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Macrophyte species distinctly affect diurnal carbon dioxide and methane fluxes on a tropical coastal lagoon

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Abstract: Macrophyte species distinctly influence carbon dioxide (CO_2) and methane (CH_4) fluxes in aquatic ecosystems, both indirectly (via diffusion and ebullition) and directly (through internal gas transport). Consequently, greenhouse gases (GHGs) fluxes may vary depending on the species stands, day-period, and gas pathways. We evaluated diurnal CO_2 and CH_4 dynamics in five macrophyte stands in Jurubatiba lagoon, a tropical humic coastal ecosystem. We expect that both CO_2 and CH_4 fluxes will vary along day according to macrophytes photosynthetic activity, and that incorporation and/or emission rates among distinct species is not homogeneous. Diurnal variability was not observed for diffusive CH_4 fluxes, but higher CO_2 uptake was registered during noon for diffusive and via-macrophytes gas pathways. Photosynthetic active radiation and plant biomass significantly influenced macrophyte CO_2 fluxes. Stands of species employing convective throughflow mechanism exhibited considerable variations in methane emissions during the daytime, but such rates were considerably higher via bubbles. Elevated CO_2 incorporation and CH_4 emission rates were detected in stands of the emergent species, driven by depth, dissolved oxygen and plant biomass variations. Our results underscore the importance of considering daily-scale variations and differences among macrophyte stands when examining their effects on C dynamics in tropical coastal aquatic ecosystems.

Key words: Carbon cycling; Diffusion; Ebullition; Internal gas transport; Littoral zone.

Espécies de macrófitas influenciam distintamente os fluxos diurnos de dióxido de carbono e metano em uma lagoa costeira tropical. Resumo: Espécies de macrófitas influenciam de modo distinto os fluxos de gás carbônico (CO_2) e metano (CH_4) em ecossistemas aquáticos, tanto indiretamente (via difusão e ebulição) quanto diretamente (via mecanismos internos de transporte de gases). Consequentemente, os fluxos desses gases de efeito estufa (GEEs) podem variar dependendo das espécies presentes, do período do dia e das vias de liberação dos gases. Avaliamos a dinâmica de CO_2 e CH_4 em bancos de cinco espécies de macrófitas ao longo do dia na lagoa de Jurubatiba, um ecossistema costeiro tropical húmico. Esperamos que os fluxos de CO_2 e CH_4 variem ao longo do dia de acordo com a atividade fotossintética das macrófitas, e que taxas de incorporação e/ou emissão não sejam homogêneas entre as diferentes espécies. Não foi observada variabilidade diurna nos fluxos difusivos de CH_4, mas maior captação de CO_2 foi registrada ao meio-dia para fluxos difusivos e via macrófitas. A radiação fotossinteticamente ativa e a biomassa vegetal influenciaram significativamente os fluxos de CO_2 pelas macrófitas. Bancos das espécies que empregam o mecanismo de fluxo convectivo apresentaram variações consideráveis nas emissões de CH_4 durante o dia, mas as taxas de emissão foram consideravelmente maiores via bolhas. Elevadas taxas de incorporação de CO_2 e emissão de CH_4 foram detectadas em bancos de espécies emergentes, associadas a variações de profundidade, concentração de oxigênio dissolvido e biomassa vegetal. Nossos resultados ressaltam a importância de considerar variações em escala diária e diferenças entre bancos de macrófitas ao examinar seus efeitos na dinâmica do C em ecossistemas aquáticos costeiros tropicais.

Palavras-chave: Ciclagem do carbono; Difusão; Ebulição; Transporte interno de gases; Zona litorânea.

Introduction

Carbon dioxide (CO_2) and methane (CH_4) are two of the main greenhouse gases (GHGs; IPCC 2023). Within natural sources of these GHGs to the atmosphere, wetlands are some of the most important on a global scale, contributing to about 2.05 Pg of C (CO_2 equivalent) annually (IPCC 2023, Bastviken et al. 2011). The emission of GHGs from wetlands can occur through distinct mechanisms. Previous studies reported that CO_2 and CH_4 concentrations in water and sediment are the main factors that regulate diffusive and ebullient emission rates of GHGs, respectively (Bastviken et al. 2011, Marotta et al. 2009, 2014). Under gas availability, diffusive rates are enhanced by water temperature and wind speed, whereas the emission via bubbles is enhanced under low hydrostatic pressures due to low water column depths (Marotta et al. 2009, Bridgham et al. 2013).

Aquatic macrophytes are also fundamental elements for GHGs exchanges between aquatic ecosystems and the atmosphere, and play a critical role in carbon (C) cycling in wetlands. Macrophytes absorb CO_2, CH_4 and other gases accumulated in water and sediment into their tissues, and then release them to the atmosphere (Knapp & Yavitt 1995, Hirota et al. 2007, Kosten et al. 2016). But these plants also act as greater C sinks due to CO_2 incorporation for biomass production and C sedimentation, counterbalancing to some extent their effects on GHGs emission (Hirota et al. 2007, Gripp et al. 2013, Peixoto et al. 2016)

Stands of distinct macrophytes, however, do not contribute to GHGs exchanges in similar ways. First, macrophyte stands have distinct abundances, and species have distinct C uptake efficiencies, stoichiometric ratios, and aerobic and anaerobic decomposition rates, which regulate the amount of C assimilation and GHGs exchanged with the atmosphere (Knapp & Yavitt 1995, Gripp et al. 2013, Marinho et al. 2010, O'Sullivan et al. 2010, Xu et al. 2014). Second, aquatic macrophytes distribution are determined by their physiological requirements and, to a certain degree, by abiotic conditions along the littoral zone (Chappuis et al. 2014). Species properties may interact with environmental aspects and affect the stands effects on C cycling. For example, although floating plants may have great anaerobic digestion potentials (O'Sullivan et al. 2010), a large proportion of the CH_4 produced on their stands may become oxidized below the superficial mat they form before escaping to atmosphere (Kosten et al. 2016, Fonseca et al. 2017), reducing methane, but increasing CO_2 emissions. On the other hand, even though emergent macrophytes present high root and rhizome oxidative potentials (Fonseca et al. 2017, Ding et al. 2004, Laanbroek 2010), CH_4 emission may be considerably larger in their stands because they are in contact with both the atmosphere and the sediment, where most of the gas is produced.

