1 **Human practices are behind the aquatic and terrestrial ecological decoupling to climate change in**

2 **the tropical Andes**

3 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 sedimentological

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)

terrestrial vegetation and aquatic ecosystems' responses to change are coupled through indirect climate

influences—that is, past climate-driven vegetation changes dictated limnological trajectories.

Alternatively, subsequently human impact in the lake-catchment system, would uncoupled the terrestrial-

aquatic dynamics. 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. Results showed that

between *ca*. 3000-400 cal years BP terrestrial vegetation, agropastoralism and diatoms fluctuated without

consistent periods of synchronous change. In contrast, positive lagged relationships (i.e., asynchrony)

between climate-driven terrestrial pollen changes and diatom responses were in operation until *ca* 750 cal

years BP. Thereafter, 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 off the links between climate-driven vegetation changes and the

aquatic community. The 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, South America, rate of change

1. Introduction

In the tropical Andes, climate warming is accelerating twice as 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 understanding on: 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). As climate change accelerate globally (Trisos et al., 2020), 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 the way 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 conquest) people had also attendant ecological effects on Andean lakes via agropastoralism practices (e.g. cultivation, fires, camelid domestication) (Velez et al., 2021). For instance, land-use change, and fish stocking were widespread in many parts of the high Andes leading to excess nutrient loads (cultural eutrophication,

76   oxygen depletion), and phytoplankton community composition changes (e.g. shift from low to high-

77   nutrient sensitive algal communities) (Van Colen et al., 2018). In Amazonian landscapes, cycles of

78   deforestation and recovery followed waves of heterogeneous occupational human histories, depending on

79   social and economic contexts (Hamilton et al., 2021). Unlike the lowlands, a fully environmental

80   retrospective assessment is only available for a small suite of mountain tropical lakes despite their crucial

81   role in water ecosystem services for millions of people (Buytaert et al., 2006). Therefore, there is a need

82   to investigate rates and magnitudes of shared climate and human influences, and the dependencies

83   between the two, on lake ecosystems if we are to predict how coupled terrestrial-aquatic ecosystems

84   respond to the abrupt climate change the tropical regions will be experiencing in the next decades (Trisos

85   et al., 2020).

86

87   Under increasing human activities in the catchment (e.g. terraces for agriculture, fire)

88   biogeochemical fluxes from terrestrial to aquatic systems can increase or decrease the input of detrital

89   sediments, nutrients, and organic matter with attendant indirect, and often lagged effects, on the aquatic

90   community (Beck et al., 2018b). Human effects can also indirectly amplify the sensitivity of lakes to

91   record climatic changes in the catchment that otherwise would be buffered by natural vegetation (Bush et

92   al., 2017). Moreover, lakes can respond directly to climate via changes in water temperature and

93   stratification (Fritz, 2008), and aquatic changes can be either independent of (Leavitt et al., 2009) or

94   synchronous with those in the catchment (Bracht-Flyears & Fritz, 2012). Factors explaining synchronous

95   responses include a shared climatic and geological template (Riera et al., 2000), whereas intrinsic

96   sensitivities to external forcing (Schneider et al., 2018) or varied signs of human activities (Bush et al.,

97   2021) can explain the decoupling of terrestrial-lake interactions to climate change.

98

99   In tropical mountain ecosystems, abundant literature revolving around the "ecological resilience"

100   concept have associated the lack of human activities as the main factor for ecosystems to remain stable,

101   even with documented climatic changes such as the Medieval Climate Anomaly (900-1100 years before

102 present) or the Little Ice Age (270–670 years before present) (Lüning et al., 2019). This notion has been

103 supported by study cases documenting forest and aquatic structure recovery after the cessation of

104 deforestation (Norden et al., 2009). However, existing analytical approaches prevent quantification of the

105 relative strength of such variable climate-lake-human interactions. Our study uses a combination of

106 advanced time-series methods to shed light on the long-term trajectories of vegetation, humans, and

107 aquatic communities in Lake Llaviucu (Ecuador), part of an important ancient 80 km-long Amazonia-

108 Andean trade route connecting the highlands in the Paramo (Tomebamba, today Cuenca) with the

109 Amazon lowlands, in Paredones. The humid environment of the Paramo and Andean moist forest

110 catchments develop thick organic soils, resulting in a tight coupling between vegetation and water

111 chemistry (Catalan and Rondón, 2016). We hypothesize that such vegetation-water chemistry dynamics

112 are an intrinsic feature of Lake Llaviucu conferring ecological resilience at long temporal scales and

113 under certain climate regimes. Under natural conditions (i.e., low human pressure), responses of past

114 vegetation to climate would predict diatom assemblage rate of change–that is, terrestrial vegetation and

115 lake dynamics would have been temporally coupled. Alternatively, when humans began impacting the

116 lake-catchment system, agropastoralism indicators (i.e. crop and disturbance pollen taxa, cattle grazing,

117 and charcoal) would have had a greater predictive power on diatom changes over climate–that is, the

118 terrestrial-aquatic dynamics would have become uncoupled.

119

120 **2. Methods**

121 **2.1 Study site**

122 Lake Llaviucu is located at 3150 m asl. in the Cajas National Park, in Ecuador: it lies below the Paramo,

123 and is surrounded by moist montane forest (Fig. 1). Lake Llaviucu is of special economic and ecological

124 interest for the city of Cuenca (old Tomebamba) because it provides 30% of the drinking water supply

125 (Mosquera et al., 2017). The lake housed a fish hatchery and a brewery from 1978 to 1998, which

126 resulted in lake eutrophication during this time (Barros et al., 2015). In the 1960s, a small weir was

127 constructed, which raised the lake level ca. 2 m (Raczka et al., 2019). Once the fish farm was closed with

128   the creation of Cajas National Park (1996), the lake recovered to meso-oligotrophic conditions today,

129   showing nutrient concentrations comparable to other lakes in the region (Van Colen et al., 2017). An

130   ancient road close to the Lake Llaviucu indicates that this catchment was long accessed for the trade by

131   pre-Incan (Cañari) (*ca* 3700-470 cal years BP) and Inca societies (480-420 cal years BP) (Prado

132   Mogrovejo, 2009).

133

134   **2.2 Core collection and sediment indicator analyses**

135   Two sediment cores were retrieved from the deepest basin of the lake (~15m depth): Llav-2009 is

136   11.5 m length and was collected using a Colinvaux-Vohnout piston corer; and Llav-2014, 1.95 m long,

137   collected with a UWITEC gravity corer. Both cores were previously studied to decipher terrestrial

138   vegetation and limnology histories of Lake Llaviucu over the last 12,000 years (Benito et al., 2021;

