

Extremophile Algae Threatened by Coastal Environmental Changes: Halophilic Microalgal Communities Are Resilient But Not Resistant

Luciene Valladares¹, João Pedro Guimarães Machado¹, Vinícius Peruzzi de Oliveira^{1*},
Laura Shizue Moriga Masuda², Angela Manzolillo Sanseverino³, Alex Enrich-Prast⁴

¹Institute of Biology, Federal University of Rio de Janeiro, Rio de Janeiro, Brazil

²Chico Mendes Institute for Biodiversity Conservation, ICMBio, Brasília, Brazil

³Grants Office, Linköping University, Linköping, Sweden

⁴Department of Environmental Change, Linköping University, Linköping, Sweden

Email: *vinicius@biologia.ufrj.br

How to cite this paper: Valladares, L., Machado, J.P.G., de Oliveira, V.P., Masuda, L.S.M., Sanseverino, A.M. and Enrich-Prast, A. (2026) Extremophile Algae Threatened by Coastal Environmental Changes: Halophilic Microalgal Communities Are Resilient But Not Resistant. *Advances in Bioscience and Biotechnology*, 17, 13-29.

<https://doi.org/10.4236/abb.2026.171002>

Received: December 16, 2025

Accepted: January 17, 2026

Published: January 20, 2026

Copyright © 2026 by author(s) and Scientific Research Publishing Inc.

This work is licensed under the Creative Commons Attribution International License (CC BY 4.0).

<http://creativecommons.org/licenses/by/4.0/>



Open Access

Abstract

We examined the responses of extremophilic microalgal communities to environmental disturbance. Salt flat microbial mats are halophilic communities that thrive in extreme environments characterized by high salinity and frequent desiccation. However, they may be vulnerable to lower, mesophilic salinity levels resulting from accelerated hydrologic cycles and sea level rise caused by climate change. Therefore, we simulated these disturbance scenarios: one of a short-term extreme rainfall event and another of a long-term sea level rise. We measured the ecological and physiological effects of these scenarios by total and relative cell density, chlorophyll-*a* concentrations, diversity, equitability, richness, relative contribution per taxon, and taxonomic composition of the microalgal mats. We found that lower salinity levels significantly altered these parameters of extremophile microalgal communities and compromised their original functional traits. Short-term salinity stress, simulating extreme rainfall events, demonstrated the resilience of the microalgal mat community. After the disturbance, parameters returned to the original values, albeit with a minor taxonomic turnover. Long-term salinity stress, simulating sea-level rise, demonstrated the halophile community's limited resistance. Community parameters quickly deviated from their original values and underwent significant changes. In both treatments, mesophilic salinities resulted in a loss of diversity and lower equitability. Maintaining high salinity levels emerged as pivotal for the stability of salt flat ecosystems. Restoration and management efforts should prioritize restoring field site salinities to previous baseline levels to facilitate the recovery of original functionality within

these ecosystems. The lack of endemism in halophilic microalgal communities and the cosmopolitan distribution of our sampled taxa support the generality and applicability of our findings to salt flat microalgal communities worldwide. This study's broader implications highlight the fragility and stenotolerance of apparently invulnerable extremophilic communities, underscoring the need for global conservation and management strategies to protect these delicate ecosystems in the face of a changing climate.

Keywords

Hypersaline Environments, Coastal Ecosystems, Benthic Microalgae, Environmental Resilience, Hydrological Disruptions

1. Introduction

Salt flats are shallow coastal ecosystems characterized by extreme physical conditions, including high salinity, elevated temperatures, and intense solar radiation, and are a vital component of coastal habitats. Harsh environmental conditions stem from high evaporation rates, limited precipitation, and infrequent tidal inundation, culminating in the formation of hypersaline lagoons and salt flats often near mangrove forests [1]. While they are poorly understood and face increasing anthropogenic disturbances, such areas play essential roles in coastal carbon flux and nutrient cycling [2]-[4].

Benthic microalgal communities or microphytobenthos in salt flats are comprised of photosynthetic microorganisms adhering to sediment surfaces. The microalgae of salt flat communities establish intricate microbial mats in concert with bacteria, producing mucilage to shield their cells from desiccation and saline stress [1] [5]. These microbial mats serve as reservoirs of essential nutrients, which are transported to nearby mangrove habitats and coastal waters through tidal and rainfall-driven wash-off [3] [4]. Benthic microalgae can account for up to 80% of total primary production within hypersaline lagoons, surpassing the contribution of phytoplankton [6]. As such, the microphytobenthos play a pivotal role in carbon and nutrient biogeochemical cycles and form crucial components of coastal ecosystem food webs [7].

However, these fragile ecosystems dependent on overall constant high salinities face imminent threats from climate change, which has the potential to disrupt precipitation patterns and tidal regimes, consequently inducing temporary fluctuations or permanent changes in salinity [8]. This environmental parameter is the key determinant of halophile microbial community diversity and functionality [9] [10]. Disturbances in salinity levels, poised to increase with climate change and other anthropogenic disturbances, are the primary threat to halophile communities, by altering their composition and function, thereby reducing ecosystem stability [11].

In ecological theory, ecosystem stability in the face of disturbance is commonly

described through the complementary concepts of resistance and resilience. Resistance refers to the ability of a community or ecosystem to withstand environmental change while maintaining its structure and functioning, exhibiting little or no immediate response to disturbance [12]. Resilience, in contrast, describes the capacity of an ecosystem to recover following disturbance, either by returning to its pre-disturbance state or by reorganizing while retaining its essential functions, processes, and feedback [13]. Together, these concepts provide a robust conceptual framework for assessing ecosystem responses to both acute and chronic environmental stressors, particularly in extreme and highly variable environments such as hypersaline coastal systems.

To address our currently poor knowledge of salt flat microalgal mats' functioning and how climate change could impact them, we modeled the responses of the keystone guild of halophile microalgae to climate change disturbance scenarios. We modeled hydrologic cycle acceleration by climate change [14] [15], by simulating extreme rainfall events [16] [17] and sea level rise [18]-[20] on halophilic microalgal mat communities. We assessed the responses of extremophile microalgal mat communities to continuous and discrete climatic changes by multiple ecological and physiological approaches to combine this with the ecological concepts of resistance or resilience. We subjected them to simulations of an extreme precipitation event for three weeks, followed by a three-week return to normal hypersaline conditions, and of sea level rise for nine weeks, in different treatment groups, respectively.

Our hypothesis posited that halophilic communities of eukaryotic microalgae and cyanobacteria would exhibit resistance and resilience to salinity fluctuations, expressed at different temporal scales. In this context, resistance was expected to be primarily manifested in the short term, whereas resilience was anticipated to occur over longer temporal scales, following initial changes in community structure and functioning. These responses were attributed to previous selective pressure imposed by natural salinity fluctuations and subsequent acclimatization to mesophilic saline conditions [21]-[23]. We also anticipated that data on these responses would be key to salt flat and broader extremophilic environmental management and conservation.

