaj et al., 2017). In this study, the rate of change of diatoms for the last 500 years were unprecedented, characterized by a dominance (40% of the total assemblage) of the oligo-mesotrophic planktic species *Discostella stelligera*, *Tabellaria flocculosa,* and *Diatoma tenuis* (Fig.4 and Fig S7). Model predictions suggest that lake mixing regimes will be impacted in the upcoming decades with continued warming (Woolway et al., 2020). In high latitude lakes, climate-driven biological regime shifts responded to reduced duration and extent of ice cover (Smol et al., 2005). However, the same mechanism does not apply in the tropical Andes because of constant growing conditions around the year. In the Ecuadorean Andes, pre-industrial (<1950) meteorological records are inexistent, which hampers the assessment of climatic drivers of thermal stratification. In Lake Llaviucu, one potential confounding effect on thermal stratification through human activity was the trout farm operating between the 1980s and 1990s. Trout stocking could have enhanced heat penetration because of top-down control effects that cleared the water column (Chraïbi and Fritz, 2020). Fecal matter and slaughtering wastes from the fish farm and the construction of the weir could further explain via increase in dissolved organic carbon the rapid increase in planktic mesotrophic ecological niches irrespective of warming (Saros and Anderson, 2015). Moreover, heavy metal influx and dust deposition from rubber tires, vehicle breaks, and industrial emissions to Lake Llaviucu, caused by contemporary heavy traffic on the nearby main highway, may have indirectly influenced the assemblages additionally (Schneider et al., 2021). Overall, our study sheds light into the multivariate nature of changes, both climate and human, explaining the relationship between recent warming and lake physical changes (Winslow et al., 2017), and emphasizes the importance of long-term perspectives in deciphering anthropogenic climate warming.

A thought-provoking result is the two opposite (i.e. negative and positive) periods of lagged agropastoralism on current diatoms after humans began to alter Lake Llaviucu significantly (Fig. 6). We interpret these as a cycle of impact by Incan societies and abandonment following European contact (750 cal years BP, ~1250-1300 CE), and a regained human impact with the establishment of European-style agricultural practices (250 cal years BP, ~1800 CE). How generalizable is this pattern within the human history of the tropical Andes? Although not referencing attending impacts on aquatic ecosystems, the most recent and comprehensive review of widespread reforestation of Amazonian landscapes after the arrival of the Europeans in South America indicate that human practices largely followed the cycle of deforestation, use, and reforestation, all beginning before the conquest (*ca.* 550 cal years BP, 1492 CE; Bush et al., 2021). In ecologically analogous lakes of the Northern Andes of Colombia and Ecuador, aquatic indicators (including diatoms and pollen) were also responding to human-driven vegetation changes (González-Carranza et al., 2012; Loughlin et al., 2018; Vélez et al., 2021). However, previous studies did not quantify time-varying past effects of human practices on aquatic responses. Decoupling between natural and human-associated pollen effects on diatoms is difficult to discern because their drivers might be temporally correlated (i.e. humans and climate). Our numerical approach is important in the sense that it shows key temporal periods when drivers (native pollen, and agropastoralism indicators) and responses (diatoms) are fluctuating within or move outside their long-term rates of change, the uncertainty of covariate's constitutions, and their lagged effects; all of this without assuming any specific dynamics in the time-series (i.e., GAM). This is a critical analytical step to provide nuances in paleoenvironmental reconstructions, with potential to complement with other drivers of change such as archaeology-based radiocarbon time-series that infer human population changes in South America (Marsh, 2015).

5. Conclusion

Our findings describe the dynamic aquatic transitions of the Lake Llaviucu best explained by time-delayed human practices in the catchment that triggered shifts in lake diatoms mediated by nutrient changes. The current Lake Llaviucu's ecological integrity may be compared with past waves of human practices in the catchment of different intensity and nature. For instance, albeit located in a protected area, current Lake Llaviucu's vicinity in the Cajas Natural Park is managed under traditional burning practices to stimulate growth of grass for cattle grazing, and herds use the lake as a water source potentially leading to lake's primary production increases. Nevertheless, current rates of livestock grazing could not have surpassed nutrient-associated baseline thresholds to alter the lake diatom assemblages as in *ca.* 1400 and 500 cal years BP. While the decrease in nutrient status can be associated with diatom changes for most of the record, anthropogenic stressors via climate change and direct in-lake impacts (i.e., weir, fish farm) appear to be the most important drivers of the lake state (i.e., the unique rapid change in assemblage-wide rate of change) after Indigenous practices long decoupled the natural aquatic-terrestrial links. Whenever similar time series are available, our framework can be used in similar settings to shed light into ecological couplings and baselines of tropical aquatic ecosystems. Our paleoecological record provided a long-term perspective on the interactive effects of human and climate stressors that may support policy addressing current global change issues, such a water quality and availability, and land-use practices.

