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Authors
Rejmánková, Eliška
Sullivan, Benjamin W
Aldana, José R Ortiz
et al.

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ORIGINAL ARTICLE

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Regime shift in the littoral ecosystem of volcanic Lake Atitlán in Central America: combined role of stochastic event and invasive plant species

Eliška Rejmánková[1] | **Benjamin W. Sullivan[2]** | **José R. Ortiz Aldana[3]** | **Jenise M. Snyder[4]** | **Stephanie T. Castle[1]** | **Fátima Reyes Morales[5]**

[1]Department of Environmental Science and Policy, University of California Davis, Davis, California

[2]Department of Natural Resources and Environmental Science & The Global Water Center, University of Nevada Reno, Reno, Nevada

[3]Centro de Estudios del Mar y Acuicultura, Universidad de San Carlos, Guatemala City, Guatemala

[4]Department of Biology, Ursuline College, Pepper Pike, Ohio

[5]Departamento de Investigación y Calidad Ambiental, AMSCLAE, Panajachel, Guatemala

Correspondence
Eliška Rejmánková, Department of Environmental Science and Policy, University of California Davis, Davis, CA.
Email: erejmankova@ucdavis.edu

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Abstract

1. Different functional groups of macrophytes vary in their impact on aquatic ecosystem structure and processes. The introduction of new species with different growth form, combined with a stochastic event, may have serious and irreversible consequences on lake functioning.
2. Our goals were to document and explain physical, chemical, metabolic and biotic changes in the littoral zones of a volcanic lake before and following two coinciding events: invasion by a submersed macrophyte, *Hydrilla verticillata* (Hydrocharitaceae), followed by a rapid increase in the lake water level (>2.5 m). We recorded plant biomass, plant tissue C:N:P stoichiometry, macroinvertebrates, water characteristics data along transects through littoral zones, and measured gas emission in controlled mesocosms and in the lake.
3. The native emergent species, *Schoenoplectus californicus* (Cyperaceae), was generally not able to survive such a rapid water level increase, and *Hydrilla* spread and formed dense mats further preventing *Schoenoplectus* regeneration. The impact of another introduced species, the free-floating *Eichhornia crassipes* (Pontederiaceae), was more localised, despite its much longer presence at the lake.
4. Although the three species had comparable standing biomass, the two invader species had lower C:N:P ratios than *Schoenoplectus*, resulting in faster decomposition rates and indicating potential shifts in nutrient cycling within the ecosystem. The oxygen profile of the water column was altered by the non-native species in a significantly different manner: in *Eichhornia*, the saturation concentrations dropped down to 30%–50% of dissolved oxygen, while oxygen supersaturation was recorded in *Hydrilla*.
5. Both *Schoenoplectus* and *Eichhornia* patches exhibited comparable carbon dioxide (CO_2) fluxes, sequestering 230 and 300 mg CO_2 m^{-2} hr^{-1}, respectively, during the day and emitting 250 and 200 mg CO_2 m^{-2} hr^{-1}, respectively, during the night. Contrary to these two species, *Hydrilla* patches sequestered CO_2 during the day (34 mg CO_2 m^{-2} hr^{-1}) and night (44 mg CO_2 m^{-2} hr^{-1}).
6. The invasive species maintained a richer community of macroinvertebrates compared to several native species (excluding *Schoenoplectus*), both in taxa diversity and in numbers of individuals.

7. When the results are considered in the regional context, an increase in nutrient supply could lead to the dominance of free-floating plants. We discussed management options more broadly considering the negative impacts of introduced species balanced against their beneficial effects, in the context of environmental changes.

KEYWORDS
CO_2 fluxes, invasive macrophyte, littoral ecosystem processes, tropical lake

1 | INTRODUCTION

To improve our ability to predict and manage macrophyte invasions in freshwater ecosystems, it is necessary to better understand the impacts of macrophyte invasions on these systems (Kuehne, Olden, & Rubenson, 2016). Plant invasions in aquatic ecosystems have received less attention than their terrestrial counterparts (Thomaz, Kovalenko, Havel, & Kats, 2015). In addition, studies focusing on invasion biology of aquatic plants in tropical fresh waters are limited, especially in the Neotropics (Thomaz, Mormul, & Michelan, 2015). This makes the assessment of the causes and consequences of invasions urgently needed for these regions. Central American lakes, specifically volcanic lakes located in the Central American Volcanic Arc, have been largely unexplored by invasion biologists and the information on the impact of invasions on this type of ecosystem is limited. Here, we report on the physical, chemical and biotic changes following macrophyte invasions of the volcanic Lake Atitlan in Guatemala and discuss the results in the context of other volcanic lakes of the region.

Widely documented patterns and processes of invasions in temperate lakes are not necessarily directly transferable to predict dynamics and outcomes of invasions in tropical lakes. The different pelagic processes between temperate and tropical lakes were summarised by Sarmento (2012): generally, tropical lakes are (1) more efficient in phytoplankton primary production on a given nutrient base than temperate lakes, (2) more often nitrogen rather than phosphorus limited and (3) typified by strong non-seasonal variation superimposed on a weaker seasonal cycle (see also Abell, Özkundakci, Hamilton, & Jones, 2012; Catalan & Donato Rondón, 2016; Downing et al., 1999; Lewis, 2010). Although these authors do not explicitly discuss macrophytes, there are reasons to assume that the impact of invasive macrophytes on ecosystem processes would differ between temperate and tropical lakes. Based on weak seasonality and stable temperatures in tropical lakes, we can expect sustained productivity of macrophytes and rapid mineralisation of organic matter (Catalan & Donato Rondón, 2016), which can potentially promote the growth of invaders. Additionally, the dynamics of macrophyte invasions in tropical ecosystems will be further impacted due to human population and economic growth; any adverse effects will likely be exacerbated by climate change (Thomaz et al., 2015). Therefore, the effects of macrophyte invasion in tropical lakes should not be extrapolated from research in temperate lakes.

The abundance of macrophytes in lakes depends on geomorphology, nutrient status and biotic interactions (Gasith & Hoyer, 1998). The relative importance of macrophyte invasion for lake processes is expected to be directly proportional to macrophyte abundance, but inversely proportional to lake size and depth. In shallow lakes, macrophytes often exert a major impact on productivity, biogeochemical cycles, food webs and habitat availability (Carpenter & Lodge, 1986; Hempel, Grossart, & Gross, 2009; Sachse et al., 2014). Therefore, the structure and function of macrophytes have been studied in much more detail in shallow lakes as compared to deep lakes. In deep lakes, macrophytes are typically restricted to shallow bays due to depth limitation and high wave energy. Despite their limited distribution, changes in littoral macrophyte abundance and composition may have wide-reaching impacts, potentially influencing transparency and the trophic state of the whole lake (Hilt, Henschke, Rücker, & Nixdorf, 2010).

The structural and functional roles of macrophytes in lakes can be combined into three categories (Gasith & Hoyer, 1998): (1) physical and chemical, relating to conditions in water and sediment; (2) metabolic, including organic matter production, nutrient cycling and sequestration/emission of gases; and (3) biotic, representing structured habitat for epiphytes and food for grazers. Different functional groups of macrophytes, that is emergent, submersed, floating-leaved and freely floating (Rejmánková, 2011), as well as their density and seasonality, will differentially impact processes in the aforementioned categories (Caraco, Cole, Findlay, & Wigand, 2006). Thus, the impact of invasive species displacing native species is expected to be greater if it represents the replacement of one life form and functional role with another (Kato, Nishihiro, & Yoshida, 2016).

Invasive macrophytes can change the structure, composition and function of freshwater ecosystems in numerous ways. Invasive macrophytes are typically faster growing and produce more biomass than native species (Herb & Stefan, 2006; Kennedy, Horth, & Carr, 2009). Macrophyte productivity impacts carbon (C) budgets of freshwater lakes directly via photosynthesis and autotrophic respiration and indirectly due to the degradation of plant litter (Carmichael, Bernhardt, Brauer, & Smith, 2014; Grasset, Abril, Guillard, Delolme, & Bornette, 2016). Therefore, significant changes in life forms of primary producers, such as those resulting from plant invasions, have the potential to change the net C flux of a lake (Attermeyer et al., 2016). Large differences in nutrient recycling among different functional groups of macrophytes can result in substantial changes in water and sediment chemistry. Macrophyte invasion can also impact higher trophic levels, as the abundance, species composition and temporal variation of aquatic vegetation are the main determinants of the composition and abundance of macroinvertebrates (Kornijów, 1989; Lodge, 1985; Rooke, 1986). Invasion-induced changes of the structure of macroinvertebrate communities could result in changing diet of fish and aquatic birds (Masifwa, Twongo, & Denny, 2001). Changes in macrophyte composition/abundance impact also the epiphytic communities (biofilms) composed of algae, cyanobacteria and heterotrophic bacteria and their role in the ecosystems (Carpenter & Lodge, 1986; Cronin, Lewis, & Schiehser, 2006).

Although numerous studies document the negative effects of invasive aquatic macrophytes, many authors argue that their potential benefits are generally underreported (Hulme et al., 2013; Hussner et al., 2017). In assessments of the socioeconomic and environmental impact of these plants (Bonanno, 2016; Havel, Kovalenko, Thomaz, Amalfitano, & Kats, 2015), it is necessary to consider not just the negative impacts, but also the positive impacts of invasive macrophytes for developing conservation, management and policy strategies (Chapman, 2016; Sax et al., 2007).

