



# Long-Term Habitat Degradation Drives Neotropical Macrophyte Species Loss While Assisting the Spread of Invasive Plant Species

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The spread of invasive macrophyte species is a pressing threat to neotropical shallow lakes. Yet there are few studies addressing the full extent of biotic and abiotic changes that may occur in response to invasive species. Less is known of how other human-induced stressors such as eutrophication and lake draining may interact over time with invasive macrophytes to influence biodiversity. We combined limnological observations with paleoecological data from Fúquene Lake, Colombia, a eutrophic neotropical shallow lake, to provide information on the current and long-term (decades-centuries) dynamics of the spread of two well-established invasive plants *Eichhornia crassipes* and *Egeria densa*. We found a unique in macrophyte species composition in areas currently dominated by *Egeria* and *Eichhornia*. *Eichhornia*-dominated areas had 14 macrophyte species, turbid (secchi=19 ± 6 cm) and poorly oxygenated (3.94 ± 2.61 ppm) waters whereas *Egeria*-rich areas supported 5 species and had clearer (secchi=51 ± 12 cm) and better-oxygenated (6.06 ± 2.4 ppm) waters. Historical macrophyte community shifts were linked to eutrophication and lake level variation and characterized by the loss of charophytes and bryophytes before 1500 CE and subsequent reductions in *Nymphaea* sp., *Potamogeton illinoensis* and *Najas guadalupensis* in the early 1900s (lake draining). *Eichhornia crassipes* (since 1500 CE) and *E. densa* (early 1900s) occurred well before proposed dates of introduction (1950s and 1990 respectively). Both species have rapidly expanded since the 1990s along with *Azolla filiculoides* in response to an inflow water diversion scheme and heavy nutrient loads. Our results suggest that the spread of *Eichhornia* and *Egeria* was not responsible for native macrophyte species loss, but that their current dominance is exerting synergistic and antagonistic secondary effects on plant assemblages through habitat modification, competitive exclusion and promotion of habitat heterogeneity across the lake. It could therefore be misleading to suggest that invasive plants causes macrophyte species loss in degraded lakes. We suggest that

aggressive species like *Eichhornia*, *Azolla*, and *Egeria* require hydrologically stable and eutrophic environments to spread; thus, management actions should focus on controlling these two factors. Our study demonstrates the need to use a long-term approach to fully-understand the effects of invasive macrophytes.

**Keywords:** *Eichhornia crassipes*, *Egeria densa*, Fúquene Lake, hydrological modification, lag-phase, multiple stressors, palaeolimnology, shallow lakes

## INTRODUCTION

The spread of invasive macrophyte species is considered to be one of the most detrimental human impacts on inland waters across the globe (Strayer, 2010; Reid A. J. et al., 2018). Invasive macrophyte species are alien species living outside their natural range. They create self-replacing populations over several life cycles, reducing freshwater biodiversity (Boylen et al., 1999; Ailstock et al., 2001; Houlahan and Findlay, 2004), stimulating plant biomass production (Farnsworth and Ellis, 2001; Kelly and Hawes, 2005), altering biogeochemical cycles (Templer et al., 1998; Angeloni et al., 2006) and causing millions of dollars (e.g., > US\$30 million year<sup>-1</sup> in the UK; Oreska and Aldridge, 2011) in damages and ecosystem remediation (Strayer and Dudgeon, 2010). The distinctive plant structure and high biomass of most invasive macrophytes can further cause strong and varied ecosystem engineering effects (Crooks, 2002; Yarrow et al., 2009). For instance, dense beds of invasive plants offer colonization space for epiphytic algae, invertebrates, and fish (Meerhoff et al., 2003), and can greatly stimulate diversity and populations of these organisms (Kelly and Hawes, 2005; Rejmánková et al., 2018). Similarly, dense stands of invasive floating plants enhance shading, reduce temperature, and cause anoxia in the underlying water that ultimately inhibit understory species (Villamagna and Murphy, 2010).

In tropical shallow lakes, notorious invasive macrophyte species include highly competitive submerged species such as *Hydrilla verticillata* (L. f.) Royle and *Egeria densa* Planchon (Byers, 2002), and several floating plant species like *Eichhornia crassipes* Mart. Solms, *Pistia stratiotes* L., *Azolla filiculoides* L., and *Salvinia molesta* Mitchell (Scheffer et al., 2003). Their effects may include reductions in the number of fish, declines in water quality, navigation obstruction (Gopal, 1987), modification of habitat structure and displacement of native macrophyte species (Yarrow et al., 2009; Rejmánková et al., 2018). The full extent of biotic and abiotic changes that may occur in response to the spread of these species is, however, poorly studied in the neotropics (Villamagna and Murphy, 2010; Rejmánková et al., 2018). Even less is known about how increasing human-induced stress factors such as eutrophication and hydrological alterations (e.g., lake level fluctuations) may interact over time with the spread of invasive macrophyte species spread to jointly influence aquatic plant biodiversity (Byers, 2002; Rejmánková et al., 2018).

To date, research on the effects of the spread of invasive macrophyte species on biodiversity loss in freshwater systems has been tested by simple correlations, where the ability of invasive species to compete against native plants results in the

suppression of resident species (Boylen et al., 1999; Levine et al., 2003). However, some macrophyte species may require an initial habitat disturbance such as increase in nutrient loads to get established, and thus, may only be successful once a disturbance decreases the competitive interference of resident macrophytes (MacDougall and Turkington, 2005). In such cases, invasive species do not drive early ecological change, rather, they are established as “passengers” (MacDougall and Turkington, 2005). Ultimately, the long-term effects of the accumulation and spread of invasive macrophyte species may have negative or positive feedbacks with eutrophication and thus become a secondary driver of change (Didham et al., 2005). Induced secondary driver effects by invasive macrophytes can be prevalent among species with strong engineering effects, such as *Egeria* (Yarrow et al., 2009) or *Eichhornia* (Villamagna and Murphy, 2010) if they create positive feedbacks which further encourage the invader species (Strayer, 2010).

There are > 4 million lakes in the tropics and subtropics (Verpoorter et al., 2014). Water hyacinth (*E. crassipes*) has invaded many freshwater systems across the globe, and according to future climate change predictions, its range of distribution is likely to expand into higher latitudes as water temperatures increase (Hellmann et al., 2008; Rahel and Olden, 2008). The lack of consensus on the relationships between the timing of the spread of invasive macrophyte species like *Eichhornia* and human induced stressors (such as eutrophication) significantly constrain our understanding of how affected shallow lakes must be managed. Further understanding in this area will assist with predicting macrophyte invasion potential (Strayer et al., 2006) in relation to multiple adverse emergent factors (Reid A. J. et al., 2018) including changing climate (Hellmann et al., 2008; Rahel and Olden, 2008) and enhance ability to manage socio-ecological and human health impacts (Pejchar and Mooney, 2009). Forecasting the combined effects of invasive macrophyte species and co-occurring stress factors in neotropical lakes is however challenging, given the lack of rigorous monitoring programmes, and so our understanding of colonization success and how these factors vary through time once established is limited (Strayer et al., 2006). The latter is of key management interest as most macrophyte invasions and environmental stress factors (such as eutrophication), typically take time to be fully manifested (decades to centuries; Strayer et al., 2006; Sayer et al., 2010), and crucial lake management aspects of early invasion stages such as lag-phases, are commonly overlooked (Pyšek and Hulme, 2005). A solution comes from the application of paleoecological techniques since most macrophyte species leave a sub-fossil remains in the sediments that can be tracked over

time (Davidson et al., 2005; Salgado et al., 2010). This is a very useful technique that allows for the detection of invasive species, of pre-colonization or pre-spreading conditions (Nogué et al., 2017) and an understanding of changes in species distributions and abundances on a long-term basis (Salgado et al., 2018a).

In this study we combined detailed limnological observations with paleoecological and historical environmental data from Fúquene Lake (Colombia, South America), a neotropical shallow lake. We provide new information on the long-term (decades-centuries) dynamics of two well-established invasive plant species: the free-floating water hyacinth (*E. crassipes*) and the submerged Brazilian Elodea (*E. densa*). More specifically, we had three objectives: (i) to examine the long-term changes in macrophyte community structure in response to multiple stress factors (i.e., spread of invasive macrophyte species, lake draining and eutrophication); (ii) to reveal the long-term dynamics of the spread of invasive species and how they are linked to eutrophication and lake draining; and (iii) to assess the contemporary consequences of invasive macrophyte species dominance on macrophyte species distributions and water quality. Our working hypothesis is that long-term (gradual) eutrophication and two hydrological alterations (lake draining and a water canal construction) initially drove native species loss, rather than the spread of invasive macrophyte species. We also hypothesized that once the invasive macrophyte species established, they exerted secondary effects on the remaining native plant communities through habitat modification (e.g., promotion of anoxic conditions and habitat heterogeneity), resource availability (shading) and community homogenization (dominance).