Data availability statement

All fossil pollen, diatom and XRF datasets, and R scripts to perform statistical analyses and generate plots are available from GitHub (https://github.com/xbenitogranell/DiatPollSync).

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Tables

Table 1 Generalized Additive Models (GAM) parameters and summary statistics for the models used. Covariable: time series used for each model; K-index: diagnostic parameter to check if k is too low (k<1); bs: smoothing basis; K: basis dimensions for the smooth term; edf: estimated degrees of freedom.

Model	Covariable	bs	k	k-index	edf	p-value
Covariates model						
Interpolated data						
Response variable: diatom PrC	Age	adaptative	20	0.65	11.1	$p<0.05$
	Agropastoralism PrC	cubic spline	10	1.03	1.20	0.03
	Pollen PrC	cubic spline	10	0.95	0.71	0.09
	Titanium	cubic spline	10	1.06	0.55	0.11
GAM-simulated data						
Response variable: diatom PrC	Age	cubic spline	-	0.82	6.38	$p<0.05$
	Agropastoralism PrC	cubic spline	-	0.93	7.94	$p<0.05$
	Pollen PrC	cubic spline	-	0.83	7.92	0.32
	Titanium	cubic spline	-	1.05	6.75	0.10
Hierarchical GAM						

Response: Diatom counts (n species=22)	Age	Factor smooth (age, species)	20	0.96	242.8	$p<0.05$
Pollen counts (n species=26)	Age	Factor smooth (age, species)	20	0.99	137.5	$p<0.05$
Agropastoralism indicator counts (n species=12)	Age	Factor smooth (age, species)	20	0.97	61.72	$p<0.05$

