

# Diversity and distribution of epiphytic diatoms on macroalgae inhabiting the Red Sea, Egypt

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**Abstract.** The epiphytic diatoms attached to marine macroalgae have been collected along the Red Sea coast in Egypt, and a total of 52 species of epiphytic diatoms were recorded. Some epiphytic diatoms exhibited host specificity on a few macroalgae, giving unialgal epiphytic flora. Other diatoms did not reveal the preceding preference pattern and persisted on most macroalgae showing a lack of selectivity. Whereas, the significant components of the epiphytic diatom flora were *Fragilariaforma virescens*, *Licmophora ehrenbergii*, *Licmophora flabellata*, *Nitzschia gracilis*, and *Nitzschia* sp.1, which were recorded on most macroalgal hosts. The other of the recorded epiphytic diatoms was considered rare. The species richness index ( $d'$ ) of epiphytic diatoms ranged between 1.569 and 5.41. Shannon Wiener's ( $H'$ ) diversity index ( $H'$ ,  $\log_e$  and  $\log_2$  based) ranged from 1.019 to 2.773 for  $H'$  ( $\log_e$ ) and from 1.47 to 4 for  $H'$  ( $\log_2$ ). Diversity and distribution of epiphytic diatom taxa varied temporally between macroalgal hosts with variations correlated with abiotic factors such as temperature, pH, magnesium, chloride, and salinity. The structure of epiphytic diatom assemblages exhibited high beta diversity and low similarity between the hosts.

**Keywords:** Macroalgae, epiphytic diatoms,  $\beta$ -diversity, distribution, and environmental factors

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## 1. Introduction

In marine environments, benthic microalgae colonize a wide variety of substrates. Living substrates are considered a highly appropriate habitat for microorganism colonization and development, especially in aquatic environments, because of the variety of interactions between epibionts and their host animals or plants (Burfeid-Castellanos et al., 2021). Although most epiphytic algae are principally facultative and are not strictly associated with the host species (Wahl & Mark, 1999), some are recognized as specific and obligate epibionts on definite hosts (Fawzy, 2016). Macroalgae are living substrata, and their surfaces are covered with organic and inorganic compounds and, therefore, disposed of for attachment of planktonic colonizers such as diatoms, fungi, bacteria, protozoa, and larvae of invertebrates (Jacobi & Langevin, 1996). Macroalgae are considered ecosystem engineers because they affect the associated biota assemblages, modulate the availability of resources, and add spatial complexity to substrata (Gestoso et al., 2010). The epiphytic algae associated with the seaweeds are mostly diatoms (Polifrone et al., 2020). Regardless of the substrate type to which they are associated, the epiphytic diatoms appear in various forms of growth, consisting of erect forms including cells attached to substrata by pads (e.g., *Synedra*, *Cyclophora*) or mucilaginous stalks (*Licmophora*, *Grammatophora*), adnate forms comprising monoraphid and biraphid taxa closely associated with substrata and rarely colonial (e.g., *Rhopalodia*, *Epithemia*, *Cocconeis*, *Amphora*), motile forms consisting of biraphid taxa freely that move over hard substrata or soft sediments and tube-dwelling colonies involving mostly of motile nitzschoid or naviculoid taxa living in mucilaginous tubes (Romagnoli et al., 2007).

Diatoms growth may be stimulated by high nutrient levels, but it is largely dependent on the individual taxa's physiology. Generally, environmental parameters significantly affect the population and the growth of epiphytic organisms. The light intensity and temperature have an essential effect on the epiphytes' growth (Lepoint et al., 2000). The occurrence of epiphytic algae in the aquatic environment depends on the substrate's availability and the biotic and abiotic environment (Mabrouk et al., 2011). In temperate regions, the seasonal succession of epiphytic algae mostly depends on climatic conditions and the trophic state of a water body. The succession of epiphytic algae cannot be explained by one factor (Adam et al., 2017). Because of the heterogeneous substrates, its patterns vary in lakes and the same lake. Snoeijs (1995) indicated that although the salinity gradient and season more influenced the epiphytic diatom communities than by preference of macroalgal host, the hosts affected the epiphytic taxonomic composition as they supported various abundances of epiphytic diatoms. Al-Handal and Wulff (2008) reported that the existence of a host effect due to a different composition of epiphytic diatom occurred on seaweed species from the same area and depth. Sutherland (2008) also suggested that the epiphytic diatom communities differed concerning dominant taxa on coralline and frondose red algae from the same area.