139   Nascimento et al., 2020). Here, the Llav-2019 core was analyzed for the pollen dataset (thereafter 'native

140   pollen'), while indicators of human activity were extracted as single data set–'agropastoralism dataset'

141   including: *Sporiormella* spores (presence of herbivors), charcoal (fire) and *Hedyosmum, Rumex,*

142   *Begoniaceae, Alnus, Cyperaceae, Cecropia, Asteracea*, *Zea mays, Phaseolus, Ipomoea* (disturbance and

143   crops such as maize, common sorrel, beans, or sweet potato) (Flantua et al., 2016). Samples were

144   processed following standard methods (Faegri and Iversen, 1989) by counting 300 terrestrial pollen grains

145   for each sample and identified using the pollen database from Florida Institute of Technology (Bush and

146   Weng, 2007). *Sporiormella* spores were counted until a total of 300 pollen grains was reached and are

147   expressed as a percentage of the pollen sum. Charcoal fragments were based on macro fragment counts

148   (>100 μm) hence indicating local fires (Whitlock and Larsen, 2001). The Llav-2014 core was processed

149   for diatom analysis following standard procedures (Battarbee et al., 2002). See Benito et al. (2021) for

150   further information on diatom data processing and species identification. Diatom, pollen, and

151   agropastoralism taxa were included in all the analyses if they occurred in more than 2 samples with a

152   relative abundance greater than 1%. The Llav-2009 was analyzed for μXRF using a ITRAX core scanner

153   at 1 mm resolution (Nascimento et al., 2019). Of the μXRF data, Titanium (Ti) was used to represent

154 changes in terrigenous erosion. The diatom core was further analyzed for Si/Ti (silica to titanium ratio)

155 and Mn/Fe (iron to magnesium) (Benito et al., 2020). These elemental ratios are commonly used as

156 indicators of aquatic paleo-productivity and paleo-redox conditions, respectively (Davies et al., 2015).

157

158 **2.3 Core chronologies**

159 For each core, a Bayesian age-depth model was generated using the R package *rbacon* (Blaauw and

160 Christen, 2011). See supplementary figures 1 and 2 for the original Bayesian age-depth models and Table

161 S1 for summary of radiocarbon and ^{210}Pb data (Arcusa et al., 2020; Benito et al., 2021; Nascimento et al.,

162 2020). The ^{210}Pb chronology was calculated using the Constant-Rate-of-Supply model (Appleby and

163 Oldfield, 1978). The entire inventory of unsupported ^{210}Pb was contained in the top 20 cm of the two

164 cores. [14]C ages were calibrated with the IntCal13 calibration curve (Reimer et al., 2013). Here, we

165 compared the original IntCal13 calibrated ages with the IntCal20 calibration curve (Reimer et al., 2020)

166 using R *Bchron* package (Haslett and Parnell 2008) (Fig. S3-4). Results showed no differences between

167 the two sets of calibrated ages. Thereby we refer the numerical analyses to the original age-depth models

168 to allow for comparison with the present study.

169

170 **2.4 Statistical analyses**

171 *2.4.1 Cores interpolation*

172 Prior to statistical analyses, diatom, pollen and agropastoralism indicators data were Hellinger-

173 transformed to accommodate different unit's variable. Sub-samples for diatom and pollen analyses were

174 extracted at ca. 25-year and 40-year resolution, respectively. To overcome discrepancy between 2009 and

175 2014 cores related to temporal resolution, we applied two complementary approaches. First, we estimated

176 a Principal Curve (PrC) on relative abundance data of diatoms, native pollen, agropastoralism indicators,

177 and Ti datasets separately using the R analogue's *prcurve* function (Simpson and Oksanen, 2016). PrC is

178 a nonlinear ordination technique that extracts a single gradient of variation from multivariate data.

179 Subsequently, we modelled temporal trends of PrCs with a Generalized Additive Model (GAM) with a

180 smoothing basis of cubic regression splines, and simulated GAM-inferred values to obtain a multiproxy

181 dataset in a common time series for the response variable (diatoms) using the *mgcv* package (Wood,

182 2017). Second, we linearly interpolated the PrCs of diatoms to the pollen sample ages using the R's base

183 function *approx*. The rationale was to infer values from the finer (diatoms) to the coarser (pollen)

184 temporal resolution dataset. Different tie-points (n=8) between the 2009 and 2014 cores were visually

185 identified using Ti data, and correlation was calculated to determine strength of tie-points (r Person=0.81)

186 to support the linear interpolation of datasets (Fig. S5). To visually explore relationships among aquatic

187 and terrestrial variables, the PrCs of diatom, pollen, and agropastoralism indicators, and titanium were

188 analyzed using an indirect gradient analysis (Detrended Correspondence Analysis; DCA). This plot shows

189 the main temporal trajectories of change in aquatic and terrestrial assemblages, representing the lake-

190 catchment links through time.

191

192 *2.4.2 Relationships between terrestrial and aquatic dynamics*

193 We applied a three-step analytical procedure to test for the relationship between Lake Llaviucu's

194 terrestrial and aquatic ecosystem trajectories (Fig. 2):

195 *Covariates model (Step 1)*– a multivariate GAM was fitted to the diatom PrCs using the mgcv's

196 *gam* function, with pollen and agropastoralism PrCs, and Ti as covariates. This allowed to identify the

197 important trends in the aquatic ecosystem as it responds to changes in the catchment by extracting the

198 contributions of the individual model covariates (pollen, agropastoralism, Ti) to the fitted values of the

199 response variable (diatom PrCs) (Fig. 2). By including both agropastoralism PrC and Ti in the model, we

200 are partially factoring out the additive effect of climate (i.e., soil erosion, Ti plus native pollen) from

201 human practices (i.e., agropastoralism) destabilizing the soil surrounding Lake Llaviucu. Variable *age*

202 was also included as covariate in the model to control against spurious temporal correlation. We would

203 expect a covariate to have a significant effect on the response after considering the passage of time alone.

204 The number of years accumulated per sample (i.e., time difference between two consecutive samples)

205 from the coarser dataset was included in gam's *weights* argument as a measure to account for change in

206 variance over time.