Figures

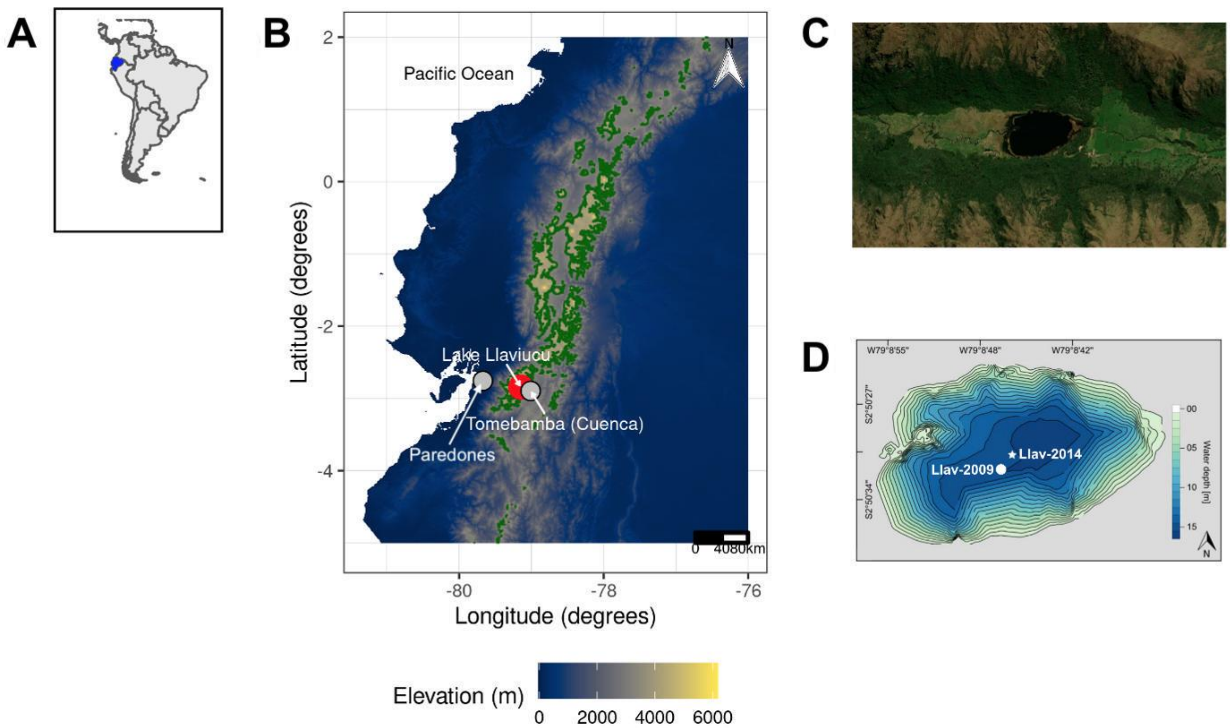

Fig. 1 Geographical location of Lake Llaviucu in Ecuador, South America (a) in relation to elevation showing the distribution of Paramo (>3500 m; green lines), the location of Tomebamba (today Cuenca) and the archaeological region of Paredones in the lowlands (b). Lake Llaviucu's aerial photography (Google Earth) showing the moist montane forest surrounding the lake and the Paramo up in the mountains (c). Lake Llaviucu's bathymetry showing the position of the diatom (Llav-2014) and pollen (Llav-2009) cores (d).

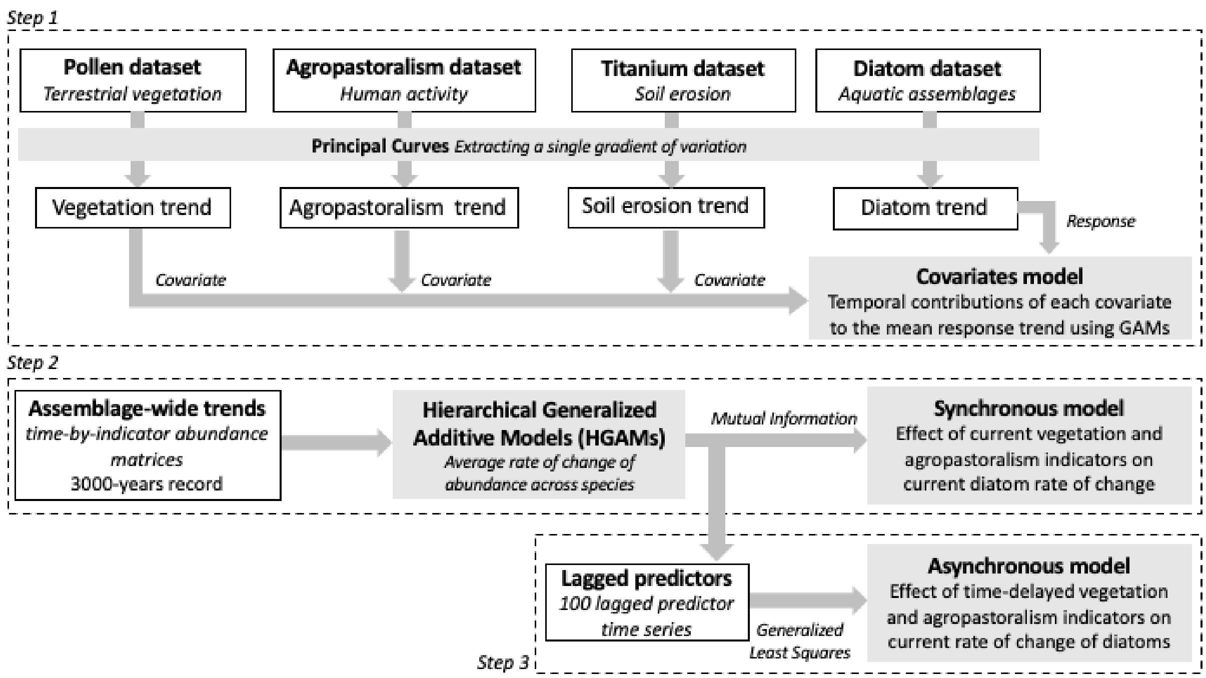

Fig. 2 Flow diagram illustrating the numerical analyses carried out in the present study, which consists in three main steps: extracting trends in temporal contributions of terrestrial vegetation, human activities and soil erosion on diatom trajectory (*Covariates model, step 1*); modeling assemblage-wide rates of change, and analyzing their coherent temporal fluctuations over time (*Synchronous model, step 2*); and generating lagged time series of predictors (pollen, agropastoralism) to test for asynchronous effects in current rate of change of diatoms (*Asynchronous model, step 3*). See text for details.