Diversity indices are the significant statistical measure for characterizing the richness (the number of species) and evenness (how uniformly abundant species are in a sample) of the species in a community (Abdelsalamet al., 2020). Also, species diversity is determined by  $\beta$ -diversity, which measures the similarity or dissimilarity degree in species composition among sites. Beta diversity examines the species turnover degree from habitat to habitat and the community to community or along any ecological gradient (Tuomisto, 2010). Therefore, different diversity indices were taken into account to illustrate their importance concerning epiphytic diatom communities. Most studies focused on the distribution and colonization of epiphytes such as bacterial communities and others, on seagrass hosts in marine and brackish water (Lachnit et al., 2011; Frankovich et al., 2006), but fewer studies focused on the diversity of epiphytic microalgae, specific diatoms on macroalgae (Al-Handal & Wulff 2008; Sanal & Demir, 2018; Burfeid-Castellanos et al., 2021). Therefore, this study evaluated the occurrence and diversity of epiphytic diatoms on Red Sea marine macroalgae in Egypt by different diversity indices. As well as determining the reasons for the epiphytic diatom community differences; sites, seasons or different macroalgal hosts that are available for attachment.

## 2. Materials and Methods

### 2.1. Research areas

Seaweed samples were collected seasonally from the intertidal region of Safaga (26°46'N, 33°56'E), Hurghada (27°12'N, 33°50'E) and Al-Quseir (26°5'N, 34°17'E) along the Red Sea coast, Egypt, between autumn 2015 and summer 2016.

### 2.2. Water analysis

Water samples (1000 mL per sample) were collected seasonally in bottles from the same areas and at the same time during macroalgae sampling (within four seasons), and all variables were measured in triplicates for each sample. Temperature of the water was measured by mercury thermometer *in situ*. The samples were filtered through Whatman glass microfibre filters GF / C (pore size 1.2  $\mu$ m) prior to seawater analysis (Grasshoff et al., 1999). A digital pH meter (pH, 211 Hanna instruments, U.S.A) was used to measure the water pH. Conductometer (YSI Model 35 yellow springs, OH, USA) measured electrical conductivity (EC). The complexometric titration method assessed calcium and magnesium (Grasshoff et al., 1999). A flame-photometry (Dr Lange Flame Photometer M 71 D type Nr / LPG 075) measured potassium and sodium. The titration with AgNO<sub>3</sub> determined chlorinity and was then used to determine salinity (Grasshoff et al., 1999). Gravimetric method was used to estimate sulfate (Grasshoff et al., 1999). Nitrate-nitrogen in concentrated sulphuric acid was measured by chromotropic acid (Bulgariu & Bulgariu, 2012). Finally, according to the Murphy and Riley (1958) process, phosphate-phosphorus was spectrophotometrically determined.

### 2.3. Collection of Macroalgae

Identification of algae at least to the genus level was made according to Jha et al. (2009), Aleem (1993), Nizamuddin (1991), Abbott and Dawson (1978). Host algal species in the intertidal zone (approx. 0.5 m depth) from the study area were handily collected in triplicate. Subsequently, algal samples were separated in the field and put in plastic polyethylene bags, then held in the icebox until examined and identified in the laboratory. Twenty-four algal samples along the four seasons representing 14 macroalgal species (8 brown algal species, 5 red algal species, and one green algal species) were presented in Table 1.

| Table 1. List of macroalgae collected from different sites and seasons in Red Sea- Egypt. |           |  |                |
|---|-----------|--|----------------|
| Season  | Site      | Macrophyte   | Algal taxonomy |
| Autumn  | Al-Quseir | <i>Palisada perforata</i> (Bory de Saint-Vincent) K.W. Nam | Rhodophyta     |
|   |           | <i>Caulerpa serrulata</i> (Forsskål) J. Agardh             | Chlorophyta    |
|   | Hurghada  | <i>Sargassum</i> sp.                                       | Ochrophyta     |
|   | Safaga    | <i>Cystoseira</i> sp.                                      | Ochrophyta     |
|   |           | <i>Sargassum</i> sp.                                       | Ochrophyta     |
| Winter  | Al-Quseir | <i>Palisada perforata</i> (Bory de Saint-Vincent) K.W. Nam | Rhodophyta     |
|   |           | <i>Cystoseira myrica</i> (S.G. Gmelin) C. Agardh           | Ochrophyta     |
|   | Hurghada  | <i>Palisada perforata</i> (Bory de Saint-Vincent) K.W. Nam | Rhodophyta     |
|   | Safaga    | <i>Palisada perforata</i> (Bory de Saint-Vincent) K.W. Nam | Rhodophyta     |
|   |           | <i>Dictyota</i> sp.  | Ochrophyta     |
| Spring  | Al-Quseir | <i>Palisada perforata</i> (Bory de Saint-Vincent) K.W. Nam | Rhodophyta     |
|   |           | <i>Padina pavonica</i> (Linnaeus) Thivy                    | Ochrophyta     |
|   |           | <i>Hydroclathrus clathratus</i> (C. Agardh) M.A. Howe      | Ochrophyta     |
|   |           | <i>Jania rubens</i> (Linnaeus) J.V. Lamouroux              | Rhodophyta     |
|   | Hurghada  | <i>Palisada perforata</i> (Bory de Saint-Vincent) K.W. Nam | Rhodophyta     |
|   |           | <i>Gracilaria arcuata</i> Zanardini                        | Rhodophyta     |
|   | Safaga    | <i>Palisada perforata</i> (Bory de Saint-Vincent) K.W. Nam | Rhodophyta     |
|   |           | <i>Dictyota pinnatifida</i> Kützing                        | Ochrophyta     |
| Summer  | Al-Quseir | <i>Palisada perforata</i> (Bory de Saint-Vincent) K.W. Nam | Rhodophyta     |
|   |           | <i>Laurencia</i> sp.                                       | Rhodophyta     |
|   | Hurghada  | <i>Palisada perforata</i> (Bory de Saint-Vincent) K.W. Nam | Rhodophyta     |
|   |           | <i>Turbinaria decurrens</i> Bory de Saint-Vincent          | Ochrophyta     |
|   | Safaga    | <i>Palisada perforata</i> (Bory de Saint-Vincent) K.W. Nam | Rhodophyta     |
|   |           | <i>Digenea simplex</i> (Wulfen) C. Agardh                  | Rhodophyta     |