2. Materials and Methods

2.1. Study Area

The research was conducted under permit #62303-1 (SISBIO. Portaria ICMBIO # 748/2022) within a hypersaline plain, also known as a tidal salt flat, situated in the vicinity of mangrove forests in Guaratiba, Rio de Janeiro, Brazil (Figure 1). This region is part of the Guaratiba Biological and Archaeological Reserve (RBAG), a protected area encompassing mangrove forests, salt flats, and coastal plains within the Sepetiba Bay region. This salt flat is a very shallow aquatic ecosystem characterized by sediments with high salinity (75), a range of pH (5-8), temperatures (20°C - 39°C), and solar radiation (320 - 2040 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), primarily attributable

to elevated evaporation rates, scarce precipitation, and infrequent tidal inundation during spring tides. The local climate is classified as tropical savanna, with an average temperature of 25 °C and an annual rainfall of approximately 1200 mm. Monthly precipitation peaks occur in January and June (156 mm), while it substantially declines in December (12 mm) [24].

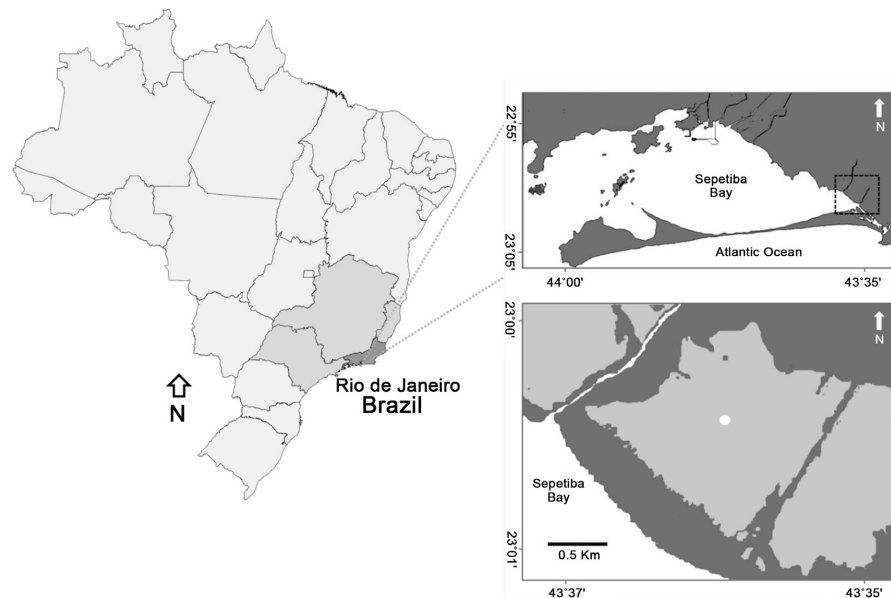


Figure 1. The white point on the map marks where samples were collected in the Guaratiba salt flat, Sepetiba Bay, RJ - Brazil (23°00'30"S, 043°36'22"W).

2.2. Sample Collection and Acclimatization

Sediment samples containing the microphytobenthic community (about 5 cm deep and 50 cm² area) were collected with a box-core and then transferred to nine mesocosms. In the laboratory, the mesocosms were daily moistened with seawater of 37 salinity and kept in a greenhouse under consistent temperature (25 °C), solar radiation (200 - 1000 $\mu\text{mol}\cdot\text{photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and a photoperiod of 12:12 h for 14 days of acclimatization.

2.3. Experimental Timeline and Salinity Conditions

After acclimatization, the environmental change experiment took place over nine weeks, divided into three separate three-week periods (P1, P2 and P3). During each period, salinity adjustments were made or maintained according to the needs of each treatment and control group. The experiment included a control group and two treatments (n = 3 mesocosms each) (Figure 2).

In the control treatment, the benthic microalgae community stayed at a salinity of 75 for three periods, reflecting the environmental salinity throughout all three periods. To simulate the short-term extreme rainfall event, salinity varied throughout the experiment, with P1 at 75, P2 at 40, and P3 at 75. To simulate sea level rise, the salinity was adjusted to 40 during three-week periods. Salinity of 40

naturally occurs in the studied environment when influenced by rare events of hefty rains or spring tides, and these values are consistent with the scenario projections of the IPCC 2023 model, referred to as Representative Concentration Pathways (RCPs) [25] [26]. Daily monitoring of salinity, pH, and temperature was conducted in the tanks throughout the experiment. Weekly, micro-core samples (10 ml) of sediments with benthic microalgal communities were collected in each treatment for biological analysis.

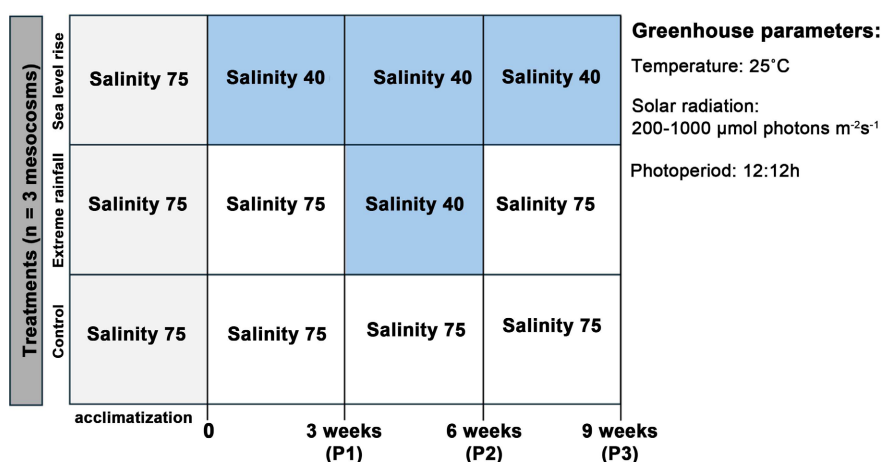


Figure 2. Schematic diagram of the experiment conducted. P1 represents the first period of the experiment, the initial three weeks, P2 represents the second period, from the fourth to the sixth week of the experiment, and P3 represents the last three weeks of the experiment. The values 75 and 40 represent the salinity (PSU) in the mesocosms.

2.4. Microphytobenthic Community Analyses

Sample preparation: The collected samples for microalgal community analysis were preserved in a 2% neutralized formaldehyde solution and stored for later examination. Before each analysis, the microbial mat was manually separated using a small brush and then diluted with seawater filtered through a GFF filter.

Quantitative analyses: We counted the microphytobenthic community using an Olympus BX51 optical microscope with a Palmer-Malloney counting chamber (0.1 ml) at 200x magnification. Microorganisms were identified to the lowest possible taxonomic level and counted accordingly. Community richness, diversity (Shannon-Weaver Diversity Index, H'), equitability (J'), relative contribution of each taxon, total cell density, and cell density for each taxon were calculated for all treatments and controls [27] [28].