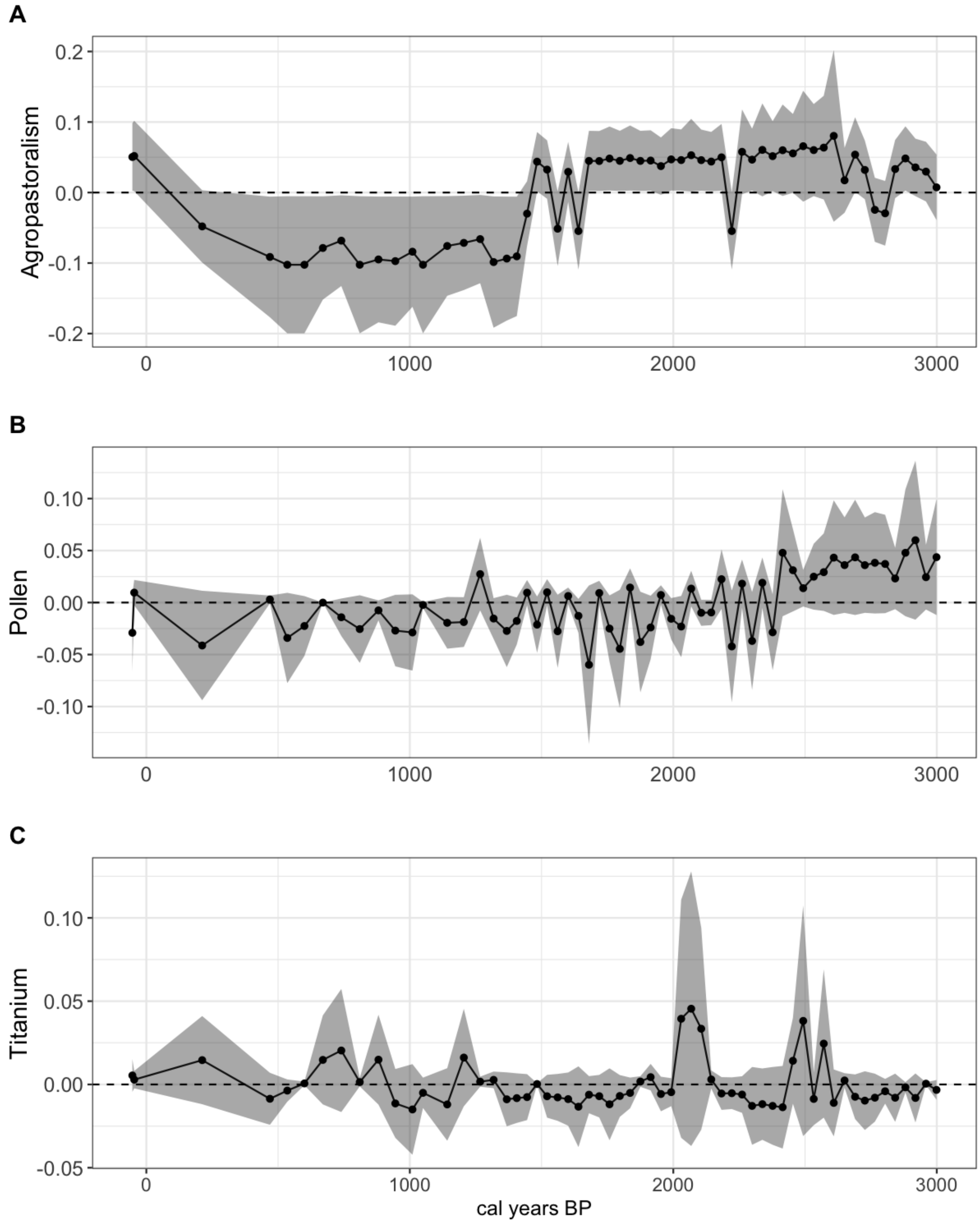

Fig. 3 The temporal contributions of a) agropastoralism, b) pollen, and c) Titanium in Generalized Additive Models (GAMs) fitted to the diatom PrC of the Lake Llaviucu (*Covariates model* in step 1 of Fig. 2). The agropastoralism PrC is the solely significant covariate (Table 1). Grey ribbon is 95%

confidence interval. Where the grey envelope includes zero line there is no statistically significant contribution of the covariate to the response. Cal years BP=calibrated years before present.

