# A wetland condition assessment to consider ecological relationships of a Maya cultural keystone species within the Lake Atitlan, Guatemala littoral zone

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# Abstract

Littoral wetland plant species such as *Typha domingensis* and *Schoenoplectus californicus* (both locally called *tul*) in Lake Atitlan provide diverse ecosystem services (ES). These ES include removal of pollutants, oxygenation, and raw material for handicrafts. Human communities, most of whom are Indigenous Maya, actively steward littoral wetlands informed by their traditional ecological knowledge (TEK). Our goal was to assess the wetland condition in four Maya Tz'utujil communities (Santiago Atitlan, San Pedro, San Juan and San Pablo La Laguna), each with different Indigenous uses and management practices. We used a three-level wetland condition assessment: 1) littoral vegetation extent measured with remote Sentinel-2 and Google Earth photographs, 2) field plant survey to measure vegetation structure and plant diversity, and 3) wetland stressor assessment. Stressors analyzed were land use, non-native macrophyte (*Hydrilla verticillata*) and lake-level fluctuations. In Santiago, where wetland plant TEK is most intact, remote sensing results showed the highest *tul* concentrations (81% of the overall 5 ha of *S. californicus* and 98% of the 5.2 ha for *T. domingensis*), and the highest structure and diversity indices (first-order Jackknife and Shannon index). San Juan showed higher plant structure (number of stalks, diameter, and cover) than San Pablo and San Pedro. Santiago and San Juan were however, the most vulnerable to water-level reduction. Traditional *Tulero* practice in Santiago, including planting and cutting *tul* and removing invasive macrophytes, has sustained these wetlands. Ecological value embedded in Indigenous resource management suggests the need to include these practices in governmental environmental management and policy.


# Introduction

Lake Atitlan, Guatemala, a volcanic lake with a long history of Maya traditional use, is now heavily impacted by land management that results in cultural and environmental degradation (Dix et al. 2003; Rejmánková et al. 2011). Littoral wetlands here are important areas for fish spawning; waterfowl nesting; and for reducing erosion, nutrient enrichment, and eutrophication (Russi et al. 2013; de Groot et al. 2018). They contribute to sustainable development goals in core areas of human well-being: food, climate, water and biodiversity (Janse et al. 2019). Wetland losses have diminished livelihoods of local peoples along Lake Atitlan´s shore (Berger 2008; López 1990). Archeological evidence indicates that Maya people have lived in this area since at least 2000 B.P. (Lothrop 1933). Their traditional ecological knowledge (TEK) has been communicated from generation to generation resulting in often rich methods of land management (Falkowski et al. 2015; Martin et al. 2010). The TEK of Lake Atitlan includes such activities as fishing, collecting crabs, and harvesting of *Typha domingensis* Pers. and *Schoenoplectus californicus* (C.A. Mey.) Soják, both locally called *tul*, and used for making mats or *petates* (Berger 2008; McBryde 1945).

LaBastille (1974) while studying the Atitlan grebe (*Podilymbus gigas* Griscom) measured the littoral vegetation as the grebe's main habitat along 25.7 km of emergent aquatic vegetation and reported that Indigenous people "harvest shoreline vegetation for weaving mats" and that they "weave sleeping mats and little seats." She found that *tul* grows rapidly; five months after clear cutting, *tul* reaches sufficient height for grebe nesting. She found that Indigenous use of shoreline vegetation was beneficial for both the grebes and the plants by: 1) developing "fresher," straighter stalks with less matting and choking (that prevent seeding and regrowth) and 2) eliminating bottom and water surface debris. Lopez (1990) reported that local people, also called *Tuleros*, harvest the shoreline vegetation. He found that the *S. californicus* was preferred for making petates over *T. domingensis.* He described the processing cycle, including cutting time and drying period (8 to 15 days) (López 1990). Dix et al. (2003) reported the aquatic macrophytes of Lake Atitlán as grouped into three categories: floating, emerging and submerged. They mentioned the importance of aquatic vegetation for biodiversity and human use, especially *tul* for mats and for "small boats in the past." Berger (2008) provided historical information and details on the cultivation and processing of *S. californicus* and the benefits for both the ecosystem and for the Maya culture. Despite the ecological, economic, and cultural importance of these plants, its cultivation has been limited by shoreline development and urbanization; these changes have reduced access to traditional uses of Lake Atitlan littoral region (Skinner Alvarado 2010).

Recent studies have focused on macrophyte ecological functions: nitrogen fixation through a case study of *S. californicus* in Lake Atitlán (Rejmánková et al. 2018a); quantifying gas emissions ($CO_2$ and $CH_4$), plant biomass, macroinvertebrates, C: N: P ratios in plant tissue for five macrophytes including *S. californicus* (Rejmánková et al. 2018b); and analysis of N and C isotopes in nine macrophyte species, fish and invertebrates (Villavicencio 2020). However, the ecological significance of native aquatic vegetation in relation to the traditional cultivation, harvesting and management by the Maya peoples has not been studied.

The purpose of this study was to assess the influence of indigenous and traditional management of *S. californicus* on ecosystem structure and macrophyte diversity using a three-level approach: 1) remote sensing of plant cover; 2) field plant surveys; and a 3) wetland condition stressor assessment. This approach was followed in four Maya-Tz'utujil territories (Santiago, San Juan, San Pedro and San Pablo) in Lake Atitlan, Guatemala. Each area has distinct biophysical characteristics and differences in their practiced relationships with wetlands.