207

208   *Synchronous model (Step 2)*– assemblage-wide and estimated average rate of change were

209 modelled among species using Hierarchical GAMs to quantify the extent to which different lake-

210 catchment components (pollen, agropastoralism, diatoms) exhibit synchronous fluctuations over time (in

211 Fig. 2). We applied a HGAM type that consists of fitting separate temporal models for each species of the

212 assemblages (i.e. diatoms, natural pollen, agropastoralism) while allowing each group-specific smoother

213 (i.e., species) have its own shape and complexity (model I in Pedersen et al., 2019). Because of the likely

214 differences in sensitivities between pollen and diatoms time series detecting local and regional changes,

215 we allowed smoothing functions of covariates to freely capture temporal variance in these time series. In

216 practice, this is achieved via the use of the *by* argument within the smooth term in the function *gam* of the

217 *mgcv* package. Models were fitted with a negative binomial distribution to guard against overdispersion

218 of the data and including lake years per sample to account for changes in variance due to sediment

219 compaction. We used Restricted Maximum Likelihood (REML) for parameter estimation fitted with a

220 thin plate smoother and k = 20-30 basis functions depending on each assemblage (Table 1) and after

221 checking if k is too low with *gam.check* function. To account for detectability across samples, we added

222 an offset equal to the log of the total count of diatom valves and pollen grains in each sample. We

223 estimated species-specific rates of change for each species of the assemblages in each year from the

224 model posterior distribution by simulating 250 estimates of counts for each species and aggregating

225 across simulations, using the methods detailed in Pedersen et al. (2020). We then calculated the average

226 rate of change of relative log-abundances (mean richness) and associated 95% confidence intervals for

227 25-years evenly spaced time series to match with the median temporal resolution of the diatom record

228 (Pedersen et al., 2020). Finally, we compared the rate of change among all assemblage-wide time series.

229 The observed mutual information value "shared" (representing the amount of information between two

230 time series) was compared against a null expectation, using the *muti* R package (Scheuerell, 2017).

231

Asynchronous model (Step 3)– 100 lagged predictor time series of assemblage-wide rate of

change of pollen and agropastoralism indicators were generated to test for asynchrony relationships

between time-delayed samples of pollen and agropastoralism indicators (predictors) and diatoms

(response) (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

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 (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

257   diatoms is indicated by the significant positive contributions in the fitted trend that occurred *ca* 2000 cal

258   years BP (Fig. 3), and it is coincident with low Mn/Fe ratio values (a proxy of hypoxia at the bottom

259   waters), and high Si/Ti values (Fig. 4 and Fig. S7). Between 1400 and 200 cal years BP, agropastoralism

260   effects were manifested with increase in abundance of diatom taxa *Achnanthidium minutissimum,*

261   *Fragilaria* cf. *capucina,* and *Cymbella cymbiformis* (Fig. 4). Mn/Fe and Si/Ti exhibited increase and

262   decrease trends, respectively (Fig. 4). A positive increasing trend, albeit not significant, in the fitted

263   diatom PrC occurred in the most recent period (last 200 years; Fig. 3). The temporal sequence of PrCs

264   and Ti within the DCA multivariate space shows that natural pollen and agropastoralism indicators are

265   positively correlated and opposed to diatoms along the first axis, suggesting a lake-catchment gradient

266   (Fig. S6). DCA axis 1 separates the samples in two groups: one *ca* 200-3000 and another one 200 cal

267   years BP. DCA axis 2 is correlated with Ti (soil erosion).

268   *Synchronous model*– Average rates of change modelled using HGAMs indicate that there is no

269   substantial period when the time-series of pollen and agropastoralism rates of change differed

270   significantly from zero (at 95% level) between *ca* 3000 and 1000 cal years BP (Fig. 5b, c). At *ca* 1000 cal

271   years BP an abrupt decrease in rate of change occurred and remain negative until present day (Fig. 5b, c).

272   The average rate of change of diatoms fluctuated significantly between 3000 and 1400 cal years BP, yet

273   the most rapid and persistent decline beginning *ca* 500 cal years BP until present day (Fig. 4a). Mutual

274   information values—representing the amount of shared information—were statistically significant

275   (*p*<0.05) at lag -4 only between past agropastoralism values and concurrent diatom rates of change (Table

276   S3).

277

278   *Asynchronous model*– The model fitted on past natural pollen rate of change predicting current

279   diatom values shows a maximum effect at *ca* 1000 cal years BP with a decreasing effect until 750 cal

280   years BP, hence converging with the asynchronous model of agropastoralism indicators (Fig. 6a-b). The

281   agropastoralism asynchronous model (i.e. the effect of time-delayed agropastoralism indicators on current

282   rate of change of diatoms) shows two periods of statistically significant increasing influence of

283 agropastoralism indicators on diatoms, one between 750-500 (R^2=0.3), and another one 250-200 cal years

284 BP (R^2=0.15) (Fig. 6b). These two asynchronous peaks show opposite influences on diatoms, negative

285 between 750-500 cal years BP, and positive between 250-200 cal years BP (Fig. 6b).

286

287 **4. Discussion**

288 The historical role of humans and climate on aquatic and terrestrial ecosystems in the tropical Andes have

289 been largely described in the literature, but independently in most cases (de Souza et al., 2019; Ekdahl et

290 al., 2008; Flantua et al., 2016; Lombardo et al., 2020), including earlier publications from Lake Llaviucu.

291 Here, we investigated when and how human activities could disrupt the links between terrestrial and

292 aquatic responses to climate change over the last three millennia. Our results supported the hypothesis of

293 the reconstructed human activities via livestock grazing, cultivation, and burning (i.e. agropastoralism

294 indicators) being stronger influences than climate-driven vegetation changes predicting post-disturbance

295 diatom trajectory over the last three millennia. Diatom ecological change and human practices were in

296 operation before the European contact through positive feedbacks resulting in agropastoralism lagged

297 effects at *ca* 750 and 200 cal years BP. These results suggest that the aquatic ecosystem is also responding

298 to the cycle of deforestation, abandonment, and re-use following Indigenous land-use, European contact,

299 and regained modern impacts, like documented in Pan-tropical terrestrial vegetation records (Hamilton et

300 al., 2021). Our study advances the notion that recent (Age?) shifts to novel diatom assemblages were

301 driven by varied, historical rates of change of anthropogenic forcings even in remote areas.