The goals of this study are to document and explain changes in littoral zones of Central American volcanic lakes following invasion by floating-leaved and submersed macrophytes, *Eichhornia crassipes* and *Hydrilla verticillata*, specifically the impact of invasions on native species, *Schoenoplectus californicus*. We combine detailed observations and experiments from Lake Atitlan, Guatemala, with available information from other lakes to examine the hypothesis that a stochastic event caused species replacement and led to change in ecosystem functioning of the lake littoral zone. We evaluate the invasion impact in terms of (1) change in macrophyte diversity, (2) biomass production and nutrient cycling, (3) impact on physical and chemical properties of water, (4) carbon sequestration/emission and (5) habitat quality for macroinvertebrates.

Although we focus on a single tropical volcanic lake, our results may apply to other tropical mountain lakes because the proximate causes of macrophyte invasion (namely eutrophication, spread of invasive species and climate change) are common throughout the region (Thomaz et al., 2015). An understanding of how littoral ecosystems respond to and cope with these changes helps to better predict future developments and suggest management options, including utilisation of beneficial functions of introduced species.

2 | METHODS

2.1 | Study location

Lake Atitlán is one of numerous volcanic lakes located in the Central American Volcanic Arc in the highlands of western Guatemala. It was formed about 84,000 years BP in a steep-sided collapsed caldera (altitude 1,555 m, maximum depth 341 m, mean depth 183 m, surface area 137 km^2, volume 24 km^3; Newhall et al., 1987). The region has two main seasons: dry (November–April) and wet (May–October); the wet season accounts for the majority of 1,500–2,000 mm annual precipitation. Lake bottom water temperatures remain at 19.5–20.0°C throughout the year, and surface water temperature fluctuates between 21 and 25°C (Rejmánková, Komárek, Dix, Komárková, & Giron, 2011). Atitlán is a hardwater lake with an average alkalinity of 3.4 mEq/L. It is nitrogen-limited and has transitioned from oligotrophic to mesotrophic during the last decade, decreasing in transparency from an average Secchi depth of 11 m in the 1970s to 6 m (Corman et al., 2015).

The first indigenous communities are thought to have settled the area at least 3,500 BP. Until about 30 years ago, low population density with low-impact sustainable agriculture prevailed in the catchment. Over the last several decades, the population has grown rapidly, and fertiliser use and logging have intensified. At present, the land cover of the lake's catchment is roughly 46% forest, both primary and secondary, and 32% agriculture. The agricultural crops include largely corn and beans, as well as market crops such as onion, potato and coffee, which are often cultivated on steep, erodible slopes. The remainder of land is urban and supports about 250,000 people, five times the basin's population size of the 1960s (LaBastille, 1974). Rapid development increased agricultural runoff and erosion, as well as inflow of untreated wastewater from nearshore municipalities. The lake undergoes annual water-level fluctuations of about 1 m, but it can be considerably higher during extreme rainfall events or seismic activity (LaBastille, 1974; Newhall et al., 1987). Such events occurred in 2010–2012 and resulted in water-level increase of over 2.5 m.

Other tropical lakes have undergone similar changes. The patterns of macrophyte invasion into Lake Atitlan may be relevant to other Central American mountain volcanic lakes; these lakes are briefly characterised in Table S1.

2.2 | Littoral of Lake Atitlán and lake macrophytes

Based on the hypsographic curve of the lake, the littoral zone (water depth of ≤10 m with vascular plants present) covers only about 4.8 km^2, which is <4% of the total lake area (Reyes Morales, Ujpan, & Valiente, 2018). Water quality differences among the littoral and pelagic zones are in Table 1. Historically, these zones were dominated by bulrush, *Schoenoplectus californicus*, and in deeper areas by a diverse group of submersed macrophytes (e.g. *Potamogeton illinoensis*, *Ceratophyllum demersum*, *Chara* spp.). First reports on macrophytes in Lake Atitlan came from Juday's limnological studies (1915), and more recently, species lists for the lake have been reported by Iturbide (2001), Ríos Palencia (2007), Dix, Fortin, and Medinilla (2003) and Rejmánková (see Table S2). Over the last several decades, large areas of the shallow bays have often been covered by the invasive water hyacinth, *Eichhornia crassipes*. During the last decade, the composition of the macrophyte flora has changed quite dramatically due to the introduction of *Hydrilla verticillata*. A massive development of green algae (mostly *Cladophora*) and a dense periphyton of dominant diatoms (genera *Cymbella*, *Gomphoneis*, *Epithemia*, *Nitzschia*) on stems and leaves of littoral vegetation occur commonly at sites near numerous inflows of sewage water. Details on the three species which are the focus of this study are as follows:

Schoenoplectus californicus is a native emergent macrophyte. It is a robust, perennial, rhizomatous wetland sedge about 3 m tall, but occasionally reaches over 7 m in height. The optimum water depth ranges from 0.5 to 2 m. This widely distributed plant frequently forms monospecific stands (Carpenter, 2009) and can impact biogeochemical cycles by providing a source of organic material and by oxygenating the rhizosphere (Thullen, Nelson, Cade, & Sartoris, 2008). At Lake Atitlán, as in many other regions, it plays an important role in the human economy, providing raw materials for the construction of all-purpose mats and handicrafts. This species utilises heterotrophically fixed N by its rhizosphere associated diazotrophs (Rejmánková et al., 2018). At Lake Atitlán, *S. californicus* has historically provided a critical habitat for a now extinct grebe, *Podilymbus gigas* (LaBastille, 1974), as well as crabs, snails and many species of fish.

Eichhornia crassipes, water hyacinth, is a floating macrophyte native to lowland tropical South America, Amazon and lower Orinoco basin (Barrett & Forno, 1982). The date of its introduction into the lake is not known, but the earliest reports of its presence were in the 1970s (LaBastille, 1974). Water hyacinth is a mat-forming, reproducing mostly vegetatively. It has a wide distribution in tropical, subtropical and warm temperate regions throughout the world (Gopal, 1987; Penfound & Earle, 1948). In waters with warm temperatures and sufficient nutrients, the plants double in number and biomass in 4–10 days (Malik, 2007). It is regarded as one of the most problematic aquatic weeds and has attracted worldwide attention due to its fast spread and congested growth, which lead to serious problems in navigation, irrigation and power generation. At Lake Atitlán, it is confined to shallow, somewhat wind-protected bays. Its spread over the whole lake surface is prevented by strong daily winds. Local communities occasionally clear the plants from the water surface to allow boat movements, but with rare exception, the plant material is not utilised. Dense root structures of water hyacinth provide an ideal habitat for diverse community of macroinvertebrates and a nursery for small fish (Barker, Hutchens, & Luken, 2014).

Hydrilla verticillata is a submersed macrophyte native to the warm regions of Asia. It was first introduced in Guatemala to Lake Izabal in the late 1990s, and around 2002, it spread to Lake Atitlán (Barrientos & Allen, 2008; Castellanos & Dix, 2009; Haller, 2002). A wide ecological amplitude, resistance organs, fast growth rates and high dispersion ability provide *Hydrilla* with great potential to invade a variety of habitats, often resulting in important physical, chemical and biotic effects on the environment (Gu, 2006; Sousa, 2011). Due to a low light compensation point, *Hydrilla* can grow at depths exceeding 10 m (Langeland, 1996). Near the water surface, it branches profusely and forms a dense canopy intercepting light to the exclusion of other submersed plants (Langeland, 1996). *Hydrilla* is photosynthetically efficient and may utilise bicarbonate as a carbon source, if the lake pH and carbonate concentrations are high. During the night, *Hydrilla* plants can also switch to C4-like carbon metabolism, fixing carbon into malate and aspartate (Holaday & Bowes, 1980; Rao, Fukayama, Reiskind, Miyao, & Bowes, 2006). Similar to water hyacinth, it is a noxious aquatic invader. In addition to outcompeting native plants, it interferes with drainage, irrigation, navigation and recreation. Hydrilla provides habitat for diverse macroinvertebrates and fish and food for aquatic birds and can enhance water transparency by reducing sediment suspension and competing for nutrients with phytoplankton (Bradshaw, Allen, & Netherland, 2015; Canfield, Langeland, Linda, & Haller, 1983; Posey, Wigand, & Stevenson, 1993). The dense foliage near the water surface also often supports diverse periphyton (Shabana & Charudattan, 1996).

2.3 | Macrophyte sampling

In September 2015 (wet season), May 2016 (dry season) and July 2017 (wet season), we sampled littoral areas near San Juan, San Pedro, San Lucas, Santa Catarina and Isla del Silencio (see Figure 1). In addition to quantitative sampling, we also surveyed macrophyte species presence in numerous trips around the lake between 2014 and 2017 and used a simple estimate of abundance: R = rare, species only occasionally seen, never at high density; C = common, occurring frequently but with low abundance; D = dominant

TABLE 1 Water nutrients (mean ± *SD*, μg/L) at five sites in the littoral zone and their means compared to open water in the centre of the lake (Student's paired *t* test, *n* = 8); for locations, see Figure 1. Statistically significant differences indicated in bold

Location	NH_4-N	NO_3-N	SRP	TN	TP	TN/TP	Inorganic N/P	Chl a
San Lucas	7.0 ± 5.5	3.7 ± 4.2	15.2 ± 7.7	537 ± 115	81 ± 27	7.1 ± 1.8	1.0 ± 1.1	12.9 ± 9.1
San Juan	5.7 ± 5.2	5.1 ± 7.6	14.7 ± 9.5	389 ± 111	57 ± 20	7.1 ± 1.6	0.9 ± 0.8	10.9 ± 5.6
Santiago	10.3 ± 6.3	7.6 ± 5.5	6.8 ± 2.1	242 ± 78	38 ± 7	6.5 ± 2.2	2.7 ± 2.1	8.3 ± 4.1
Isla	1.4 ± 0.4	<1.0	16.1 ± 4.1	601 ± 326	106 ± 38	5.4 ± 1.2	0.2 ± 0.1	24.2 ± 15.8
Santa Catarina	12.2 ± 2.4	6.4 ± 1.2	5.1 ± 3.3	310 ± 120	43 ± 2	7.3 ± 2.6	4.3 ± 1.7	Not measured
Littoral zone average	7.0 ± 5.5	4.8 ± 5.5	12.7 ± 7.9	421 ± 179	64 ± 30	6.8 ± 1.8	1.5 ± 1.7	14.1 ± 7.0
Centre of lake	2.7 ± 3.2	2.2. ± 1.9	6.1 ± 3.7	188 ± 60	32 ± 11	7.1 ± 4.1	0.8 ± 0.4	2.3 ± 0.5
p value	**.043**	.211	**.031**	**.001**	**.005**	.771	.248	**.001**

(Table S2). To evaluate the impact of *Hydrilla verticillata* between the initial stages of invasion and present, we compared species presence and abundance in three transects of nine originally surveyed in 2006 (Ríos Palencia, 2007). The transects were located perpendicular to the shore, and species with their respective numbers of individuals were recorded in five to six 50 × 50 cm sampling quadrats spaced along each 50- to 100-m-long transect. For HV, each stem was counted as an individual. To assess the longevity of HV, we tagged 10 young individuals and checked them periodically for signs of senescence.