Finally, GHG exchanges at macrophyte stands also vary with day-period. Carbon dioxide is essential for biomass production, and photosynthetic rates in aquatic macrophytes is associated with light availability (Knapp & Yavitt 1995, Peixoto et al. 2016). The magnitude of diel variations in plant-mediated CO_2 and CH_4 exchanges also depends on gas flow mechanisms (Ding et al. 2004, Greenup et al. 2000, Käki et al. 2001, Konnerup et al. 2011). Plants which rely solely on molecular diffusion for gas transport do not show large variations in GHGs emission rates along the day (Greenup et al. 2000, Whiting & Chanton 1992). On the other hand, pressurized gas flow in some aquatic macrophytes is regulated by plant functioning and daily stomatal aperture variations that are induced by hormonal and environmental signals, such as CO_2 concentration, radiation intensity, air humidity and temperature (Armstrong et al. 1996, Armstrong & Armstrong

1990, Bendix et al. 1994, Dacey 1980). As a result, diurnal variations in GHGs exchanges from plants employing pressurized gas flow tend to be greater than from plants that rely on molecular diffusion. Thus, sites dominated by floating-leaved and, mainly, emergent macrophytes may be considerably heterogeneous on C incorporation and emission throughout the day.

Therefore, diurnal and spatially explicit variations in macrophyte distribution along littoral zones must be considered to understand the role these plants play as C sources or sinks in aquatic ecosystems, mainly in low-latitude wetlands such as tropical coastal lagoons, which the current study targeted. Tropical aquatic ecosystems emit the largest portion of CO_2 and CH_4 to the atmosphere on a global scale (Marotta et al. 2009, Zhang et al. 2017). Also, the largest discrepancies and uncertainties in the estimates of GHGs emissions are reported on tropical aquatic ecosystems, due to: i) a considerable sub-representation of studies in this region (Sobek et al. 2005); ii) the great spatial and temporal variation in production and emission of GHGs (Bastviken et al. 2011, Marotta et al. 2009, Sobek et al. 2005); and iii) a lack of studies evaluating GHGs pathways (i.e. diffusive, ebullient, via aquatic macrophytes, etc; Bastviken et al. 2011, Bodmer et al. 2024). So, understanding how CO_2 and CH_4 exchanges are regulated by ecosystem properties and vary within spatial and temporal scales and between distinct pathways is essential for assessing their importance, and for monitoring and modelling C dynamics on tropical aquatic ecosystems. This work aims to evaluate the dynamics of CO_2 and CH_4 emission and uptake from/to atmosphere in stands of five aquatic macrophytes throughout the daytime in a southeastern Brazilian coastal lagoon. The macrophyte species evaluated belongs to three distinct life forms: floating, floating-leaved and emergent. We hypothesize that: i) CO_2 incorporation rates – a proxy for primary production – are higher during periods of greater light incidence (noon); and ii) the incorporation of CO_2 and the emission of CH_4 by emergent stands are greater than for floating ones. We also report trends in ebullient gas flows between distinct macrophyte stands, since it contributes to our understanding of general patterns on GHGs dynamics in aquatic ecosystems.

Material and Methods

Study Area: The study was conducted in Jurubatiba Lagoon (22º24’ S, 41º42’ W), situated at the Restinga de Jurubatiba National Park, in the northern region of Rio de Janeiro state, Brazil (Fig. 1). Jurubatiba is a pristine freshwater coastal lagoon, characterized by black water resulting from large inputs of colored terrestrial dissolved organic matter originated from the surrounding restinga ecosystem (Suhett et al. 2013, Genovez et al. 2024). The lagoon features a shallow water column and dendritic morphometry which support the establishment and growth of a diverse array of aquatic macrophyte species (Panosso et al. 1998). The climate in the region is characterized as tropical sub-humid/humid, with an annual precipitation of approximately 1,165 mm, mostly concentrated between November and January, and mean monthly temperature ranging from 19 to 25 °C (Caliman et al. 2010).

Data Sampling: We estimated C flux on a representative stand of five common species in Jurubatiba lagoon (Fig. 1 and Fig. 2), belonging to three distinct life forms: floating (*Salvinia biloba* Raddi), floating-leaved (*Nymphaea pulchella* DC. and *Pontederia azurea* Sw.) and emergent species (*Typha domingensis* (Pers.) and *Schoenoplectus californicus* (C.A. Mey.) Soják). Representative stands were defined as sites covering at least 100m², where these species were dominant, accounting for more than 80% of the macrophytes cover. On each stand, the rates of CO_2 and CH_4 fluxes by diffusion across the water surface, via bubbles and via macrophytes were estimated during daytime in September, 2009.

Diffusive and macrophyte fluxes were sampled during three distinct day-periods: morning (6 - 8:30 AM), noon (11 AM - 1:30 PM) and afternoon (4 – 6:30 PM). Carbon dioxide and methane fluxes originating from these mechanisms were estimated using single-component static closed chambers, varying in size (area and internal volume), material composition, sampling duration, and frequency, designed to evaluate plant species with distinct sizes and forms, and to minimize measurement problems (Livingston & Hutchinson 1995, Denmead 2008), based on previous tests (see Fig. 2 for details).

Diffusive gas fluxes were estimated on six 0.09m² acrylic floating chambers with a 5L internal air volume over 15 minutes. Air samples were collected from the chamber headspace at the beginning and 5-minute intervals, using 3mL gas syringes sealed with a stop-cock. Fluxes via floating

Figure 1. (a) Delimitation of Jurubatiba lagoon. (b) Open water and macrophytes cover at Jurubatiba lagoon in 2008, based on NDVI index. Red squares indicate the stands of the species *Salvinia biloba* (Sb), *Nymphaea pulchella* (Np), *Pontederia azurea* (Pa), *Typha domingensis* (Td), and *Schoenoplectus californicus* (Sc), evaluated in the present study.

and floating-leaved macrophytes were estimated on six chambers similar to those referred above, for 9 minutes, with air samples collected at the beginning and 3-minute intervals. Fluxes via emergent macrophytes were estimated using six transparent plastic chambers (0.0765m² x 2m height; Vulcan - 0.6 mm), for the same period and frequency as previously described for non-emergent macrophytes. The same six sites and set of macrophytes were sampled during the three day-periods, for diffusive and macrophyte fluxes, respectively. Sampling intervals for each gas flow mechanism were determined based on preliminary tests. Diffusive fluxes measurements were performed between plants, ensuring no leaves were present inside or below the chamber. Special care was also taken during sampling in order to avoid bubbling inside the chambers, and data indicating clear signals of bubbling effects on fluxes were eventually removed from the analyses.

Ebullient fluxes from stands were estimated on six 0.07m² inverted funnels, with 50mL tubes attached at the top, deployed for 23 to 26 hours. CO_2 and CH_4 concentrations in the headspace of the tubes (for ebullient flow) and syringes (for diffusive and via macrophytes flows) were determined in the lab by gas chromatography, using a Shimadzu GC-2010 equipped with a flame ionization detector (FID). Samples were stored in a refrigerator (~ 4ºC) prior to the analysis and were analyzed up to two days after sampling. For FID detection, the gas in the samples was burned together with ultra-pure N_2 used as the carrier gas, in the presence of H_2 and synthetic air. The injection, detection and column temperatures were maintained at 120ºC, 200ºC, and 85ºC, respectively.