2.5. Pigment Analyses

Sample preparation. The collected samples for chlorophyll-a concentration analysis were quickly frozen and stored at -20°C until further processing. Afterwards, pigment extraction was carried out using 90% (v/v) acetone for 24 hours at -20°C in darkness. Quantitative analyses. The concentrations of chlorophyll-a were quantified employing the spectrophotometric method [29] and the equations out-

lined by [30]. Absorbances were measured in a spectrophotometer at a wavelength of 664 nm. These procedures were executed for all treatments and controls every three weeks.

2.6. Statistical Analyses

All data were initially tested for normality (Kolmogorov-Smirnov test) and homocedasticity (Levene test). Then, a two-way analysis of variance (ANOVA) was employed to assess significant variances in microphytobenthic community parameters (density, diversity, equitability and chlorophyll-a concentrations) across treatments (control, extreme rainfall event, and sea level rise) and periods (P1, P2, and P3). A Tukey post hoc test was conducted to identify specific significant differences between treatments and periods with a significance level set at $p < 0.05$. The statistical analyses were executed utilizing the R software [31].

3. Results

3.1. Microphytobenthic Community Parameters

Throughout the experiment, there were no significant differences in abiotic parameters between the control and treatment groups. The microphytobenthic community, however, showed density fluctuations across treatments (control, extreme rainfall and sea level rise) and periods (P1, P2 and P3) as illustrated in **Figure 3**. In the control group, mean cell density varied between 4 and 5×10^7 cells·L⁻¹ during each three-week experimental period (P1, P2, and P3). Under the extreme rainfall treatment, the highest density occurred in P2, where values roughly doubled those of the control, reaching about 1×10^8 cells·L⁻¹. Similarly, in the sea level rise treatment, the peak density also occurred in P2, with a mean of roughly 1.5×10^8 cells·L⁻¹, exceeding both the control and the extreme rainfall treatment (**Figure 3**).

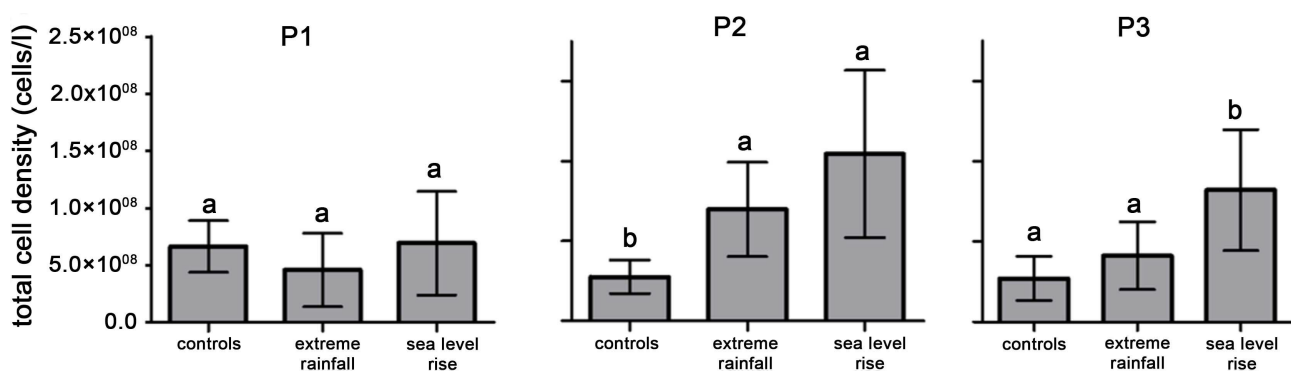


Figure 3. Cell density (mean \pm SD) in the control group, sea level rise and extreme rainfall event simulation treatments, during each three-week experimental period (P1, P2, and P3). Different letters denote statistical significance ($p < 0.05$).

The microphytobenthic community exhibited variations in diversity (Shannon-Weaver Diversity Index, H') and equitability (J') across different treatments (control, extreme rainfall, and sea level rise) and periods (P1, P2, and P3). In the con-

trol group, both indices fluctuated during the P1 (mean $H' = 0.37$ and $J' = 0.49$), followed by a progressive increase from this period, reaching the highest values near the end of the experiment ($H' = 0.79$ and $J' = 0.85$). Within the extreme rainfall treatment and sea level rise, diversity and equitability showed a progressive increase during P2 and achieved the highest values also in P3 (Figure 4).

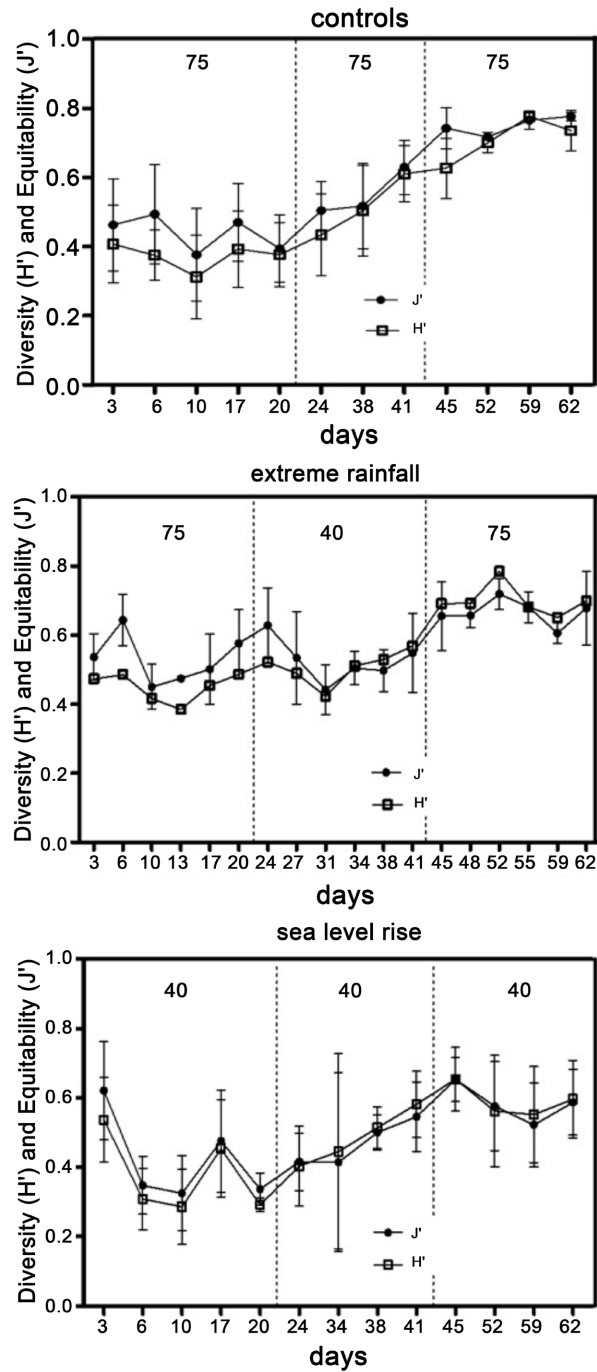


Figure 4. Diversity and equitability in sea level rise, extreme rainfall event simulation treatments, and in the control group during each three-week experimental period (P1, P2, and P3). Different letters denote statistical significance ($p < 0.05$; repeated measures ANOVA).