To assess the biomass of *Eichhornia crassipes*, we collected plants from 3 to 4 50 × 50 cm quadrats randomly placed at each location (note that *Eichhornia* was present only at San Lucas and Isla del Silencio). After sampling, the plant material was divided into leaves with petioles and roots. By contrast, *Hydrilla* was sampled in two ways: in 2015 and 2016, we sampled the upper *Hydrilla* canopy using a 30 × 30 cm quadrat frame. It included 40-cm-long metal spikes located every 5 cm that were lowered down once the frame was placed on the surface of the *Hydrilla* mat, effectively caging the cube of the *Hydrilla* mat layer that was then cut and extracted to the depth of about 30–40 cm; we did not collect leafless stems. According to Haller and Sutton (1975), about 60% of *Hydrilla* biomass occurs in the upper 40 cm of the water column. Based on this estimate, we added 40% to account for stems when expressing total *Hydrilla* biomass. Clearly, the disadvantage of this method is that it cannot be used in those stands where the canopy does not reach the surface. Therefore, in 2017, we employed the diver quadrat method recommended by Madsen and Wersal (2017) and collected total biomass of *Hydrilla* from 50 × 50 cm quadrats placed on the bottom. The 2017 sampling was made at the transect points described in the previous paragraph. In each quadrat, we counted the number of stems and divided plants into two parts: leafless stems and canopy layer; we recorded the length of each of these two layers. In three quadrats, we also collected roots. Because *Hydrilla* root biomass for all three plots was between 5% and 10% of the total biomass, we used 7.5% of total biomass as a proportion of root biomass for future estimates.

For *Schoenoplectus californicus*, we sampled non-destructively to avoid conflict with local Mayan residents because the population of *Schoenoplectus* is in decline in the lake. Structurally, *Schoenoplectus* is a simple plant, with highly reduced leaves, and consisting primarily of green photosynthesising spike-like stems. As a result, its biomass is frequently estimated based on morphometric data (Daniels, Cade, & Sartoris, 2010). We expressed biomass as a product of average number of stems x average height x specific stem weight. The average stem numbers and heights were assessed in replicated randomly placed 50 × 50 cm sampling quadrats. Specific stem weight calculated for 50 randomly collected stems ranged from 0.037 to 0.044 g dry weight/cm (mean value of 0.0405 g/cm was used for biomass assessment). The data for the relationship between water depth and *Schoenoplectus* stem density, and biomass were obtained at the lake before *Schoenoplectus* decline, during 2010 and 2012 training courses in aquatic ecology (Rejmánková, personal observation). *Schoenoplectus* stems from randomly placed quadrats in numerous patches of *Schoenoplectus* around the lake were collected, measured, dried and weighed, concomitantly with measuring water depth at each patch. To estimate the belowground biomass, we used shoot/root ratio of 0.7 that was established for a different study (Castle, 2016), which reflects a robust rhizome and root system of *Schoenoplectus*. To assess the longevity of stems of *Schoenoplectus*, we tagged 10 young stems and re-measured them periodically for 1 year. Samples of two other native species (*Ceratophyllum*

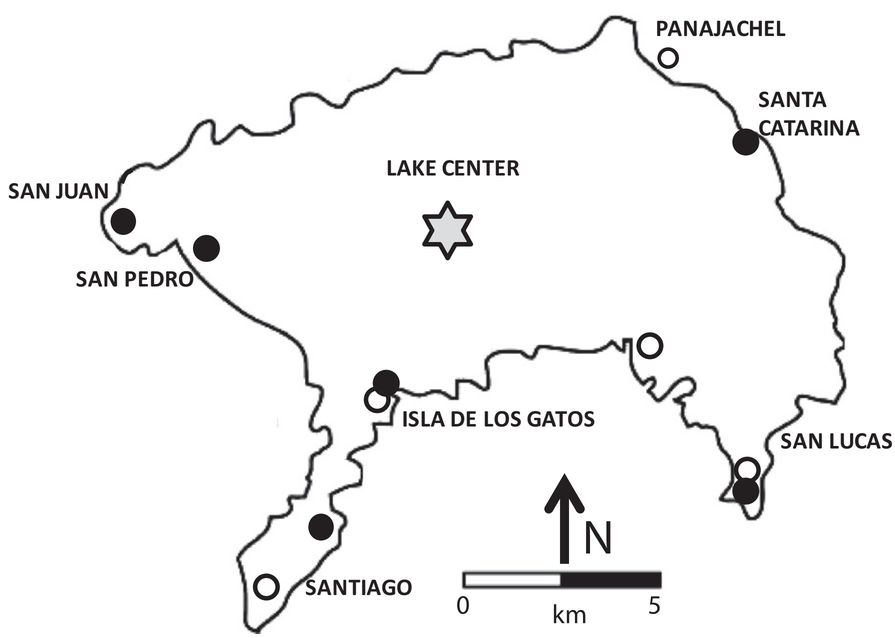

FIGURE 1 Lake Atitlán, Guatemala, with sampling locations for macrophytes (filled circles) and macroinvertebrates (open circles)

demersum, *Potamogeton illinoensis*) were collected only for tissue nutrient analysis and not quantitatively for biomass.

Plant samples were dried at 70°C to constant weight, and representative subsamples were ground for tissue carbon (C), nitrogen (N) and phosphorus (P) concentration. Total P was measured spectrophotometrically using ascorbic acid reduction in phosphomolybdate complex after combustion and consequent acid digestion (McNamara & Hill, 2000). Total C and N and their stable isotopes were measured by continuous flow isotope ratio mass spectrometry using a PDZ Europa ANCA-GSL elemental analyser interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). We used the $\delta^{13}C$ to indicate the type of photosynthesis of the macrophytes, while $\delta^{15}N$ was used as an indication of potential nitrogen fixation.

2.4 | Macroinvertebrate sampling

Macroinvertebrate diversity and abundance in monospecific stands of *Hydrilla* and *Eichhornia*, and other native macrophytes (*Ceratophyllum demersum*, *Azolla filiculoides* and *Polygonum* sp.), were assessed semi-quantitatively in May and September of 2014. We used the catch-per-unit-effort (CPUE) method (Foote & Rice Hornung, 2005). At each sampling site (see map Figure 1), a sampling effort of 1 hr/one species was performed. Approximately, the same amount of biomass of each macrophyte present was collected and washed on a white plastic tray to release the macroinvertebrates. The organisms that remained on the tray were collected and preserved in 90% ethyl alcohol (Van den Berg, Coops, Noordhuis, Van Schie, & Simons, 1997). The specimens were later identified and quantified using a stereomicroscope. The identification of the organisms was carried out to the lowest taxonomic level possible using taxonomic keys (Gutiérrez Fonseca, 2010; Menjívar Rosa, 2010; Merritt, Cummins, & Berg, 2008; Pacheco-Chaves, 2010; Sermeño Chicas, Pérez, Gutiérrez Fonseca, & Springer, 2010). Samples were not collected in *Schoenoplectus*, because its stems are extremely depauperate in macroinvertebrates. Besides occasional attached snails, no other species were found in association with *Schoenoplectus*. Macroinvertebrates found with *Schoenoplectus* are located in its rhizosphere (Lima Silveira, Gonçalves Rodrigues, de Souza, Würdig, & Luiza, 2011) and their sampling was not compatible with the methods used in this study.

2.5 | Water characteristics

Temperature, dissolved oxygen (DO), pH and specific conductivity were recorded at each sampling point at 10–20 cm below the water surface with hand-held YSI 556 m (DO sensor calibrated daily). All sites were surveyed between 9 and 11 a.m. in September 2015 and May 2016. In November 2015 and July 2017, water column profiles (0–400 cm) of the same parameters were recorded in Santa Catarina, San Lucas Bay and San Pedro. Water samples collected from the upper layer (0–20 cm) were analysed for inorganic N (NH_4-N, NO_3–N), soluble reactive P (SRP), total N and P, and chlorophyll a (Chl *a*). Water samples for NO_3–N, NH_4–N and SRP were filtered through a 0.45-μm filter within an hour after sampling and frozen until analysis. Nitrogen species and total N were analysed on a Lachat 8000 (Hach Company, Loveland, CO, USA) flow injection analyser using method # 10-107-04-1-B (cadmium column reduction), method # 10-107-06-1-F (indophenol) and a modified method # 10-115-01-4-F (persulphate digestion) for NO_3–N, NH_4–N and total N, respectively. SRP was analysed by the ascorbic acid method of Murphy and Riley (1962). Samples for Chl *a* analysis were filtered onto Whatman® GF/C glass microfiber filters (1.2 μm pore size), extracted with methanol and analysed fluorometrically for Chl *a*; acid-corrected values for Chl *a* are reported.