During field sampling, stand depth, air temperature (estimated using a bulb thermometer), salinity (YSI-30 probe), water temperature and oxygen concentration (YSI-95 probe), wind speed (anemometer Kestrel 2000), and the intensity of photosynthetically active radiation (PAR; LI-COR radiometer LI-1000, estimated as the photosynthetic photon flux density) were determined at all sampling sites. At the end of the samplings, the six sets of macrophytes sampled at each stand were collected to determine their aerial biomass (dry weight above the water column) in an oven, at 70ºC.

Figure 2. Pictures of stands of *Salvinia biloba* (a and b), *Nymphaea pulchella* (c and d), *Pontederia azurea* (e and f), *Typha domingensis* (g and h), and *Schoenoplectus californicus* (i and j) sampled in Jurubatiba lagoon along this study. Pictures also present the equipments and methods employed for determination of diffusive fluxes (b), macrophyte fluxes with small (d) and big chambers (h), ebbulitive fluxes (f), and plant biomass (j).

Data Analysis: Flux determination: Considering that gas concentration continually change (increases or reduces) in closed static chambers due to the small amount of air in their headspace (Denmead 2008), we integrated the air samples taken from each chamber and used a linear model to estimate gas fluxes. The flux measurements with $R^2 < 0.5$ were rejected. Diffusive and via macrophyte gas fluxes - F_g ($mg.m^{-2}.h^{-1}$) were then calculated using the formula:

$$F_g = (V/A).dpg/dt, \qquad \text{(Equation 1)}$$

where V (cm^3) is the volume of the headspace, A (m^2) is the surface area covered by the chamber, dpg ($mg.cm^{-3}$) is the GHG concentration in the air entering or leaving the chamber and t (hour) is the time.

The ebullient flux E_g ($mg.m^{-2}.h^{-1}$), measured by inverted funnels, was estimated as:

$$E_g = V.C/A.dt, \qquad \text{(Equation 2)}$$

where V is the gas volume stored on the tube, C is the gas concentration of the sample, A is the funnel area, and *d*t is the time interval (Keller & Stallard 1994).

Statistical analysis: To assess the importance of species for CO_2 and CH_4 ebullient flow, a one-way ANOVA was performed, using the "anova" function in the software R v. 4.4.1 (R Core Team 2024), considering bubble fluxes as the response variable and macrophyte species as a fixed factor. The coefficient of determination (R^2) from the underlying linear model is reported as the measure of effect size. The assumptions of analysis of variance, including normality of residuals and homogeneity of variances, were tested using the Shapiro-Wilk and Levene tests, respectively.

Differences in diffusive and via macrophytes CO_2 and CH_4 fluxes between species and along day-time were evaluated using a mixed-effects modeling approach, considering the "lme" function from the "nlme" package available in R, following the recommendations of Zuur et al. (2009). The effects of macrophyte species, period of the day and their interaction on the response variables (diffusive and via macrophyte CO_2 and CH_4 fluxes) were tested as fixed factors, and the sampled sites along day-time as random factors. Ebullitive CH_4 fluxes were log transformed, and diffusive and macrophyte CO_2 and CH_4 fluxes were log-modulus transformed prior to analyses, what is indicated when a variable ranges over several orders of magnitude in both positive and negative directions (John & Draper 1980). Outliers were identified on the residual plots for each model and eliminated from the analyses. When significant differences ($\alpha = 0.05$) were identified for any factor or if there was an interaction between factors, multiple comparisons were performed using the functions available in the "multcomp" package in R. When the effect of interaction was significant, a priori planned contrasts were used to test for the effects of the three distinct levels of day-period within and among the five macrophyte species stands on diffusive and macrophytes gas fluxes.

To test how abiotic factors and how these factors and macrophytes biomass drive the dynamics of diffusive and macrophyte GHGs fluxes, respectively, we used multiple linear regressions. They were calculated considering the "lm" function and the selected models were chosen using the "stepAIC" function, that performs backward model selection, from the package 'MASS', available in R. For each selected model, the variance inflation factor (VIF) were estimated using the "vif" function from the package 'car'. All models' predictors presented VIF scores smaller than 3, and were considered in the models. Outliers were identified considering Cook's distance (threshold greater than 4 times the mean), and were excluded from the models. This procedure affected 5.8% of the total measurements. Once implemented, it removed influential points that violated the key assumptions of linear models, specifically homogeneity of variance and normality of residuals, and excluded biologically implausible data that were inconsistent with the prevailing environmental conditions (e.g., strong positive macrophyte CO_2 fluxes during peak photosynthetic periods).

Results

Macrophyte stands in Jurubatiba lagoon exhibited substantial variations in depths and biomass, but not salinity (Supplementary material Table SI). During sampling, *T. domingensis* stand was considerably shallow (0.48 ± 0.02m), whereas the *P. azurea* stand was the deepest (0.97 ± 0.04m). The *T. domingensis* stand also displayed the highest aerial biomass per area (2,913.1 ± 1,833.8 $g.m^{-2}$), which was, on average, almost 6-times and 100-times higher than the second most (*S. californicus* - 522.6 ± 161.2 $g.m^{-2}$) and the least abundant species (*N. pulchella* - 21.5 ± 16.0 $g.m^{-2}$). Water and air temperature and PAR exhibited considerable diurnal variation, generally peaking at noon, except for PAR during *N. pulchella* stand samplings due to cloud cover (Supplementary material Table SI). Dissolved oxygen concentrations (DO) and wind speed were higher in the *T. domingensis* stand (6.9 – 7.9 mg.L^{-1}; 6.8 to 9.4 m.s^{-1}) and lower in the *S. biloba* stand (about 1.1 to 1.7 mg.L^{-1}; 0.1 to 1.3 m.s^{-1}), with values moderately variable across day-periods, without any clear pattern (Supplementary material Table SI).

Diffusive fluxes ranged from -25.2 to 49.3 mg CO_2.m^{-2}.h^{-1} and from -15.2 to 182.4 mg CH_4.m^{-2}.h^{-1} (Figure 3). Species and day-period independently affected diffusive CO_2 flux (Table I). *S. biloba* stands emitted larger amounts of CO_2 compared to other species stands, particularly during the morning and afternoon rather than at noon (Fig. 3a). Conversely, there were no significant effects of species and day-period, nor an interactive effect of these factors, on diffusive CH_4 fluxes (Table I; Fig. 3b).