## Methods

# Study Site

Lake Atitlan is located in Guatemala's highlands as described by Newhall (1987) at an altitude of 1555 m, a maximum depth of 341 m, mean depth of 183 m, surface area of 137 km$^2$, and a total volume of 24 km$^3$. The lake is not in hydrological equilibrium (LaBastille 1974); it fluctuates seasonally and periodically depending on the rainfall and storm events. The wet season is from May to October, and the dry season from November to April. Lake Atitlan watershed is dominated by mixed pine oak forest, coffee, and annual agriculture of maize and vegetables. Evidence of inhabitation dates to at least 2,000 years before present (BP). A human population of 256,039 currently live in the watershed. The majority of residents are from three Mayan linguistic groups: Kaqchikel, K'iche' and Tz'utujil (AMSCLAE 2020b). This study centers on the territories of the Tz'utujil communities. Figure 1 shows the location of sampling sites in four Maya-Tz'utujil communities: Santiago, San Juan, San Pablo, and San Pedro. Here we describe briefly information about each community and their working relationship with the wetlands.

Santiago covers an area of 136 $km^2$ and has a population of 41,877 inhabitants; the majority are Maya-Tz’utujil (SEGEPLAN 2016, INE 2018). Traditional cultivation and harvesting continue to be shared from generation to generation. Community members mainly use *S. californicus* to weave sleeping mats and seating pads (LaBastille 1974). They are organized in a group named the *Comité de Tuleros de Santiago Atitlán* (*Tuleros*). The sleeping mats (petates) are their main traditional product sold in markets in the Guatemalan highlands (López 1990). *T. domingensis* is used for ceremonial decorations; no evidence of cultivation has been noted for this species.

San Juan has a population of 12,162 people in an area of 37.18 $km^2$, 87% of that area drains to Lake Atitlan and 96% of the population that live in that area is Maya-Tz'utujil people (Segeplan 2018, INE 2018). The fishing association *Chajil Chupup* practice *S. californicus* cultivation as described in Berger (2008).

San Pablo has the smallest area of the study communities of 12 $km^2$. It has a population of 7,276 of which 99% is Maya-Tz’utujil people (INE 2018). Few families have artisans who know how to weave mats, and they are mainly women. The mats and crafts produced are sold in markets or in the streets. Few men of those families harvest the *S. californicus* fibers of San Pablo and San Juan or purchase them in Santiago. Planting of *S. californicus* have been completed by governmental agencies, NGOs and volunteers (AMSCLAE 2020a).

In San Pedro, the second largest Maya-Tz’utujil community (24 $km^2$ and 10,705 inhabitants) showed no evidence of traditional cultivation and harvesting practices. Recent planting done by residents, governmental agencies, or non-profit volunteers were not observed during the fieldwork period.

# Establishing research scope with communities and interviews

Planning and site visits started in summer 2017 with meetings in three communities: Santiago, San Juan, and San Pablo. The relevance of *S. californicus* in the area was stressed by community members, indicating their role as a cultural keystone species (CKS). Planning meetings included conversations to determine the scope and process of the study, and semi-structured interviews were conducted with *tuleros* in Santiago (n = 3), fishermen in San Juan (n = 3) and artisans of San Pablo (n = 3). Institutional Review Board (IRB) approval was through SUNY College of Environmental Science and Forestry (through Syracuse University), IRB#16–221. A research license was also approved from the Authority of Sustainable Management of Lake Atitlan Watershed (AMSCLAE, acronym in Spanish), license No.02-2018. An exploratory survey, for sampling site selection, was conducted in January 2021.

# Remote sensing of vegetation

Coverage of littoral vegetation dominated by stands of the CKS *S. californicus* and *T. domingensis* was mapped using Google Earth images of 2018, as described in Garcia Polo et al. (2021); other remote sensing like Sentinel-2 were less valuable due to the high resolution required for the small patch size. The method consisted of analyzing Google Earth images from December 2018 through visual photointerpretation (Tiner, Lang, and Klemas 2015). The resolution of the images permitted identifying and measuring *S. californicus* and *T. domingensis* cover. Classification guided by characteristics of the green colorations, difference in texture, shape patterns, and location near the shoreline aided in discerning between the two species and other vegetation cover (agricultural zones and submersed macrophytes). The non-native macrophyte *H. verticillata* was mapped using Sentinel-2; 10 m resolution images were calibrated with the color combination of bands IR, R, G (8,4,3) to identify spectral firm of *H. verticillata*, further image segmentation and calculations generated distribution maps and cover data. A field validation was conducted February to May 2020, resulting in a verified map of the cover of *H. verticillata*, *S. californicus* and *T. domingensis* (Garcia-Polo et al. 2021).

# Field plant community assessment

In November 2018, a plant survey was conducted in two territories, Santiago and San Juan, to identify differences in vegetation structure and macrophyte diversity. In Santiago, the Committee of *Tuleros* collaborated in providing access to their traditional *tul* planting sites, a total of 15 sites, and arranged a *cayuco* (local names for wooden canoes) for aquatic transportation. Plant surveying in San Juan was conducted in collaboration with *Chajil Chupup.* This organization provided guidance to the planting sites walking along the shore from the public dock. Four sites were surveyed. Due to the size of the planting sites (3 to 6 m width), two plots (1x1 m) were placed, one on the upland terrestrial edge of the wetland and the other one in the center of the wetland. In each plot, we measured three parameters of vegetation structure: stem counts, average above ground height (height) and cover (%) using a visual estimation within six cover categories (Braun-Blanquet 1932). Water depth was measured in each plot as an explanatory factor.