#### 2.4. Separation of Epiphytic diatoms

Each algal host had been prepared to isolate epiphytic diatoms in three replicas. Epiphytic diatoms were scraped from the surface of seaweed and cleaned with HCl following the method of von Stosch's in Hasle and Syvertsen (1997). After washing with little filtered seawater, segments of fresh algal tissue were placed into glass bottles containing about 20 mL filtered seawater. Samples were subsequently passed through a 100 µm mesh sieve to remove algal host and large particles and then completed to 50 mL for a microalgae concentrate. The identification of diatoms to the lowest possible taxonomic rank has been made possible by the oxidation of the organic components of the diatom frustules. The identification of diatoms was performed according to De Stefano and Romero (2005); De Stefano et al. (2000; 2008); Kooistra et al. (2009); Witkowski et al. (2000); Snoeijs (1993).

#### 2.5. Data analysis

The diversity indices, including Margalefs Diversity (d) and Shannon-Wiener diversity ( $H'$ ,  $\log_e$  and  $\log_2$  based), were calculated using the DIVERSE procedure of PRIMER package (Primer V. 6.0, Primer-E). Two-factor permutational multivariate analysis of variance (PERMANOVA) can be used to discern statistical differences in the diatom assemblages at species and genera levels between different seasons and sites (i.e., to examine the contribution of seasonal and geographic variability to the diatom assemblages). Thus two factors were considered: site (Si), a three-level fixed factor (Safaga, Hurghada, and Al-Quseir),

and season (Se), a four-level random factor (autumn, winter, spring, and summer). PERMANOVA was conducted using permutation of residuals under a reduced model (999 permutations), based on Jaccard similarity ( $S_{jac}$ ). A pair-wise comparison (999 permutations) was carried out to explore the variations between all pairs of the levels of factors examined when PERMANOVA indicated a significant difference. Multivariate analysis was conducted with the PRIMER v.6+PERMANOVA program (Anderson et al., 2008).

Under the Distance-based Linear Model Analysis (DISTLM) routine, analysis of non-parametric multiple regression was used to investigate the relationship between diatom assemblage dissimilarity data and environmental variables and identify specific subsets of variables that are better at demonstrating the variability of data species (McArdle & Anderson, 2001). In this analysis, each environmental variable was first analyzed in the marginal test separately (without the other variables) to examine the probable relationship with multivariate community data. The variables were then exposed to a forward selection process (sequential test,  $R^2$  selection criterion), in which the amount of variation represented by each variable added to the model is conditional on the variables previously in the model. The significance of the marginal test results was assessed using a permutation test (9999 permutations) of the non-normalized and transformed data. After that, the sequential tests under the reduced model were obtained using 9999 permutations of residuals (Anderson, 2001). In this study, the analysis of DistLM was performed based on Jaccard and taxonomic similarity of the data of diatom species and environmental variables.

The algal taxa turnover among the hosts was determined using Podani et al. (2013).  $\beta$ -Diversity method defined as a method of SDR-abun Simplex by the software of SDR-abun Simplex. The principle of the method was to divide the data of presence/absence for a pair of algal hosts into three components; differences in species richness (D; the amount by which the total number of species in either sample exceeds the total of the other), similarity (S; based on the Jaccard index for the data of presence/absence), and species replacement (R; abundances of species in either sample replaced by abundances pertaining to different species in the other sample). After the normalization to unit sum, these amounts determine the position of a given sample pair in the two-dimensional SDR simplex plot by program of ProSim Ternary Diagram. The algal taxa turnover among the hosts was determined using Podani et al. (2013).