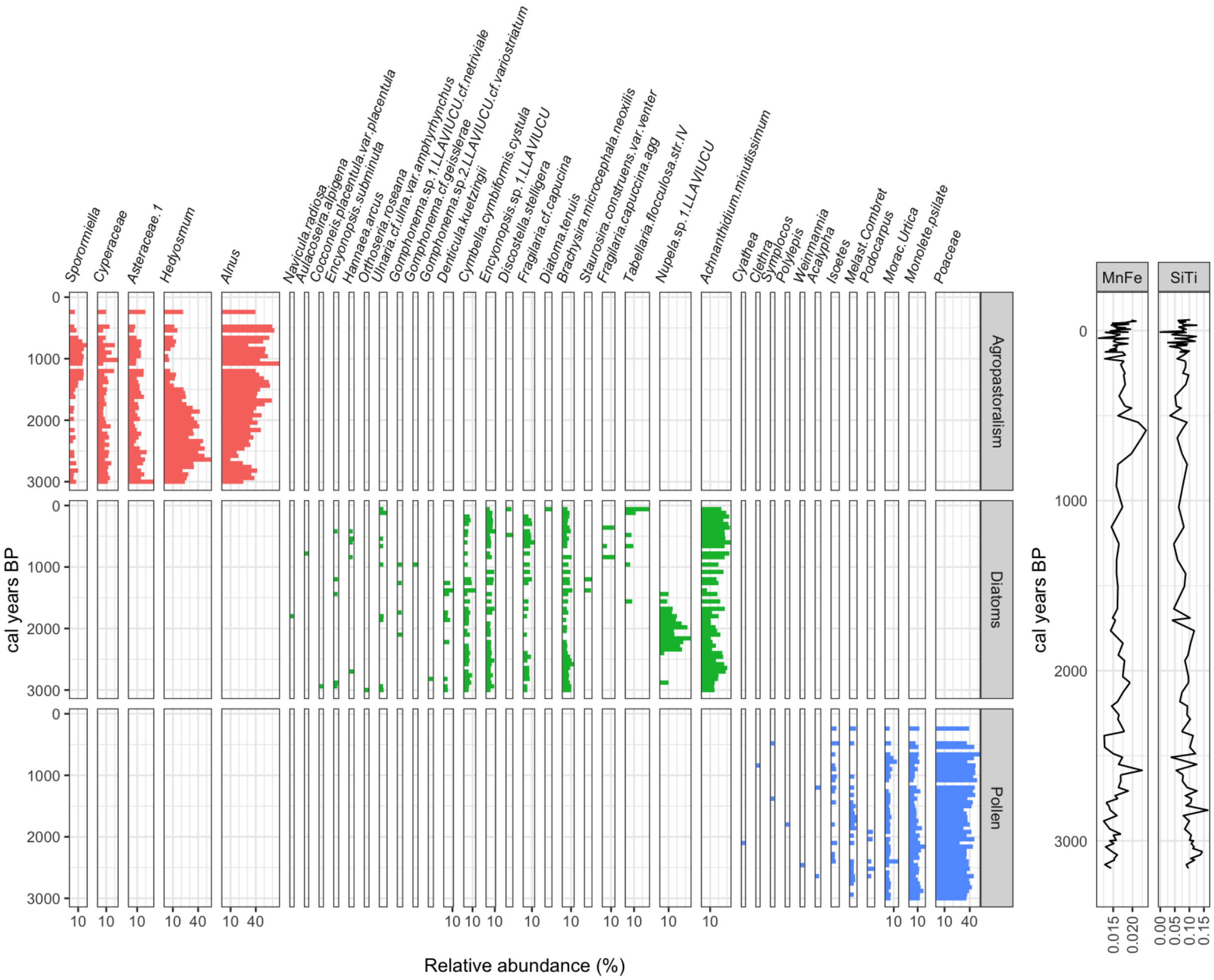

Fig. 4 Summary stratigraphic plots of the Lake Llaviucu, showing (from *left*) the relative abundance (%) of selected taxa (i.e., those occurring having more than 3% relative abundance) of agropastoralism, diatom, and native pollen assemblages arranged by increased abundance (x-axis) over time (y-axis), and downcore distribution of Mn/Fe and Si/Ti ratios (Llav-2014 core).