During a brief window without restrictions for COVID-19 from March - May 2021, four sites per village (Santiago, San Juan, San Pablo and San Pedro; Fig. 1), were visited to assess littoral vegetation. Field methods were similar to 2018 using three 1x1 m plots: one located on the upland edge of the wetland, one located in the one in the center of the wetland and the other in the deeper water edge, by foot or *cayuco* when needed. In addition to stem counts, height of *S. californicus* and cover per plant species, we measured average diameter (cm) by measuring with a vernier caliper the diameter of the ten tallest stems per plot. Water depth was measured in each plot as an explanatory factor. Water quality was measured using a handheld WTW Multi 3430 SET F (Wissenschaftlich Technische Werkstätten, Weilheim, Germany) in the center or each wetland for water temperature, dissolved oxygen, pH, and conductivity, for reference information. The Committee of *Tuleros* provided guidance and access to their planting sites in the bay of Santiago Atitlan. Students from the Faculty of Engineering of Universidad del Valle de Guatemala Altiplano Campus assisted with data collection in all sampling sites.

# Wetland condition assessment

We conducted a wetland condition assessment on *S. californicus* stands considering three stressors for analysis: land use/land cover (LULC) stressors, cover of invasive non-native macrophyte *Hydrilla verticillata*, and water level change as a hydrologic indicator. An on-screen approach was followed, detailed in Shappell et al. (2016), to estimate cover and scores for LULC features. This method is feasible for developing countries where access to high-resolution (commercial) aerial/satellite images is limited. The procedure was adapted due to the low number and size of patches for the native vegetation. Four sites (*S. californicus* stands) in each village were selected from the field exploratory survey, and a 100 m radius polygon with a 10x10 m grid was deployed on Google geodata in QGIS 3.4.5 (https://qgis.org). A chart per site was generated (see Fig. S1 in the supplementary material) where land use features were visually classified. The number of grid-cells per class (agriculture, agroforestry, vacation houses- real estate, public beaches, forest, impervious surfaces, other natural vegetation, and *tul*); cover of *H. verticillata* and open water were counted but not included in data analysis for LULC Score estimation. Water level change was also measured on-screen for the same site coordinates, measuring the nearest distance (m) between the water level in 2018 to water level in 2021 using Google Earth Pro, using negative (-) values if the water level was lower than 2018 or positive (+) if water levels were higher than 2018.

# Statistical analyses

# Remote sensing of vegetation

Cover data of each dominant macrophyte, the native *S. californicus* and *T. domingensis* and the non-native invasive *H. verticillata*, were used and compared among management territories Santiago, San Juan, San Pablo and San Pedro by estimating the proportion of each species from their total cover. Landscape level metrics were calculated for each species included, a) Class Area in hectares (CA):

$$CA = \sum a_{ij}/10{,}000$$

1

Where $a_{ij}$ is the area ($m^2$) of patch ij. b) Number of Patches (NP):

$$NP = n_i$$

2

Where $n_i$ is the number of patches of species i; c) Patch Density (PD) is the number of patches per hectare:

$$PD = NP/TA$$

3

Where TA in this context is the total area of the studied littoral region. And d) Largest patch index (LPI):

$$LPI = \left(Max_{a_{ij}}/TA\right) \times 100$$

4

Where TA is in $m^2$ (McGarigal et al. 1995; McGarigal 2006).

## Field plant community assessment

All statistical analyses were performed in R (R Development Core Team 2021). To analyze macrophyte diversity for plant survey 2018 and 2021 frequency data, we used first-order Jacknife (Jacknife 1) for estimated species richness and Shannon Index as a metric of heterogeneity, with the vegan package (Oksanen, Simpson, and Blanchet 2019), using the *poolspec* and *diversity* functions, respectively.

For the 2021 plant survey, *S. californicus* structure response variables (stem counts, height, and diameter) were analyzed using a generalized linear model (GLM) with management as explanatory variable with four factors (i.e., *tulero* management- Santiago; fishermen management- San Juan; external management- San Pablo; and no management- San Pedro). Stem counts GLM used a quasi-Poisson distribution with a log link, after checking for overdispersion with a Poisson distribution (residual deviance degrees of freedom). After confirming non-normality for height and diameter GLM, we used a Gamma distribution with an inverse link. A pairwise comparison using estimated marginal means and the Tukey method was computed with the package *emmeans* (Lenth 2022).

Macrophyte species composition was analyzed with the vegan package (Oksanen, Simpson, and Blanchet 2019) using a non-Metric Multidimensional Scaling (NMDS), function *metaMDS*. The cover (%) data were square root transformed and Wisconsin standardized. Significance was tested with permutational multivariate analysis of variance (PERMANOVA) using the *adonis* function, with a Bray Curtis distance and 999 permutations.

## Wetland condition assessment

Percentages for each LULC class were estimated with the grid-cells counts and the total grids in the terrestrial and shoreline area. Each class was assigned a weight based on the impact on wetlands (e.g.: impervious surfaces = 4, forest = 0), and LULC score was estimated using the equation:

$$LULCscore = \sum LULC_i * W_i/10$$

5

Where $LULC_i$ is the cover (%) of class i and $W_i$ is the corresponding weight to class *i*, based on Shappell et al. (2016). For all LULC classes, *H. verticillata* and water level change, mean and standard error were estimated per territory.

## Water depth effect model

The influence of water depth on the response variables was analyzed using a generalized linear mixed models (GLMM) with random effects, with water depth as fixed effect and site nested in management territory as random effect. Response variables, diameter and height were analyzed using the *glmer* function of lme4 package (Bates et al. 2021) with a Gamma distribution and an inverse link. The stem count GLMM with a Poisson distribution and a log link was checked for overdispersion with the blmeco R package, then stem count was analyzed with a quasipoisson distribution using the function *glmmPQL* of the MASS package (Ripley 2023). We tested water depth in categorical variables defined as 'zero' (water level = 0 cm) and 'above zero' (water level > 0 cm). A pairwise comparison using estimated marginal means and the Tukey method was computed with the package *emmeans* (Lenth 2022).