## 2.6. Taxonomic $\beta$ -diversity

To measure the taxonomic beta diversity (Izsak & Price, 2001), the taxonomic similarity index ( $\Delta_s$ ) index was used.  $\Delta_s$  is a similarity index derived from the taxonomic distance (TD) calculated from the presence/absence of species data. Taxonomic distance is the average minimum path length between any two species recorded in different sites on the algal host (Izsak & Price, 2001). The taxonomic path lengths would be 0 (same species), 1 (different species but same genus), 2 (different genus but same family), and 3 (different family but same order). The species were classified into genera, families, orders, and various sites. However, the length of the path shows species in different sites rather than in only one site (Izsak & Price, 2001). Taxonomic similarity ( $\Delta_s$ ) was calculated as follow:

$$\Delta_s = 1 - (TD / (L - 1))$$

where, L: the taxonomic level number used to classify the species. PRIMER software measured the index of taxonomic distance, where it is the Gamma<sup>+</sup> index in the program (Clarke & Gorley, 2001). For all pair-wise comparisons of species recorded on algal hosts at three sites throughout the same season or various seasons at the same site, taxonomic beta diversity was known as an average taxonomic similarity. Among all pair-wise comparisons of seasons and sites, the slope of linear regression equations was computed to assess the relationship between various similarity matrices. The Mantel test with Pearson's product-moment correlation was used to detect the significant correlation, with p-values being based on 10,000 permutations using the XLSTAT program v7.

## 3. Results

Diatoms formed the dominant group of epiphytes on the macroalgae studied, with some rare filamentous cyanobacteria and metaphyton not included in community study. Table 2 displays all of the epiphytic diatom taxa seen on the thalli surface of the 14 species of seaweed. During the study period, 52 taxa represented the epiphytic diatom group on all the macroalgae (Table 2). Three genera contributed about 28.85% of them: *Nitzschia* (6 species), *Cymbella* (5 species), and *Licmophora* (4 species). There were noticeable differences in the number of species between the host species through the different sites and seasons (Table 2). On *Palisada perforate* present in Safaga during the spring (16 species) and on *Digenea simplex* present also





Table 2.Continue

|  |    |    |   |   |    |   |   |   |   |    |    |   |    |    |   |    |    |   |    |    |   |    |    |    |   |
|--|----|----|---|---|----|---|---|---|---|----|----|---|----|----|---|----|----|---|----|----|---|----|----|----|---|
| <i>Synedra acus</i> Kützing  | -  | -  | - | - | -  | - | - | - | - | -  | -  | - | -  | -  | - | -  | -  | - | -  | +  | - | +  | -  | -  | + |
| <i>Synedra ulna</i> (Nitzsch)<br>Ehrenberg   | -  | -  | - | - | +  | - | - | - | - | -  | +  | - | -  | -  | - | +  | -  | - | +  | -  | - | -  | -  | -  | - |
| <i>Synedra</i> sp.   | -  | -  | - | - | -  | - | - | - | - | -  | -  | - | -  | -  | - | +  | +  | + | +  | -  | + | -  | -  | -  | - |
| <i>Trachysphenia australis</i><br>P.Petit  | -  | -  | - | - | -  | - | + | - | - | +  | +  | + | -  | -  | + | -  | -  | + | +  | -  | - | -  | -  | -  | - |
| Total algal species  | 10 | 11 | 2 | 9 | 11 | 3 | 9 | 6 | 3 | 14 | 11 | 8 | 10 | 10 | 8 | 14 | 16 | 9 | 14 | 12 | 6 | 10 | 14 | 15 |   |
| Note. <i>H. clathratus</i> – <i>Hydroclathrus clathratus</i> ; <i>T. decurrens</i> – <i>Turbinaria decurrens</i> |    |    |   |   |    |   |   |   |   |    |    |   |    |    |   |    |    |   |    |    |   |    |    |    |   |

Table 3. Community parameters at Red Sea. Number of species (S), Margalefs Index (d'), Shannon-Wiener diversity (H', log<sub>e</sub> and log<sub>2</sub> based).