3.2. Chlorophyll-A Concentrations

Chlorophyll-a concentrations in the microphytobenthic community varied across treatments (control, extreme rainfall, and sea level rise) and periods (P1, P2, and P3). In the control group, mean chlorophyll-a concentration was $1420 \text{ mg}\cdot\text{m}^{-3}$ at P1, followed by a slight decline at P2 ($1127 \text{ mg}\cdot\text{m}^{-3}$) and values similar to P1 at P3 ($1422 \text{ mg}\cdot\text{m}^{-3}$). Under the extreme rainfall treatment, chlorophyll-a increased from $830 \text{ mg}\cdot\text{m}^{-3}$ at P1 to $2400 \text{ mg}\cdot\text{m}^{-3}$ at P2 and subsequently decreased to $1176 \text{ mg}\cdot\text{m}^{-3}$ at P3. In the sea level rise treatment, mean chlorophyll-a concentration was highest at P3 ($4215 \text{ mg}\cdot\text{m}^{-3}$), followed by P1 ($2107 \text{ mg}\cdot\text{m}^{-3}$), and lowest at P2 ($1323 \text{ mg}\cdot\text{m}^{-3}$) (Figure 5).

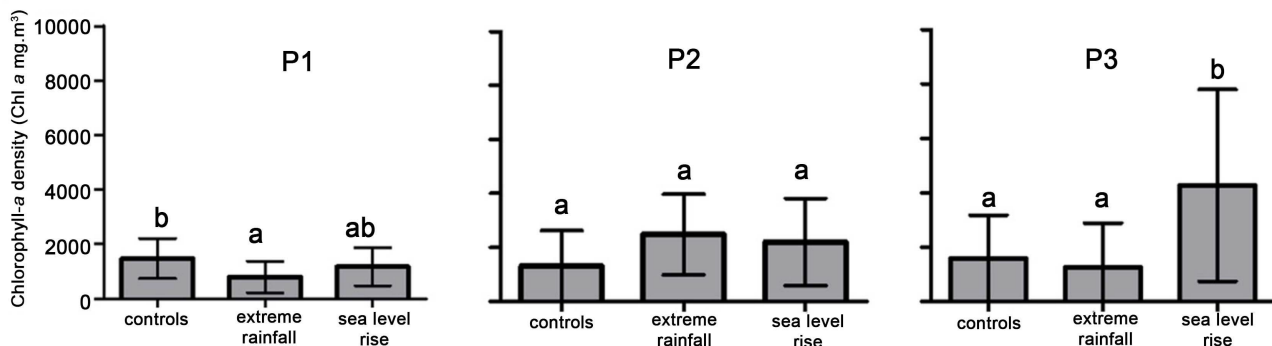


Figure 5. Chlorophyll-a (Chl a) in sea level rise, extreme rainfall event simulation treatments, and in the control group during each three-week experimental period (P1, P2, and P3). Different letters denote statistical significance ($p < 0.05$; repeated measures ANOVA).

3.3. Microphytobenthic Community Composition

In the salt flat microbial mats, a total of 16 microalgal taxa were identified, all of which have a cosmopolitan distribution. The composition of the microphytobenthic community exhibited variations across treatments (control, extreme rainfall, and sea level rise) and periods (P1, P2, and P3). Cyanobacteria and Bacillariophyceae (diatoms) were the first and second most abundant groups, respectively, throughout all treatments and periods. Among the cyanobacterial taxa, the genera *Microcoleus* / *Leptolyngbya* and *Lyngbya* exhibited significantly higher abundance in the sea level rise treatment compared to the control. In the sea level rise simulation, they constituted 74% of the total abundance in the microalgal community, whereas in the controls, their representation was 39%. Among the diatom taxa, the genus *Nitzschia* showed significantly higher abundance in the extreme rainfall simulation (9%) compared to the control (0.6%). The comparison between the extreme rainfall simulation with the control at P3, showed no significant differences in diversity and equitability. The other abundant taxa included *Phormidium* and *Pleurosigma* / *Gyrosigma*. The relative abundances of these taxa fluctuated within and across treatments and periods but showed no significant pattern when analyzed in isolation from other taxa. (Figure 6 and Figure 7).