## Results

# Remote sensing of vegetation

The vegetation cover and distribution map of the three macrophyte species *S. californicus*, *T. domingensis*, and *H. verticillata* (Fig. 2), illustrate the dominance of *H. verticillata* in the littoral region studied in Lake Atitlan. Comparing between villages, Santiago showed the highest cover for all three species, 81% of the total area of *S. californicus*, 98% of *T. domingensis*, and 90% of *H. verticillata* (Fig. 3). San Pedro showed the lowest cover of *S. californicus* (3%), San Pablo with no cover of *T. domingensis*, and San Pedro and San Juan with lowest cover of *H. verticillata*. Landscape metrics (Fig. 3) were found for *S. californicus* to have highest values of CA and NP in Santiago. San Pablo was highest for PD, and LPI. *T. domingensis* had the highest metrics (CA, NP and PD) in Santiago. Only LPI was higher in San Juan. *Hydrilla verticillata* showed highest metrics for CA and NP in Santiago, PD in San Juan and LPI in San Pablo.

# Field plant community assessment

# Richness and diversity index

Santiago showed a higher macrophyte richness and diversity compared to San Juan in 2018 (Table 1). In 2021, Santiago showed higher observed species (17) followed by San Juan, San Pedro and only four species were observed in San Pablo. Species richness estimator, Jackknife 1 showed that Santiago had the highest estimated species richness and San Pablo with the lowest, and similar in San Juan and San Pedro. Likewise, Shannon diversity index suggested that Santiago had the highest and San Pablo the lowest plant diversity, and was similar in San Pedro and San Juan.

# Vegetation structure and management territories

Santiago showed the highest stem counts, height, and diameter EM means (Table 2), followed by San Juan in stem counts and diameter EM means and San Pablo in height EM mean. San Pedro had the lowest stem counts and diameter EM mean, and San Juan had the lowest height EM mean. The EM mean contrast showed Santiago diameter EM mean was significantly different among the other territories (Table 2). Differences in height EM means were not statistically significant among territories. Similar was observed with stem counts EM means with no significant difference, the lowest $p$-value was between Santiago and San Pedro ($p = 0.0555$).

# Macrophyte species composition

The NMDS indicated that macrophyte compositions showed similarities among territories (Fig. 4A). When *H. verticillata* was excluded from the analysis, NMDS showed a different plant composition in Santiago and San Pablo (Fig. 4B), and when *S. californicus* was excluded, distinct composition in Santiago (Fig. 4C). The PERMANOVA found significant differences of plant composition among the four management territories ($p < 0.01$). The plant community composition also was significantly different among territories when excluding *S. californicus* ($p < 0.05$) and *H. verticillata* ($p < 0.05$) from the PERMANOVA.

# Wetland condition stressors assessment

The LULC scores (Table 3) suggested San Pedro and San Pablo experienced a greater impact from land use, Santiago presented the lowest LULC score (18.2 ± 2.8). Invasive non-native macrophyte *H. verticillata* was more abundant in San Pedro and San Pablo, and Santiago and San Juan had similar cover of *H. verticillata* (6.6% ± 1.9 and 5.6% ± 1.1, respectively). Water level from 2018 to 2021 decreased in all territories, but San Juan and Santiago was found to have a larger retreated distance of the water level (-41.5 ± 9.0 and − 27.4 ± 4.0, respectively).

# Water depth effects on vegetation structure

The diameter EM means of *S. californicus* (Table 4) were the lowest in water level 'zero' depth, significantly different from the 'above zero' category ($p < 0.05$). Our models, GLMM, suggest that water level 'zero' negatively affected both height and diameter EM means. GLMM suggested that stem count be higher in the water depth 'zero' category than 'above zero'; however, it was not statistically significant (Table 4).

## Discussion

Wetland condition assessment incorporates multi-levels including landscape-level and field-based rapid and intensive surveys (Kentula 2007). On a landscape scale, wetland mapping and extent have been used extensively as an indicator of wetland health (Fennessy et al. 2007; Patience and Klemas 1993). Mapping different wetland types using GIS for integration and analysis of geospatial data and aerial imagery has been a standard for landscape-level wetland assessment (Tiner 2018), and includes using high-resolution aerial imagery like Google Earth as an alternative for locations where wetland inventories and maps are not available (Tiner 2018; Tiner et al. 2015). Similar remote sensing methodologies have been used before in Lake Atitlan to assess water quality and cyanobacteria blooms (Flores-Anderson et al. 2020). In this study we conducted a landscape-level assessment by using remote sensors Sentinel-2 and Google Earth images to map the wetland types and cover distributions for the first time in Lake Atitlan (Garcia-Polo et al. 2021). In addition to the landscape-level methods, the field surveys of vegetation structure, cover and plant diversity conducted for this study can be used as indicators of wetland condition and ecological integrity (Faber-Langendoen et al. 2019; Fennessy et al. 2007). In future studies we suggest considering other organisms for testing diversity indices such as macroinvertebrates, diatoms, or fish assemblages (Reiss and Brown 2007).

Our results suggest that Santiago, where wetland plant TEK is most intact of the four sites, informs the actions and practices for coping with biophysical stressors and adapting to environmental changes, as in many other traditional resource management systems (Berkes 2017) showing the best condition based on wetland indicators of extent, structure, and plant diversity and composition. San Juan wetland indicators of extent and structure suggest better wetland conditions than San Pablo and San Pedro, affected mainly by the water level reduction, San Juan's littoral wetland area has been sensitive to water level fluctuations (Berger 2008; Rejmánková et al. 2018b). Despite water level reductions and potential *H. verticillata* invasion, Santiago had better wetland conditions and ecological integrity compared to wetlands in the other Tz'utujil territories. These conditions suggest that TEK of *Tuleros* in Santiago has a major influence on the wetland sustainability in Lake Atitlan.