Macrophyte CO_2 fluxes ranged from -2,915.7 to 937.8 mg CO_2.m^{-2}.h^{-1} (Fig. 4a). Stands and day-period significantly affected macrophyte CO_2 fluxes (Table II; Fig. 4a). Carbon dioxide uptake was significantly higher in *T. domingensis* and *P. azurea* stands, particularly during mid-day than afternoon, for all species stands (Fig. 4a). In general, macrophyte CO_2 influxes predominated over effluxes for all species stands, whereas the opposite was observed for CH_4 fluxes. Macrophyte CH_4 fluxes ranged from -118.1 to 210.9 mg CH_4.m^{-2}.h^{-1}, and were influenced by plant species stands but not

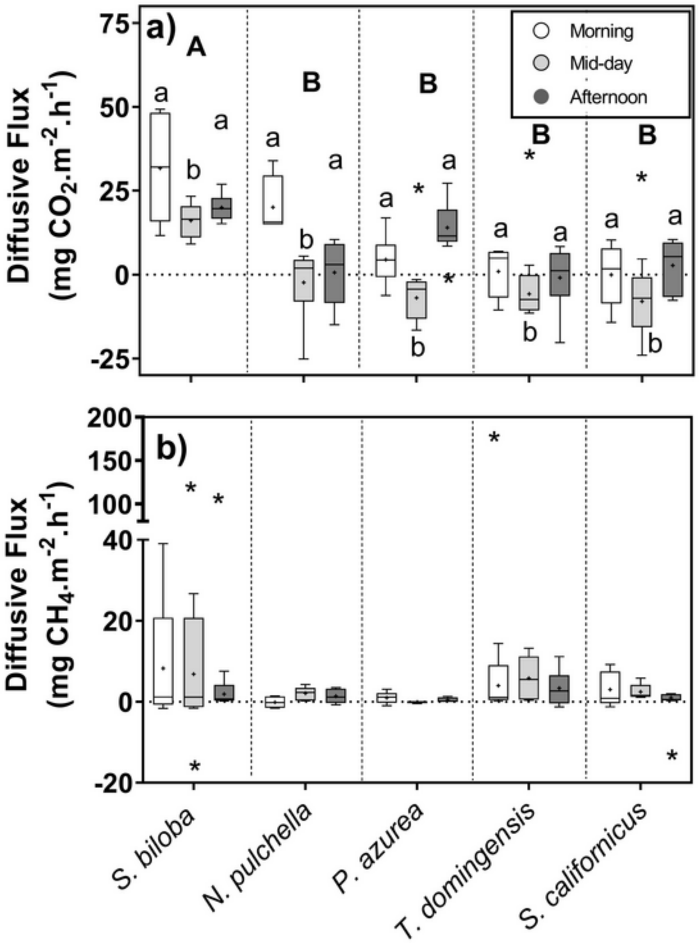

Figure 3. Diffusive CO_2 (a) and CH_4 (b) fluxes (mg.m^{-2}.h^{-1}) by stands of *Salvinia biloba*, *Nymphaea pulchella*, *Pontederia azurea*, *Typha domingensis*, and *Schoenoplectus californicus* at morning, mid-day and afternoon. Negative and positive values represent uptake from and emission to the atmosphere, respectively. Box-plots show the median (central bar), the 10–90% percentiles (boxes) and outliers (asterisks). Cross symbols (+) inside bars indicate mean values. In (a), distinct uppercase (highlighted) and lowercase letters indicate significant differences among macrophyte species stands and day-periods, respectively. Letters are positioned above or below the data points to indicate the direction of the net flux. On (b) no significant differences were detected.

day-period (Table II; Fig. 4b). However, the effects of day-period on macrophyte CH_4 emission varied within and among species (Table II), increasing and decreasing from early morning to afternoon for *P. azurea* and *S. californicus*, respectively, while mid-day presented intermediate rates (Fig. 4b). In the early morning, both emergent species (*T. domingensis* and *S. californicus*) exhibited significantly greater macrophytes CH_4 effluxes than floating species (*P. azurea* and *N. pulchella*), whereas only *T. domingensis* displayed greater CH_4 effluxes than *P. azurea* and *S. biloba* in the afternoon (Fig. 4b).

Ebullient fluxes ranged from 0 to 16.5 mg $CO_2.m^{-2}.h^{-1}$ and from 0.16 to 634.6 mg $CH_4.m^{-2}.h^{-1}$ (Fig. 5). Macrophyte species stands significantly affected ebullient CO_2 ($R^2 = 0.517$; $p < 0.001$) and CH_4 fluxes ($R^2 = 0.243$; $p < 0.001$; Table III). Carbon dioxide emissions were significantly higher in *S. biloba* and *S. californicus* stands than in *N. pulchella* and *P. azurea* ones, but not in *T. domingensis*, which presented intermediate rates (Fig. 5a). Methane emissions through bubbling were significantly higher on the *P. azurea* than in *S. biloba* stand, but not in *N. pulchella*, *S. californicus* nor *T. domingensis* stands (Fig. 5b).

Macrophyte stands and their characteristics distinctly affected GHGs fluxes, except for diffusive CH_4 fluxes, which were not significantly associated with any modeled variable (Adj. $R^2 = 0.0196$; $F_{(1, 73)} = 2.48$; $p = 0.12$; Table IV). Models accounted for 50%, 35.3% and 30.4% of total variation in diffusive CO_2, and macrophyte CO_2 and CH_4 fluxes, respectively (Table IV). Diffusive CO_2 fluxes were negatively affected by DO concentrations (78.1%; $p<0.001$; Table IV). Macrophyte CO_2 fluxes were negatively associated with PAR and plant biomass, and positively with water temperature, contributing to 32% of the total variation explained by the model (Table IV). Macrophyte CH_4 fluxes were negatively associated with water column depth and wind speed, but positively associated with DO concentrations, accounting for 78.4% of the total variation explained by the model (Table IV). Salinity, although important for gas dynamics, did not present a considerable variability between sites and day-periods (Supplementary material Table SI), and was not considered on the analyses.

Table I. Results of linear mixed models to test the effects of macrophyte species stand (S), day-period (P) and their interaction (S x P) on CO_2 and CH_4 diffusive fluxes ($mg.m^{-2}.h^{-1}$).

	Num d.f.	**Dend.f.**	**F value**	**p value**
		Diffusive CO_2 flux		
S	4	53	11.92	**< 0.001**
P	2	10	10.55	**0.003**
S x P	8	53	2.06	0.057
Intercept	1	53	21.91	<0.001
		Diffusive CH_4 flux		
S	4	43	2.03	0.108
P	2	10	0.28	0.763
S x P	8	43	0.58	0.785
Intercept	1	43	27.86	< 0.001

Table II. Results of linear mixed models to test for macrophyte species stand (S), day-period (P) and their interaction (S x P) on macrophyte CO_2 and CH_4 fluxes ($mg.m^{-2}.h^{-1}$).