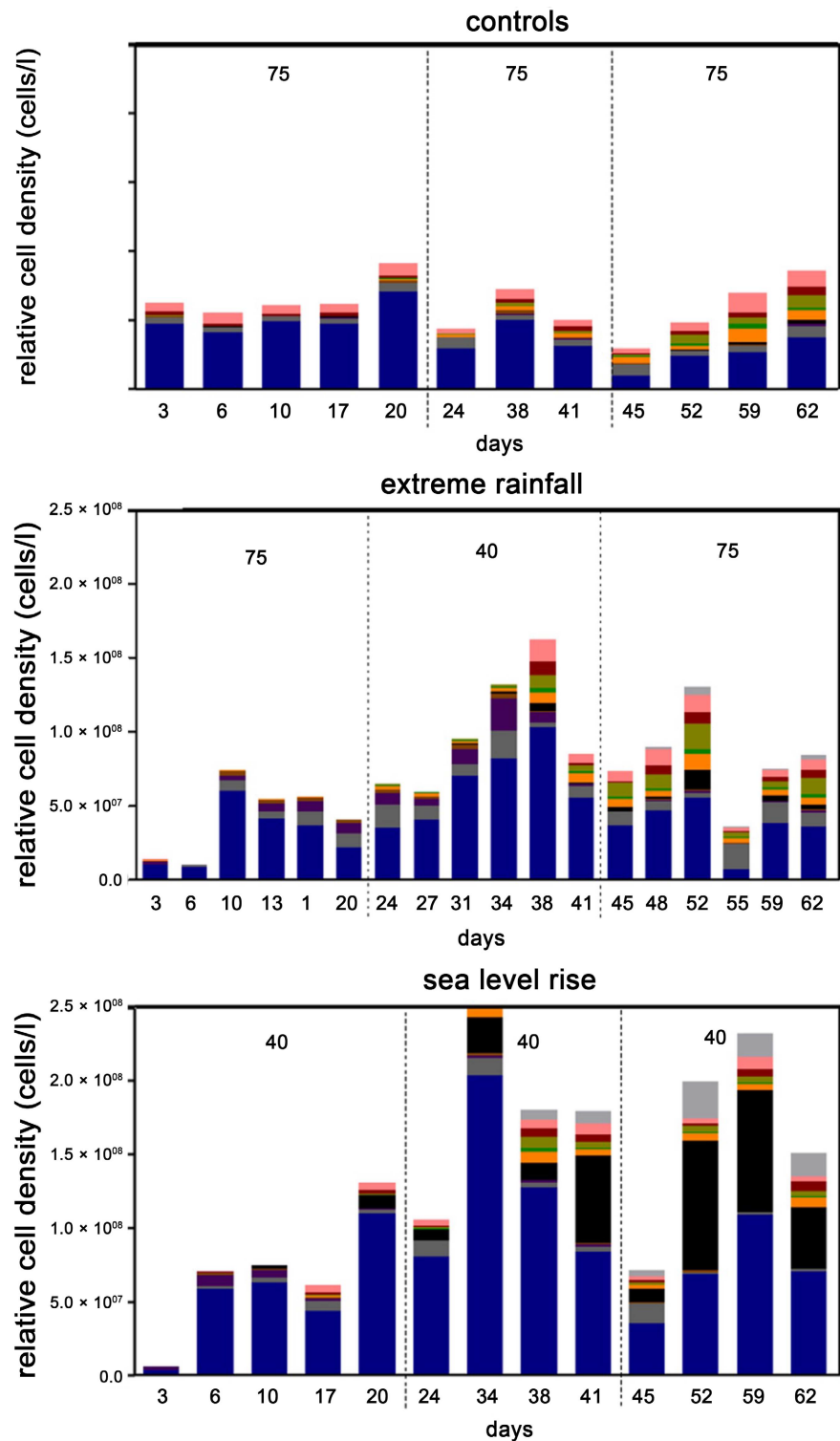


Figure 6. Relative cell density per taxon in sea level rise, extreme rainfall event simulation treatments, and in the control group during each three-week experimental period (P1, P2, and P3). Salinities in PSU are shown for every period, being separated by dashed lines. *Microcoleus/Leptolyngbya* in dark blue, *Lyngbya* in black, *Nitzschia* in gray, *Pleurosigma/Gyrosigma* in orange, *Phormidium* in magenta, and remaining rare taxa in other colors.

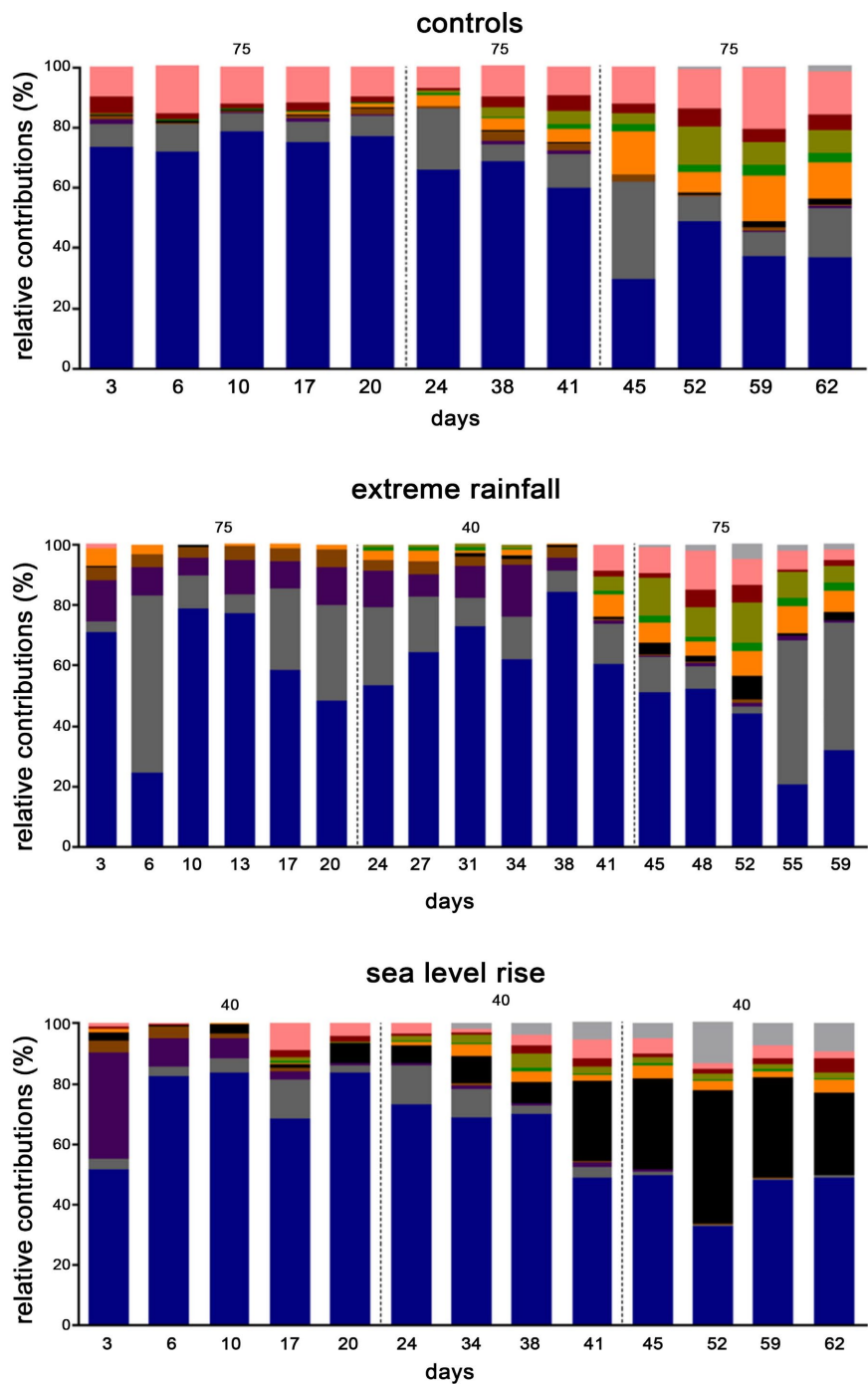


Figure 7. Relative contributions per taxon in sea level rise, extreme rainfall event simulation treatments, and in the control group during each three-week experimental period (P1, P2, and P3). Salinities in PSU are shown for every period, being separated by dashed lines. *Microcoleus/Leptolyngbya* in dark blue, *Lyngbya* in black, *Nitzschia* in gray, *Pleurosigma/Gyrosigma* in orange, *Phormidium* in magenta, and remaining rare taxa in other colors.

4. Discussion

Disturbances in natural salinity baselines are poised to increase with climate

change-induced hydrologic cycle acceleration and sea level rise. While the salt flat halophilic microalgal communities thrive in high salinity environments and often face desiccation, their responses to mesophilic salinity levels are poorly known. To address this problem, we simulated two scenarios of disturbance by salinity reduction: one of a short-term intense rain event and another of a long-term sea level rise.

The controls remained at 75 PSU in every period and no significant alterations were observed in total and relative cell density, chlorophyll-a concentrations, diversity, equitability, richness, relative contribution per taxon, and taxonomic composition of the microalgal mats, as expected.