### Traditional Tulero Practice

As mentioned earlier, the Tuleros in Santiago have a long-standing tradition of growing tul and using fibers for making *petates* (López 1990; LaBastille 1974). Their TEK informs aquatic plant use, cultivation and management actions to cope with stressors of plant growth. For example, the *Tuleros* explained the actions during water level fluctuations. *"If the lake goes down, the tul stays outside and dries up. We must move it. And if the lake rises the tul drowns, we must also take it to the shore."* They also described actions for tul growth and maintenance that involves "planting and more planting", where more than 65 active *Tuleros* each plant a minimum of ten plugs in about a 10 m long fringe with constant care: *"…planting tul, we clean the tul and then we cut them and so we dry them in the sun; then we make the bundles and later when we get home, we measure which ones we make petates*". Cleaning includes collection of litter but also the extraction of the invasive species *H. verticillata*. These traditional practices act as a small-scale disturbance that helps wetland renewal (Falkowski et al. 2020; Berkes 2017). For example clear cutting the *tul* in small areas is a small-scale and intensive disturbance that benefits waterfowl and the wetland by making fresher and straighter stalks with less matting and choking, allowing seeding and regrowth, and eliminating debris accumulated in soil and water surface (LaBastille 1974). In San Juan the main goal of *Chajil Chupup* fishermen for transplanting *tul* is to maintain fish habitat (only one fisherman makes *petates* and handicrafts), but at same time they sell *S. californicus* patches to San Pablo's artisans. Two times each year *Chajil Chupup* transplants plugs of *S. californicus* from patches left out of the lake. They tie a stone in the roots and use a cayuco to move the *tul* to areas 2 to 4 m deep, and it is buried preferably in muddy soils (Berger 2008). San Pablo's artisans harvest and sun dry *tul* fibers in the shoreline of San Pablo and San Juan, but also buy fibers in the market from Santiago to make petates. No evidence was found of artisans planting *tul* on San Pablo's littoral region. However, the government and volunteers created two planting areas in San Pablo in 2019 of 100 plugs, and two planting in 2020 of 185 plugs in 140 linear meters (AMSCLAE 2020a).

## Comparison to Past Studies

We were unable to directly compare with previous studies because of different methods and scales, but the data reported can provide additional evidence of reference wetland conditions and trends. In 1967 the extent of the lake shoreline covered by aquatic vegetation was 25.8 km of the shoreline with the 63.7% of *S. californicus* and 20.1% of *T. domingensis* (LaBastille 1974). Wetland size declined from 25 km of shoreline covered by both species in 1968 to 10.5 km in 1980, mainly because the lake level dropped 4.5 m after the 1976 earthquake (7.5 magnitude). A slight recovery was recorded in 1983 up to 14 km mostly on the southern shore of Lake Atitlan (LaBastille 1989). A water level increase is another stressor of wetland growth, as mentioned by *Tuleros*. During the events of higher water levels increase, the deeper water weakens *S. californicus* rhizome system limiting resprout growth, especially when shading by *H. verticillata* limits photosynthesis and outcompetes for nutrients and space (Rejmánková et al. 2018). The literature agrees with TEK of *Tuleros* that the water level fluctuations are stressors of *S. californicus* growth. We agree on the relevance of considering water depth and other hydrology indicators in wetland research (Tiner 2016); water depth, water level fluctuations, or soil moisture had a significant role in shaping wetland vegetation (Kua et al. 2020; Jones et al. 2021). Our results show the influence of water depth on the structure in *S. californicus* stands, where plots of water level zero (drier soils) showed lower heights and diameters, and plots in deepest waters showed the lowest measurements (stem densities, height and cover) where rhizome stress and abundant *H. verticillata* may limit stalk regrowth (Rejmánková et al. 2018b). In addition, we provided evidence of a current period of accelerated water level reduction in agreement with the government lake level monitoring (AMSCLAE, 2020b). Therefore, traditional management practiced by *Tuleros* appears to be playing a role under a dynamic hydroperiod with annual and interannual fluctuation, especially with the increasing impacts of climate change; predictions had set a reduced water availability in the Lake Atitlan watershed and in general for the freshwater ecosystems in Latin America (Garcia-Oliva et al. unpublished, Castellanos et al. 2022).

# Conclusion

This study used indicators of wetland health and ecological integrity, centered on the role of different traditional wetland uses and management currently present in Lake Atitlan, Guatemala. Our results provide evidence of the ecological value of Indigenous resource management for wetland extent, structure, and plant diversity and composition. This work is another example of how prioritizing Indigenous resource managers could enhance society’s ability to adapt to local and global changes. Traditional management, such as *Tulero* practice, could be central to policy initiatives prioritizing livelihood through stewardship for ecological restoration.

For holistic watershed stewardship, inclusion of wetland TEK is vital for watershed sustainable management plans and other environmental management programs (i.e., restoration, alien plant management, climate change adaptation). Access to land for wetland uses for managers will nurture this long-standing tradition and revitalize the cultural practices of the Maya people in Lake Atitlan, growing pride, identity, and self-determination. Legal actions and innovations for granting rights and security of customary wetland will lead to social justice and equity. In addition to the need for interventions supporting market development for wetland plant-based products as an economic dimension, in Lake Atitlan a joint project emerged with participation of *Tuleros*, government, academia, and the private tourism sector through Community-Based Tourism initiatives for conservation. The “*Tour del Tul Atitlan*” provides a novel experience for tourists; while rowing wooden canoes along the marshes, they learn to plant and care for the *tul*, craft making, plant diversity, and landscape, and in return, support the *Tuleros* livelihood and the management of healthy diverse wetlands systems. Transdisciplinary initiatives are encouraged using solid ecological indicators and methods coupled with social and cultural values.