302

303 4.1 Terrestrial-aquatic dynamics and ecological decoupling

304   Titanium concentrations in lake sediments can be associated with catchment disturbances (e.g.

305 deforestation) or climate (e.g. precipitation changes). For instance, Schneider (2018) found an increased

306 precipitation frequency after 1300 AD (*ca* 700 cal yr BP) coinciding with Inca occupation of the Lake

307 Llaviucu's catchment. In mountain and lowland tropical lakes, human activities amplified subtle climatic

308 signal that otherwise could have been buffered by natural vegetation (Åkesson et al., 2020; Bush et al.,

12   12

309 2017). In our study, the difficulty in teasing apart sources of natural and human factors on long-term

310 limnological change has been partially resolved by two lines of independent evidence. First, our results

311 indicated that agropastoralism effects are independent from climate change, here interpreted as the

312 additive effects of soil erosion and native pollen in the GAM covariates model (Fig. 3). Second, the DCA

313 analysis showed that terrestrial vegetation changes (i.e., pollen and agropastoralism PrCs) are highly

314 correlated but independently associated with soil erosion (Ti). Taken together, we interpret that soil

315 erosion is likely not sourced from precipitation changes but originated from human-driven catchment

316 disturbances (i.e., agropastoralism). Here, we must acknowledge that the lack of statistically significant

317 temporal contributions of native pollen and Ti on the diatom trajectory could well be because of the

318 analyzed proxies come from two different records, and data were interpolated. Nevertheless, our results

319 are robust because we attempted two independent cross-core correlation methods yielding similar results

320 (Table 1). Previous studies in Lake Llaviucu also demonstrated the overriding effect of human practices

321 (Nascimento et al., 2019). On larger spatial scales and longer time scales, agropastoralism spread across

322 South America (Riris and Arroyo-Kalin 2019), and humans were involved in the extinction of megafauna

323 in the Ecuadorean Andes (Raczka et al., 2019), despite harsh climate events such as droughts during the

324 Mid Holocene Dry Event.

325

326   Between ~3000 and 500 cal years BP, the diatom trajectory (PrC) suggests a complex ecological

327 history due to varied contributions of terrestrial vegetation and agropastoralism indicators. The

328 dominance of the benthic diatoms *Nupela* sp., *Encyonopsis* sp., *Denticula kuetzingii, Gomphonema* sp.

329 between *ca* 3000-1400 cal years BP, suggest a stable benthic habitat characterized by light limitation,

330 slightly acidic and mesotrophic waters (Wojtal, 2009). The coeval dominance of upper forest montane

331 taxa and Poaceae (up to 90% of the total pollen assemblage) (Fig. 4 and Fig. S8) indicates a catchment

332 covered with native forest and grasses and well-developed soils that potentially provided large

333 concentrations of nutrients and dissolved organic matter into the lake reducing light availability

334 conditions while likely enhanced lake productivity and acidity (Beck et al., 2018a). These trends are

13   13

335 supported by higher nutrient availability, as indicated by higher Si/Ti ratios (Fig. 4). Subsequently,

336 prominent peaks in *Sporiormella* (proxy of herbivory presence) and charcoal (proxy of local fires) at *ca*

337 1400 cal years BP were coincident with a diatom shift towards an assemblage of less acidophilus,

338 disturbance, and oligotrophic species (*Achnanthidium minutissimum, Fragilaria* cf. *capucina, Cymbella*

339 *cymbiformis*) (Tapia et al., 2006; Velez et al., 2011), which is interpreted as evidence for a reduced

340 nutrient availability in the lake. Reduced nutrient inputs were likely driven by greater slope stability

341 associated with human practices (i.e. terracing). These are consistent with changing land use practices

342 across the tropical Andes at that time as seen in the Peruvian Andes (Matthews-Bird et al., 2017),

343 highlands of Colombia (Vélez et al., 2021), and Bolivian Altiplano (Marsh, 2015). Fire could be another

344 human-associated disrupting factor on terrestrial material inputs resulting in a less productive system

345 (Beck et al., 2018), which may also be the case here because of the high relative increase in

346 *Achnanthidium minutissimum* as a characteristic opportunistic taxon in the Ecuadorean Andes (Benito et

347 al., 2019). Overall, our data suggest a strong link between terrestrial vegetation and aquatic systems likely

348 driven by nutrient changes. Accurately interpreting such links require attention to factors that could

349 influence lake nutrient status, which might include direct climate effects via thermal stratification, indirect

350 climate-driven vegetation changes (as discussed above), or both.

351

352 Despite its deep waters, dominance of benthic diatoms between 3000 and 500 cal years BP in

353 Lake Llaviucu supports the view of an aquatic basin characterized by sunlit gradual slopes covered by

354 macrophyte vegetation. Shifts in benthic vs planktic diatoms have been widely attributed to lake level

355 changes resulting from precipitation variability under warm/dry climates (Weide et al., 2017). For

356 instance, the Medieval Climate Anomaly (MCA) triggered lower lake levels and it was recorded on many

357 different tropical Andean paleolimnological records (Lüning et al., 2019). Although the signal of MCA on

358 Lake Llaviucu's sediments is inconclusive (Benito et al., 2021), one consequence of potential

359 warming/drying is an enhanced lake productivity promoted by less mixing within the water column, as

360 seen in analogous moist forest Andean lakes (Loughlin et al., 2018). Lake Llaviucu's mesotrophic diatom

361 assemblages between *ca* 3000-1400 cal years BP were supported by low Mn/Fe ratio values, which could

362 reflect reduced oxygenation because of a gradual trend towards a reduced mixing (Boyle, 2001) (Fig. 4).

363 Our data suggest that an increase in nutrient cycling towards mesotrophic conditions is a plausible

364 alternative explanation to indirect climate-driven vegetation cover changes (Jenny et al., 2016).

365 Nonetheless, either forcing is suggested to be in operation under natural conditions: climate-driven

366 terrestrial vegetation change preceded change in diatom assemblages.

367

368 4.2 Time-varying aquatic responses to human impacts

369   The asynchronous model of pollen and agropastoralism indicators converged at 750-years lag,

370 and time-delayed pollen effects on current rate of change of diatoms did not resume after, indicating a

371 decoupling once Indigenous activities began to insensitively impact the catchment. It may seem

372 counterintuitive that such a large time interval (750-years lag) characterized the time-delayed diatom

373 responses, but for instance, Beck et al. (2018b) identified a 1600-year lag of aquatic (cladoceran)

374 responses to pollen changes in a Tasmanian lake. Nonetheless, there are no similar quantitative studies on

375 the long-term linkages between different components of the catchment (vegetation, precipitation, humans)

376 in the tropical Andes. One potential explanation could be a non-analogue situation between the type of

377 responses of diatoms and the disturbance regime: there are no equivalent current benthic dominated

378 assemblages responding to cumulative human pressures in the catchment with slow processes and small

379 variability (e.g., Williams and Jackson, 2007). Benthic diatoms respond in more complex ways to axes of

380 trophic conditions (i.e., organic matter, acid-base conditions, cation exchanges) as opposed to planktic

381 species that are more subjected to water column variability such as light regimes or mixing (Juggins et al.,

382 2013; Rivera-Rondón and Catalan, 2020). Another explanation could be found in the variability of

383 Indigenous land-use. Terracing practices may have begun earlier downstream than upstream because of

384 more favorable terrain or different societal needs (Kendall, 2013). As consequence, agropastoralism

385 effects on lake diatoms were delayed until a larger portion the Llaviucu's catchment was occupied with

386 more sophisticated systems to control runoff and slope stabilization for cultivation (Chepstow-Lusty &

387   Jonsson, 2000). We cannot discard the possibility that diatoms or pollen records were not accurately

388   responding to forcing drivers in the catchment, and therefore, additional aquatic geochemical proxies

389   (e.g., organic matter, nutrient isotopes, sedimentary pigments) could help to generate a stronger inference

390   from multiproxy paleoenvironmental records.