## METHODS

### Study Area

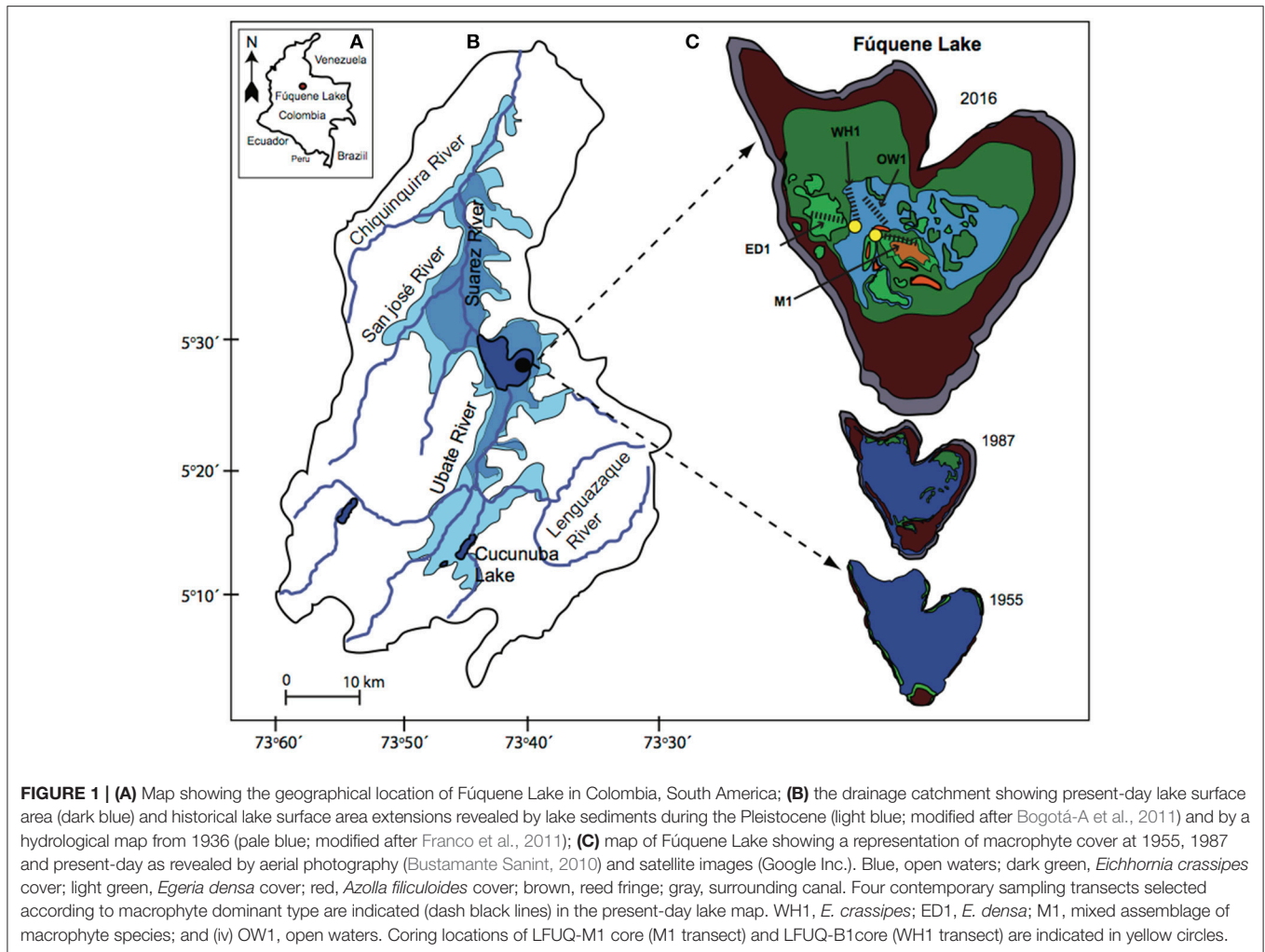
Fúquene Lake is a large (30 km<sup>2</sup>) and shallow (average depth 2 m, maximum depth 6 m), Andean lake (2,560 m a.s.l.) located on the eastern Cordillera of the Colombian Andes (5°27'55" N, 75°46'19" W) (Figure 1). The Ubaté, Lenguazaque and Suta rivers are the main inflows and the outflow to the north forms the Suárez River, a key tributary of the Magdalena River. Fúquene Lake is an important provider of natural habitats for native aquatic birds, fish, and macrophytes and offers many benefits to local inhabitants including water and food (Vidal and Perez, 2007).

Fúquene Lake was once regarded as one of the largest natural Andean shallow lakes in Colombia (approx. area of 112 km<sup>2</sup>; Franco et al., 2011). Archaeological records and pollen data from the lake catchment area have shown that humans occupied and modified the landscape for agriculture well before 1500 CE (Van Geel and Van der Hammen, 1973; Langebaek, 1995). After the Spanish conquest at 1500 CE there were major increases in population densities at nearby settlements (Langebaek, 1995) marked by large-scale land-use shifts from small-cultivated areas into large grazing areas (Etter et al., 2008). Europeans introduced several non-native grazing animals such as cattle, goats, sheep, and horses, which quickly transformed the landscape from natural montane forests/cultivated areas to large extensions of

pasture lands (Etter et al., 2008). Since the late 1800s Fúquene Lake was further subjected to several draining episodes which aimed to increase land for agriculture and livestock. By the mid-1930s the lake had lost almost 70% of its original surface area (Figure 1; Table 1; Vidal and Perez, 2007). More recently, in 1987, the lake hydrology was further affected through the construction of a canal along the lake shorelines which was built to stop further expansion of agricultural lands (Franco et al., 2011). This engineering work impeded lateral hydrological connectivity of the lake, diverted most of the inflow waters, and increased the water retention time of the lake, which are thought to have stimulated lake productivity and the spread of invasive species (Table 1; Vidal et al., 2015). The lake is currently in a hypertrophic state (total phosphorus [TP] > 0.40 mg/L) with well-established populations of *Eichhornia* and *Egeria* (Franco et al., 2011; Figure 1). The date of introduction of *Eichhornia*, which is believed to be a native plant to the lowland Amazon and lower Orinoco basins (Barrett and Forno, 1982), is not fully clear but locals affirm that the plant was transplanted into the lake sometime around the mid-1950s. In contrast, *E. densa*, native to the southern Hemisphere (Yarrow et al., 2009), was deliberately introduced in 1990 as a phytoremediation strategy (Duque and Donato, unpublished) to improve the poorly oxygenated (dissolved oxygen of 4.41 ppm) eutrophic (total phosphorus-TP of 1.73 mg/L) waters at the time (Table 1; Donato et al., 1987).

### Contemporary Macrophyte and Water Quality Sampling

We selected four sampling transects of approx. 1 km long across the lake to characterize the present-day macrophyte species composition and environmental conditions (Figure 1). Each transect was defined according to the dominant macrophyte type and designated with a code (in parentheses): (i) *E. crassipes* (WH1); (ii) *E. densa* (ED1); (iii) mix assemblage of macrophyte species (M1); and (iv) open waters (OW1) (Figure 1). At each transect we collected macrophyte data at approximately 50 m intervals ( $n = 18$  sampling points), during five fieldwork sessions (December 2015–April 2017). Surveys were undertaken from a boat and at each sampling point we used a combination of bathyscope and double-headed rake sampler, and macrophyte species cover percentages within a 1 m<sup>2</sup> area were recorded. Due to difficulties in accessing inner areas of the dense floating mats of *Eichhornia*, macrophyte-sampling points at transect WH1 were assessed from the margins. Concurrent with the macrophyte surveys, we collected three measurements of water depth, secchi depth, water temperature, conductivity, salinity, total dissolved solids (TDS) and dissolved oxygen (DO) at the beginning, middle, and end of each transect. For transect WH1, we removed or displaced a few plant individuals of *Eichhornia* at each environmental sampling point and waited for a few minutes to let hydrological conditions settle back before measuring the limnological variables. Physical and chemical parameters were measured at the surface water and at 0.5 m depth using a YSI<sup>®</sup> DO and conductivity meter.



## Long-Term Changes in Macrophyte Assemblages

We used a corer of 10 cm diameter (Aquatic Instruments Inc.) to collect a large volume of sediment whilst preserving undisturbed surface sediments (Patmore et al., 2014). We retrieved two short sediment cores with lengths of 100 cm (LFUQ-M1) and 50 cm (LFUQ-WH1) from two of the contemporary sampling transects (M1, and WH1, respectively; **Figure 1C**). The core LFUQ-M1 was retrieved at the end of transect M1 (5°27'13.86"N, 73°44'59.33"W) at a water depth of 100 cm and core LFUQ-WH1 was collected at the mid-point of the transect at a water depth of 90 cm (5°27'45.35"N, 73°45'48.61"W). Each core was extruded in the field at 1 cm intervals and changes in lithostratigraphy were recorded prior to extrusion.

## Core Dating and Geochemistry

We dated the longer core LFUQ-M1 by combining  $^{210}\text{Pb}$  and  $^{14}\text{C}$ . Radionuclide measurements of  $^{210}\text{Pb}$  (half-life 22.3 years),  $^{137}\text{Cs}$  and  $^{241}\text{Am}$  were performed on the most recent samples (0–20 cm; Appleby et al., 1986). Dates were ascribed using the

Constant Rate of Supply (CRS) model (Appleby and Oldfield, 1978).  $^{14}\text{C}$  analysis on plant macrofossil remains via accelerator mass spectrometry analysis (AMS; Beta Analytic Inc.) was used to date older sediments at depths of 30, 75, and 98 cm. A combined age-depth model was calculated using the CLAM 2.2 software in R (Blaauw, 2010; R Development Core Team, 2016) to ascribe dates below the  $^{210}\text{Pb}$  age model. Radiocarbon ages were calibrated using the Northern Hemisphere calibration curve and an age model used linear loess interpolation (lower AIC and no time reversals). The final age model that best matched the environmental history of the lake resulted from using the maximum error standard  $^{210}\text{Pb}$  dates for the top 15 cm intervals and the minimum error standard dates derived from the CLAM model for 15–100 cm sediment intervals (**Figure 3; Table 2**).

Geochemical element concentrations were measured on 1 cm-thick discrete samples using X-Ray Fluorescence (XRF). For the cores LFUQ-M1 sampling resolution was at 2-cm intervals (0–20 cm) and at 4-cm intervals from 20 to 100 cm. For the core LFUQB1 we analyzed contiguous sediment intervals (0–20 cm) and every 3-cm between 20 and 50 cm. The XRF analyses were measured in the laboratory using



**TABLE 1** | Historically records of environmental data, macrophytes and water hyacinth spread in Fúquene Lake (modified after Franco et al., 2011).