| Seasons | Sites     | Macrophyte                      | S  | d'    | H'(log <sub>e</sub> ) | H'(log <sub>2</sub> ) |
|---------|-----------|---------------------------------|----|-------|-----------------------|-----------------------|
| Autumn  | Al-Quseir | <i>Palisada perforata</i>       | 10 | 3.909 | 2.303                 | 3.322                 |
|         |           | <i>Caulerpa serrulata</i>       | 11 | 4.16  | 2.383                 | 3.437                 |
|         | Hurghada  | <i>Sargassum</i> sp.            | 2  | 1.569 | 1.019                 | 1.47                  |
|         | Safaga    | <i>Cystoseira</i> sp.           | 9  | 3.641 | 2.197                 | 3.17                  |
|         |           | <i>Sargassum</i> sp.            | 11 | 4.16  | 2.383                 | 3.437                 |
| Winter  | Al-Quseir | <i>Palisada perforate</i>       | 3  | 1.82  | 1.099                 | 1.585                 |
|         |           | <i>Cystoseira myrica</i>        | 9  | 3.641 | 2.197                 | 3.17                  |
|         | Hurghada  | <i>Palisada perforate</i>       | 6  | 2.736 | 1.689                 | 2.437                 |
|         | Safaga    | <i>Palisada perforate</i>       | 3  | 1.82  | 1.099                 | 1.585                 |
|         |           | <i>Dictyota</i> sp.             | 14 | 4.926 | 2.639                 | 3.807                 |
| Spring  | Al-Quseir | <i>Palisada perforata</i>       | 11 | 4.16  | 2.383                 | 3.437                 |
|         |           | <i>Padina pavonica</i>          | 8  | 3.366 | 2.079                 | 3                     |
|         |           | <i>Hydroclathrus clathratus</i> | 10 | 3.909 | 2.303                 | 3.322                 |
|         |           | <i>Jania rubens</i>             | 10 | 3.909 | 2.303                 | 3.322                 |
|         | Hurghada  | <i>Palisada perforate</i>       | 8  | 3.366 | 2.079                 | 3                     |
|         |           | <i>Gracilaria arcuata</i>       | 14 | 4.926 | 2.639                 | 3.807                 |
|         | Safaga    | <i>Palisada perforate</i>       | 16 | 5.41  | 2.773                 | 4                     |
|         |           | <i>Dictyota pinnatifida</i>     | 9  | 3.641 | 2.197                 | 3.17                  |
| Summer  | Al-Quseir | <i>Palisade perforate</i>       | 14 | 4.926 | 2.639                 | 3.807                 |
|         |           | <i>Laurencia</i> sp.            | 12 | 4.427 | 2.485                 | 3.585                 |
|         | Hurghada  | <i>Palisada perforate</i>       | 6  | 2.736 | 1.689                 | 2.437                 |
|         |           | <i>Turbinaria decurrens</i>     | 10 | 3.909 | 2.303                 | 3.322                 |
|         | Safaga    | <i>Palisada perforate</i>       | 14 | 4.926 | 2.639                 | 3.807                 |
|         |           | <i>Digenea simplex</i>          | 15 | 5.17  | 2.708                 | 3.907                 |

A distance-based permutational multivariate variance analysis, PERMANOVA, has analyzed the variations in the epiphytic diatom community structure between the two studied variables (season and site). Two way-PERMANOVA of epiphytic diatom assemblages between the two factors studied (site and season) revealed that temporal variation was the most important factor causing variation in epiphytic diatom assemblages (Table 4). Temporal variation affected the diatom species and the level of diatom genera using the Jaccard and taxonomic similarity ( $p \leq 0.05$ ; Table 4). On the other hand, the diatom species and genera level did not vary among sites based on the Jaccard and taxonomic similarity ( $p \geq 0.05$ ; Table 4). Significant site-season interactions on epiphytic diatom assemblages using taxonomic similarity ( $p \leq 0.05$ ) were observed; however, site-season

interactions could not show the difference between diatom species and diatom genera based on Jaccard similarity ( $p \geq 0.05$ , Table 4).

| Source of variation                      | df | SS     | MS     | Pseudo-F | P(perm) | Unique permutations |
|--|----|--------|--------|----------|---------|---------------------|
| <b>Diatoms species level<sup>a</sup></b> |    |        |        |          |         |                     |
| Si                                       | 2  | 8761.9 | 4380.9 | 1.2666   | 0.256   | 999                 |
| Se                                       | 3  | 16260  | 5420   | 1.8234   | 0.002   | 997                 |
| Si × Se                                  | 6  | 21245  | 3540.8 | 1.1912   | 0.13    | 998                 |
| Res                                      | 12 | 35670  | 2972.5 |          |         |                     |
| Total                                    | 23 | 81246  |        |          |         |                     |
| <b>Diatoms genera level<sup>a</sup></b>  |    |        |        |          |         |                     |
| Si                                       | 2  | 4579   | 2289.5 | 0.93746  | 0.557   | 999                 |
| Se                                       | 3  | 11619  | 3873   | 1.6344   | 0.028   | 995                 |
| Si × Se                                  | 6  | 14727  | 2454.5 | 1.0358   | 0.373   | 998                 |
| Res                                      | 12 | 28436  | 2369.7 |          |         |                     |
| Total                                    | 23 | 60104  |        |          |         |                     |
| <b>Diatoms<sup>b</sup></b>               |    |        |        |          |         |                     |
| Si                                       | 2  | 1198.2 | 599.12 | 0.7879   | 0.605   | 999                 |
| Se                                       | 3  | 4688.5 | 1562.8 | 3.2568   | 0.001   | 997                 |
| Si × Se                                  | 6  | 4845.8 | 807.63 | 1.683    | 0.036   | 999                 |
| Res                                      | 12 | 5758.5 | 479.88 |          |         |                     |
| Total                                    | 23 | 16587  |        |          |         |                     |