2.6 | Mesocosms

Twelve mesocosms were established in Santa Catarina near the lake shore in May 2015. They consisted of oval PVC tanks (Rubbermaid® Structural Foam Stock Tanks, 380 L capacity) filled with 150 L of washed pumice as an inert substrate and were irrigated with lake water. Each mesocosm was planted with young individuals of either *Schoenoplectus californicus*, *Eichhornia crassipes*, *Hydrilla verticillata* or not planted (control), each in three randomly placed replicates. Plants were allowed to grow to maturity and become well established (equivalent densities to those naturally occurring in the lake) before being used for gas exchange measurements (described below).

2.7 | CO_2 and CH_4 fluxes measurements

Gas fluxes were measured in the 12 mesocosms during daytime and night-time periods (11:00 a.m.–13:00 p.m. and 02:00 a.m.–04:00 a.m., respectively), in July and November of 2016. In addition, in July and November of 2016, we conducted daytime measurements in the lake (Santa Catarina and San Lucas) in the homogeneous stands of the respective macrophyte species and open water (each in three replicates). In both the mesocosm and the lake, we measured gas fluxes in transparent floating chambers made of PVC pipe (25 cm diameter) with floats attached to the chambers; different positioning of floats allowed for height adjustment of the chambers according to vegetation type. The chamber height was between 10 and 15 cm for *Hydrilla* and open water, 20–30 cm for *Eichhornia* and 50–60 cm for *Schoenoplectus* (note that taller shoots of *Schoenoplectus* were bent to fit in). Chamber headspace samples were collected 1, 5, 15 and 25 min after placing the chamber in the mesocosm. Headspace gas was collected with a syringe and injected into 12-ml evacuated Exetainers (Labco Limited, Lampeter, Wales, UK). Before sampling, the air inside the chambers was mixed by pumping the syringe several times while it was attached. The sampling set-up provided data on combined plant-mediated flux measurements with open water fluxes. Gas samples were analysed for CO_2 and CH_4 concentrations using a Shimadzu GC-2014 greenhouse gas analyser (Shimadzu Scientific, Kyoto, Japan). Both CO_2 and CH_4 were pre-conditioned and separated using two packed columns (1 m HayeSep T, 4 m HayeSep D). Methane eluted directly onto a flame ionisation detector (FID). Carbon dioxide was further conditioned on a 1.5 m HayeSep N packed column before eluting through a methaniser, which reduced CO_2 to CH_4 prior to measurement on the FID. Methane and CO_2 concentrations of gas samples were calculated as peak area relative to two known standards higher and lower than ambient atmospheric concentrations. The rate of gas changes within chambers was calculated from the linear regression of concentration measured and time since chamber was installed (1–25 min). Using the ideal gas law, the rate of gas concentration change and the volume of the chamber, we calculated emission fluxes in mg CO_2 or CH_4 m^{-2} hr^{-1}.

2.8 | Data analysis

Two diversity indices were calculated: Simpson index of dominance (I) and Shannon index of diversity (H') with $I = \Sigma p_i^2$ and $H' = -\Sigma p_i * \ln(p_i)$, where p_i = the relative proportion of species *i* (Pielou, 1975). Statistical analyses were performed using Statview (SAS Institute Inc., 1998). Student's paired *t* test was used to test the difference between means of biomass and tissue nutrient data from the wet and dry season; since there were no significant differences, data from both seasons were combined for further analysis. One-way analysis of variance (ANOVA) with plant species as a factor was used to test differences between biomass and between tissue nutrients. Biomass data were log-transformed. Angular (arcsine) transformation was used on percentage data. Two-way ANOVA was used to test the difference between (1) CO_2 emissions from the mesocosms and macrophytes in the lake, with plant species and location as factors, and (2) CO_2 emissions from different species during the day and night with plant species and time as factors. When ANOVA produced significant overall differences, the post hoc Scheffé's multiple comparison test was used to evaluate differences between means. To test for differences of the impact of HV, EC and SC on dissolved oxygen, temperature and conductivity along depth profiles, we used the ANCOVA with species as a factor and depth as covariable; the Scheffé's test was used to test the mean differences between species. A Wilcoxon nonparametric test was performed to evaluate differences in richness and abundance of macroinvertebrates between native and invasive species using R (R Development Core Team, 2006).

3 | RESULTS

3.1 | Change in macrophyte abundance and diversity

In 2017, about 15 years after the invasion of *Hydrilla verticillata*, the presence of macrophyte species in the lake has not changed, as documented by the fact that all species reported by Iturbide (2001) before the invasion and Ríos Palencia (2007) in the early years of invasion were found during the 2014–2016 surveys (Table S2). What has changed dramatically is the species dominance. The littoral zone is dominated by *Hydrilla* except for areas cleaned by local people to enable boat operations. In 2006, the Simpson dominance index ranged from 0.22 to 0.64, indicating that the abundance of plant species was relatively even, while in 2017, the values ranged from 0.96 to 0.99 due to the nearly complete dominance of *Hydrilla* (Table 2). Concurrently, the Shannon index of diversity dropped from 0.54 to 1.65 range in 2006 to 0.1 or less in 2017.

3.2 | Biomass and nutrients

The average biomass across all the sampling sites did not differ significantly among the three dominant species due to relatively large spatial variability, and ranked 2,218, 1,362 and 1,243 g dry weight/m^2 for *Hydrilla*, *Eichhornia* and *Schoenplectus*, respectively (Figure 2a). However, there was a major difference in the depth distribution of *Hydrilla* and *Schoenoplectus* (Figure 2b,c). For *Hydrilla*, the biomass of both stems and leaves was positively correlated with water depth (stems: R^2 = .68, p = .0002; leaves R^2 = .35, p = .02; Figure S1c). The opposite was true for *Schoenoplectus*, whose biomass rapidly decreased at water depths over 2 m (Figure 2c). Stem numbers of *Schoenoplectus* decreased with increasing water depth (Figure S1a), while stems of *Hydrilla* were highest at medium depths (Figure S1b). Data on *Hydrilla* biomass presented in Figure 2 were based on the sampling using the diver quadrat method. The biomass assessments based on sampling of only the upper 40 cm of the canopy underestimated the total biomass values, especially at greater depths (Table S3). While the biomass of the three dominants is in the same range, there were significant differences in their longevity. Stems of *Schoenoplectus* take, on average, 3 months to reach their full length, and they stay alive for about a year unless broken by wind (50% of tagged stems were live 1 year after tagging). By contrast, 90% of tagged stems and leaves of *Hydrilla* were senescent after 3 months, and similarly, the longevity of *Eichhornia* ranged from 2 to 4 months (Esquit de Leon, personal communication).

Tissue nutrient composition also differed, with *Schoenoplectus* containing a significantly higher proportion of C than the relatively soft tissues of *Eichhornia* and *Hydrilla* (Table 3). This resulted in *Schoenoplectus* having significantly higher C:N, C:P and N:P ratios relative to *Eichhornia* and *Hydrilla*. The plant tissue $\delta^{13}C$ of *Schoenoplectus* and *Eichhornia* was -27.9 ‰, typical of C3 plants, but the $\delta^{13}C$ of *Hydrilla* was -13.8 ‰, indicating the unique C4 photosynthesis of this species. The relatively wide range of $\delta^{13}C$ in *Hydrilla* (see high standard deviation in Table 3) was likely caused by the plants switching photosynthesis between C3 and C4 pathways.

3.3 | Impact on water physical and chemical characteristics

The three species differentially impacted physical (temperature) and chemical (dissolved oxygen and conductivity) conditions along the water profile (Figure 3, Table S4). Water profile of *Schoenoplectus* was similar to open water with no vegetation for all three variables. Areas dominated with *Eichhornia* had much lower dissolved oxygen concentration, decreasing from about 70% near the surface to <50%

TABLE 2 Comparison of number of aquatic plant species and individuals (density of stems), and indices of dominance and diversity at three locations around Lake Atitlán (see map Figure 1) for the years 2006 and 2017. Data from 2006 are from a thesis by Ríos Palencia (2007)

	Santa Catarina		San Lucas		San Pedro	
	2006	2017	2006	2017	2006	2017
Total number of species	2	4	7	4	4	4
Total number of individuals	156	436	672	862	294	662
Simpson index of dominance	0.643	0.959	0.215	0.986	0.433	0.958
Shannon index of diversity	0.541	0.118	1.652	0.081	1.054	0.119

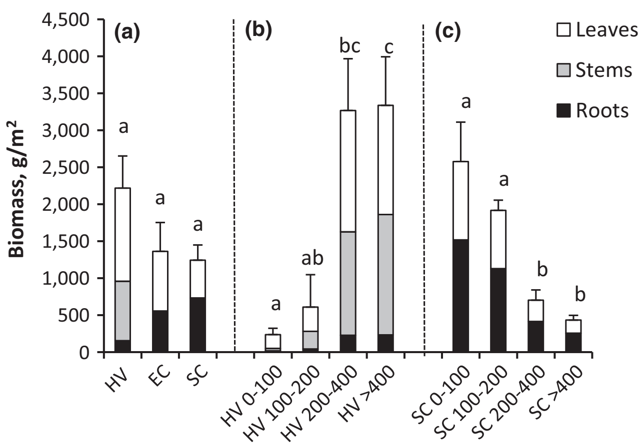

FIGURE 2 Biomass of *Hydrilla verticillata* (HV), *Eichhornia crassipes* (EC) and *Schoenoplectus californicus* (SC), in g dry weight/m^2. (a) Average values over all sampling locations, 2015–2017. (b) Average biomass of HV for discrete depth ranges along transects (2017). (c) Average biomass of SC for discrete depth ranges (2010–2012). For SC, the category "roots" includes roots and rhizomes. Error bars indicate the standard error of mean, n = 8. Treatments sharing the same letter are not significantly different from each other (Scheffé's; p > .05)

near the bottom. Contrary to *Eichhornia*, the upper two metres of the water column in *Hydrilla* were supersaturated with oxygen. Two profiles are presented for *Hydrilla* (Figure 3), one for locations where the plants broke the water surface (surface canopy) and one for sites where the main *Hydrilla* canopy ranged between −50 and −150 cm depth (deep submersed canopy). The deep submersed canopy of *Hydrilla* shows the highest DO around −100 cm corresponding to the highest presence of photosynthetically active tissue. Temperature was significantly lower in water dominated by *Eichhornia*, while temperature in the surface mat of *Hydrilla* was significantly higher than in the stands of other species. Water in *Hydrilla* canopy had consistently lower conductivity values than other locations by about 15 μS/cm^2. The pH of surface water was 8.5 (±0.21), 9.1 (±0.19), 8.1 (±0.42) and 8.7 (±0.15) for *Schoenoplectus*, *Hydrilla*, *Eichhornia* and open water, respectively (mean and standard deviation).