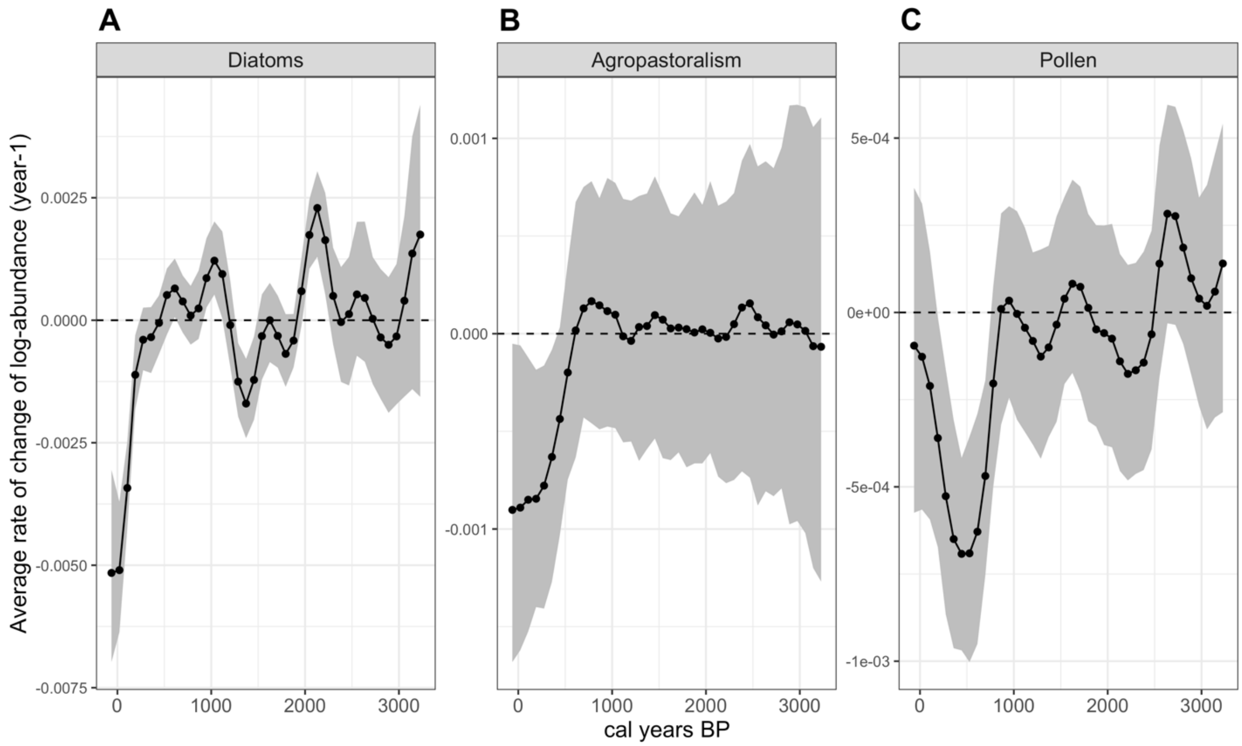

Fig. 5 Assemblage-wide rate of change (y-axis) over time (calibrated years before present; x-axis), estimated from Hierarchical generalized additive models (HGAMs) fitted to the most common taxa (those present in more than 2 samples): diatoms (a), agropastoralism (b), and native pollen (c). Zero dashed line represents mean rate of change of abundance, averaged across species. Where the grey ribbon (95% pointwise confidence intervals on the fitted models) includes the zero dashed line, there is no significant increase or decrease in abundances at that time.