Year	Open water (Ha.)	Aquatic vegetation	Water hyacinth(Ha.)	TP (mg/L)	DO (ppm)	References
1890	3,203	0				Vidal and Perez, 2007
1940	2,768	0				Garzón, 2005
1955	2,657	23	4.0			Garzón, 2005, Bustamante Sanint, 2010
1963	2,355	38				Garzón, 2005
1974				0.39	5	Donato et al., 1987
1978	2,141	79	9.3			Garzón, 2005, Bustamante Sanint, 2010
1983			10.8			Bustamante Sanint, 2010
1986				1.73	4.41	Donato et al., 1987
1987	1,770	617				Fundación Humedales
1987	1,909	710				Montenegro, 2004
1993	1,490	585	13.9			Garzón, 2005; Bustamante Sanint, 2010
1999	1,363	697				JICA-Agencia de Cooperación Internacional Del Japón, 1999
1999	1,344	750				Montenegro, 2004
2002	446	2,015		0.12		Montenegro, 2004
2003	1,081	1,004				Garzón, 2005
2003	332	1,720			3.1	Fundación Humedales
2005	923	1,277				Fundación Humedales
2009	725	1,390	21.5			Fundación Humedales, Bustamante Sanint, 2010
2010				0.4		Franco et al., 2011

**TABLE 2** | Chronology of the dated depth profiles of core LFUQ-M1.

Depth (cm)	<sup>210</sup> Pb age (yr)	<sup>14</sup> C Age (yr)	Date (CE)	(±)	Clam model ±	Selected age (yr)	Selected date (CE)	Sed. rates (cm/yr)
0	0		2016			0	2016	3
1.5	1		2015	1	1	0	2016	3
3.5	2		2013	2	2	3	2013	3
6.5	6		2006	3	3	6	2010	1
9.5	19		1999	4	4	12	2004	0.33
12.5	25		1990	5	5	20	1995	0.167
17.5	48		1967	7	7	39	1975	0.33
30.5		340	1676	30	86	361	1697	0.003
75.5		510	1506	40	84	515	1511	0.005
98.5		1370	1299	30	86	556	1460	1

Different dates and ages and its standard deviation (±) are presented according to <sup>210</sup>Pb radiometric analysis, <sup>14</sup>C AMS analysis, a combined <sup>210</sup>Pb and <sup>14</sup>C age model (Clam), and the final selected ages and dates with its associated sedimentation rates.

a portable XRF analyzer spectrometer, XMET 7500. Dry sediment samples were ground and homogenized in the laboratory using a mortar and pestle. Approximately 3 g of sediment sample were used and covered with Chemplex thin-film sample support. Mean values of each element were determined and plotted using two readings per sample. Calcium (Ca), Potassium (K), Iron (Fe), Manganese (Mn), Rubidium (Rb), and Titanium (Ti) results were selected for this study. Given that Ti is an unambiguous indicator of allochthonous inputs from the catchment, we used this element for normalization (Cohen, 2003). We calculated four different but complementary index ratios according to Davies et al. (2015) to investigate changes in: weathering regimes (Rb/K), physical erosion of the lake catchment area (K/Ti),

lake level fluctuation (Ca/Ti) and lake reduction conditions ([Fe/Mn]/Ti). We also used loss-on-ignition (LOI) (Dean, 1974) to determine the organic fraction of contiguous sediment intervals (0–50 cm) in the cores LFUQ-M1 and LFUQ-WH1, and of 2-cm intervals from 50 to 100 cm in core LFUQ-M1.

As funds were not available for dating core LFUQ-WH1, we used a similar approach to Sayer et al. (2010), correlating the core with LFUQ-M1 according to specific independent paleo-markers: changes in LOI profiles, changes in lithostratigraphy, changes in geochemical proxies, and changes in pollen abundance of *Pinus* spp. which was introduced in the lake catchment during the early 1900s (Vidal and Perez, 2007).

## Plant Macrofossil Analysis

We analyzed 25 (LFUQM1) and 19 (LFUQB1) sediment samples (1-cm thick) for plant macro remains at 2-cm intervals for the top 20 and at 5 cm intervals lower down each core, respectively. Between 20 and 40 cm<sup>3</sup> of wet sediment was disaggregated in 10% potassium hydroxide (KOH) before sieving. Macrophyte remains were retrieved from the residues of sieved core material (using mesh sizes of 355 and 125 μm) following standard methods (Birks, 2001). Plant remains included seeds and fruits, leaf-spines, leaf fragments (including water lily leaf sclereid cells), charophyte oospores and characteristic *Eichhornia* root-caps. Plant remains data were standardized as the number of fossils per 100 cm<sup>3</sup> and identified by comparison with reference material and by using relevant taxonomic keys (e.g., Birks, 2001; <https://tmi.laccore.umn.edu/is>). Due to poor macrofossil preservation, we estimated temporal variations of *Egeria* via pollen analysis using the method for determining absolute pollen concentration (Moore et al., 1991). Fifteen sediment samples were analyzed for pollen analysis for LFUQ-M1 core and 12 samples for LFUQ-WH1.

## Data Analysis

We assessed relationships between current macrophyte species occurrences and variation in physical and chemical parameters across transects via multivariate regression tree (MRT) analysis (De'ath and Fabricius, 2000). Prior to analysis, we excluded variables with collinearity (i.e., conductivity and TDS; see **Table S1.1** in Appendix S1), defined as those with a variance inflation factor >8 (Zuur et al., 2007). To match the number of environmental data points at each transect, we split the macrophyte data from each transect into 3 groups according to proximity to the beginning, middle or end of each transect. The occurrences of each macrophyte species within each group transect were then transformed as frequencies of occurrence (i.e.,  $[number\ of\ observations/total\ number\ of\ sampling\ points\ per\ group\ transect] \times 100$ ), and environmental data were  $\log(x+1)$  transformed prior to analysis (Legendre and Gallagher, 2001). Cross-validation was applied to determine the optimal number of splits in the tree (De'ath and Fabricius, 2000) and the best predictive tree with one standard error was selected (De'ath and Fabricius, 2000). Given that the MRT algorithm uses random numbers as a starting point, we ran several ( $n = 15$ ) MRT analyses using the *set.seed* algorithm in R (R Development Core Team, 2016) and compared the multiple runs for the same model (De'ath and Fabricius, 2000). The mean value of the best predictive trees was then used to describe the variation in the macrophyte and environmental variables. MRT analysis was carried out using the MVEPART library (version 1.4; De'ath and Fabricius, 2000) in R (R Development Core Team, 2016). Principal component analysis (PCA) was then used to visualize macrophyte species distributions according to the MRT selected groups.

To reduce the variation between differentially produced plant macrofossil structures (e.g., root-caps, leaves and seeds), we  $\log(x+1)$  transformed the plant macrofossil abundance (Legendre and Gallagher, 2001). In order to assess major temporal zones of community change, we combined the data sets from the two cores into a single species matrix and

applied a univariate regression tree analysis using core depth as the explanatory variable. To explore any potential variability between different tree models, we ran 10 different analyses using the *set.seed* algorithm in R (R Development Core Team, 2016). The mean value of the best predictive trees was then used to describe the variation in the plant macrofossil data. A PCA was used for visualization of major compositional temporal changes in macrophyte assemblages across the cores. Plant macrofossil stratigraphy for each core was achieved using the "Rioja" Package in R (Juggins, 2009; R Development Core Team, 2016).

To assess long-term dynamics of invasive macrophyte species spread, we focused on the variation of *Eichhornia* fossil abundances (longer history of occurrences and good fossil preservation). We modeled the variation of *Eichhornia* log-abundances through time as a two distinct spread processes using piecewise regression analysis (Aikio et al., 2010). This analysis models early stages of spread (i.e., stable periods of low abundances; lag-phase) as a linear process while the subsequent exponential growth phase is modeled as a non-linear component (Aikio et al., 2010). The significance of a potential breaking point between the two-modeled slopes was tested using a Davies test (Davies, 1987). Analyses were run using the "fragmented" package in R (R Development Core Team, 2016; Muggeo and Muggeo, 2017).

## RESULTS

### Contemporary Macrophyte and Environmental Data

A total of 14 macrophyte species and filamentous algae (undifferentiated) were recorded across the four studied transects including *Azolla filiculoides*, *E. crassipes*, *E. densa*, *Limnobium laevigatum* Humb. & Bonpl. ex Willd. Heine, *Ludwigia peploides* Kunth P.H.Raven, *Myriophyllum aquaticum* (Vell.) Verdc., *Hydrocotyle ranunculoides* L. f. (VVV), *Potamogeton pusillus* L., *Utricularia gibba* L., *Typha angustifolia* Pers., and *Schoenoplectus californicus* (C.A. Mey.) Steud (**Table 3**). Plantless areas were a common feature (mean = 38.9% ± 31.9) across the open water transect (OW1) and, when present, *E. densa* dominated the assemblages (mean = 51 ± 34.8%). Other species such as *E. crassipes* (mean = 20 ± 26.1%), *P. pusillus* L. (mean = 6.7 ± 15.2%), and *A. filiculoides* (mean = 5.6 ± 8.1%) occurred irregularly. In the *Eichhornia* type transect (WH1) we recorded 14 species including *E. crassipes*, *L. laevigatum*, *L. peploides*, *M. aquaticum*, *H. ranunculoides*, and *U. gibba*. Emergent species like *Bidens laevis* (L.) Britton Sterns Poggenb., *T. angustifolia*, and *S. californicus*, also occurred in a few sample locations. In ED1 (*E. densa* type) transect *Egeria* dominated and a few species such as *A. filiculoides*, *L. laevigatum* and *U. gibba* occurred sporadically (**Table 2**). For the transect M1 (mixed assemblage of species) we observed 10 macrophyte species with *E. densa* (100%), *A. filiculoides* (mean = 97.8 ± 8.6%) and *Eichhornia* (mean = 78.9 ± 18.3%) being the most common ones.

A summary of measured environmental variables is presented in **Table 4**. Transects OW1 (137 ± 36.5 cm), M1 (114.8 ± 48 cm) and WH1 (103 ± 41.4 cm) were generally deeper than the ED1

**TABLE 3** | Summary of macrophyte species data measured over five quarterly fieldwork campaigns (December 2015–April 2017) at four contemporary sampling transects selected according to dominant macrophyte type: WH1, *Eichhornia crassipes*; ED1, *Egeria densa*; M1, mixed assemblage of macrophyte species; and OW1, open waters.