	Num d.f.	**Dend.f.**	**F value**	**p value**
		Macrophytes CO2 flux		
S	4	53	11.19	**< 0.001**
P	2	10	10.76	**0.003**
S x P	8	53	0.72	0.672
Intercept	1	53	17.15	<0.001
		Macrophytes CH4 flux		
S	4	48	13.82	**< 0.001**
P	2	10	0.30	0.745
S x P	8	48	3.73	**0.002**
Intercept	1	48	118.84	<0.001

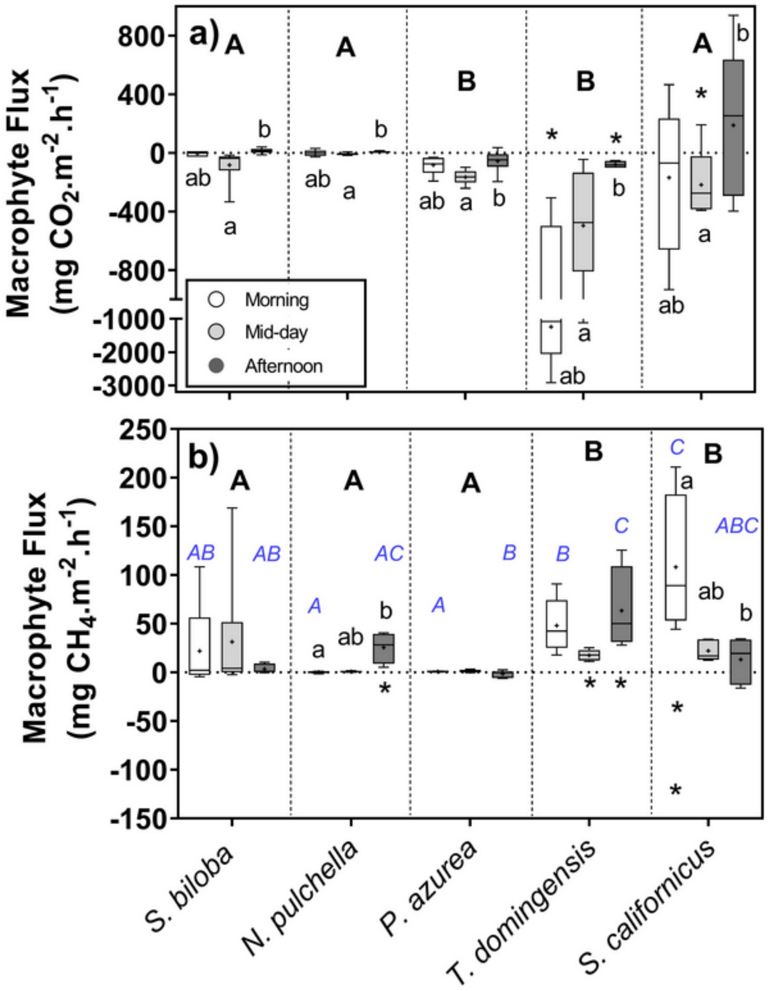

Figure 4. Macrophytes CO_2 (a) and CH_4 (b) fluxes ($mg.m^{-2}.h^{-1}$) by stands of *Salvinia biloba*, *Nymphaea pulchella*, *Pontederia azurea*, *Typha domingensis*, and *Schoenoplectus californicus* at morning, mid-day and afternoon. On (a) and (b), distinct uppercase-highlighted, uppercase-blue and lowercase letters indicate significant differences between macrophyte species stands, among day-periods between species stands and among day-period within species stands, respectively. See Figure 3 legends for details.

Discussion

The presence of aquatic macrophytes makes the littoral zone of coastal aquatic ecosystems an important site for the dynamic of GHGs (Hirota et al. 2007, Gripp et al. 2013, Xu et al. 2014). In tropical humic coastal lagoons, macrophyte detritus plays a crucial role in the sediment stoichiometry of the littoral zone, serving as the primary substrate for CO_2 and CH_4 production (Marinho et al. 2010, 2025, Fonseca et al. 2017, Fonseca et al. 2013). Macrophyte detritus also contributes to the composition of suspended particulate organic carbon (POC) (Marinho et al. 2010), whereas dissolved organic carbon (DOC) is mainly derived from the decomposition of terrestrial plants from the surrounding restinga vegetation (Suhett et al. 2013). The high concentrations of humic DOC in these lagoons inhibit pelagic primary production and favor heterotrophic processes (Thomaz et al. 2001). Additionally, photochemical reactions break down this DOC, generating low C weight molecules and CO_2 (Suhett et al. 2013), resulting in elevated pCO_2 and diffusive CO_2 emissions from both limnetic and litoral zones (Gripp et al. 2013, Marotta et al. 2010). Thus, the combined presence of aquatic macrophytes and allochtonous organic material makes the littoral zone of these coastal lagoons an important hotspot for CO_2 and CH_4 emissions to the atmosphere (Marotta et al. 2009, Gripp et al. 2013, Petruzzella et al. 2015).

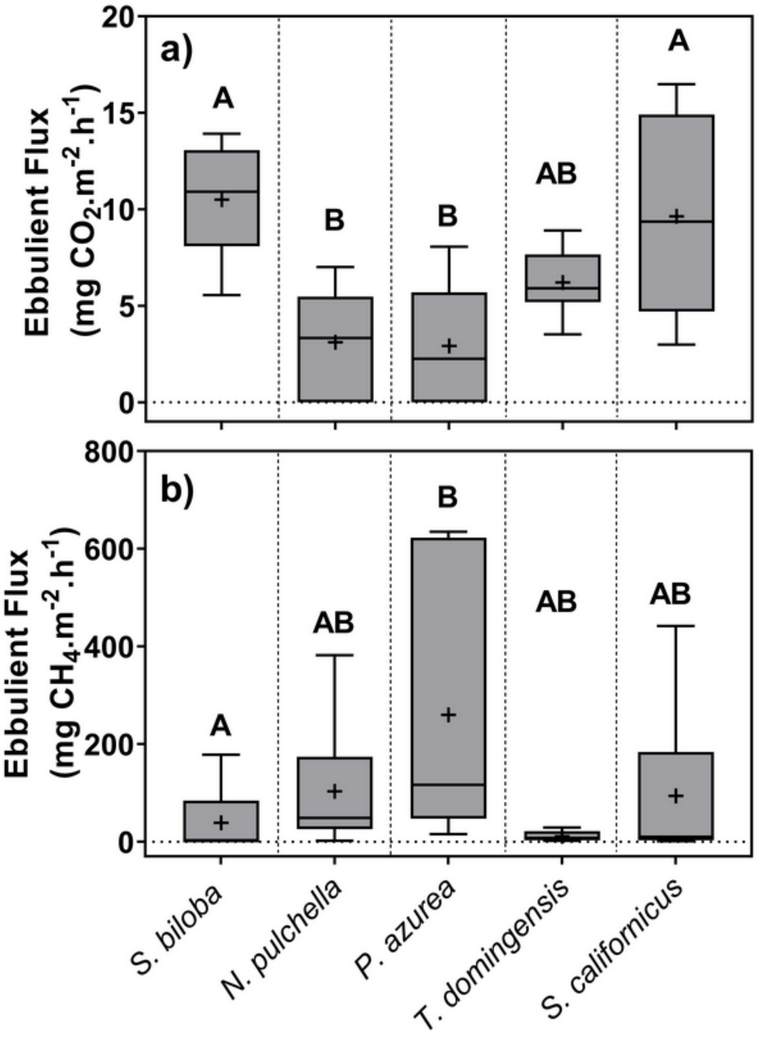

Figure 5. Ebullitive CO_2 (a) and CH_4 (b) fluxes (mg.m^{-2}.h^{-1}) by stands of *Salvinia biloba*, *Nymphaea pulchella*, *Pontederia azurea*, *Typha domingensis,* and *Schoenoplectus californicus*. See Figure 3 legends for details.