391

392   Certain tropical Andean Lakes have suffered recent physical habitat changes coinciding with the

393   onset of wind speed reductions and rising temperatures (Michelutti et al., 2016). Associated changes in

394   thermal structure led to biotic regime shifts favoring proliferation of planktic assemblages (Giles et al.,

395   2018; Labaj et al., 2017). In this study, the rate of change of diatoms for the last 500 years were

396   unprecedented, characterized by a dominance (40% of the total assemblage) of the oligo-mesotrophic

397   planktic species *Discostella stelligera, Tabellaria flocculosa,* and *Diatoma tenuis* (Fig.4 and Fig S7).

398   Model predictions suggest that lake mixing regimes will be impacted in the upcoming decades with

399   continued warming (Woolway et al., 2020). In high latitude lakes, climate-driven biological regime shifts

400   responded to reduced duration and extent of ice cover (Smol et al., 2005). However, the same mechanism

401   does not apply in the tropical Andes because of constant growing conditions around the year. In the

402   Ecuadorean Andes, pre-industrial (<1950) meteorological records are inexistent, which hampers the

403   assessment of climatic drivers of thermal stratification. In Lake Llaviucu, one potential confounding

404   effect on thermal stratification through human activity was the trout farm operating between the 1980s

405   and 1990s. Trout stocking could have enhanced heat penetration because of top-down control effects that

406   cleared the water column (Chraïbi and Fritz, 2020). Fecal matter and slaughtering wastes from the fish

407   farm and the construction of the weir could further explain via increase in dissolved organic carbon the

408   rapid increase in planktic mesotrophic ecological niches irrespective of warming (Saros and Anderson,

409   2015). Moreover, heavy metal influx and dust deposition from tire rubbers, vehicle breaks, and emissions

410   to Lake Llaviucu, caused by contemporary heavy traffic on the nearby main highway, may have indirectly

411   influenced the assemblages additionally (Schneider et al., 2021). Overall, our study sheds light into the

412   multivariate nature of changes, both climate and human, explaining the relationship between recent

413 warming and lake physical changes (Winslow et al., 2017), and emphasizes the importance of long-term

414 perspectives in deciphering anthropogenic climate warming.

415

416   A thought-provoking result is the two opposite (i.e. negative and positive) periods of lagged

417 agropastoralism on current diatoms once after humans began to alter Lake Llaviucu significantly (Fig. 6).

418 We interpret these as a cycle of impact by Incan societies and abandonment following European contact

419 (750 cal years BP, ~1250-1300 CE), and a regained human impact with the establishment of European-

420 style agricultural practices (250 cal years BP, ~1800 CE). How generalizable is this pattern within the

421 human history of the tropical Andes? Although not referencing attending impacts on aquatic ecosystems,

422 the most recent and comprehensive review of widespread reforestation of Amazonian landscapes after the

423 arrival of the Europeans in South America indicate that human practices largely followed the cycle of

424 deforestation, use, and reforestation, all beginning before the conquest (*ca* 550 cal years BP, 1492 CE;

425 Bush et al., 2021). In ecologically analogous lakes of the Northern Andes of Colombia and Ecuador,

426 aquatic indicators (including diatoms and pollen) were also in concert with human-driven vegetation

427 changes (González-Carranza et al., 2012; Loughlin et al., 2018; Velez et al., 2021). However, previous

428 studies did not quantify time-varying past effects of human practices on aquatic responses. Decoupling

429 between natural and human-associated pollen effects on diatoms is difficult to discern because their

430 drivers might be temporally correlated (i.e. humans and climate). Our study is important in the sense that

431 it shows key temporal stages of when diatom assemblages are changing, and the uncertainty of

432 covariates' contributions and their lagged effects without assuming any specific dynamics in the time-

433 series (i.e., GAM). This is a critical analytical step to provide nuances in paleoenvironmental

434 reconstructions, with potential to complement archaeological models that infer cultural changes in South

435 America (Marsh, 2015).

436

437 **5. Conclusion**

438   Our findings describe the dynamic aquatic transitions of the Lake Llaviucu best explained by

439   time-delayed human practices in the catchment that triggered changes in lake nutrient status. The current

440   Lake Llaviucu's ecological integrity may be compared with past waves of human practices in the

441   catchment of different intensity and nature. For instance, albeit located in a protected area, current Lake

442   Llaviucu's vicinity in the Cajas Natural Park is managed under traditional burning practices to stimulate

443   growth of grass for cattle grazing, and herds use the lake as a water source potentially leading to lake's

444   primary production increases. Nevertheless, current rates of livestock grazing could not have surpassed

445   nutrient-associated baseline thresholds to alter the lake diatom assemblages as in *ca* 1400 and 500 cal

446   years BP. While the decrease in nutrient status can be associated with diatom changes for most of the

447   record, anthropogenic stressors via climate change and direct in-lake impacts (i.e., weir, fish farm) appear

448   to be the most important driver of the lake state (i.e., the uniqueness rapid change in assemblage-wide rate

449   of change) after Indigenous practices long decoupled the natural aquatic-terrestrial links. Whenever

450   similar time series are available, our framework can be used in similar settings to shed light into

451   ecological couplings and baselines of tropical aquatic ecosystems. Our paleoecological record provided a

452   long-term perspective on the interactive effects of human and climate stressors that may support policy

453   addressing current global change issues, such a water quality and availability, and land-use practices.

454

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710 **Tables**
711
712 **Table 1** Generalized Additive Models (GAM) parameters and summary statistics for the models used.

713 Covariable: time series used for each model; K-index: diagnostic parameter to check if k is too low (k<1);

714 bs: smoothing basis; K: basis dimensions for the smooth term; edf: estimated degrees of freedom.

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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

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719 **Figures**

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722 **Fig. 1** Geographical location of Lake Llaviucu in Ecuador, South America (a) in relation with elevation

723 showing the distribution of Paramo (>3500 m; green lines), the location of Tomebamba (today Cuenca)

724 and the archaeological region of Paredones in the lowlands (b). c) Lake Llaviucu's aerial photography

725 (Google Earth) showing the moist montane forest surrounding the lake and Paramo up in the mountains.