During the initial three weeks of the experiment (P1), salinities were kept at average field site levels of 75 PSU for the extreme rainfall simulation. In the sea level rise simulation, salinity was decreased from 75 to 40 PSU, a difference numerically the same as going from average seawater to distilled water. In P1, no significant alterations were observed in the analyzed ecological and physiological variables between treatments and controls. At the start of week four (P2), salinity was lowered to 40 PSU to simulate an extreme rain event that would affect the salt flat for only three weeks. A minor yet significant alteration in some community parameters occurred in the extreme rainfall simulation during P2. However, after six weeks of lowered salinity, a major community shift happened in the sea level rise simulation, primarily due to the increased abundance of two taxa that were already dominant under natural extremophilic conditions (*Microcoleus/Leptolyngbya* and *Lyngbya*).

The taxonomic composition and relative contribution per taxon, which altered little in the first three weeks in P1, showed a gradual, steep turnover at the start of week four in P2. In this context, the abundance of *Microcoleus/Leptolyngbya* and *Lyngbya* was associated with the reduction in osmotic stress under mesophilic conditions, which likely relaxed physiological constraints and allowed competitively superior taxa to proliferate, thereby contributing to the observed increases in cell density, changes in community composition, and growth of chlorophyll-a density, mainly during the P3. This was likely due to less harsh environmental conditions, as evidenced by increased chlorophyll-a and cell densities, as also reported by Bento *et al.* 2017 [32]. However, this ecological disturbance also led to a significant reduction in diversity and equitability in relation to control levels. Therefore, the data after three weeks of salinity disturbance in both simulations show that the community showed overall resistance only in the short term.

At the start of week seven (P3) for the extreme rainfall simulation group, the salinity was returned to natural extremophilic levels (75 PSU). The return to extreme salt concentrations and harsh environment resulted in a return to previous control values of cell and chlorophyll-a densities, similar taxonomic composition, relative abundance, and taxon densities. This resulted in a return to a low density and low productivity characteristic of a stress-tolerant community within just four days (from day 41 to day 45). Therefore, the salt flat extremophile microalgal com-

munity was resilient, successfully facing short-term stress caused by climate change, as parameters similar to those present before the simulated stressor were reattained.

In weeks seven to nine (P3) for the sea level rise simulation group, the salinity was kept at mesophilic seawater levels (40 PSU). The continuity of lower salt concentrations kept a mesophilic environment for a previously extremophile-selected microalgal community. The continuity of less harsh environmental conditions resulted in the same high values of cell and chlorophyll-*a* densities, but different taxonomic composition, relative abundance, and taxon densities from P2. Values were not expected to be even higher due to the maximum density having been reached already by P2, due to the self-thinning rule being at play [33]. Under the sea level rise scenario, the prolonged-term osmotic stress due to subjecting extremophiles to mesophilic conditions resulted in an increased community restructuring, away from low-density and low-productivity halophile microalgal mats selected for stress-tolerance and towards mesophilic communities. Therefore, the salt flat extremophile microalgal community was not resistant, as parameters similar to those present before the simulated stressor were not reattained, as it faced long-term stress caused by climate change. Under the sea level rise scenario, even if the salt flat were not entirely flooded, changing conditions would gradually restructure the salt flat ecosystem, endangering its sensitive extremophile microalgal mat community. Long-term environmental disturbance also increased diversity loss in this treatment, which poises this community for further instability in a feedback loop [34].

Overall, in our simulated scenarios, the environmental disturbance generated by climate change led to shifts in dominance, equitability, and diversity. However, it depended on whether disturbances were temporary or long-term. Under temporary salinity stress (extreme rainfall simulation), the microalgal mat community displayed resilience, returning to parameters similar to the original values, but with some taxonomic changes. Under long-term salinity stress, in the sea level rise simulation, the microalgal mat community did not display resistance, since its parameters increasingly departed from the original values. As a previously extremophilic environment shifted to a mesophilic one, the high diversity, high equitability community dominated by stress-strategist extremophiles was supplanted by a low diversity, low equitability competitive-strategist mesophilic community [35] [36]. Extremophilic communities are generally less diverse than [35]. Still, the lowered diversity and equitability in relation to P1 levels are due to the new disturbance event (salinity decrease), which is expected to lower diversity and equitability regarding the previous baseline in the short term [34]. Experimentally, Bartha (2022) [37] found a decrease in diversity and equitability in extremophilic bacterial community cultures, with the eventual presence of a single taxon per culture from previously mixed cultures. This was in accordance with our results on eukaryotic extremophiles, for even in the controls, there was a gradual decrease in equitability and diversity. In the extreme rainfall treatment group, after the sa-

linity levels returned to baseline (P3), there was a partial recuperation of initial diversity and equitability values.

However, it should not be expected that extremophilic communities would return to the same previous state after disturbances and stresses ended, as our results showed in the extreme rainfall simulation in P3 compared to P1 and further corroborated by Zhou *et al.* (2023) [38] results on microbial community change after disturbance. These factors, even if short-term, would alter ecosystemic interactions and population dynamics of every taxon, increasing the likelihood of extirpations or extinctions whose vacancies could be filled by new immigrant taxa, but not necessarily to the same functional consequence.

It should be recognized that mesocosm-based experiments, while enabling controlled manipulation of key environmental drivers, do not entirely capture the complexity of natural salt flat ecosystems, including factors such as grazing pressure, spatial heterogeneity, and large-scale nutrient fluxes, which may modulate community responses in field conditions. Although we studied microorganisms from a single collection site, there is currently no evidence supporting biogeographical regionalization for extremophilic, especially halophilic, microbial communities [39], and the 16 microalgae taxa we identified were cosmopolitan, consistent with current literature on extremophile biogeography [37]. Therefore, we can reasonably expect our findings to be applicable broadly to salt flat microalgal communities worldwide.

5. Conclusions

This study demonstrates that halophilic microalgal mat communities inhabiting salt flats are resilient but not resistant to climate change-driven salinity disturbances. Short-term salinity reductions simulating extreme rainfall events induced temporary changes in community structure, biomass, and productivity; however, the rapid recovery of density, chlorophyll-a concentration, and taxonomic composition following the restoration of hypersaline conditions highlights a strong capacity for resilience. In contrast, prolonged exposure to mesophilic salinity levels, simulating sea level rise, resulted in persistent shifts in community structure, reduced diversity and equitability, and the failure to return to pre-disturbance conditions. These findings indicate that halophilic microalgal communities are unable to resist chronic salinity changes.

Accordingly, our initial hypothesis that extremophile microalgal communities would exhibit both resistance and resilience to salinity fluctuations was only partially supported. While resilience to short-term disturbances was confirmed, resistance to long-term salinity reduction was clearly rejected. Sustained mesophilic conditions promoted community restructuring away from low-diversity, stress-tolerant extremophile assemblages toward altered states with compromised functional traits.