Transect	<i>Azolla fillicoides</i>	<i>Bidens laevis</i>	<i>Egeria densa</i>	<i>Eichhornia crassipes</i>	Filamentous algae	<i>Hydrocotyle ranunculoides</i>	<i>Lemna minuta</i>	<i>Lemna valdiviana</i>	<i>Limnobium laevigatum</i>	<i>Ludwigia peploides</i>	<i>Myriophyllum aquaticum</i>	<i>Potamogeton pusillus</i>	<i>Scheuchzeria palustris</i>	<i>Typha angustifolia</i>	<i>Utricularia gibba</i>	Plant-less areas	Species richness
M1	97.8 ± 8.6	5.6 ± 10.3	100	78.9 ± 18.3	22.2 ± 33.1	3.3 ± 9.3	4.4 ± 9.9	51.1 ± 29.9	33.3 ± 28.2	3.3 ± 6.9	1.1 ± 4.3						10
OW1	5.6 ± 8.1		51.1 ± 34.8	20.0 ± 26.1	16.7 ± 25.2						6.7 ± 15.2					38.9 ± 31.9	4
WH1	64.4 ± 30.1	47.8 ± 26.6	40.0 ± 23.4	100		27.8 ± 17.4	4.4 ± 9.9	45.6 ± 24.0	71.1 ± 25.6	52.2 ± 15.3	37.8 ± 27.8	6.7 ± 15.2	13.3 ± 14.4	4.5 ± 7.6	15.6 ± 19.4		14
ED1	37.8 ± 32.4		100	11.1 ± 15	22.2 ± 31.3				15.6 ± 18.3						5.6 ± 8.1		5

A total of 18 sampling points clustered into three groups (beginning, middle and end) per transect were collected during each campaign and the presence/absence of each macrophyte species within a group were expressed as frequency of occurrences. The mean frequency values (expressed as %) and standard deviations per transect from the combined five campaigns are presented.

**TABLE 4** | Summary of environmental data measured over five fieldwork campaigns (December 2015–April 2017) measured at the sampling transects described in Table 3.

Transect	DO <sub>s</sub> (ppm)	DO <sub>w,col</sub> (ppm)	Secchi (cm)	Salinity (ppt)	CD <sub>s</sub> (μS/cm)	CD <sub>w,col</sub> (μS/cm)	TDS <sub>s</sub> (ppm.)	TDS <sub>w,col</sub> (ppm.)	T <sub>s</sub> (°C)	T <sub>w,col</sub> (°C)	Depth (cm)
M1	11.4 ± 2.8	5.4 ± 1.9	50.8 ± 11.7	0.12 ± 0.07	267 ± 117.8	264 ± 119.3	173 ± 77.3	173 ± 76.5	19.8 ± 2.4	17.4 ± 1.1	114.8 ± 48
OW1	12.3 ± 2.9	10.5 ± 2.1	40 ± 18.7	0.1 ± 0.25	259 ± 53.5	252 ± 46.1	169 ± 39.5	165 ± 34.9	19.4 ± 1.2	18.6 ± 0.9	137 ± 36.5
WH1	6.7 ± 2.6	3.9 ± 2.6	19.3 ± 6.1	0.1 ± 0.01	284 ± 67.9	287 ± 65.5	188 ± 32.9	194 ± 34.5	20.2 ± 1.8	19.2 ± 2.9	103 ± 41.4
ED1	11.8 ± 2.1	6.1 ± 2.5	55 ± 17.9	0.25 ± 0.05	351 ± 103.8	357 ± 99.8	230 ± 64.6	242 ± 62.6	20.6 ± 1.5	18.4 ± 1.1	86 ± 31.1

DO, Dissolved oxygen; CD, Conductivity; TDS, Total dissolved solids; T, temperature; s, surface; w.col, water column. A total of three measurements per transect (beginning, middle, and end) were collected at each campaign and mean values and standard deviations per transect from all five campaigns are presented.

( $86 \pm 31.1$  cm) transect. In a descending order, DO surface values varied from  $12.3 \pm 2.9$  ppm at OW1,  $11.8 \pm 2.1$  ppm at ED1,  $11.4 \pm 2.8$  ppm at M1 and  $6.7 \pm 2.6$  ppm at WH1. Similarly, DO in the water column had the lowest values at the WH1 ( $3.9 \pm 2.6$  ppm) transect. Highest secchi depths were recorded at the E1 ( $55 \pm 17.9$  cm) and M1 ( $50.8 \pm 11.7$  cm) transects, while lowest values ( $19.3 \pm 6.1$  cm) were observed at the WH1 transect. Salinity ( $0.25 \pm 0.05$  ppt), conductivity ( $357 \pm 99.8$   $\mu\text{S}/\text{cm}$ ) and TDS ( $242 \pm 62.6$  ppm) were also greater at the ED1 transect than at the other three transects.

### Multivariate Tree Analysis (MRT)

The MRT analysis identified surface DO, secchi disk depth and salinity as the most important environmental variables explaining the current macrophyte species distributions across the transects (Figure 2A). Nine out of the 15 analyzed trees split the macrophyte data into five main groups explaining  $67.3 \pm 3.4\%$  of the plant variation (Figure 2A; Table S2.1 in Appendix S2). PCA on the macrophyte frequency of occurrences showed that the MRT tree splits generally concur with different macrophyte cover types of each sampling transect (Figure 2B). The tree was initially split in two main branches, where the majority of macrophyte data points of transect WH1 clustered in an independent group (lower right hand side in Figure 2B) characterized by DO surface values  $<7.6$  ppm. Three sampling points characterized by *Eichhornia* dominance clustered, as an independent group with DO values above 7.6 ppm. Macrophyte data points from transect OW1, ED1, and M1 grouped together on the left branch of the tree according to DO surface values  $\geq 7.7$  ppm (Figure 2A). The MRT separated most macrophyte data associated with the OW1 transect according to DO water column values  $\geq 7.73$  ppm, whereas higher salinity for ED1 ( $\geq 0.15$ ) and higher secchi depths ( $\geq 30$  cm) split most ED1 data from M1 data. The PCA analysis showed that macrophyte associations of these three groups overlap in some instances (Figure 2B).

### Chronology and Long-Term Changes in Geochemical Elements

Our age-depth calibration of the core LFUQ-M1 resulted in a chronological model spanning the last *c.* 600 years, with the last two centuries in the top 20 cm (Figure 3; Table 2). Due to the non-monotonic variation of unsupported  $^{210}\text{Pb}$  in the core, radiometric chronologies were calculated using the CRS dating model (See Appendix S4 for details). The simple CRS model placed the 1963 depth above 17 cm, likely due to low unsupported  $^{210}\text{Pb}$  activities and to earlier reductions in unsupported  $^{210}\text{Pb}$ . Chronologies and sedimentation rates were therefore corrected under the CRS model by assigning a date of 1963 to sediments at 19 cm in accordance to the  $^{137}\text{Cs}$  record. The  $^{14}\text{C}$  AMS analysis dated the macrofossil samples at 30, 75, and 98 cm to  $1676 \pm 30$ ,  $1506 \pm 40$ , and  $1370 \pm 86$ , respectively (Table 2). Sedimentation rates in our age-depth calibration showed a U-shaped pattern being relatively high (1 cm/yr.) between 98 and 76 cm, dropping to a mean of 0.0065 cm/yr between 75 and 20 cm and gradually increasing above 20 cm to reach a mean value of 2.5 cm/yr in the most recent samples (6–1 cm) (Figure 4).

Temporal variations in lithostratigraphy, LOI and XRF index ratios were highly consistent across the two cores, showing three

zones of change that allowed us to correlate the dated core LFUQ-M1 with the LFUQ-WH1 core with good confidence (Figure 4). The three zones correspond to: (i) a historical phase with distinctive dark sediments, high organic matter, high Ca/Ti, (Fe/Mn)/Ti and Rb/K ratios, and low K/Ti ratio (100–75 cm in LFUQ-M1; 50–41 cm in LFUQ-WH1); (ii) a transitional phase with distinctive pale gray sediments, low organic material, low Ca/Ti, (Fe/Mn)/Ti and Rb/K ratios, and high K/Ti ratio (74–20 cm in LFUQ-M1; 38–13 cm in LFUQ-WH1); (iii) a recent phase with distinctive dark sediments, high organic matter, Ca/Ti, (Fe/Mn)/Ti and Rb/K ratios and poor K/Ti ratio (19–0 cm in LFUQ-M1; 13–0 cm in LFUQ-WH1 cm). Similarly, the independent pollen record of *Pinus* spp. was highly consistent across the two cores showing a reduction at 9–10 cm, an increase at 7.5 and a reduction at 2 cm (see Figure S5.1 in Appendix S5).

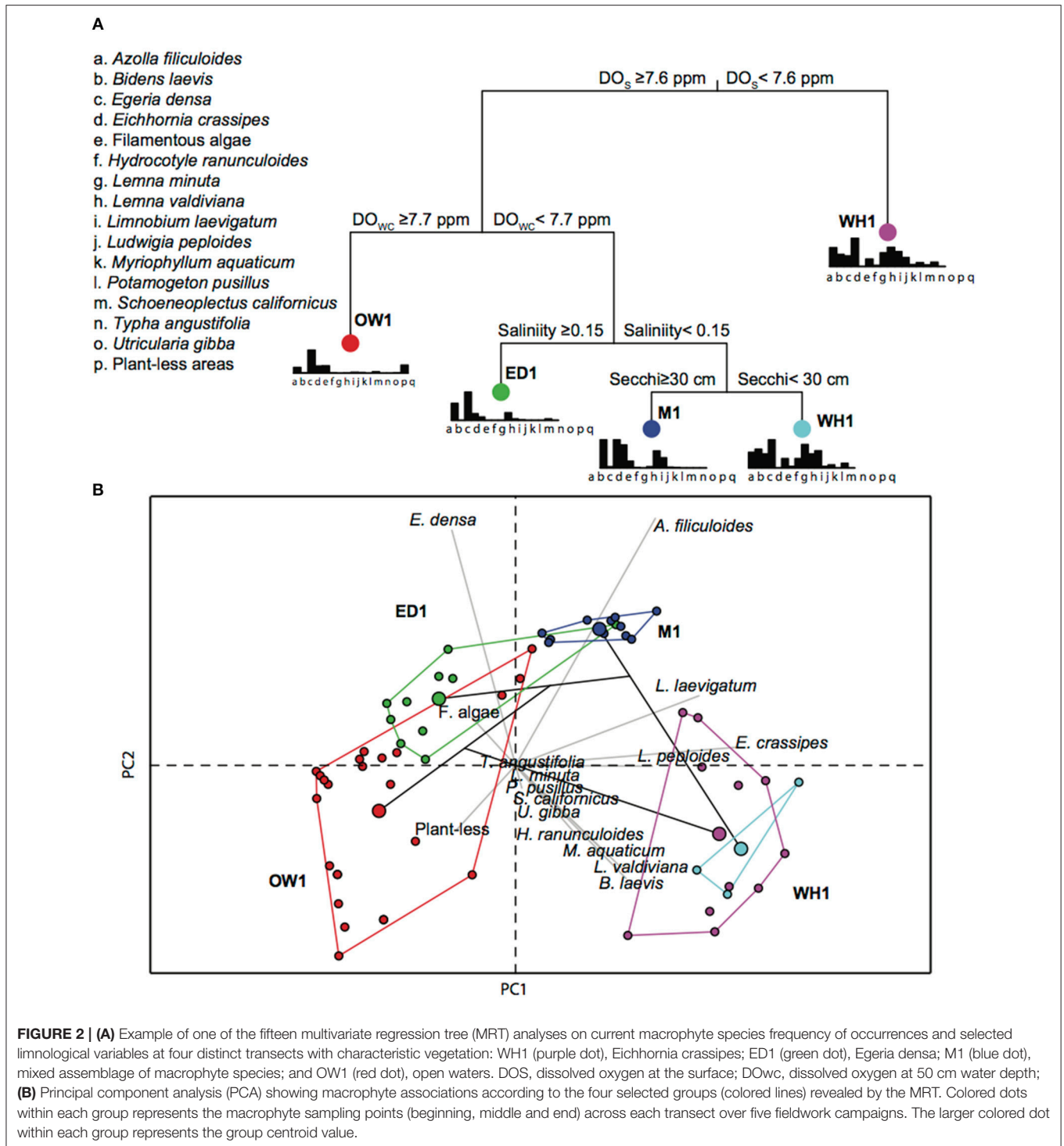
### Long-Term Changes in Macrophyte Assemblages