3.4 | Replacement of *Schoenoplectus* by *Hydrilla*

The increase in water level by about more than 2.5 m in 2010 and 2011, combined with the invasion of *Hydrilla*, led to a major loss and degeneration of *Schoenoplectus* stands in many areas of the lake (Figures 4 and 5). The increased water depth had a negative impact on SC growth and biomass production (Figure 2c, Figure S3a). Both stem density and aboveground biomass decreased with increasing water depth, and, at depths over 3 m, the plants were barely surviving. *Schoenoplectus* was not able to persist at depths over 5–6 m for longer than 3 years. Following the weakening and consequent loss of *Schoenoplectus*, *Hydrilla* spread and became established into the abandoned habitat. The dense canopy of *Hydrilla* in the water layer intercepted the majority of the incoming light and inhibited the growth of other plants, including *Schoenoplectus*.

3.5 | CO_2 and CH_4 fluxes

Both *Schoenoplectus* and *Eichhornia* showed comparable atmospheric CO_2 fluxes in mesocosms, though with high diel variability. SC and EC sequestered 241 and 304 mg CO_2 m^{-2} hr^{-1}, respectively, during the day and emitted 262 and 224 mg CO_2 m^{-2} hr^{-1}, respectively, during the night (Figure 6). In contrast to these two species, *Hydrilla* sequestered small, but consistent, amounts of CO_2 during the day (34 mg CO_2 m^{-2} hr^{-1}) and night (44 mg CO_2 m^{-2} hr^{-1}) in mesocosms. The effect of species, time of the day, and their interaction were significant at p = .005, p = .0001, p = .0001, respectively (Table S5). The significant interaction between the two factors confirmed that the day and night pattern differed between species. Net CH_4 emissions were only detected in the *Schoenoplectus*-containing mesocosms, which had low and consistent CH_4 emissions with mean value of 1.24 mg CH_4 m^{-2} hr^{-1} (range 0.41–2.45).

A series of *in situ* measurements in Atitlán during daylight hours confirmed the general patterns we observed in the mesocosms. *In situ* CO_2 flux rates in open lake water (unaffected by macrophytes) were low (−4.7 and +0.4 mg CO_2 m^{-2} hr^{-1} for day and night, respectively) relative to both mesocosms with macrophytes and locations in the lake with macrophytes. Daytime lake measurement in natural stands of these macrophytes ranged between −183 and −473 mg CO_2 m^{-2} hr^{-1} in *Schoenoplectus*, −37 to −42 mg CO_2 m^{-2} hr^{-1} in *Hydrilla*, −151 to −487 mg CO_2 m^{-2} hr^{-1} in *Eichhornia* and −22.6 to +23 mg CO_2 m^{-2} hr^{-1} in open water (Figure 7). The differences between the mesocosm and lake natural stand fluxes were not statistically significant, and there was no significant interaction between species and location (Table S6). Additionally, we found similar CH_4 flux rates in the lake measurements as the mesocosms. Most lake locations lacked significant net CH_4 emissions. However, *Hydrilla* at San Lucas

TABLE 3 Average (±*SD*) tissue nutrient content, C and N stable isotope signature, ash content and C:N:P stoichiometry (mass ratios) from combined wet and dry season samples; *n* = number of replicates; *SD* indicates the standard deviation. Same letters indicate means that are not significantly different (Scheffé's, $p < .05$). *Schoenoplectus californicus*, *Hydrilla verticillata*, *Eichhornia crassipes*, *Potamogeton illinoensis*, *Ceratophyllum demersum*; Lake Atitlán, Guatemala

Species	*n*	C %	N %	P %	$\delta^{15}N$ ‰	$\delta^{13}C$ ‰	Ash %	C/P	C/N	N/P
Schoenoplectus	11	43.8 ± 0.9 a	1.8 ± 0.2 a	0.13 ± 0.02 a	0.7 ± 3.5 a	−27.9 ± 0.6 a	7.8 ± 1.2 a	340 ± 64 a	25 ± 2.5 a	13.5 ± 1.9 a
Hydrilla	14	31.6 ± 3.4 b	2.0 ± 0.4 a	0.24 ± 0.08 bc	2.2 ± 2.5 a	−13.8 ± 3.7 b	26.7 ± 3.6 b	147 ± 47 bd	16 ± 3.4 bc	8.1 ± 1.3 b
Eichhornia	8	36.1 ± 1.4 c	1.8 ± 0.2 ab	0.23 ± 0.05 cd	2.4 ± 1.0 a	−27.9 ± 0.6 a	11.5 ± 2.7 ac	159 ± 50 bd	20 ± 2.4 ac	7.9 ± 1.6 b
Potamogeton	8	36.3 ± 1.2 c	1.4 ± 0.3 b	0.15 ± 0.05 abd	0.0 ± 1.1 a	−12.5 ± 0.9 b	23.5 ± 6.4 b	260 ± 49 abc	28 ± 6.3 ad	9.3 ± 1.9 b
Ceratophyllum	3	36.7 ± 0.6 c	2.8 ± 0.5 c	0.37 ± 0.05 e	3.9 ± 1.7 a	−25.7 ± 2.2 b	21.2 ± 3.3 b	101 ± 16 d	14 ± 2.2 ce	2.5 ± 1.5 b
p value		<.001	<.001	<.001	.168	<.001	<.001	<.001	<.001	<.001

(Figure 1) released large amounts of CH_4 to the atmosphere (112.4 and 704.4 mg CH_4 m^{-2} hr^{-1} in July and November 2016, respectively). No net CH_4 uptake was recorded in either the mesocosms or lake sampling events.

3.6 | Macroinvertebrates

A total of 1,714 individuals of aquatic macroinvertebrates were collected, 817 in May and 897 in September. These belonged to 34 taxa corresponding to 29 families, 14 orders and seven classes (Table S7). The most abundant classes that were present in all sites were Malacostraca (49.18%) and Insecta (24.73%), followed by Gastropoda (18.32%); the remaining groups were below 4%. The three dominant taxa were the genus *Hyalella* sp. (Hyalellidae: Amphipoda) with 843 organisms, followed by the family Physidae (Gastropoda: Mollusca) and the genus *Nehalennia* sp. (Coenagrionidae: Odonata) with 302 and 211 individuals, respectively (Table S7). Both EC and HV had a greater number of macroinvertebrate species and also a higher abundance of individuals compared to macroinvertebrates in native plant communities (Figure 8, Table S8); however, the differences were not statistically significant ($Z = 3.7$, $p > .05$).

4 | DISCUSSION

The volcanic lakes in Central America span the range of trophic states from oligotrophic (e.g. Ayarza, Chicabal), with few invasions, to strongly eutrophic and heavily invaded (e.g. Amatitlán, Ilopango; see Table S1). At most lakes, *Eichhornia* is present; this species has been reported from Central American waters for decades (Standley & Record, 1936). Many lakes have also been already invaded by *Hydrilla*, which spread to Central America after the 1990s (Haller, 2002). While some information on the impact of *Eichhornia* and *Hydrilla* in the lakes listed in Table S1 is available from grey literature and anecdotal evidence, little other information currently exists. The detailed data from Lake Atitlán confirm the hypothesis that disturbance-induced species replacement leads to major changes in ecosystem functioning of the lake littoral zone. Disturbance, represented by rapid change in water level, was exacerbated by anthropogenically mediated nutrient loading. The following discussion is focused on Atitlán with references to the other lakes as appropriate.