726 d) Lake Llaviucu's bathymetry showing the position of the diatom (Llav-2014) and pollen (Llav-2009)

727 cores (b).

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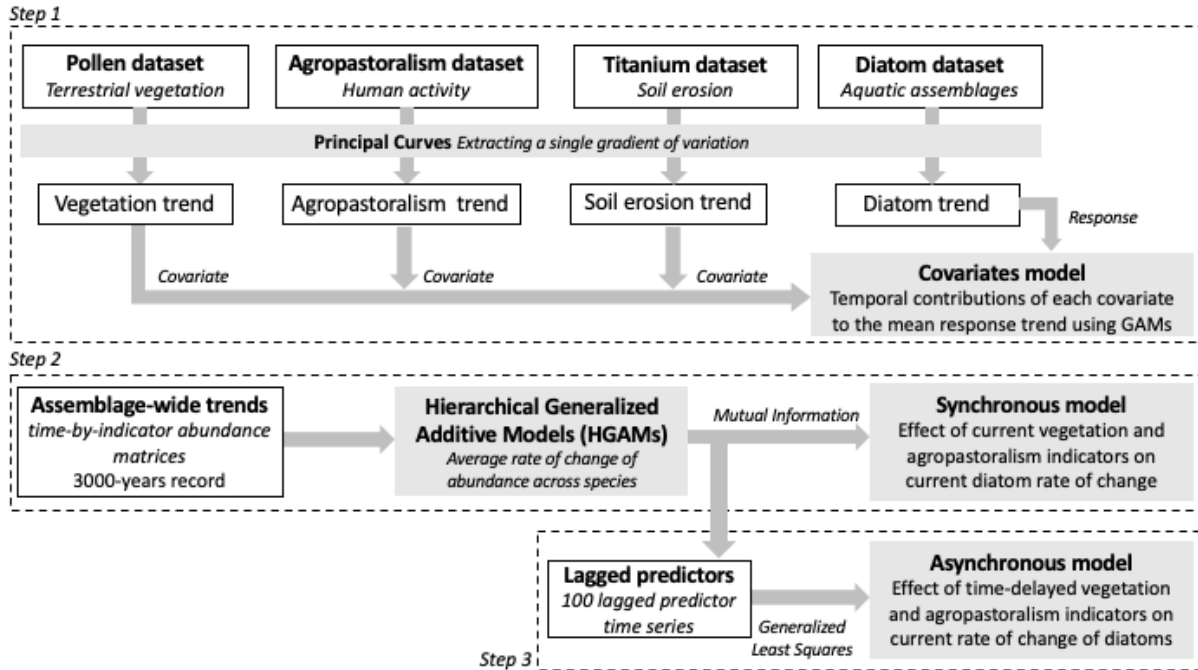
Fig. 2 Flow diagram illustrating the numerical analyses carried out in the present study, which consists in three main steps: extracting trends in temporal contributions of terrestrial vegetation, human activities and soil erosion on diatom trajectory (*Covariates model, step 1*); modeling assemblage-wide 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.

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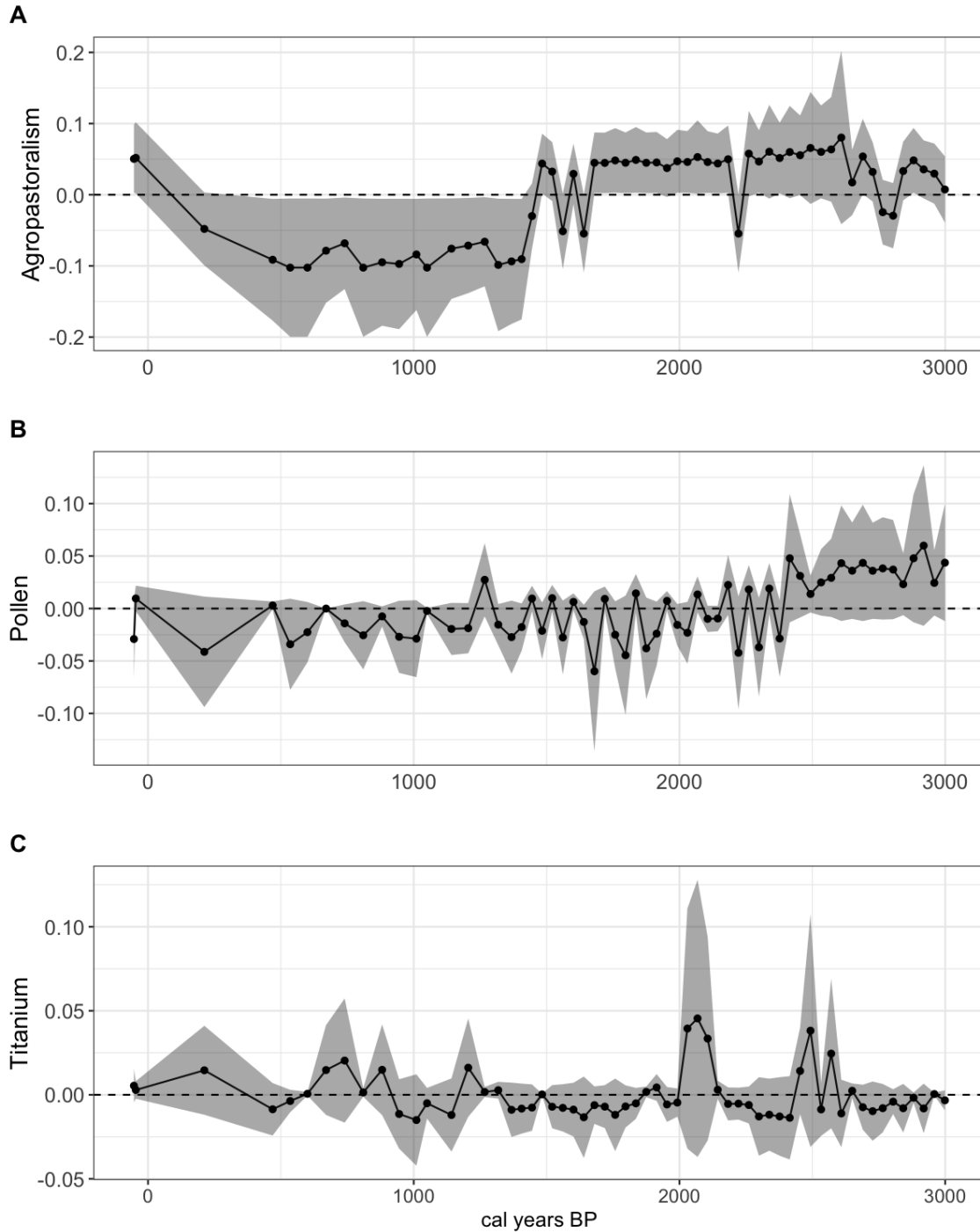
Fig. 3 The temporal contributions of a) agropastoralism, b) pollen, and c) Titanium in Generalized

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%

745   confidence interval. Where the grey envelope includes zero line there is no statistically significant

746   contribution of the covariate to the response. Cal years BP=calibrated years before present.