From an ecological and conservation perspective, our results underscore the critical importance of maintaining high salinity regimes for the stability and func-

tionality of salt flat ecosystems. Management and restoration strategies should prioritize restoring and preserving natural salinity baselines, as failure to do so may lead to irreversible changes in community composition and ecosystem functioning. Given the cosmopolitan distribution of the taxa observed and the lack of evidence for biogeographic regionalization in halophilic microalgae, these findings are likely applicable to salt flat ecosystems globally. Overall, our study highlights the fragility of seemingly robust extremophilic systems in the face of ongoing climate change.

Acknowledgements

We extend our profound gratitude to the Leopoldo Américo Miguez de Mello Research and Development Center (CENPES) for the research fellowships awarded to L.V. This research was further sustained by projects financially backed by CAPES, CNPq, and FAPERJ. Specific project resources were sourced through the support of CNPq INCT-MAR-COI and PELD-Baía da Guanabara initiatives. A.E.P. expresses his gratitude for the CNPq fellowship he received.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

References

- [1] Pinckney, J.L. (2023) Benthic Microalgal Community Structure, Primary Productivity, and Fiddler Crab (*Leptuca pugilator*) Grazing in an Estuarine Salt Panne. *Estuaries and Coasts*, **46**, 1316-1325. <https://doi.org/10.1007/s12237-023-01208-8>
- [2] Lin, W.J., Wu, J. and Lin, H.J. (2020) Contribution of Unvegetated Tidal Flats to Coastal Carbon Flux. *Global Change Biology*, **26**, 3443-3454. <https://doi.org/10.1111/gcb.15107>
- [3] Shadrin, N.V. and Anufrieva, E.V. (2020) Structure and Trophic Relations in Hyper-saline Environments. *Biology Bulletin Reviews*, **10**, 48-56. <https://doi.org/10.1134/s2079086420010065>
- [4] Ferreira, A.C., Freire, F.A.M., Rodrigues, J.V.M. and Bezerra, L.E.A. (2022) Mangrove Recovery in Semiarid Coast Shows Increase of Ecological Processes from Biotic and Abiotic Drivers in Response to Hydrological Restoration. *Wetlands*, **42**, Article No. 80. <https://doi.org/10.1007/s13157-022-01603-0>
- [5] Oren, A. (2015) Halophilic Microbial Communities and Their Environments. *Current Opinion in Biotechnology*, **33**, 119-124. <https://doi.org/10.1016/j.copbio.2015.02.005>
- [6] Vadeboncoeur, Y., Lodge, D.M. and Carpenter, S.R. (2001) Whole-Lake Fertilization Effects on Distribution of Primary Production between Benthic and Pelagic Habitats. *Ecology*, **82**, 1065-1077.
- [7] Chen, Z.L. and Lee, S.Y. (2022) Tidal Flats as a Significant Carbon Reservoir in Global Coastal Ecosystems. *Frontiers in Marine Science*, **9**, Article 900896. <https://doi.org/10.3389/fmars.2022.900896>
- [8] Costa, C.S.B. and Herrera, O.B. (2016) Halophytic Life in Brazilian Salt Flats: Biodiversity, Uses and Threats. In: Khan, M.A., Boër, B., Öztürk, M., Clüsener-Godt, M.,

- Gul, B. and Breckle, S.W., *Sabkha Ecosystems. Volume V: The Americas*, Springer International Publishing, 11-27.
- [9] Banda, J.F., Lu, Y., Hao, C., Pei, L., Du, Z., Zhang, Y., *et al.* (2019) The Effects of Salinity and pH on Microbial Community Diversity and Distribution Pattern in the Brines of Soda Lakes in Badain Jaran Desert, China. *Geomicrobiology Journal*, **37**, 1-12. <https://doi.org/10.1080/01490451.2019.1654568>
- [10] Uritskiy, G., Getsin, S., Munn, A., Gomez-Silva, B., Davila, A., Glass, B., *et al.* (2019) Halophilic Microbial Community Compositional Shift after a Rare Rainfall in the Atacama Desert. *The ISME Journal*, **13**, 2737-2749. <https://doi.org/10.1038/s41396-019-0468-y>
- [11] FitzGerald, D.M. and Hughes, Z. (2019) Marsh Processes and Their Response to Climate Change and Sea-Level Rise. *Annual Review of Earth and Planetary Sciences*, **47**, 481-517. <https://doi.org/10.1146/annurev-earth-082517-010255>
- [12] Van Meerbeek, K., Jucker, T. and Svenning, J. (2021) Unifying the Concepts of Stability and Resilience in Ecology. *Journal of Ecology*, **109**, 3114-3132. <https://doi.org/10.1111/1365-2745.13651>
- [13] Serejo, M.L., Franco Morgado, M., García, D., González-Sánchez, A., Méndez-Acosta, H.O. and Toledo-Cervantes, A. (2020) Environmental Resilience by Microalgae. In: *Microalgae Cultivation for Biofuels Production*, Elsevier, 293-315. <https://doi.org/10.1016/b978-0-12-817536-1.00019-9>
- [14] Cheng, L., Trenberth, K.E., Gruber, N., Abraham, J.P., Fasullo, J.T., Li, G., *et al.* (2020) Improved Estimates of Changes in Upper Ocean Salinity and the Hydrological Cycle. *Journal of Climate*, **33**, 10357-10381. <https://doi.org/10.1175/jcli-d-20-0366.1>
- [15] Benestad, R.E., Lussana, C., Lutz, J., Dobler, A., Landgren, O., Haugen, J.E., *et al.* (2022) Global Hydro-Climatological Indicators and Changes in the Global Hydrological Cycle and Rainfall Patterns. *PLoS Climate*, **1**, e0000029. <https://doi.org/10.1371/journal.pclm.0000029>
- [16] Fowler, H.J., Ali, H., Allan, R.P., Ban, N., Barbero, R., Berg, P., *et al.* (2021) Towards Advancing Scientific Knowledge of Climate Change Impacts on Short-Duration Rainfall Extremes. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, **379**, Article 20190542. <https://doi.org/10.1098/rsta.2019.0542>
- [17] Martel, J.L., Brissette, F.P., Lucas-Picher, P., Troin, M. and Arsenault, R. (2021) Climate Change and Rainfall Intensity-Duration-Frequency Curves: Overview of Science and Guidelines for Adaptation. *Journal of Hydrologic Engineering*, **26**, Article 03121001. [https://doi.org/10.1061/\(asce\)he.1943-5584.0002122](https://doi.org/10.1061/(asce)he.1943-5584.0002122)
- [18] He, Q. and Silliman, B.R. (2019) Climate Change, Human Impacts, and Coastal Ecosystems in the Anthropocene. *Current Biology*, **29**, R1021-R1035. <https://doi.org/10.1016/j.cub.2019.08.042>
- [19] Saintilan, N., Khan, N.S., Ashe, E., Kelleway, J.J., Rogers, K., Woodroffe, C.D., *et al.* (2020) Thresholds of Mangrove Survival under Rapid Sea Level Rise. *Science*, **368**, 1118-1121. <https://doi.org/10.1126/science.aba2656>
- [20] Nicholls, R.J., Lincke, D., Hinkel, J., Brown, S., Vafeidis, A.T., Meyssignac, B., *et al.* (2021) A Global Analysis of Subsidence, Relative Sea-Level Change and Coastal Flood Exposure. *Nature Climate Change*, **11**, 338-342. <https://doi.org/10.1038/s41558-021-00993-z>
- [21] Abomohra, A.E.F., El-Naggar, A.H., Alaswad, S.O., Elsayed, M., Li, M. and Li, W. (2020) Enhancement of Biodiesel Yield from a Halophilic Green Microalga Isolated