# Declarations


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### Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

### Author Contributions

JGP and SAWD did study conception and design. JGP performed material and equipment preparation and data collection. JGP and SAWD wrote a first draft. TBF advised statistical analysis. DJL reviewed earlier versions of the manuscript and provided significant editions and comments. All authors contributed to commenting on previous versions and approved the final version of the manuscript.

### Data Availability

The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

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# Tables

Table 1 Vegetation structure and macrophyte diversity. Average values per parameter measured during the plant surveys of November 3-10, 2018 and March 3 - May 24, 2021 in Lake Atitlan, Guatemala. Means ± standard error values provided. nd: not determined.

| Parameters | | Survey | 2018 Plant survey | | 2021 Plant survey | | | |
|---|---|---|---|---|---|---|---|---|
| | | Treatments | Santiago | San Juan | Santiago | San Juan | San Pablo | San Pedro |
| | | #Plots | 30 | 8 | 12 | 12 | 12 | 12 |
| Structure | Stem count | stems/m2 | 113.4 ± 3.9 | 151.9 ± 5.3 | 137.8 ± 10.6 | 126.8 ± 13.9 | 95.5 ± 11.2 | 88.0 ± 16.5 |
| | Height | cm | 284.1 ± 9.4 | 266.0 ± 12.7 | 247.5 ± 8.6 | 199.2 ± 15.1 | 223.9 ± 16.1 | 180.5 ± 25.9 |
| | Cover | % | 76.6 ± 1.7 | 84.4 ± 4.5 | 60.4 ± 2.5 | 51.3 ± 4.3 | 40.2 ± 4.6 | 37.7 ± 7.5 |
| | Diameter | cm | nd | nd | 1.2 ± 0.09 | 0.9 ± 0.05 | 0.8 ± 0.04 | 0.7 ± 0.10 |
| | Depth | cm | 19.1 ± 3.5 | 17.0 ± 6.0 | 15.2 ± 4.4 | 10.2 ± 3.0 | 24.1 ± 7.0 | 34.6 ± 10.0 |
| Diversity | Richness | No. species | 15 | 6 | 17 | 12 | 4 | 11 |
| | | Jackknife 1 | 19.8 ± 2.5 | 9.5 ± 2.9 | 26.2 ± 4.6 | 19.3 ± 6.0 | 5.8 ± 1.3 | 17.4 ± 3.6 |
| | Heterogeneity | Shannon | 0.79 ± 0.09 | 0.19 ± 0.09 | 0.85 ± 0.07 | 0.52 ± 0.14 | 0.47 ± 0.06 | 0.55 ± 0.14 |

Table 2 Estimated marginal (EM) means of the Generalized Linear Model (GLM) for management territories (explanatory variable - 4 levels) over the three response variables of *S. californicus* structure, stems count, above ground height (cm) and diameter (cm). GLM with a quasi-Poisson distribution with a log link (for stem counts) and with a Gamma distribution with an inverse link (for height and diameter). Pairwise comparison using the Tukey method resulted in statistically significant differences for diameter EM means among sites as shown with a shared letter for each contrast, where *p*-value for a is $p = 0.0036$, for b is $p = 0.0006$, and for c $p = 0.0054$.

| Parameters | Generalized linear models (GLM) for management territories | | | |
|---|---|---|---|---|
| | Santiago | San Juan | San Pablo | San Pedro |
| Diameter | 1.19 ± 1.05 [a,b,c] | 0.89 ± 0.05 [a] | 0.84 ± 0.05 [b] | 0.88 ± 0.05 [c] |
| Height | 247 ± 17.7 | 199 ± 14.3 | 224 ± 16.1 | 207 ± 16.1 |
| Stem counts | 137.8 ± 15.3 | 126.8 ± 14.6 | 95.5 ± 12.7 | 88.0 ± 12.2 |

Table 3 Wetland condition stressor assessment results for the four Maya-Tz'utujil communities, San Juan, San Pablo, San Pedro and Santiago. Mean ± standard error is presented per Land Use and Land Cover (LULC) category in percentage (%), LULC scores, cover of the invasive non-native macrophyte *H. verticillata*, and water level change in meters (m) linear distance from water level in 2018 to water level in 2021.

| **Parameters** | **Survey** | **2021 Wetland condition stressor assessment** | | | |
|---|---|---|---|---|---|
| | **Treatments** | **Santiago** | **San Juan** | **San Pablo** | **San Pedro** |
| | #Sites | 4 | 4 | 4 | 4 |
| LULC Analysis (%) | Impervious surfaces | 5.1 ± 4.4 | 1.5 ± 1.0 | 0.3 ± 0.3 | 33.1 ± 15.8 |
| | Real state and beaches | 1.7 ± 1.7 | 3.3 ± 3.3 | 0.6 ± 0.6 | 14.2 ± 5.4 |
| | Agriculture | 51.4 ± 10.6 | 62.3 ± 2.8 | 87.3 ± 2.4 | 26.5 ± 16.4 |
| | Agroforestry | 0 | 8.0 ± 5.5 | 0 | 0 |
| | Forest/ trees | 39.2 ± 9.5 | 6.1 ± 3.8 | 7.6 ± 1.8 | 17.7 ± 8.5 |
| | Other vegetation | 2.5 ± 0.5 | 18.8 ± 6.8 | 4.2 ± 0.7 | 8.5 ± 3.5 |
| | LULC Scores | 18.2 ± 2.8 | 22.2 ± 1.3 | 26.5 ± 0.5 | 27.0 ± 3.8 |
| Invasive macrophyte | *H. verticillata* (%) | 6.6 ± 1.9 | 5.6 ± 1.1 | 15.7 ± 8.3 | 23.0 ± 5.7 |
| Hydrology | Water level change (m) 2018-2021 | -27.4 ± 4.0 | -41.5 ± 9.0 | -12.6 ± 7.3 | -9.3 ± 3.7 |