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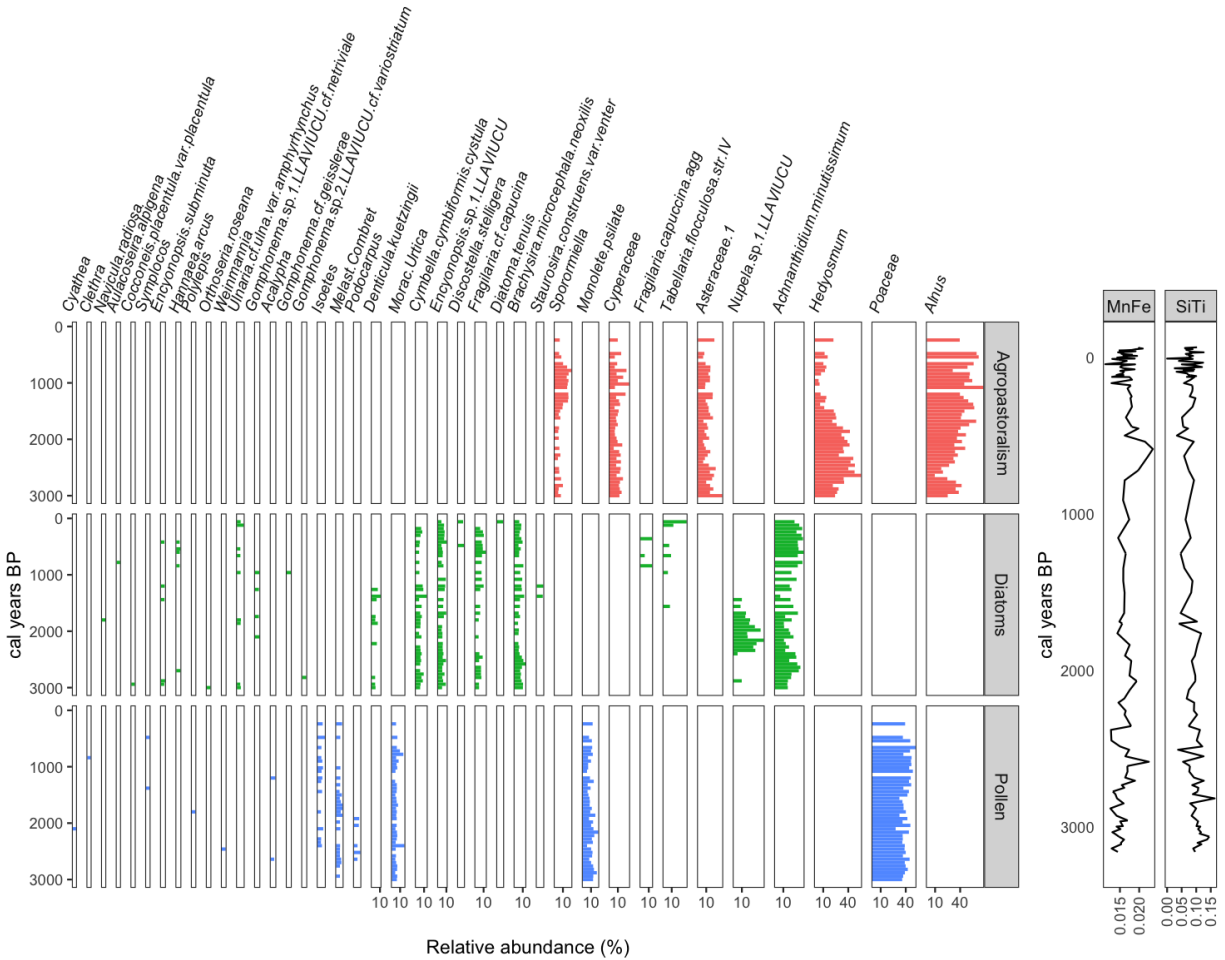
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749   **Fig. 4** Summary stratigraphic plots of the Lake Llaviucu, showing (from *left*) the relative abundance (%)

750   of selected taxa (i.e., those occurring having more than 3% relative abundance) of the agropastoralism,

751   diatom, and pollen assemblages arranged by increased abundance (x-axis) over time (y-axis), and

752   downcore distribution of Mn/Fe and Si/Ti ratios (Llav-2014 core).

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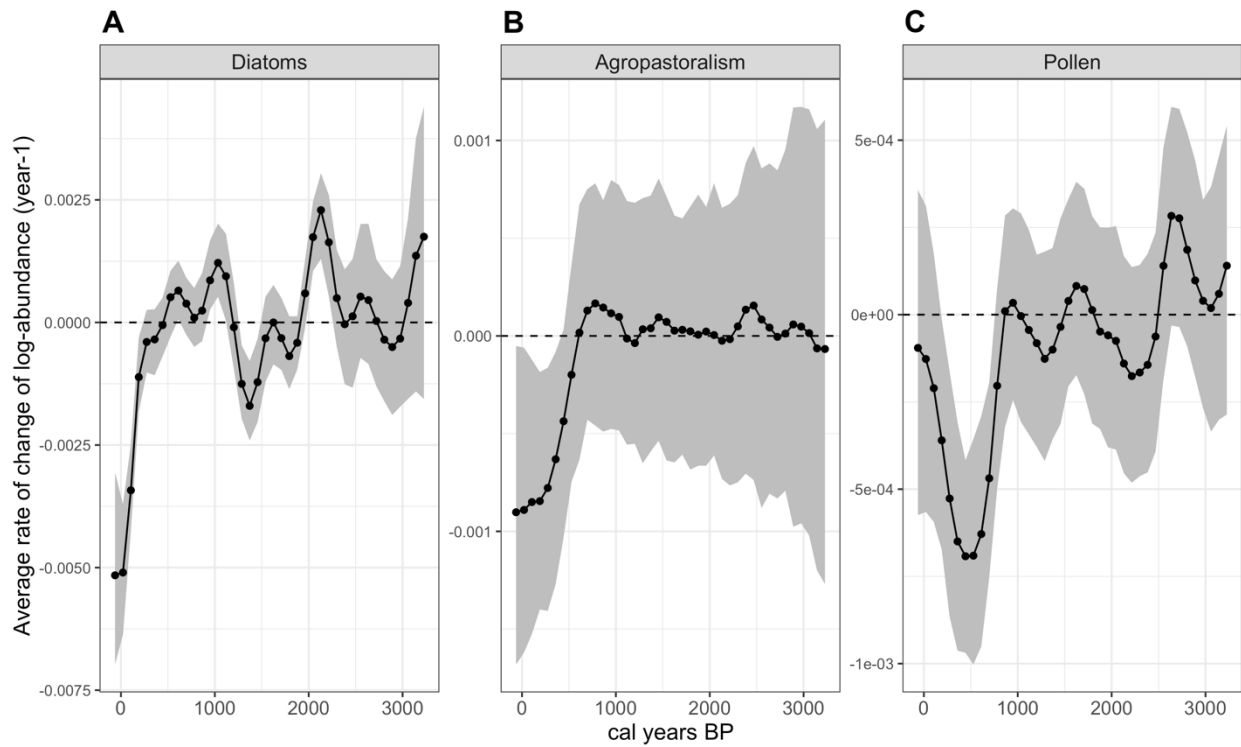
Fig. 5 Assemblage-wide rate of change (y-axis) over time (calibrated years before present; x-axis),