<sup>a</sup>Based on Jaccard similarity.  
<sup>b</sup>Based on taxonomic similarity. Two similarity matrices were used for the analysis: Jaccard similarity and taxonomic similarity. df, degrees of freedom; SS, sum of squares; MS, mean squares; Res, residuals.

| Marginal Tests   |         |          |       |        | Sequential Tests |         |          |       |        |         |         |
|------------------|---------|----------|-------|--------|------------------|---------|----------|-------|--------|---------|---------|
| Variable         | SS(tr.) | Pseudo-F | P     | Prop.  | R <sup>2</sup>   | SS(tr.) | Pseudo-F | P     | Prop.  | Cum.    | res. df |
| Water temp.      | 6949.8  | 2.0579   | 0.008 | 0.0855 | 0.085            | 6949.8  | 2.0579   | 0.002 | 0.0855 | 0.0855  | 22      |
| pH               | 8094.8  | 2.4345   | 0.001 | 0.0996 | 0.13985          | 4412.9  | 1.3261   | 0.109 | 0.0543 | 0.13985 | 21      |
| E.C.             | 3326.4  | 0.9392   | 0.58  | 0.0409 | 0.17304          | 2696.5  | 0.8027   | 0.744 | 0.0332 | 0.17304 | 20      |
| Na <sup>+</sup>  | 3104.9  | 0.87416  | 0.681 | 0.0382 | 0.21649          | 3529.9  | 1.0536   | 0.389 | 0.0434 | 0.21649 | 19      |
| K <sup>+</sup>   | 5696.5  | 1.6588   | 0.018 | 0.0701 | 0.3024           | 6979.7  | 2.2167   | 0.004 | 0.0859 | 0.3024  | 18      |
| Ca <sup>2+</sup> | 4473.2  | 1.2818   | 0.132 | 0.0551 | 0.35831          | 4542.6  | 1.4813   | 0.064 | 0.0559 | 0.35831 | 17      |
| Mg <sup>2+</sup> | 7044.1  | 2.0885   | 0.001 | 0.0867 | 0.41033          | 4226.5  | 1.4115   | 0.125 | 0.0520 | 0.41033 | 16      |
| Cl <sup>-</sup>  | 5690.3  | 1.6569   | 0.013 | 0.0700 | 0.44387          | 2725    | 0.90466  | 0.576 | 0.0335 | 0.44387 | 15      |
| Salinity         | 5690.3  | 1.6569   | 0.014 | 0.0700 | 0.44387          | 0.0006  | 0        | 1     | 0.0786 | 0.44387 | 15      |
| Phosphate        | 3100.5  | 0.87288  | 0.688 | 0.0382 | 0.48938          | 3697.4  | 1.2477   | 0.243 | 0.0455 | 0.48938 | 14      |
| Sulphate         | 2824.1  | 0.79225  | 0.8   | 0.0348 | 0.52929          | 3242.7  | 1.1023   | 0.364 | 0.0399 | 0.52929 | 13      |
| Nitrate          | 4115.9  | 1.174    | 0.237 | 0.0507 | 0.56097          | 2573.5  | 0.86579  | 0.649 | 0.0317 | 0.56097 | 12      |

E.C.: Electrical conductivity, Prop.: proportion of total variation explained, Cum.: cumulative.