4.1 | Change in macrophyte dominance following the invasion

So far, no loss of native species has been recorded at Lake Atitlán, but the abundance of submersed native species has declined (Table S2). Between 2006 and 2017, *Hydrilla* became dominant as shown by changes in species richness and diversity indices. While *Hydrilla* has been spreading rapidly since its introduction and specifically after the water-level increase of 2010, abundance of *Eichhornia* has been stable and even declining. This brings up the question: Why is *Eichhornia* not outcompeting *Hydrilla*? There are many

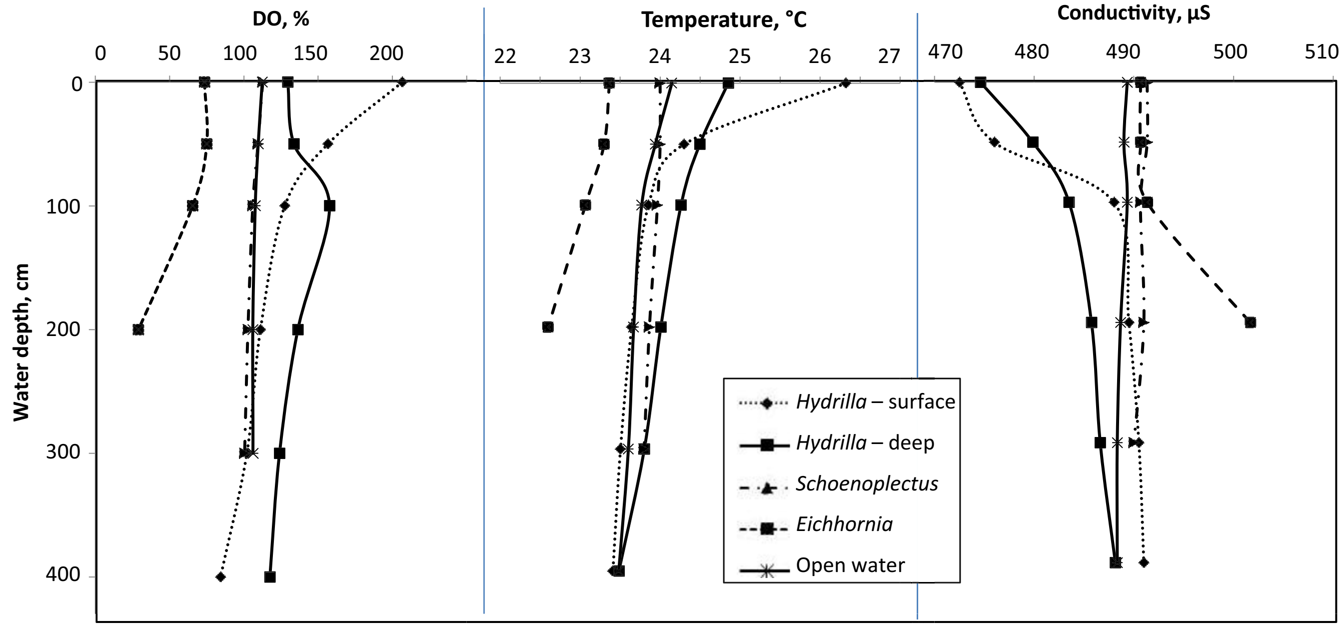

FIGURE 3 Mean values of depth profiles of dissolved oxygen (DO, %), water temperature (T, °C) and conductivity (µSiemens/cm), measured in stands of *Schoenoplectus californicus*, *Hydrilla verticillata* and *Eichhornia crassipes* in July 2017 between 10 a.m. and noon at San Lucas, Santa Catarina and San Pedro, Lake Atitlan. *Hydrilla*—surface indicates values for a stand where the canopy is breaking water surface, *Hydrilla*—deep indicates stands with the canopy 50–150 cm below the water surface

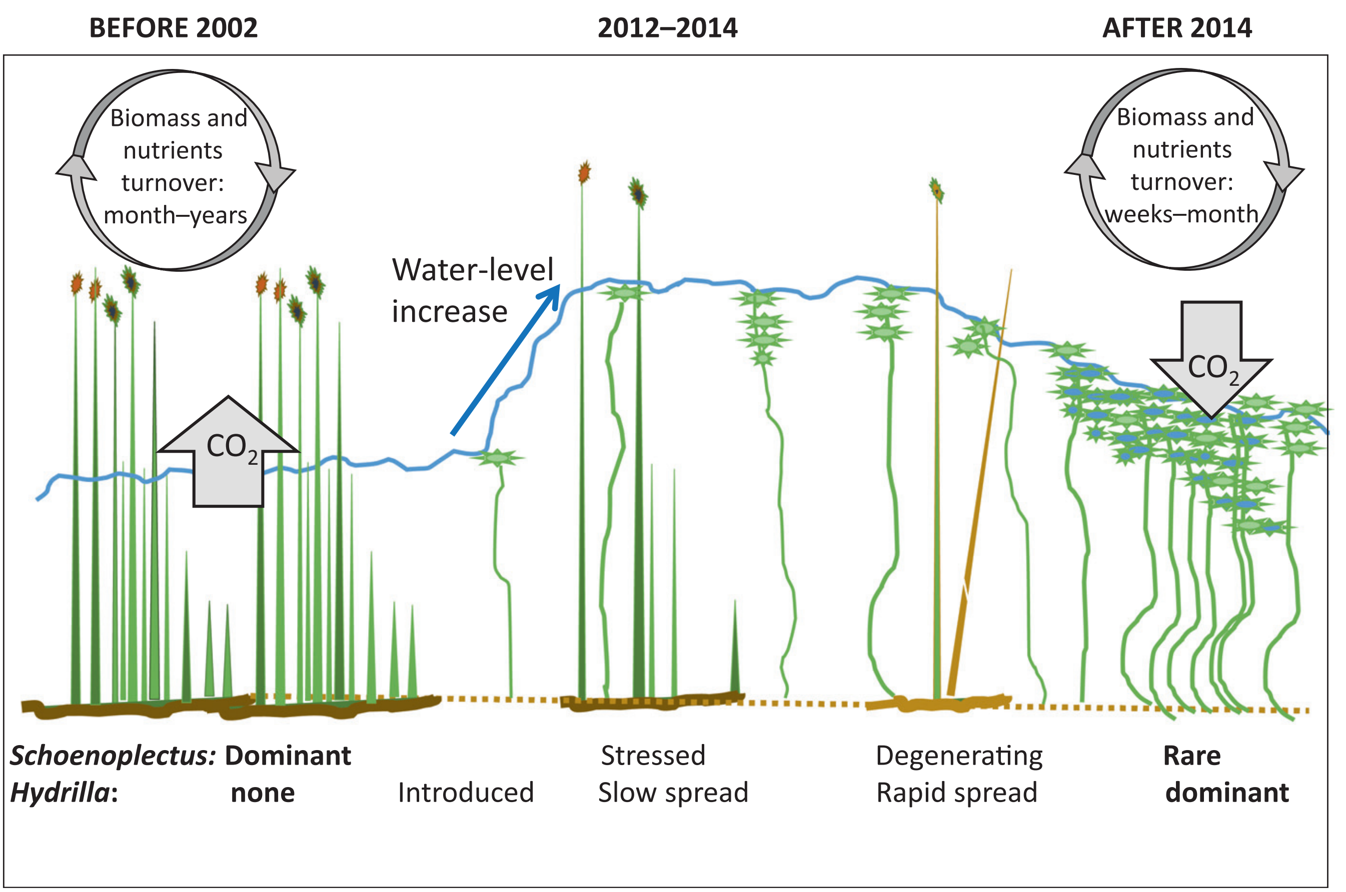

FIGURE 4 Regime shift in the littoral zone of Lake Atitlán, Guatemala, with replacement of *Schoenoplectus californicus* (SC) by invasive *Hydrilla verticillata* (HV)

FIGURE 5 Healthy stand of *Schoenoplectus californicus* near San Juan in 2002; the same area in 2015, dominated by *Hydrilla verticillata* with *Schoenoplectus* completely missing. Lake Atitlán, Guatemala

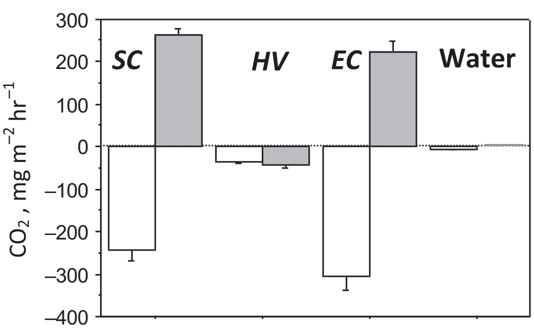

FIGURE 6 Effects of macrophyte species and time of day on CO_2 fluxes in mesocosms. White and grey columns represent CO_2 fluxes during day and night, respectively. EC, *Eichhornia crassipes*; HV, *Hydrilla verticillata*; SC, *Schoenoplectus californicus*; water, open water. Error bars indicate the standard error of the mean

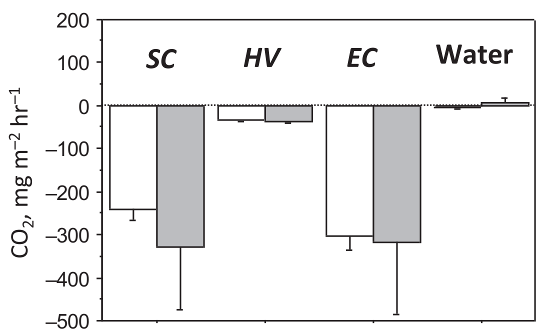

FIGURE 7 Effects of macrophyte species and location (mesocosm/lake) on CO_2 fluxes under daylight. White and grey column represent CO_2 fluxes in the mesocosms and lake, respectively. Error bars indicate the standard error of the mean

examples of *Eichhornia* outcompeting submersed macrophytes including *Hydrilla* (Li et al., 2015; Villamagna & Murphy, 2010), and there is a general consensus that floating plants typically outcompete submersed plants and phytoplankton due to shading (Scheffer et al., 2003). *Eichhornia* appears to outcompete *Hydrilla* in nutrient-rich waters. As summarised by Szabo et al. (2010), submerged plants, which are capable of utilising nutrients from both sediment and water column (Blanchet, Maltais-Landry, & Marange, 2012), can sustain their dominance over floating plants under low nutrient loadings. In Lake Atitlán, N concentrations may be suboptimal for *Eichhornia* (see Table 1). The optimal N level for *Eichhornia* growth is around 5 mg N/L, that is, orders of magnitude higher than available in Lake Atitlán (Reddy, Agami, & Tucker, 1989). Additional reasons for the