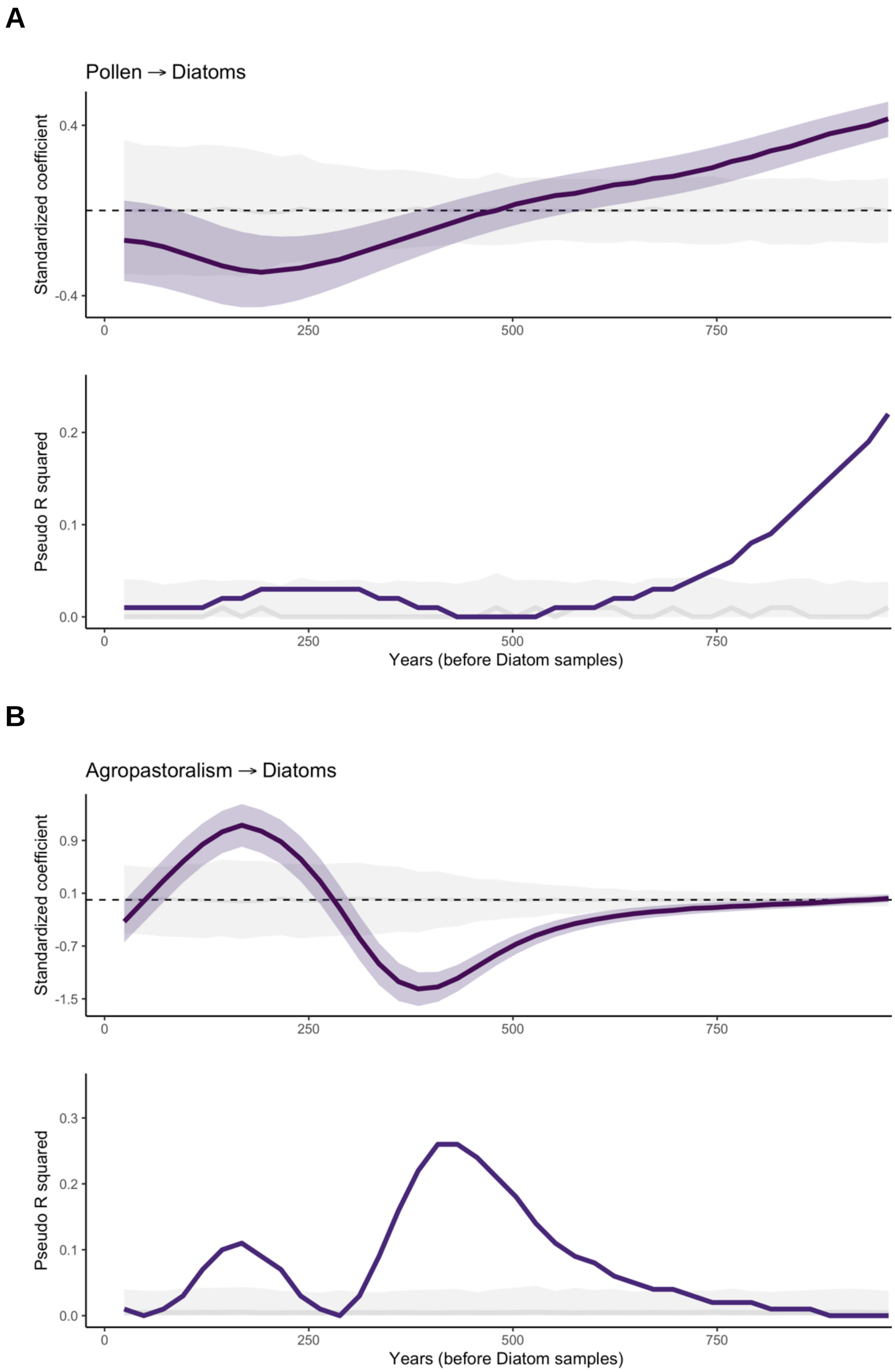

Fig. 6 Asynchrony models (standardized coefficients and pseudo R^2) fitted on lagged predictors to assess the effect of past pollen (a) and agropastoralism (b) rate of change on diatom rate of change. Grey ribbons

represent standardized coefficients and pseudo R^2 for the null model. Standardized coefficients indicate the direction (positive or negative) of the relationship between the lagged predictors and current diatom rate of change. Pseudo R squared indicates the predictive accuracy (i.e., goodness of fit) of the regression asynchronous model between lagged predictors and the response. Where lines intersect the grey ribbon, there is no statistically significant effect of past predictor values (pollen or agropastoralism) on the response (diatoms).