The plant macrofossil analysis resulted in 14 macrophyte taxa occurring throughout the cores (Figures 5, 6). Plant assemblage representation across the two cores was highly congruent resulting in nine out of 10 consistent regression trees explaining the macrophyte variation of  $53\% \pm 4.1$  (Figure 7; Table S3.1 in Appendix S3). Three major temporal zones of change were identified: Zone 1– CE *c.* pre-1506 (100–75 cm in LFUQ-M1; 50–41 cm in LFUQ-WH1); Zone 2– 1506–1904 CE (74–20 cm in LFUQ-M1; 38–13 cm in LFUQ-WH1); and Zone 3– 1905 CE–present (19–0 cm in LFUQ-M1; 13–0 cm in LFUQ-WH1 cm). In Zone 1 charophytes (*Chara* sp. and *Nitella* sp.), bryophytes (agg.), *Ceratophyllum demersum* L., and *P. pusillus*, dominated the assemblages. Leaf-sclereid cells (probably *Nymphaea* sp.), *Potamogeton illinoensis* Morong., the previously unreported *Najas guadalupensis* (Spreng.) Magnus, *A. filiculoides* and *E. crassipes* also occurred in abundant numbers. In Zone 2 charophytes, bryophytes and *C. demersum* disappeared from the fossil record, while *Nymphaea* spp., *P. illinoensis*, and *N. guadalupensis* dominated until the end of the 1800s when abundances gradually decreased. *Eichhornia* and *A. filiculoides* occurred in relatively low abundances, presenting a slight increase from 1640. At zone 3 (1905–present), *Nymphaea* sp., disappeared while *N. guadalupensis* and *P. illinoensis* further declined. At the beginning of this zone *E. densa* colonized the lake whilst *E. crassipes* and *A. filiculoides* gradually increased. The species *L. valdiviana* and *M. aquaticum* also become apparent during the late periods of this zone and since the mid-1990s the lake was typified by marked expansions in *Eichhornia*, *A. filiculoides*, *Egeria*, *M. aquaticum* and *L. peploides*. At this point *P. illinoensis* disappeared from the fossil record while *N. guadalupensis* only occurred in low numbers throughout the LFUQ-WH1 core (Figure 6).

### Long-Term Dynamics of Invasive Macrophytes Spread

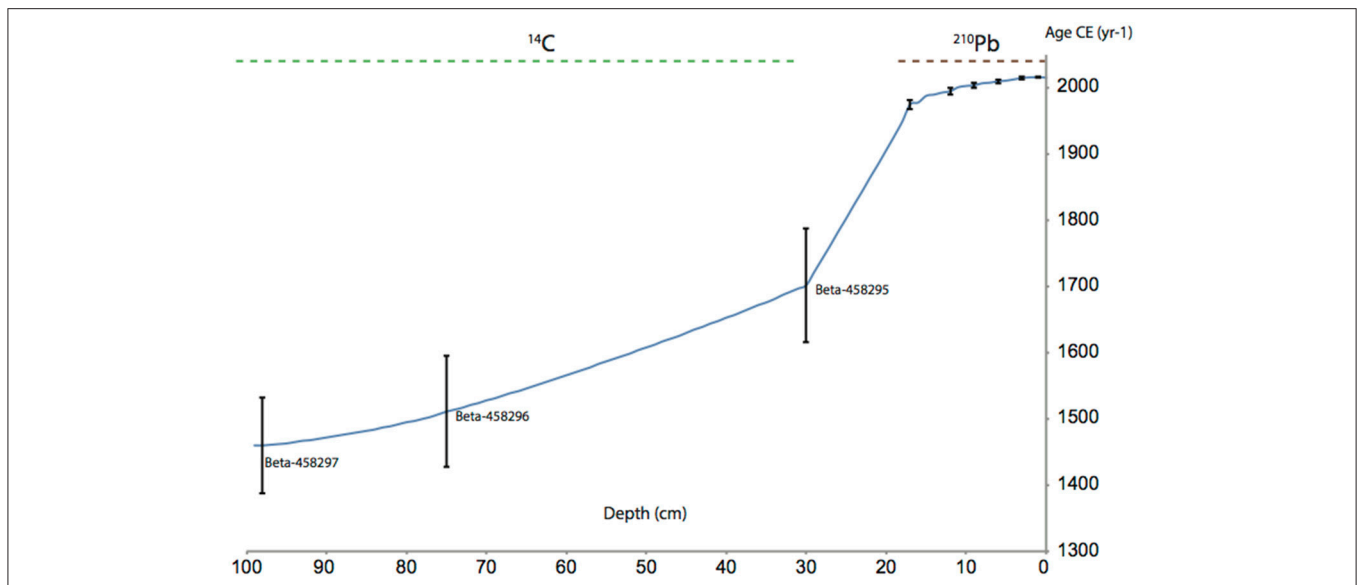
The palaeo-data suggest that both *Eichhornia* and *Egeria* have been present in Fúquene Lake well before the proposed date of introduction in the 1950s and 1990, respectively (Figures 5, 6). Our data suggest that *Egeria* colonized the



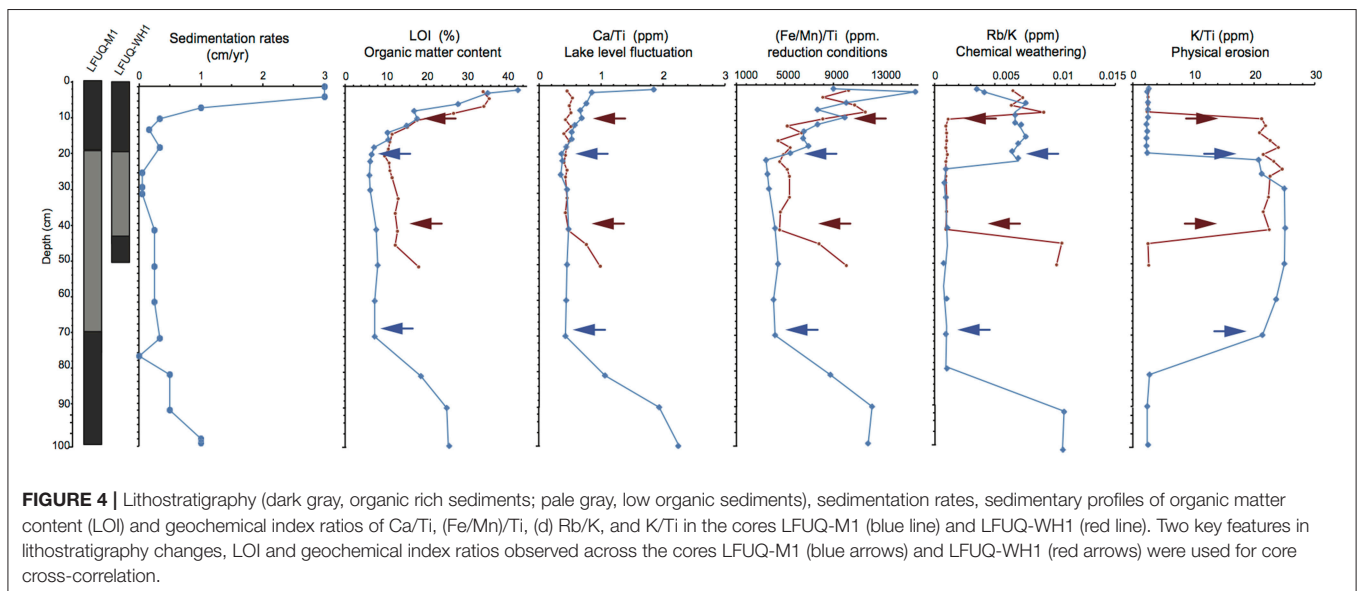


lake around the early 1900s, while *Eichhornia* appeared at 1500 CE. Piecewise regression analysis on *Eichhornia* temporal variation showed two phases of spread explaining 86.4% of the adjusted variation ( $_{adj}R^2$ ) with a highly significant ( $P < 0.0001$ ) breaking point at  $9.2 \pm 0.6$  cm, which corresponds to 1995–2000 (Figure 8). Accordingly, the

Davies test revealed a highly significant ( $P < 0.0001$ ) change in slopes at 11.5 cm (1995) characterized by large increases in fossil abundances that almost doubled the historical values (Figure 8). These patterns are highly consistent with the historical records of *Eichhornia* spread in the lake (Figure 1; Table 1).



**FIGURE 3** | Chronology of the dated depth profiles of core LFUQ-M1. Dates and ages and standard deviations are presented according to our combined age model using  $^{210}\text{Pb}$  radiometric analysis and  $^{14}\text{C}$  AMS analysis on plant macrofossil material (seeds and leaves). The  $^{14}\text{C}$  AMS publication codes are presented for each of the analyzed samples (31–32 cm; 75–67 cm; 98–99 cm).