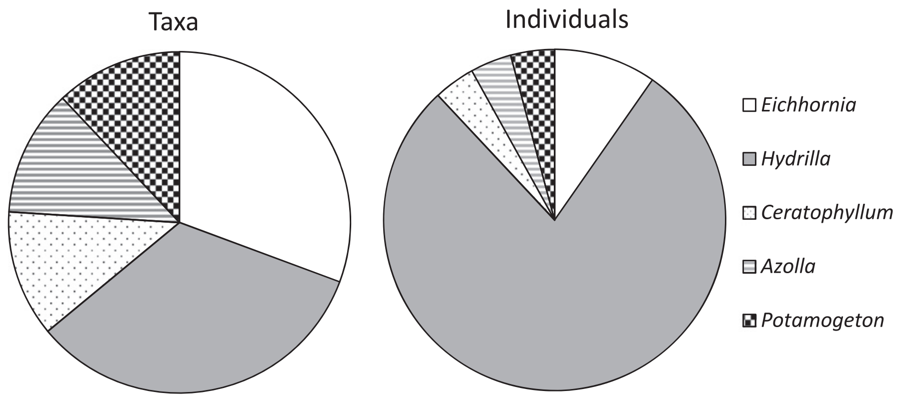

FIGURE 8 Proportion of macroinvertebrate taxa and individuals associated with five macrophyte species: *Eichhornia crassipes*, *Hydrilla verticillata*, *Ceratophyllum demersum*, *Azolla filliculoides* and *Potamogeton* sp

reduced competitiveness and invasiveness of *Eichhornia* include relatively low water temperature (average annual surface temperature of Lake Atitlan is 23°C, while *Eichhornia* grows best in the temperature range of 28–30°C) (Wilson, Holst, & Rees, 2005) and high wave action, which appears to prevent stand formation in other lakes (Wilson et al., 2007). Areas of *Eichhornia* infestation near villages are periodically harvested by locals, and since the spread of *Hydrilla*, *Eichhornia* is not re-colonising as fast as it used to (Esquit de Leon, personal communication). With relatively low nutrient loading of Lake Atitlán, *Hydrilla* will likely outcompete native species and an earlier invader, *Eichhornia*. The opposite situation exists in the eutrophic Lake Amatitlán (Table S1), where total N concentrations are higher (in the range of 1–7 mg/L; Tetzaguic Car, 2003). Amatitlán has been dominated by *Eichhornia* with only a small areas infested with *Hydrilla*.

4.2 | Biomass production and nutrient cycling

The average biomass per square metre does not differ significantly among the three species and falls in the range given for these species from mesotrophic to eutrophic locations (Bowes, Holaday, & Haller, 1979; Hopson & Zimba, 1993; Robles, Madsen, & Wersal, 2015; Singh, Pandey, & Kumari, 2012). What has changed with the invasion of *Hydrilla* was the total biomass production and its depth distribution. Most littoral areas formerly dominated by *Schoenoplectus* are now dominated by *Hydrilla*. The invasion of *Hydrilla* actually increased the littoral zone (defined as occupied by macrophytes) because *Hydrilla* now forms dense plant beds at depth up to 7–8 m, which were previously mostly devoid of vascular macrophyte vegetation. It is also clear that the littoral is now much more productive than in the past. Biomass of *Hydrilla* is highest in the depth range of 2–6 m, while *Schoenoplectus*, where it survived or has been replanted, maintains the maximum biomass in the 0.5–2 m depth range. In addition, the fate of the biomass is different due to species-level differences in biomass turnover and tissue-nutrient composition. The two invasive species grow fast and produce soft leaves with a short turnover, measured in weeks (Bianchini, Cunha-Santino, Milan, Rodrigues, & Dias, 2010). The native *Schoenoplectus* is a species with very slow turnover, with the average stem longevity of several months up to a year. Similarly, the litter decomposition of *Schoenoplectus* is very slow with a half-life of many months (Castle, 2016). We have observed that the soft tissues of *Hydrilla* and *Eichhornia* can decompose in a matter of weeks (Snyder, unpublished data), a pattern also documented by Dierberg (1993), Battle and Mihuc (2000), Li, Wang, Ye, and Ba (2014), Quintão, Rezende, and Gonçalves (2013) and Balasubramanian, Arunachalama, Das, and Arunachalam (2012). Stable water temperature (19–24°C) assures high metabolic rates of decomposers and corresponding rapid nutrient mineralisation throughout the whole year.

Without rapid nutrient recycling, *Hydrilla* and *Eichhornia* would be unable to grow so vigorously except in areas with direct inflow of wastewater. Like many volcanic lakes (Diaz, Pedrozo, Reynolds, & Temporetti, 2007), Lake Atitlán is nitrogen-limited (as indicated by low N and low N:P ratios in Table 1). Nitrogen limitation has been explored in relation to phytoplankton, specifically cyanobacteria and N-fixation (Corman et al., 2015; Rejmánková et al., 2011), but how do the littoral macrophytes cope with this N limitation? Tissue composition of Atitlán macrophytes indicates N concentrations in the range typical of the respective species growing in N-unlimited conditions (Demars & Edwards, 2007). *Schoenoplectus* apparently utilises N produced by N-fixation by heterotrophic bacteria in its rhizosphere, with estimated contribution of this N to be 19% of the plant N budget (Rejmánková et al., 2018). While research on N-fixation associated with invasive *Eichhornia* and *Hydrilla* is a subject of a recent project, preliminary data indicate an important role of N-fixation by both autotrophic and heterotrophic fixers that live in epiphytic biofilms on leaves and stems of *Hydrilla*. We have also found active heterotrophic N-fixers in the rhizosphere of *Eichhornia* (Rejmánková, personal observation). In addition to N-fixation, a rapid recycling of decomposing plant material releases inorganic N from organic N compounds as documented by high activities of extracellular aminopeptidases (Rejmánková, personal observation). The littoral zones are richer in total N, the majority of which is dissolved organic N (see Table 1 comparing TN in littoral versus pelagial). Clearly, N limitation has not prevented the spread of invasive species in Lake Atitlan as both natives and invasives seem capable of utilising various mechanisms to overcome it.

Hence, the switch from low-productive littoral zones dominated by *Schoenoplectus* to high-productive littoral zones dominated by submersed *Hydrilla* represents a major acceleration of biogeochemical cycling in these lake zones (Figure 4). It is not known how much the increased input of organic material to the littoral zone sediment will impact *Hydrilla* in the long run as excessive proportion of organic matter has been reported to inhibit its growth (Barko & Smart, 1983).

4.3 | Impact on physical and chemical properties of water

The two invasive species impact the conditions in the water column very differently, specifically in terms of oxygen concentration. *Hydrilla*, as a submersed species, releases O_2 to the water column leading to high O_2 supersaturation. Filamentous green algae growing attached to surface-breaking *Hydrilla* (see Figure 5, year 2015) undoubtedly contribute to extremely high (>200%) DO concentration. Unlike *Hydrilla*, freely floating *Eichhornia* releases O_2 to the air. It also shades the water column below, eliminating phytoplankton, and maintains much lower DO (typically 60% and lower). Because of its high photosynthetic rates, dense stands of *Hydrilla* tend to deplete CO_2 in the water column, raising the pH values up to >9, a pattern also reported by Bowes et al. (1979) and Sousa (2011). The reduction in conductivity is probably due to increased $CaCO_3$ precipitation resulting from high pH during HV photosynthesis. The highly saturated oxygen conditions and structured habitat of HV make its stands ideal environment for macroinvertebrates and fish (see below).

4.4 | Carbon sequestration/emission

Macrophytes can be an important component of lake C cycling (Attermeyer et al., 2016; Peixoto, Marotta, Bastviken, & Enrich-Prast, 2016). While our results clearly support this concept, the wide range of CO_2 fluxes measured among macrophyte species and time of day (Figure 6) demonstrate the different functional impact of various macrophyte life forms on the C cycle. The emergent *Schoenoplectus* and freely floating *Eichhornia* have their photosynthetic apparatus in the air and the values of both C sequestration and C emission fluctuate widely between the day and night. In contrast to these two species, the fully submersed *Hydrilla* obtains CO_2 from the water column and is taking up CO_2 also during the night utilising the single-cell C4 metabolism. At high pH, during the day, free CO_2 becomes depleted and *Hydrilla* can switch to using bicarbonate (Bowes, 2011; Salvucci & Bowes, 1983). The high physiologic plasticity and various mechanisms by which *Hydrilla* adapts to low amount of CO_2 in the water column contribute to its invasive capabilities (Hussner, Mettler-Altmann, Weber, & Sand-Jensen, 2016; Raven, Beardall, & Giordano, 2014).

We have only nascent knowledge of the interplay between eutrophication and aquatic C fluxes in tropical lakes (Almeida et al., 2016). Our data indicate that the invasive macrophytes in nutrient-enriched littoral zones are sequestering CO_2, *Schoenoplectus* is a net emitter of CO_2, and fluxes from open water are negligible. Recent studies in temperate ecosystems revealed that when eutrophication increases, lakes and reservoirs tend to emit less CO_2 efflux to the atmosphere because of high CO_2 uptake by primary production (Gu, Schelske, & Coveney, 2011; Jeppesen et al., 2016; Pacheco, Roland, & Downing, 2013), although such generalities mask complexity in lake C cycling (Perga et al., 2016). We do not have continuous 24-hr measurements to express the average daily CO_2 fluxes, but calculating them as a mean of day and night fluxes, we get +240, −936, −960 and −48 mg CO_2 m^{-2} day^{-1} for *Schoenoplectus*, *Eichhornia*, *Hydrilla* and open water, respectively. Such values are in the range of CO_2 flux estimates generated by Gu et al. (2011) for a subtropical eutrophic lake (−3640 to 770 mg CO_2 m^{-2} day^{-1}). Clearly, the CO_2 fluxes associated with different types of macrophytes need to be accounted for when calculating a lake CO_2 balance.