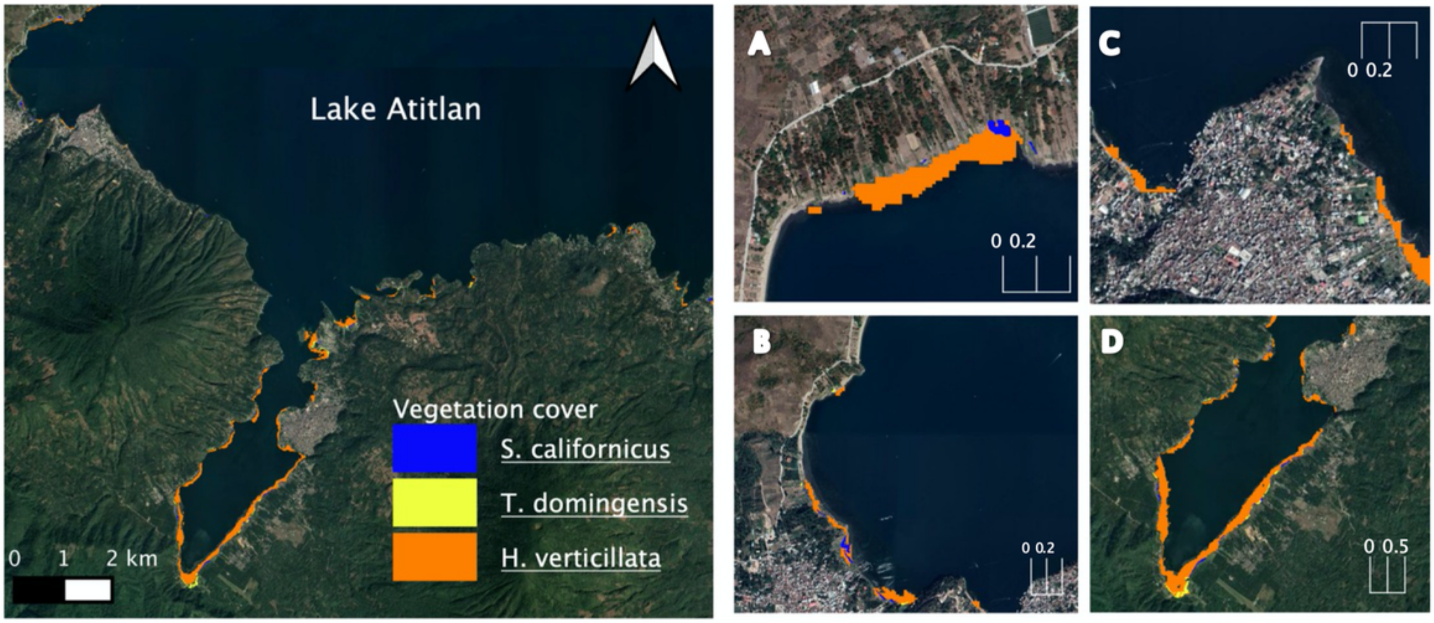
Table 4 Estimated marginal (EM) means of the Generalized Linear Mixed Model (GLMM) with both fixed effects (water level categories) and random effects (sites nested in management territories) for three response variables (diameter, height, and stem count). Pairwise comparison using the Tukey method were statistically significantly different for diameter EM means as shown with a shared letter, where *p*-value for a is $p = 0.0127$.

| **Parameters** | **Zero (0 cm water depth)** | **Above zero (>0 cm water depth)** |
|---|---|---|
| Diameter | 0.84 ± 0.07 [a] | 0.91 ± 0.08 [a] |
| Height | 204 ± 15.9 | 222 ± 15.5 |
| Stem counts | 115 ± 13.7 | 109 ± 11.7 |