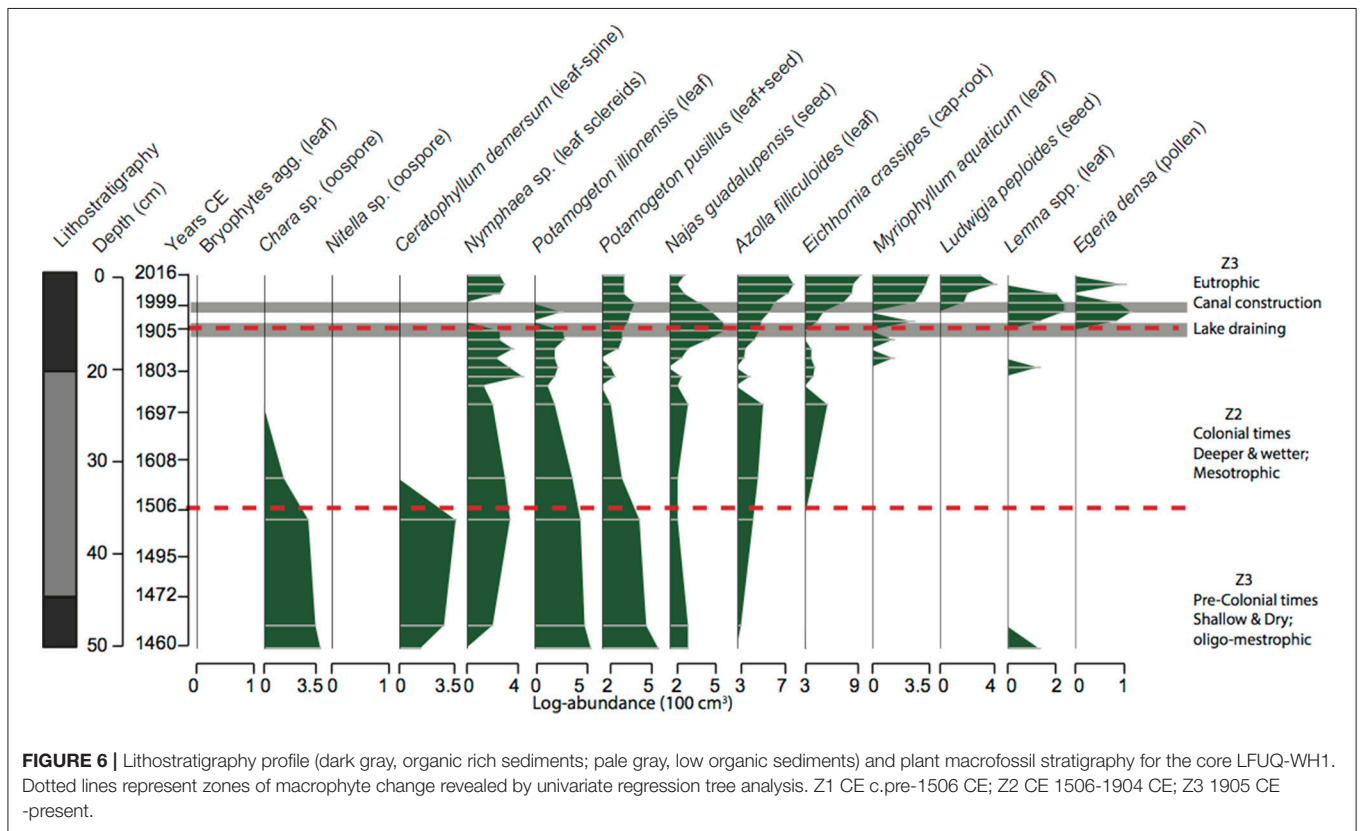
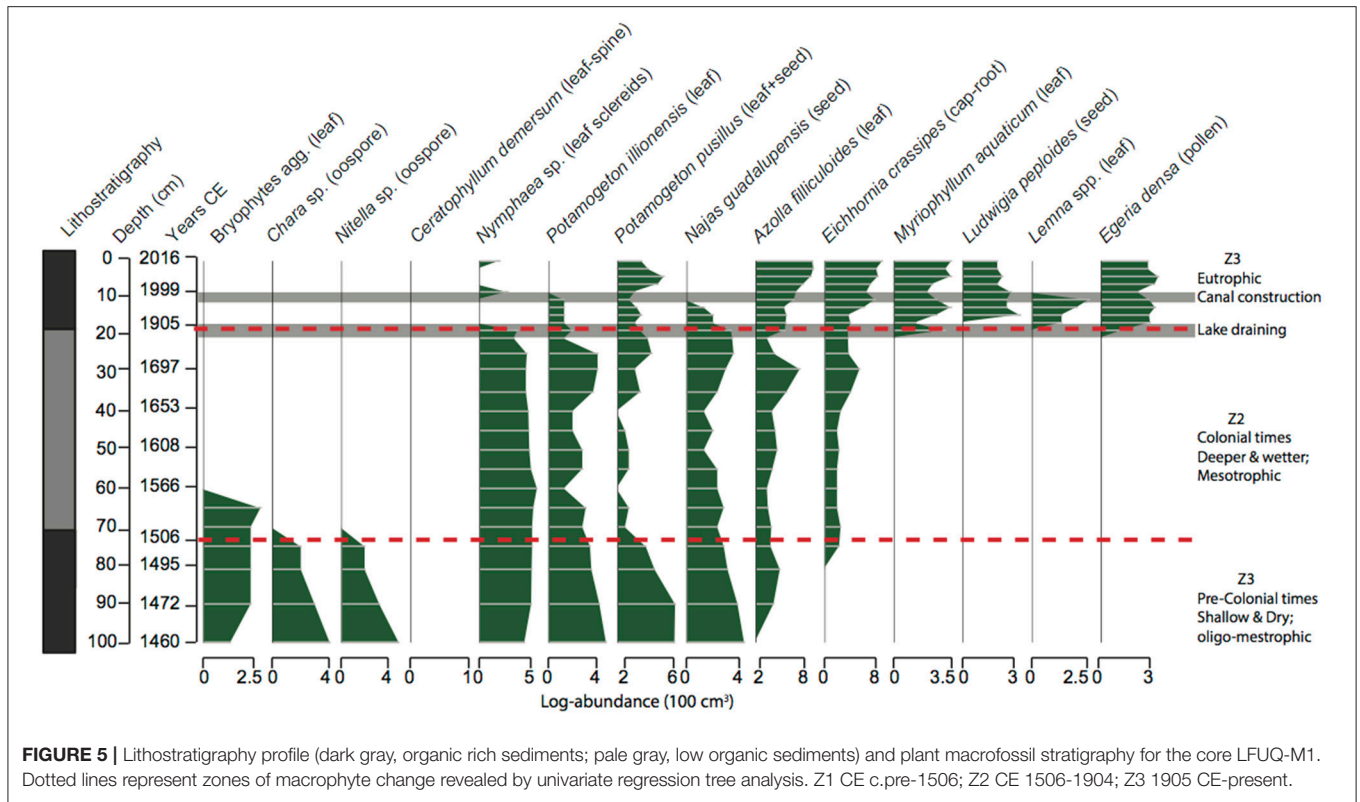
**FIGURE 4** | Lithostratigraphy (dark gray, organic rich sediments; pale gray, low organic sediments), sedimentation rates, sedimentary profiles of organic matter content (LOI) and geochemical index ratios of Ca/Ti, (Fe/Mn)/Ti, (d) Rb/K, and K/Ti in the cores LFUQ-M1 (blue line) and LFUQ-WH1 (red line). Two key features in lithostratigraphy changes, LOI and geochemical index ratios observed across the cores LFUQ-M1 (blue arrows) and LFUQ-WH1 (red arrows) were used for core cross-correlation.