We did not expect high CH_4 emissions for several reasons. The lake water profile is still mostly oxygenated with the exception of occasional anoxia at the bottom; thus, any CH_4 moving through diffusion would likely be oxidised. In the macrophyte-dominated areas, only *Schoenoplectus* is known to provide a good conduit for CH_4, due to well-developed aerenchyma in its stems (Armstrong, 1979). *Eichhornia* is not rooted in sediments and *Hydrilla* lacks well-developed aerenchyma to serve as a conduit of gas flux through plant tissue (Silveira, Harthman, Michelan, & Sousa, 2016). In the mesocosm measurements, CH_4 emissions occurred only in association with *Schoenoplectus*. Mesocosom CH_4 emissions were in the same range as CH_4 fluxes in lake *Schoenoplectus* stands as well as in *Schoenoplectus*-dominated areas of other lakes (<1 mg CH_4 m^{-2} hr^{-1}, Koebsch, Glatzel, & Jurasinski, 2013; 1–1.7 mg CH_4 m^{-2} hr^{-1}, Kankaala et al., 2003). Surprisingly, we measured high rates of CH_4 emissions from *Hydrilla* in San Lucas Bay during both sampling events in July and November. In this case, the bay was overgrown with aquatic vegetation, mostly with *Hydrilla*, and was receiving wastewater from a nearby laundry washing station utilised by area residents. This organic carbon- and nutrient-rich outflow likely stimulated growth of *Hydrilla* and contributed to anaerobic decomposition in sediments providing substrate for CH_4 production. We attribute these high CH_4 fluxes to CH_4 ebullition from the anoxic sediments rather than transport through plants.

Consequently, invasive macrophytes significantly changed the carbon cycling of the littoral zone of lake Atitlán. While the littoral region of tropical lakes may be small by volume, macrophyte invasion in this region may have an overall impact on the lake C balance proportionally greater than would be expected based on infestation spatial extent alone.

4.5 | Habitat quality for macroinvertebrates

Habitat structural complexity is important for associated macroinvertebrates (Cronin et al., 2006; Kurashov, Telesh, Panov, Usenko, & Rychkova, 1996), and since submersed macrophytes are typically highly structured, it is not surprising that we found more taxa and higher organism abundance associated with *Hydrilla* and *Eichhornia* relative to native species. Similar results have been documented from other *Hydrilla* dominated areas such as Lake Tanganyika (Copeland et al., 2012), Parana River (Mormul, Thomaz, Higuti, & Martens, 2010) and Lake Tutira, New Zealand (Hofstra & Clayton, 2014). Freely floating macrophytes such as duckweeds or aquatic ferns (*Azolla*, *Salvinia*) generally provide less favourable habitat due to much lower complexity of their simple root structures (Fontanarrosa, Chaparro, & O'Farrell, 2013). The exception is *Eichhornia*, because its extensive aquatic root mass has a more structurally complex surface with fine roots serving as a substrate for microbial communities and thus providing a rich food environment for epiphytic macroinvertebrates (Barker et al., 2014; Kouamé et al., 2010; Masifwa et al., 2001; Toft, Simenstad, Cordell, & Grimaldo, 2003; and others). This higher abundance, however, may be accompanied by lower species diversity (Coetzee, Jones, & Hill, 2014).

Gasith and Hoyer (1998) argue that while physical and metabolic effects of macrophytes in deep lakes may primarily impact littoral zones, their importance extends to pelagic zones by providing structured habitat that affects biotic interactions of higher trophic levels. In Atitlán, the replacement or suppression of native macrophytes by *Eichhornia* and *Hydrilla* certainly contributed to richer and more abundant macroinvertebrate populations, with important consequences for fish populations (Villavicencio, personal communication). *Hydrilla* forms much denser and more spatially extensive stands than native macrophytes; thus, in addition to providing more macroinvertebrates per specific area, its importance as a valuable fish food provider may be even higher because of its large total area.

4.6 | *Replacement of* Schoenoplectus *by* Hydrilla *and consequences for the lake*

There are many examples of invasive species supplanting native species; many of these represent a replacement of submersed by floating-leaved or floating macrophytes (Goodwin, Caraco, & Cole, 2008; Li et al., 2015; Villamagna & Murphy, 2010). The natural order of lake succession is for plant functional groups to shift from submersed to floating-leaved, to emergent. Succession is assumed to be controlled by accretion of sediments and changes in resource availability (Barko & Smart, 1983; Van der Valk & Bliss, 1971). The replacement of emergent macrophytes by submersed plants does not typically happen unless the emergent population/community first declines due to a disease or herbivory (muskrat grazing; Vermaat, Bos, & van der Burg, 2016). In the present case, the weakening of native *Schoenoplectus* may have been precipitated by the rapid and sustained lake water-level rise. This more than likely led to exhaustion of *Schoenoplectus* rhizome system, similar to what has been reported for other Cyperaceae species, *Eleocharis cellulosa*, by Macek, Rejmánková, and Houdková (2006). Weakened *Schoenoplectus* rhizomes are less capable of subsidising the growth of new ramets (Rejmánková, Rejmánek, Djohan, & Goldman, 1999), especially when the required resources to subsidise new growth increase due to deeper water. When this stress is combined with strong shading by *Hydrilla* mats limiting photosynthesis of newly growing ramets, and potentially stronger competition of fast-growing *Hydrilla* for nutrients, *Schoenoplectus* regeneration is even further constrained and nearly impossible. In Table S9, we present four potential scenarios of interactions between *Schoenoplectus* and *Hydrilla* that can be relevant to other lakes in the Central American volcanic region.

Both negative and positive impacts of invasive aquatic species have been reported elsewhere. What are negative impacts of the macrophyte species replacement in Atitlán? *Schoenoplectus* has been traditionally harvested by local "tuleros" and used for mat-weaving (Dix et al., 2003); tuleros are directly impacted by the *Schoenoplectus* decline. There are records indicating that *Schoenoplectus* degeneration in Atitlán has caused significant losses in terms of bird habitat (Garcia, Davila, & Noriega, 2011), although reports from other aquatic ecosystems show that most waterfowl species appear to benefit from the presence of *Hydrilla* (Rybicki & Landwehr, 2007). While no loss of bird species has been recorded due to *Hydrilla* invasion, the native flora of submersed macrophytes is less abundant than it used to be (Table 2). As mentioned previously, dense growth of both *Hydrilla* and *Eichhornia* impedes boat traffic.

What are positive impacts of *Hydrilla* invasion? According to a study from Guatemala's Lake Izabal, *Hydrilla* supported the highest fish biomass in comparison with other habitats, although fish density and composition differed among the macrophytes (Barrientos & Allen, 2008). The authors concluded that *Hydrilla* was not detrimental to the fish community. While we do not have evidence from Lake Atitlán, local fishermen suggest that *Hydrilla* provides an excellent fish habitat (Villavicencio, personal communication). *Hydrilla* has also been reported as efficient in removing cyanotoxins from water (Nimptsch, Wiegand, & Pflugmacher, 2008) and Romero-Oliva, Contardo-Jara, and Pflugmacher (2015) recommended *Hydrilla* as a suitable species for phytoremediation. This may be highly relevant to Lake Atitlán and other tropical lakes where cyanobacterial blooms are becoming more frequent and it is a topic deserving of more research (Romero-Oliva et al., 2015).

Biological invasions of freshwater ecosystems have a large number of known and potential impacts on community structure and ecosystem function including impacts on higher trophic levels (Havel et al., 2015). Typically, these impacts have been perceived as negative but as Ewel and Putz (2004) point out: "Blanket condemnation of alien species in restoration efforts is counterproductive. Where their presence does not unduly threaten surrounding ecosystems, alien species can be tolerated or even used to good advantage, if they provide essential ecological or socioeconomic services." This certainly applies to *Hydrilla*. While it has been identified as the most problematic invasive aquatic plant in fresh waters (Gu, 2006), examples listed in this study show that its presence can have positive impact on the ecosystem.

4.7 | Management options

Because of the large size of the lake and rapid reproduction of both invasive macrophytes, *Hydrilla* and *Eichhornia* are unlikely to be eliminated from Lake Atitlán (cf. Rejmánek & Pitcairn, 2002). Some of the communities around the lake are already aware of the benefits of the nutrient-rich biomass, which they remove from the lake to enable boat traffic and then compost to improve crop production on land. To restore *Schoenoplectus*, at least in some parts of the lake, a strategy of local *Hydrilla* control will have to be designed. Until a more efficient control of sewage inflow to the lake is realised, the littoral buffer zones of both *Eichhornia* and *Hydrilla* can help to intercept excessive nutrients and pathogens before they reach the pelagic zone. A comprehensive life cycle analysis (Evans & Wilkie, 2010) of economic cost associated with harvest of *Hydrilla* and *Eichhornia*, and their utilisation for compost production needs to be performed.

4.8 | Needs for future research

More data on plant invasion dynamics and their ecological impacts are needed from other Neotropical volcanic lakes. To provide management recommendations, it is important to focus on obtaining a better understanding of nutrient recycling processes and carbon balance in littoral zones dominated by *Hydrilla* and their potential impact on pelagic zones. Understanding how invasive species are able to exploit pathways for N acquisition under limiting conditions may be imperative for management of invasive species in nutrient-limited systems. Considering that the direct metabolic consequences of lake warming are likely to be felt most strongly at low latitudes (Kraemer et al., 2017), response of littoral communities to increased temperature should also be assessed. Finally, quantitative data on the nutrients, pathogens and cyanotoxin interception by the buffer zones *of Hydrilla* need to be obtained.

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ORCID

Eliška Rejmánková http://orcid.org/0000-0001-7539-0232

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