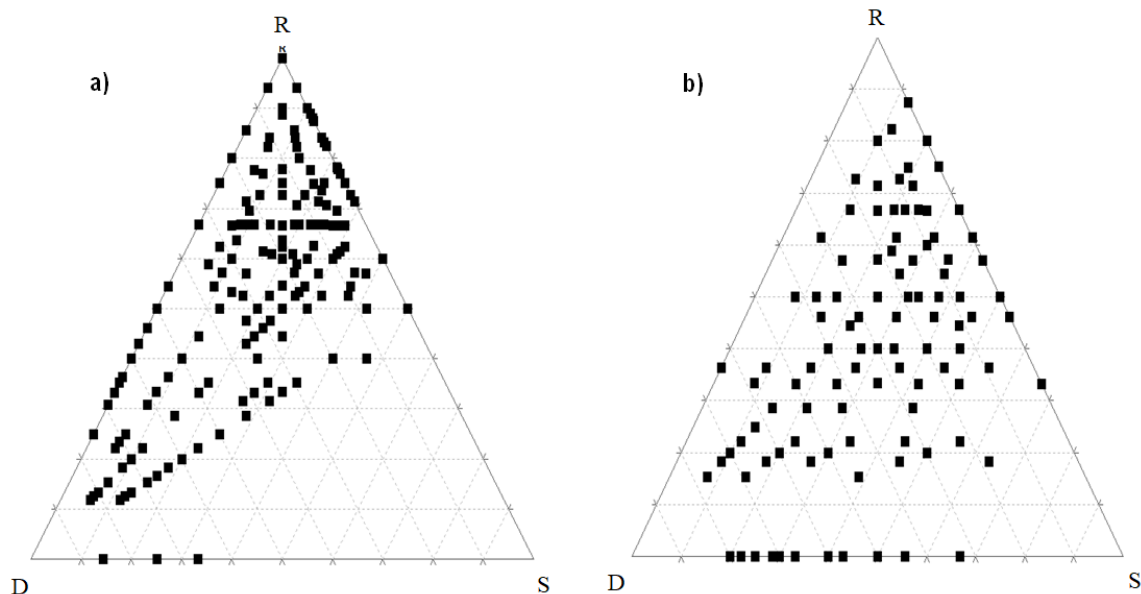
The DISTLM marginal analysis showed that water temperature, pH, magnesium, chloride, and salinity had significant influences on the structure of the diatom assemblages using Jaccard and taxonomic similarity (i.e. the main sources of variability). The results of the marginal tests suggest the separate effect of each environmental parameter, but the results of the sequential tests show the combined model's impact of parameters on the diatom species (Table 5, 6). Table 5, 6 shows the best



fitting model, based on the retained environmental variables which explained the diatom assemblages. These results show the water temperature, pH, magnesium, chloride, and salinity explained 8.55, 9.96, 8.67, 7.0, 7.0% and 16.8, 17.5, 11.4, 9.9, 9.9% of the variance found for the diatom assemblages based on Jaccard and taxonomic similarity, respectively. The cumulative amount explained by all variables is 56% of the total variability based on Jaccard similarity and 64.3% based on taxonomic similarity for the diatom species (Table 5, 6).

| Marginal Tests   |         |          |       |        | Sequential Tests |         |          |       |        |         |         |
|------------------|---------|----------|-------|--------|------------------|---------|----------|-------|--------|---------|---------|
| Variable         | SS(tr.) | Pseudo-F | P     | Prop.  | R <sup>2</sup>   | SS(tr.) | Pseudo-F | P     | Prop.  | Cum.    | res. df |
| Water temp.      | 2800.5  | 4.469    | 0.005 | 0.1688 | 0.16884          | 2800.5  | 4.469    | 0.003 | 0.1688 | 0.16884 | 22      |
| pH               | 2912.9  | 4.6865   | 0.002 | 0.1756 | 0.22028          | 853.33  | 1.3856   | 0.231 | 0.0514 | 0.22028 | 21      |
| E.C.             | 421.75  | 0.57397  | 0.772 | 0.0254 | 0.23979          | 323.55  | 0.51318  | 0.801 | 0.0195 | 0.23979 | 20      |
| Na <sup>+</sup>  | 790.41  | 1.1008   | 0.375 | 0.0477 | 0.3201           | 1332.1  | 2.2442   | 0.04  | 0.0803 | 0.3201  | 19      |
| K <sup>+</sup>   | 1348.2  | 1.9463   | 0.083 | 0.0813 | 0.39951          | 1317.2  | 2.3804   | 0.027 | 0.0794 | 0.39951 | 18      |
| Ca <sup>2+</sup> | 1474.9  | 2.1471   | 0.054 | 0.0889 | 0.47379          | 1232.2  | 2.3999   | 0.032 | 0.0743 | 0.47379 | 17      |
| Mg <sup>2+</sup> | 1899.5  | 2.8452   | 0.017 | 0.1145 | 0.52129          | 787.76  | 1.5873   | 0.17  | 0.0475 | 0.52129 | 16      |
| Cl <sup>-</sup>  | 1656.1  | 2.4402   | 0.038 | 0.0998 | 0.54398          | 376.44  | 0.7465   | 0.648 | 0.0227 | 0.54398 | 15      |
| Salinity         | 1656.1  | 2.4402   | 0.039 | 0.0998 | 0.54398          | 0.0007  | 0        | 1     | 0.0405 | 0.54398 | 15      |
| Phosphate        | 644.95  | 0.8900   | 0.505 | 0.0389 | 0.62539          | 1350.3  | 3.0424   | 0.005 | 0.0814 | 0.62539 | 14      |
| Sulphate         | 469.08  | 0.6403   | 0.697 | 0.0283 | 0.64315          | 294.66  | 0.64715  | 0.64  | 0.0178 | 0.64315 | 13      |
| Nitrate          | 931.77  | 1.3094   | 0.245 | 0.0562 | 0.65283          | 160.54  | 0.33454  | 0.92  | 0.0097 | 0.65283 | 12      |