Indeed, on the stands of five of the most common species in Jurubatiba lagoon, CO_2 and CH_4 effluxes tended to predominate over influxes for diffusive, ebullitive and macrophytes-mediated (only for CH_4 fluxes) gas pathways, aligning with previous studies characterizing coastal ecosystems as substantial sources of C to the atmosphere (Hirota et al. 2007, Xu et al. 2014, Marotta et al. 2011). However, diurnal CO_2 influxes were also registered for diffusive and mainly macrophytes-mediated gas pathways, what reinforces that C incorporation by these primary producers may partly offset its emission in coastal ecosystems (Hirota et al. 2007). So, some particularities of macrophyte species stands and their diurnal dynamics may limit generalizations about such coastal ecosystems as GHG sources. In fact, C fluxes presented a considerable spatial (due to macrophyte species stands) and temporal variability (across day-period), and their effects on CO_2 and CH_4 fluxes varied depending on gas transport pathways.

Despite the high CH_4 production rates in littoral zones (Fonseca et al. 2017) and the distinct anaerobic digestion potentials of aquatic macrophytes (O'Sullivan et al. 2010, Fonseca et al. 2013) - that may affect methane production, concentration and emission - neither species stands nor day-period significantly affected diffusive CH_4 fluxes. This implies that pCH_4 and diffusive methane emissions are spatially and daily homogeneous, despite distinctions in environmental and biotic factors regulating this process (stand density, water

Table III. Summary of the ANOVA results testing the effects of macrophyte species stand (S) on ebullitive CO_2 and CH_4 fluxes ($mg.m^{-2}.h^{-1}$).

	Num d.f.	MQ	F value	p value
		Ebulitive CO_2 flux		
S	4	75.49	6.69	< **0.001**
Residuals	25	11.29		
		Ebullitive CH_4 flux		
S	4	13.00	3.29	**0.027**
Residuals	25	3.94		

and roots oxidative potentials, etc). Previous studies corroborate that Jurubatiba lagoon presents low CH_4 concentrations in the water column, with no distinctions between limnetic and littoral zones dominated by aquatic macrophytes (Fonseca et al. 2004). Thus, the differences observed among macrophye stands may not be sufficient to promote significant differences in diffusive CH_4 fluxes between them.

Regarding diffusive CO_2 fluxes, higher rates were detected on *S. biloba* stand than on emergent and floating-leaved stands, irrespectively of the day-period. *Salvinia* sp. typically forms dense floating stands and constitutes an important source of C for decomposition in aquatic ecosystems (Passerini et al. 2016). The dense floating stands reduce water movement, wind fetch and solar incidence, which usually reduce oxygen availability in the water column by limiting diffusion of atmospheric oxygen and aquatic primary production (Kosten et al. 2016), hence, potentially reducing respiration rates, CO_2 production and emission (Peixoto et al. 2016). However, the considerable radial oxygen loss through the roots of floating species makes them important oxidative microsites, allowing CO_2 production to prevail on *Salvinia* stands even under anaerobic conditions (Kosten et al. 2016, Passerini et al. 2016). Apart from *S. biloba*, higher ebullient CO_2 rates were also detected on the stands of emergent species (mainly *S. californicus*) compared to floating-leaved stands. Aerobic reactions usually occur on the bottom of the sediment, and may increase in the presence of emergent macrophytes, that promote great rates of sediment oxygenation via their rhizosphere, even in deeper sediment fractions (Armstrong et al. 1996, Armstrong & Armstrong 1991). These conditions stimulate CO_2 production and increase concentrations in the sediment, and eventually, on the bubbles formed on the stands of emergent species.

Notably, diurnal variations in diffusive CO_2 fluxes were consistent, decreasing during noon and even becoming negative at emergent and floating-leaved species stands. These fluctuations in diffusive CO_2 fluxes in the littoral zone of aquatic ecosystems over the course of the day may be linked to the constant disequilibria in aquatic metabolism, resulting from the imbalance between heterotrophic (respiration) and autotrophic (primary production) processes rates (Hirota et al. 2007, Peixoto et al. 2016). Although macrophytes and high water colour in humic coastal lagoons may limit phytoplankton activity (Thomaz et al. 2001), macrophytes provide substrates for periphytic algae, which have demonstrated high productivity at the study site (Guariento et al. 2009, Sanches et al. 2011) and may surpass CO_2 respiration rates under conditions of high light energy availability.

Diurnal variations in macrophyte CO_2 fluxes were also observed across the stands, confirming our hypothesis that CO_2 incorporation rates tend to be higher at noon, nor only for diffusive fluxes but also via macrophytes. However, comparable CO_2 uptake rates were registered on the first hours of the day, especially for emergent species. Previous studies have demonstrated that photosynthesis can be intensified in the early hours of the day due to high CO_2 supplementation from plant respiration at night (Constable & Longstreth 1994). Diel variations on macrophyte CO_2 fluxes were expected, primarily associated with solar irradiance (Knapp & Yavitt 1995, Peixoto et al. 2016, Große 1996). Carbon dioxide incorporation and primary production rates are strongly linked to internal gas transport capacity and plant biomass, which are generally greater and more variable for emergent macrophytes (Hirota et al. 2007, Brix et al. 1992, Zhou et al. 2009). Consequently, water temperature, PAR and plant biomass were significantly associated with macrophyte CO_2 fluxes. For species of the genus *Typha*, for instance, temperature, solar irradiance and humidity are the main driving forces of pressurized flows, regulating net primary production, stomatal conductance, and internal gas flows (Knapp & Yavitt 1995, Bendix et al. 1994). Maintaining internal pressure is crucial for oxygenating rhizomes of emergent macrophytes situated in the anaerobic sediment (Armstrong et al. 1996, Armstrong & Armstrong 1991). Therefore, CO_2 supplementation and the higher temperature and solar irradiance during the morning and noon

Table IV. Results of multiple regression analysis for predicting diffusive and via macrophytes CO_2 and CH_4 fluxes from abiotic variables and macrophyte biomass (only for fluxes via macrophytes). Selected variables are depicted in the table. R^2 (%) indicates the contribution (and percent contribution) of each selected variable to model R^2. AIC indicates the Akaike's Information Criterion value for the selected model, while ΔAIC indicates the difference between the selected model from the model containing all variables.