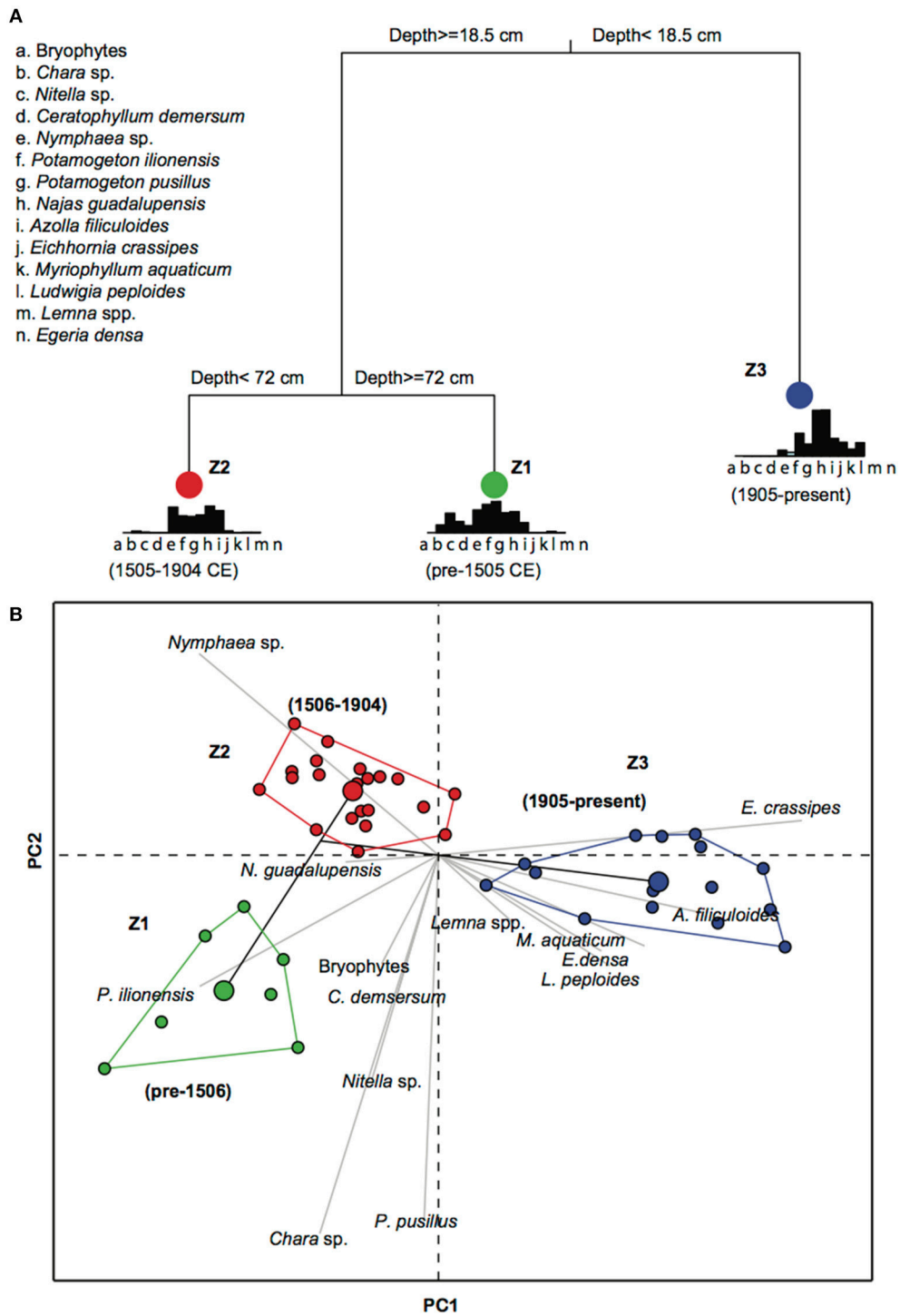
## DISCUSSION

### Long-Term Changes in the Lake Catchment and Macrophyte Assemblages

Our combined biological and geochemical palaeolimnological approach showed that over the last *c.*600 years macrophyte community dynamics in Fúquene Lake have gradually changed in response to long-term natural and human induced variations in lake catchment dynamics, hydrological modifications (lake size), reductions in water quality and the invasion of macrophyte species. For instance, the high Ca/Ti ratio suggests

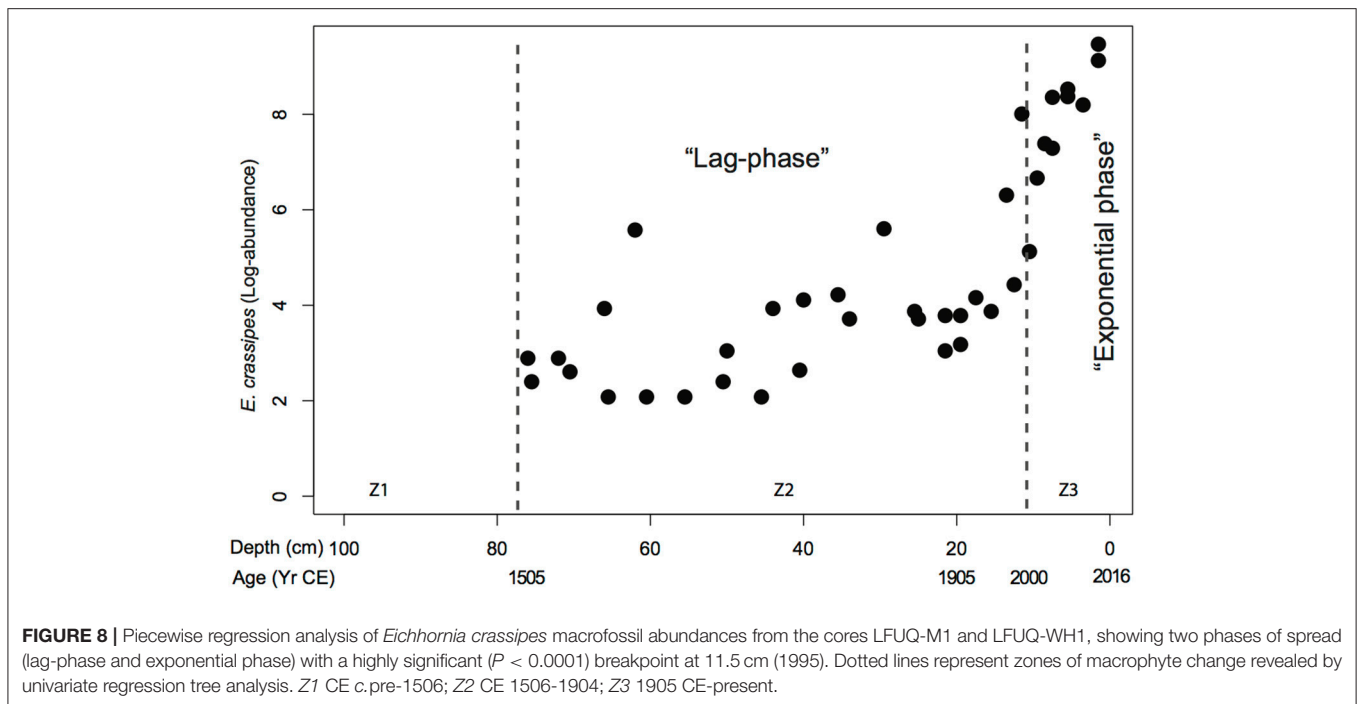
that pre-1500 climatic conditions were dry and the mean lake water balance was negative (Haberzettl et al., 2009). Shallower lake conditions would stimulate lake productivity (high LOI) and associated reductive conditions in the lake sediments (high [Fe/Mn]/Ti ratio). Chemical weathering (high Rb/K) from exposed catchment soils would have been more intense (Davies et al., 2015). The occurrence of sensitive macrophyte species such as charophytes (*Chara* sp. and *Nitella* sp.), bryophytes (agg.), and *P. illinoensis* further suggests oligo-mesotrophic conditions at the time (Kolada et al., 2014).





**FIGURE 7 | (A)** Example of one of the 10 univariate regression tree analyses showing the main zones of plant macrofossil variation recorded in the cores LFUQ-WH1 and LFUQ-M1; **(B)** Principal component analysis (PCA) showing plant macrofossil associations at the three temporal zones denoted by regression tree analysis. Green, Z1 CE c.pre-1506 BD; red, Z2 CE 1506-1904; blue, Z2 1905 CE-present. Color dots within each group represent the plant macrofossil sampling intervals in both cores. The larger color dot within each group represents the group centroid value.





Variations in the geochemical composition after 1500 CE suggest an environmental shift toward a wetter climate and lake expansion (low Ca/Ti; Haberzettl et al., 2009). This climatic pattern was described by Bird et al. (2018) in a nearby neotropical Andean lake (Ubaque Lake, Colombia). As indicated by the high K/Ti ratio (Figure 4), physical erosion may also have increased during this time period in response to larger river inputs and human activities in the catchment area (Arnaud et al., 2012). Macrophyte compositional shifts at this time suggest incipient signs of nutrient-enrichment and/or reductions in water transparency with the disappearance of charophytes and bryophytes from the fossil record. These two macrophytes are commonly associated with low-nutrient, clear waters and decrease as more nutrient-enriched and turbid waters develop (Poikane et al., 2014; Ecke, 2018). Although archaeological and paleoecological records from the lake catchment area have shown that humans occupied and modified the landscape for agriculture well before 1500 CE (Van Geel and Van der Hammen, 1973; Langebaek, 1995) it is likely that this change of lake water quality is linked to major shifts in agriculture and increases in population densities after the Spanish conquest at 1500 CE (Langebaek, 1995). The inferred wetter conditions during this colonial time period, together with technological changes in agricultural (large numbers of grazing livestock) and mining practices initiated by European arrival (Etter et al., 2008) would have resulted in greater sediment and nutrient runoff into the lake. Compositional shifts in lake biota associated with the onset of European settlement have been similarly reported across subtropical lakes (e.g., Bickford et al., 2008; Reid, 2008; Reid M. A. et al., 2018).

Abundances of some existing macrophyte species (*Nymphaea* sp., *N. guadalupensis*, *P. illinoensis*, *E. crassipes*, and *A.*

*filiculoides*) initially increased after 1500 CE with the land use transformations and wetter conditions (Figures 5, 6). However, *N. guadalupensis*, *P. illinoensis* and *Nymphaea* sp. started to decline around the late 1800s. By the mid 1800's CE, agricultural areas had doubled in size (Etter et al., 2008), likely resulting in greater nutrient load into the lake. Further reductions of *N. guadalupensis*, *P. illinoensis*, and *Nymphaea* sp. after the early 1900s CE coincides with the lake drainage schemes (as supported by the increases in Ca/Ti and [Fe/Mn]/Ti ratios) which aimed to further expand grazing land (Figure 1; Franco et al., 2011). Such hydrological alteration would have resulted initially in turbid waters coupled with heavier nutrient loads (Table 1), which are unfavorable for *N. guadalupensis*, *P. illinoensis*, and *Nymphaea* sp. (Wentz and Stuckey, 1971; Skubinna et al., 1995; Egertson et al., 2004). In particular, *N. guadalupensis*, and *P. illinoensis* have been reported to expand under mesotrophic conditions (Wentz and Stuckey, 1971; Egertson et al., 2004), and to be extirpated as turbidity and/or nutrient-enrichment progresses up to eutrophic levels (Skubinna et al., 1995; Brush and Hilgartner, 2000; Egertson et al., 2004).

The marked expansion of *Eichhornia*, *Azolla* and other associated taxa were most likely the result of significant increases in nutrients (0.41 mg/L by 2010) and further shifts in lake hydrology (Table 1; Figure 4). The eutrophic conditions coupled with the implementation of the surrounding water canal would have created ideal conditions for floating plants to thrive, in particular *Eichhornia* and *Azolla* (Scheffer et al., 2003; Villamagna and Murphy, 2010). The high capacity of *E. densa* to obtain nutrients from both the sediments and the water column, and to grow under low light conditions (Barko and Smart, 1981; Yarrow et al., 2009) may have facilitated its spread. Population

growth, along with the deliberate introduction of new *Egeria* plant propagules in 1990, would have helped to out-compete the already declining populations of *N. guadalupensis* and *P. illinoensis*.