estimated from Hierarchical generalized additive models (HGAMs) fitted to the most common taxa (those

present in more than 2 samples). 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.

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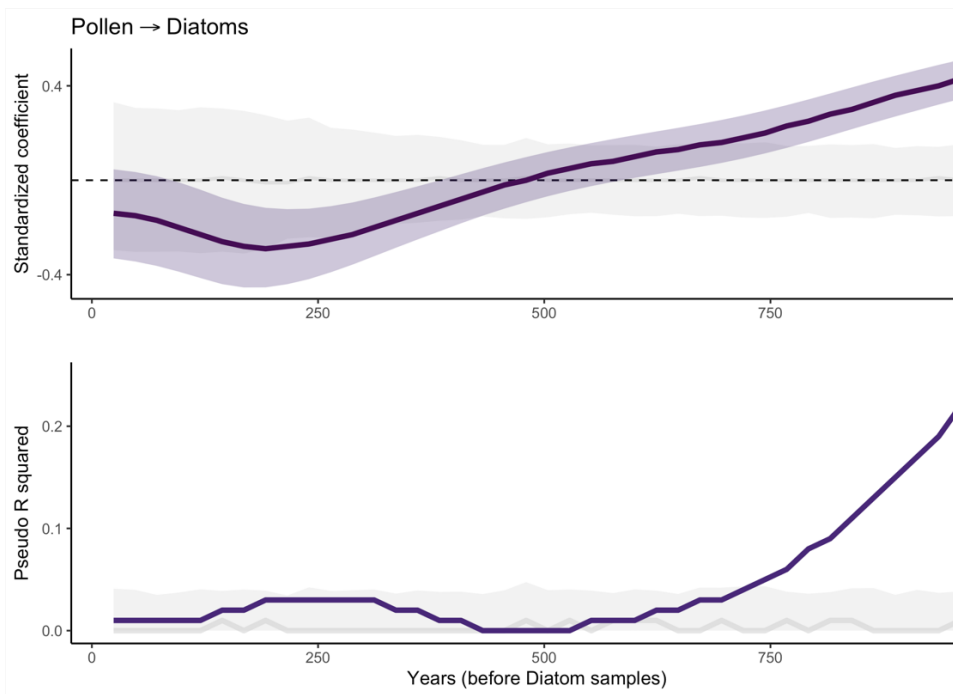
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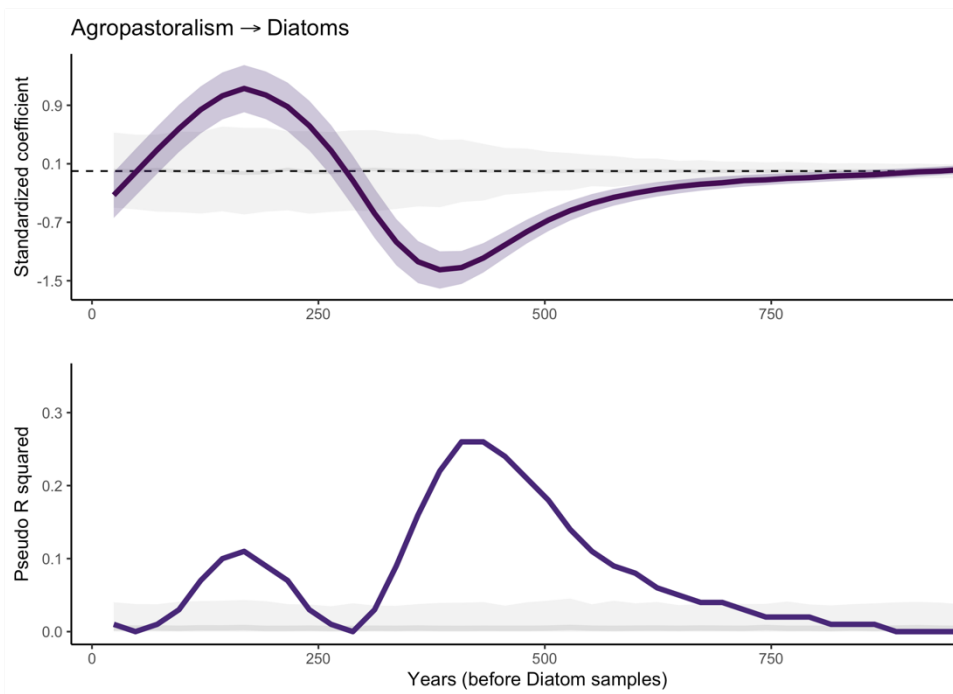
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764 **Fig. 6** Asynchrony models (standardized coefficients and pseudo R^2) fitted on lagged predictors to assess

765 the effect of past pollen (a) and agropastoralism (b) rate of change on diatom rate of change. Grey ribbons

766   represent standardized coefficients and pseudo R^2 for the null model. Standardized coefficients indicate

767   the direction (positive or negative) of the relationship between the lagged predictors and current diatom

768   rate of change. Pseudo R squared indicates the predictive accuracy (i.e., goodness of fit) of the regression

769   asynchronous model between lagged predictors and the response. Where lines intersect the grey ribbon,

770   there is no statistically significant effect of past predictor values (pollen or agropastoralism) on the

771   response (diatoms).