Variable	Coefficient	Std Error	t value	p value	R^2 (%)	AIC	ΔAIC
Model - Diffusive CO_2 flux							
($R^2 = 0.5246$; Adj $R^2 = 0.4995$; $F(4, 75) = 20.69$; $p < 0.001$)						*337.85*	*3.91*
Wtemp	-2.3519	1.223	-1.923	0.058	0.014 (2.80)		
Depth	-1.8348	1.1481	-1.598	0.114	0.082 (16.42)		
DO	-8.9867	1.2582	-7.143	**<0.001**	0.390 (78.10)		
PAR	-1.5076	1.012	-1.49	0.141	0.013 (2.68)		
Intercept	5.2084	0.9025	5.771	< 0.001			
Model - Diffusive CH_4 flux							
($R^2 = 0.0328$; Adj $R^2 = 0.0196$; $F(1, 73) = 2.476$; $p = 0.1199$)						*284.36*	*7.25*
Depth	-1.205	0.766	-1.573	0.119			
Intercept	2.315	0.759	3.05	< 0.001			
Model - Macrophyte CO_2 flux							
($R^2 = 0.3934$; Adj $R^2 = 0.3529$; $F(5, 75) = 9.727$; $p < 0.001$)						*881.94*	*3.79*
Wtemp	120.06	33.34	3.602	**< 0.001**	0.009 (2.42)		
Atemp	-76.82	41.39	-1.856	0.067	0.240 (67.99)		
DO	53.13	30.92	1.719	0.090	0.001 (0.13)		
PAR	-100.85	34.73	-2.904	**0.005**	0.058 (16.39)		
Biomass	-90.29	35.81	-2.521	**0.014**	0.046 (13.07)		
Intercept	-97.77	24.94	-3.919	< 0.001			
Model - Macrophyte CH_4 flux							
($R^2 = 0.3494$; Adj $R^2 = 0.3035$; $F(5, 71) = 7.624$; $p < 0.001$)						*456.88*	*2.93*
Depth	-8.253	2.576	-3.204	**0.002**	0.155 (51.21)		
Wind	-8.058	3.371	-2.39	**0.019**	0.007 (2.25)		
DO	6.317	3.15	2.006	**0.049**	0.076 (24.97)		
PAR	3.675	2.261	1.625	0.109	0.035 (11.58)		
Biomass	4.558	2.336	1.951	0.055	0.030 (9.99)		
Intercept	13.037	2.138	6.098	< 0.001			

Atemp = Air temperature; Biomass = Leaf biomass; DO = dissolved oxygen concentration; PAR = Photosynthetically Active Radiation; WTemp = Water temperature; Wind = Wind speed.

explain the larger CO_2 influxes during the beginning of the day. However, as the day progresses, CO_2 incorporation may decrease due to both a decrease in irradiance and photosynthetic activity, and hence, a lower efficiency of gas flows (Knapp & Yavitt 1995, Brix et al. 1992).

Carbon dioxide uptake was consistently higher on *T. domingensis* and *P. azurea* stands, the dominant species at Jurubatiba lagoon (Gripp et al. 2013). Species of the genus *Typha* are among the most productive organisms in aquatic ecosystems (Jervis 1969). Previous studies indicated even greater CO_2 uptake at *T. domingensis* than *P. azurea* stands in this ecosystem (Gripp et al. 2013). However, this study was restricted to a single period of the day (10 a.m. to 3 p.m.). By evaluating diel variations in gas fluxes, we revealed that lower CO_2 incorporation rates in the afternoon may compensate higher CO_2 uptake along the day in both species stands, making their average contributions equivalent. This highlights the importance of temporal approaches to better understand species contribution to C cycling in aquatic ecosystems.

Macrophyte CH_4 fluxes were also substantially affected by species stands, indicating that GHG fluxes are considerably distinct depending on the dominant species present in the stands. As predicted, methane emission rates by stands of the emergent species were substantially higher - on average, 3 to 91 times - than on floating and floating-leaved species. Pressurized gas flow in *T. domingensis* stimulates methane emission throughout the day (Käki et al. 2001, Whiting & Chanton 1996). Additionally, the high gas transport resistance on single culms of *S. californicus*, that makes convective gas throughflow very slow and may reduce diurnal gas exchanges on *Schoenoplectus* species (Brix et al. 1992) may be counterbalanced by the great abundance of culms, enhancing CH_4 emission in such stands. However, emergent species consistently improved methane emission only during the early morning, whereas only *T. domingensis* significantly increased methane fluxes in the afternoon. During the night, gas throughflows are considerably reduced in aquatic macrophytes (Brix et al. 1992) and, thus, the great amount of methane produced and accumulated on emergent culms are released during the morning (Ding et al. 2004, Käki et al. 2001, Whiting & Chanton 1996).

Diel methane dynamics seem to be affected by species stands, in accordance with what we predicted based on previous studies reporting that, at least for species employing pressurized gas flow, diurnal variations may be common (Hirota et al. 2007, Käki et al. 2001, Whiting & Chanton 1992, 1996). Higher and lower CH_4 fluxes in the afternoon in *N. pulchella* and *S. californicus* stands, respectively, are likely associated with convective throughflow, driven by a gas-pumping system powered by higher solar radiation during these periods in leaves and culms of these species (Große 1996, Brix et al. 1992). Reduced wind speed, higher DO concentrations and mainly lower stand depths were associated to higher macrophyte CH_4 fluxes, particularly because the most productive and wind-protected emergent species stands are situated on the shallower parts of the lagoon. Notably, higher CH_4 ebullitive fluxes were recorded in *P. azurea* stands, potentially reducing the availability of this GHG for emission via macrophytes. The sediment is the main site for methane production (Fonseca et al. 2017; Fonseca et al. 2004), and bubbles tend to be the dominant pathway for CH_4 emission from shallow ecosystems, which have low hydrostatic pressure (Bastviken et al. 2004). Our study supports these findings, since methane emission through bubbles contributed to about 68% of total methane fluxes, on average.