## Long-Term Dynamics of Invasive Macrophytes Spread

Contrary to previous suppositions, our data from two cores showed that *E. densa* and *E. crassipes* have been present in Fúquene Lake well before the suggested dates of introduction (Figures 5, 6). According to herbarium collections, *E. densa* has been present in the Colombian Eastern Andean Cordillera since at least the mid-1950s (Schmidt-Mumm, 1996) and Fúquene Lake technical reports suggested its presence since 1986 (JICA-Agencia de Cooperación Internacional Del Japón, 1999). Although the origin of *E. crassipes* is probably Brazilian Amazonia (Barrett and Forno, 1982), the species spread north, and had colonized many countries of Central America and the Caribbean by the end of the nineteenth century (Barrett and Forno, 1982). It is therefore probable that these two species occurred in Fúquene well before current assumptions but given its low abundances they might have been overlooked (Pyšek and Hulme, 2005).

Our data showed that both *Eichhornia* and *Egeria* demonstrated classic invasion behavior (*sensu* Blackburn et al., 2011): they had already crossed an environmental barrier to spread, they showed a distinct lag-phase before the 1990s CE (low abundances) and grew exponentially to high levels after the 1980s (Figure 8). This bi-phasic temporal behavior shows that during moderate nutrient conditions (pre-1930s), both invasive species coexisted with native aquatic plants, but when conditions became eutrophic they thrived. *Eichhornia* occurs as a free-floating or, to a lesser extent, as a submerged or emergent plant (Gopal, 1987). Thus, it can endure extreme habitat disturbances such as those observed in Fúquene Lake (Gopal, 1987). The lake surface area reduction during the 1930s may have resulted in large, exposed, littoral areas and shallower waters (as suggested by the high Ca/Ti and Rb/K ratios) with stable daily and seasonal average water temperatures, all of which have shown to stimulate seed germination and plant growth (Wilson et al., 2005; Albano Pérez et al., 2011). Ultimately, the more steady hydrological conditions and the heavy nutrient load derived from the surrounding canal constructed the mid 1980s would have stimulated *Eichhornia* proliferation to the current dominant levels (Figure 1; Reddy and DeBusk, 1984; Villamagna and Murphy, 2010). Thus the loss of resident macrophyte species may not be fully accounted for by the spread of invasive *Eichhornia* and *Egeria* but through habitat degradation that decreased the competitive capacities of resident species such as *Nymphaea* sp., *N. guadalupensis* and *P. illinoensis* whilst simultaneously assisting the spread of two invasive macrophytes (MacDougall and Turkington, 2005). The gradual increases in (Fe/Mn)/Ti since the mid-1900s along with the contemporary monitoring data indicate that, once fully dominant, these two invasive species along with *Azolla* may have been exerting secondary effects on the remaining biota via reductions in DO,

intensification of light limitation in the case of *Eichhornia* and *Azolla* (Table 2; Albright et al., 2004; Villamagna and Murphy, 2010) and via competitive exclusion in the case of *Egeria* (Yarrow et al., 2009).

We are aware that the use of paleolimnological data to infer past communities has limitations. Due to preservation and a strong likelihood of missing rare or distantly-located macrophyte taxa (Zhao et al., 2006), not all species present historically will leave remains in sediment cores. Nevertheless a substantial portion of current-day macrophyte species (in this case 60%) was represented in the surface sediments of the two sediment cores (in agreement with Davidson et al., 2005; Salgado et al., 2010). Uncertainties in the chronology model, particularly for dates below the <sup>210</sup>Pb record, might have introduced some discrepancies regarding the exact dates of invasive species colonization (Figure 3; Table 2). Nonetheless, our data showed that *E. densa* and *E. crassipes* were present in Fúquene Lake well before the suggested dates of introduction when dating errors are accounted for.

## Consequences of Invasive Macrophytes

Our study suggests that once invasive species dominate, they exert positive (e.g., enhancing lake macrophyte biodiversity) and negative (e.g., reductions in DO) secondary effects on the remaining resident submerged species, and influence variability in environmental parameters across the lake. For instance, at the lake scale, the clear spatial separation between areas dominated by *Egeria* and *Eichhornia* and their unique associations with other macrophyte species and limnological variables suggest that these species are currently creating significant lake habitat heterogeneity. Such spatial patterns seem to be helping to maintain a relatively diverse macrophyte community, at least in the short-term, even under the current highly eutrophic conditions (Figure 2). These patterns in macrophyte community, environmental heterogeneity and species richness may help to increase lake resistance to nutrient enrichment (Olden et al., 2004; Salgado et al., 2018b).

*Egeria* areas had low macrophyte diversity and were highly homogenous in macrophyte composition. These patterns confirm previous studies on *Egeria* that have shown that it outcompetes other submerged macrophytes and so, dominates under stressful conditions (Roberts et al., 1999; Yarrow et al., 2009). Competitive adaptations include fast-growth rates, aggressive vegetative propagation, and a capacity to grow under low light conditions (Barko and Smart, 1981; Yarrow et al., 2009). *Egeria* is apparently a suitable plant for phytoremediation because it increases DO under the current eutrophic conditions (Table 3). As a submerged species this plant releases O<sub>2</sub> directly into the water column, thus helping increasing oxygen levels (Yarrow et al., 2009). Higher secchi depths across dense stands of *Egeria* relative to the other transects, also supports the idea that stands of this species help to decrease water movement, reduces sediment resuspension and improves water transparency (Yarrow et al., 2009). *Egeria* forms denser and more spatially extensive plant stands than the struggling native submerged *N. guadalupensis*, and *P. illinoensis*, (Yarrow et al., 2009). Therefore, its dominance may be providing greater habitat opportunities

to associated faunal organisms (e.g., fish and invertebrates) that depend on macrophytes for food or as a substrate.

As documented elsewhere (Villamagna and Murphy, 2010), we found low levels of DO and reduced water clarity across *Eichhornia* areas. Unlike *Egeria*, the dense floating mats of *Eichhornia* releases oxygen into the atmosphere while preventing light reaching the water column (Villamagna and Murphy, 2010). Thus, anoxic conditions and light limitation beneath the floating mats constrain the survival of phytoplankton and submerged macrophytes such as *N. guadalupensis* and *P. illinoensis* which are poorly adapted to low light conditions (Davis et al., 1985; Brush and Hilgartner, 2000; Egertson et al., 2004). *Eichhornia* areas appear to be macrophyte rich (Figure 2). The floating mats create ideal island-like conditions for other emergent plant species, in this case *B. laevis*, *L. peploides*, *S. californicus*, and *T. angustifolia*, to grow (Gopal, 1987); These free-floating mats also create a series of temporary open water inlets and semi-enclosed basins with low wave exposure offering temporal refugia for other floating-plants such as *A. filiculoides*, *H. ranunculoides*, *L. laevigatum*, and also submerged species like *M. aquaticum*, *E. densa*, *P. pusillus* and, *U. gibba* (Figure 2).

## Eutrophication and Floating-Plant Dominance?

Studies on the effects of eutrophication on neotropical/subtropical lake macrophytes suggest that nutrient enrichment reduces the resilience of the system against a shift to a state dominated by floating plants (Scheffer et al., 2003). In accordance, *Eichhornia*, *L. laevigatum*, *L. peploides*, and *Azolla* currently cover large areas of Lake Fúquene. Our data do not suggest a sudden tipping point toward a shift in floating plant dominance. Instead, we see gradual transitions in composition through time (Figures 5, 6) where, despite large nutrient load and associated increases in turbidity, the extensive floating-plant mats still co-exist with dense stands of submerged plants (Figure 2). Co-existence of floating and submerged plant species is largely due to the recent spread of *Egeria*, highlighting that alternative regime shifts to a floating-plant dominated state may not fully depend on nutrient availability but also on the competitive ability of submerged species to endure the light-limited conditions imposed by eutrophication. The transition between submerged and floating macrophytes over time provides support for the growing recognition that in some natural shallow lakes, macrophyte communities may not change abruptly between ecological regime shifts (Scheffer et al., 2003) but gradually over long-term scales in response to eutrophication (Sayer et al., 2010).

## Study Implications

To date, there are few studies addressing the full extent of abiotic and biotic changes that may occur in response to the spread of invasive macrophyte species in neotropical lakes (Villamagna and Murphy, 2010; Rejmánková et al., 2018). Even less is known of the ecological conditions prior to invasion and the long-term dynamics of spread linked to other co-occurring stressors such as eutrophication (Strayer et al., 2006). Our results suggest that equating macrophyte biodiversity loss

with the spread of invasive macrophytes in degraded lakes could be misleading. Instead, we found that habitat degradation is a major driving force of biodiversity loss and invasive species spread. However, once invasive macrophyte species dominate, they may exert both synergistic and antagonistic secondary effects on plant biodiversity by modifying habitat structure (e.g., shading and anoxic conditions), by excluding remaining resident species through direct resource competition (e.g., *Egeria*) and/or by exerting habitat heterogeneity across the lake.

## Management Options

Our data show that Fúquene Lake is in a delicate hybrid ecosystem state (*sensu* Hobbs et al., 2009), where, despite the depletion of most native submerged species, the lake still retains some historically characteristic species like *E. crassipes*, *A. filiculoides*, and *P. pusillus* (Figures 5, 6). The current dominance and function of *Eichhornia* and *Azolla* lies outside its historic range of variability and is working synergistically with eutrophication. Furthermore, *Eichhornia*, *Azolla* and *Egeria* are extremely difficult to eradicate once they dominate, and any further nutrient inputs will encourage their spread across the lake. Thus, restoring the lake to a state closer to its historical conditions is likely impossible and/or economically impractical (Hobbs et al., 2009). We therefore suggest focusing management objectives on reducing nutrient inputs and further controlling the spread of the two invasives along with *Azolla* to enhance open water areas that may potentially allow the currently threatened historical submerged macrophytes *N. guadalupensis* and *P. illinoensis* to re-grow. Addressing the way the surrounding canal is currently managed and restoring the lateral and longitudinal hydrological connectivity are likely key to accomplishing these conservation goals.

## AUTHOR CONTRIBUTIONS

This study is the direct work of a postdoctoral study by JS, which was supervised by CG-A. JS designed the study and collected the contemporary and paleo data in collaboration with LC-T, JV-I, LB-G, CG-A, NM-M, and LL-C performed pollen laboratory paleoecological analysis. JS analyzed the plant macrofossil data and LC-T, JV-I, LB-G analyzed the LOI and XRF data. JS wrote the first manuscript and all other authors contributed essentially to the interpretation and wording of the final version. The study was made in collaboration with MV at the University of Regina, and she also contributed substantially to the interpretation and wording of the manuscript.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2019.00140/full#supplementary-material>

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