- under Extreme Hypersaline Conditions through Stepwise Salinity Adaptation Strategy. *Bioresource Technology*, **310**, Article 123462. https://www.sciencedirect.com/science/article/pii/S0960852420307343?casa_token=zBTzhhI4sO0AAAAA:zOs32xsTCA03SUJ6-R_CfCwKyTjYh6V5k7wDPO-mAIRW7tsVMVULxrQtfKH1qSLas3TOdEisju4q
- [22] Barut, D., Enuh, B.M., Derkuş, B., Güler, Ü., Salih, B. and Aytar Çelik, P. (2023) The Relationship between Bacterial Outer Membrane Vesicles and Halophilic Adaptation. *Molecular Omics*, **19**, 174-181. <https://doi.org/10.1039/d2mo00259k>
- [23] Yoo, Y., Lee, H., Lee, J., Khim, J.S. and Kim, J. (2023) Insights into Saline Adaptation Strategies through a Novel Halophilic Bacterium Isolated from Solar Saltern of Yellow Sea. *Frontiers in Marine Science*, **10**, Article 1229444. <https://doi.org/10.3389/fmars.2023.1229444>
- [24] INPE (2023) Centro de Previsão de Tempo e Estudos Climáticos. <http://clima.cptec.inpe.br/>
- [25] Chaves, F., Gomes, J., Soares, M., Estrada, G., Almeida, P.M. and Cavalcanti, V. (2013) Contribution to Knowledge and Conservation of the Guaratiba Coastal Plain—Sepetiba bay, Rio de Janeiro-Brazil. *Journal of Integrated Coastal Zone Management*, **13**, 123-136.
- [26] Intergovernmental Panel on Climate Change (2023) Climate Change 2023: Synthesis Report. IPCC. <https://www.ipcc.ch/report/ar6/syr/>
- [27] Panja, A.K., Vasavdutta, S., Choudhary, M., Thiyagarajan, I., Shinde, A.H., Ray, S., *et al.* (2023) Interaction of Physico-Chemical Parameters with Shannon-Weaver Diversity Index Based on Phytoplankton Diversity in Coastal Water of Diu, India. *Marine Pollution Bulletin*, **190**, Article 114839. <https://doi.org/10.1016/j.marpolbul.2023.114839>
- [28] Tarafdar, L., Kim, J.Y., Srichandan, S., Mohapatra, M., Muduli, P.R., Kumar, A., *et al.* (2021) Responses of Phytoplankton Community Structure and Association to Variability in Environmental Drivers in a Tropical Coastal Lagoon. *Science of the Total Environment*, **783**, Article 146873. <https://doi.org/10.1016/j.scitotenv.2021.146873>
- [29] Siedlewicz, G., Žak, A., Sharma, L., Kosakowska, A. and Pazdro, K. (2020) Effects of Oxytetracycline on Growth and Chlorophyll a Fluorescence in Green Algae (*Chlorella vulgaris*), Diatom (*Phaeodactylum tricornutum*) and Cyanobacteria (*Microcystis aeruginosa* and *Nodularia spumigena*). *Oceanologia*, **62**, 214-225. <https://doi.org/10.1016/j.oceano.2019.12.002>
- [30] Jeffrey, S.W. and Humphrey, G.F. (1975) New Spectrophotometric Equations for Determining Chlorophylls A, B, C1 and C2 in Higher Plants, Algae and Natural Phytoplankton. *Biochimie und Physiologie der Pflanzen*, **167**, 191-194. [https://doi.org/10.1016/s0015-3796\(17\)30778-3](https://doi.org/10.1016/s0015-3796(17)30778-3)
- [31] R Core Team (2023) R Development Core Team R: A Language and Environment for Statistical Computing 2023. R Core Team.
- [32] Bento, L., Masuda, L.S.M., Peixoto, R.B. and Enrich-Prast, A. (2017) Regulation in the Metabolism and Community Structure of a Tropical Salt Flat after Rainfall. *Journal of Coastal Research*, **332**, 304-308. <https://doi.org/10.2112/jcoastres-d-15-00179.1>
- [33] Creed, J.C., Vieira, V.M.N.C.S., Norton, T.A. and Caetano, D. (2019) A Meta-Analysis Shows That Seaweeds Surpass Plants, Setting Life-on-Earth's Limit for Biomass Packing. *BMC Ecology*, **19**, Article No. 6. <https://doi.org/10.1186/s12898-019-0218-z>

- [34] Borics, G., Abonyi, A., Salmaso, N. and Ptacnik, R. (2021) Freshwater Phytoplankton Diversity: Models, Drivers and Implications for Ecosystem Properties. *Hydrobiologia*, **848**, 53-75. <https://doi.org/10.1007/s10750-020-04332-9>
- [35] Shu, W.S. and Huang, L.N. (2022) Microbial Diversity in Extreme Environments. *Nature Reviews Microbiology*, **20**, 219-235. <https://doi.org/10.1038/s41579-021-00648-y>
- [36] Couso, L.L., Soler-Bistué, A., Aptekmann, A.A. and Sánchez, I.E. (2023) Ecology Theory Disentangles Microbial Dichotomies. *Environmental Microbiology*, **25**, 3052-3063. <https://doi.org/10.1111/1462-2920.16495>
- [37] Bartha, E. (2022) Investigating Extremotolerant Microbes in Non-Extreme Environments and Altering the Salinity Growth Limits of Halophiles. Ph.D. Thesis, University of Essex. <https://repository.essex.ac.uk/33275/>
- [38] Zhou, X., Chen, X., Qi, X., Zeng, Y., Guo, X., Zhuang, G., *et al.* (2023) Soil Bacterial Communities Associated with Multi-Nutrient Cycling under Long-Term Warming in the Alpine Meadow. *Frontiers in Microbiology*, **14**, Article 1136187. <https://doi.org/10.3389/fmicb.2023.1136187>
- [39] Clark, D.R., Mathieu, M., Mourot, L., Dufossé, L., Underwood, G.J.C., Dumbrell, A.J., *et al.* (2017) Biogeography at the Limits of Life: Do Extremophilic Microbial Communities Show Biogeographical Regionalization? *Global Ecology and Biogeography*, **26**, 1435-1446. <https://doi.org/10.1111/geb.12670>