# Figures

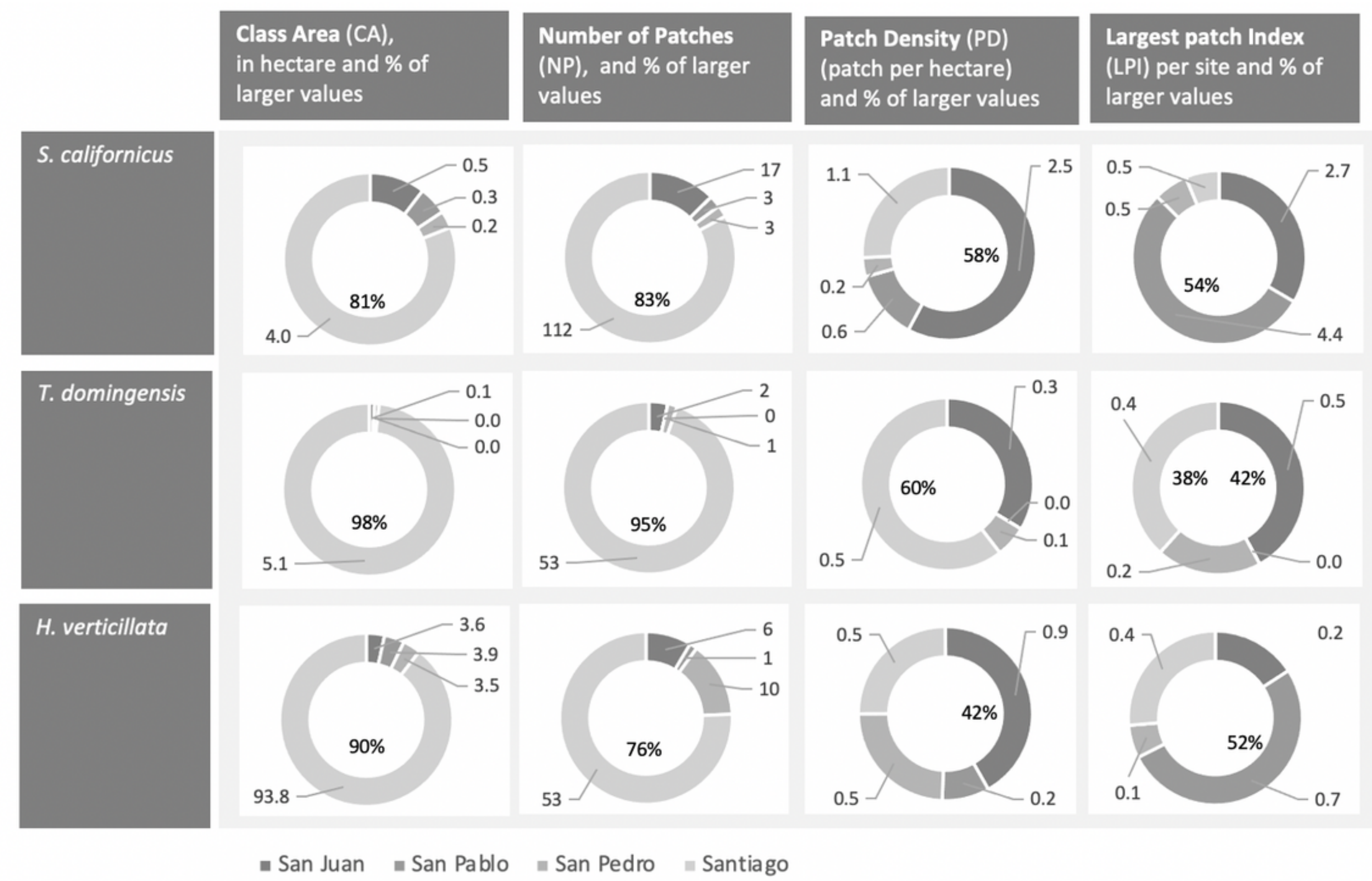

**Figure 1**

Location of Lake Atitlán, Guatemala with watershed boundaries. Study sites located in the four Maya-Tzutujil territories. The four images (lower right side) show the sampling site locations used for the wetland condition stressor assessment and 2021 plant survey, San Pablo (A), San Juan (B), San Pedro (C) and Santiago (D)




#### Figure 2

Cover of native vegetation *S. californicus* and *T. domingensis* in the four Maya-Tz'utujil territories in Lake Atitlan shore, Guatemala. Species were identified and classified manually from Google Earth photo of December 2018. The four images on the right show a zoom in each territory's plant cover distribution, San Pablo (A), San Juan (B), San Pedro (C) and Santiago (D)




## Figure 3

Cover metrics of (A) *S. californicus*, (B) *T. domingensis*, generated from Google Earth photographs and (C) *H. verticillata* from Sentinel-2 in the four Maya-Tz'utujil sites, San Juan, San Pablo, San Pedro and Santiago Atitlan. For each species their proportion from the total sum cover for the four sites was calculated and four landscape metrics: 1) class area (CA), the sum of all patch areas of each species in hectare; 2) number of patches (NP), the sum or patches per site; 3) patch density (PD), patch area per hectare in each site; and 4) largest patch index (LPI), the patch maximum area in relation to the total littoral area per site. Number inside circles consist of percentages of the largest values per metric for each species

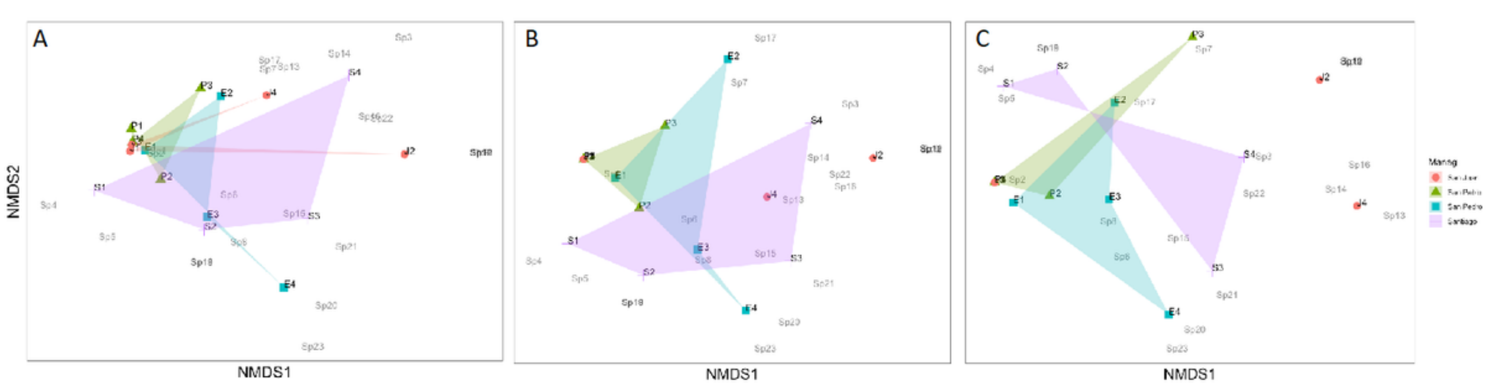


**Figure 4**

Multivariate analysis of the macrophyte species composition, per site in each Maya-Tz'utujil management territories. Results of the non-Metric Multidimensional Scaling (NMDS). Cover data in percentage was square root and Wisconsin transformed and significance tested with PERMANOVA, (A) cover of all macrophyte registered, significant difference among managed territories (stress = 0.13, k = 2, $p < 0.01$), (B) excluding *S. californicus* cover (stress = 0.11, k = 2, $p < 0.05$), and (C) excluding *H. verticillata* cover (stress = 0.13, k = 2, $p < 0.05$)

# Supplementary Files

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