The diel patterns and magnitude of CO_2 and CH_4 fluxes observed in the littoral zone of Jurubatiba lagoon align with and help refine the understanding of macrophyte-mediated GHG dynamics in coastal ecosystems globally. For instance, the pronounced midday peak in CO_2 uptake by emergent macrophytes like *T. domingensis* is consistent with patterns observed for *Phragmites australis* and *Typha latifolia* in boreal lakes (Käki et al., 2001) and temperate wetlands (Zhou et al., 2009), underscoring the universal role of irradiance in driving photosynthetic gas transport. Furthermore, the disproportionately high CH_4 emissions from emergent stands, particularly via pressurized flow in *Typha* sp., mirror findings from northern peatlands (Whiting & Chanton, 1992, 1996) and temperate marshes (Ding et al., 2004), suggesting that this plant trait is a key driver of methane flux across biomes. This finding is strongly supported by the recent global synthesis by Bodmer et al. (2024), which confirms that vegetated habitats in inland waters sustain extremely high CH_4 fluxes and that emissions from areas dominated by emergent macrophytes are consistently higher than those from non-vegetated habitats. However, the exceptionally high contribution of ebullition (~68% of total CH_4 fluxes) observed here is a feature shared with other shallow, tropical systems (Bastviken et al., 2004; Keller & Stallard, 1994), where warm temperatures and low hydrostatic pressure enhance bubble formation and release. This contrasts with cooler temperate and boreal systems where plant-mediated transport often dominates CH_4 emissions (Greenup et al., 2000; Laanbroek, 2010), reinforcing that the dominant pathway of emission varies greatly between ecosystems and plant functional types (Bodmer et al. 2024). Thus, while the fundamental mechanisms of gas transport (e.g., convective throughflow) are globally consistent, the ultimate expression of GHG fluxes - specifically the dominant pathway and its diel intensity - is strongly modulated by local to regional factors such as climate, hydrostatic pressure, and macrophyte community composition. Our results from a tropical coastal lagoon provide critical data for a geographic region (South America) and ecosystem type (coastal lagoons) identified as significantly understudied (Bodmer et al. 2024), helping to reduce the bias in global datasets and improve the accuracy of future budget estimates.

In summary, our results reinforce the importance of considering diel variations and macrophyte species composition when examining CO_2 and CH_4 dynamics in the littoral zone of tropical aquatic ecosystems (Knapp & Yavitt 1995, Käki et al. 2001, Ding et al. 2004, Peixoto et al. 2016). A consistent pattern emerging from our study is that stands of emergent species disproportionately affect C fluxes, both incorporating much more CO_2 and emitting more CH_4 compared to stands dominated by common floating and floating-leaved species. While C incorporation rates throughout the day may compensate for C respiration and methane emission rates in stands of the dominant and highly productive species *T. domingensis* and *P. azurea*, the littoral zone of Jurubatiba lagoon may be considered as a C sink. However, the considerably high methane emission rates in the littoral zone of this lagoon may make it a substantial source of radiative forcing to the atmosphere. It is also important to highlight that our study focused on daytime fluxes; therefore, nocturnal measurements remain an essential gap to be addressed in order to fully resolve diel C dynamics, and may substantially alter net daily balances, underscoring the need for future studies that integrate both day and night periods. Finally, future efforts should focus on exploring distinct spatial properties of coastal lagoons (within and between limnetic and littoral zones), macrophyte communities (spatial structure, diversity, etc.), and temporal scales (daily, seasonally and inter-annually) to achieve a more comprehensive understanding of C balance in coastal lagoons.

Ethical statement

Collection of biological samples was conducted following all applicable ethical regulations regarding collection of biological samples. Investigation was performed under permit 23217-1 issued by Chico Mendes Institute for Biodiversity Conservation (ICMBio).

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Supplementary material

Macrophyte species distinctly affect diurnal carbon dioxide and methane fluxes on a tropical coastal lagoon

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Supplementary Table S.1 – Abiotic and biotic variables in macrophyte stands and day periods at Jurubatiba lagoon. Values indicate mean ± standard deviations. Atemp = Air temperature; Biomass = Plant biomass; DO = dissolved oxygen concentration; PAR = Photosynthetically Active Radiation; Wind = Wind speed; WTemp = Water temperature.

Species	Day period	Depth (m)	Salinity (‰)	Wtemp (ºC)	Atemp (ºC)	Wind (m.s^{-1})	PAR (µmol.m^{-2}.s^{-1})	DO (mg.L^{-1})	Biomass (g.m^{-2})
Salvinia biloba	Morning	0.72 ± 0.16	0.1 ± 0.0	25.0 ± 0.1	26.0 ± 2.8	0.1 ± 0.11	338 ± 331	1.7 ± 0.07	237.5 ± 55.4
	Noon			30.0 ± 0.2	32.3 ± 2.0	1.3 ± 0.27	1,340 ± 63	1.06 ± 0.35	
	Afternoon			28.5 ± 0.5	25.3 ± 0.9	0.2 ± 0.05	430 ± 323	1.62 ± 0.67	
Nymphaea pulchella	Morning	0.58 ± 0.02	0.1 ± 0.1	24.4 ± 0.2	24.7 ± 2.0	7.2 ± 1.53	753 ± 68	5.82 ± 0.33	21.5 ± 16.0
	Noon			25.0 ± 0.1	25.8 ± 0.8	4.4 ± 0.71	173 ± 39	5.82 ± 0.97	
	Afternoon			24.8 ± 0.1	24.7 ± 1.0	7.2 ± 0.22	1,327 ± 121	6.11 ± 0.14	
Eichhornia azurea	Morning	0.97 ± 0.04	0.1 ± 0.1	23.5 ± 0.1	20.1 ± 0.7	1.8 ± 0.44	983 ± 243	6.07 ± 0.04	369.1 ± 112.2
	Noon			24.6 ± 0.2	27.5 ± 3.0	3.6 ± 0.77	1,003 ± 451	5.42 ± 0.04	
	Afternoon			23.9 ± 0.1	21.6 ± 1.1	4.0 ± 0.22	288 ± 33	4.75 ± 2.03	
Typha domingensis	Morning	0.48 ± 0.02	0.1 ± 0.1	23.3 ± 0.1	26.6 ± 3.3	6.8 ± 2.85	1,367 ± 889	6.86 ± 0.08	2,913.1 ± 1,833.8
	Noon			27.7 ± 0.3	37.1 ± 3.2	9.4 ± 2.03	2,308 ± 112	7.87 ± 0.48	

Species	**Day period**	**Depth (m)**	**Salinity (‰)**	**Wtemp (ºC)**	**Atemp (ºC)**	**Wind (m.s^{-1})**	**PAR (µmol.m^{-2}.s^{-1})**	**DO (mg.L^{-1})**	**Biomass (g.m^{-2})**
	Afternoon			27.9 ± 0.3	28.8 ± 3.4	6.8 ± 3.07	458 ± 395	7.02 ± 0.06	
Schoenoplectus californicus	Morning	0.53 ± 0.01	0.1 ± 0.1	26.4 ± 0.3	29.8 ± 4.7	1.8 ± 1.52	1,120 ± 930	6.19 ± 0.59	522.6 ± 161.2
	Noon			27.7 ± 0.6	34.4 ± 4.0	4.7 ± 0.91	1,974 ± 699	6.56 ± 0.52	
	Afternoon			26.8 ± 0.1	23.1 ± 0.7	5.1 ± 0.33	146 ± 117	5.77 ± 0.72	