E.C.: Electrical conductivity, Prop.: proportion of total variation explained, Cum.: cumulative.

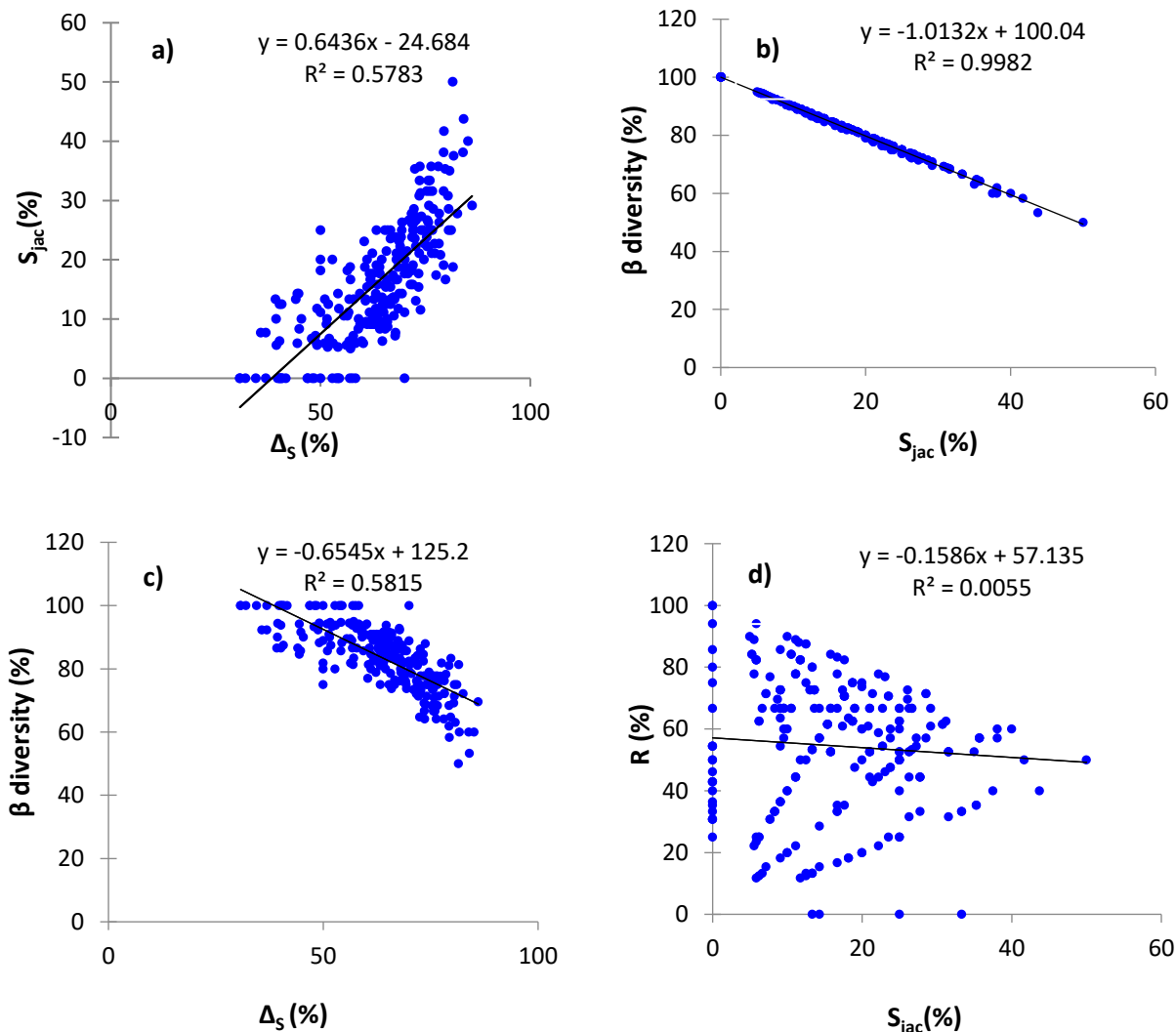


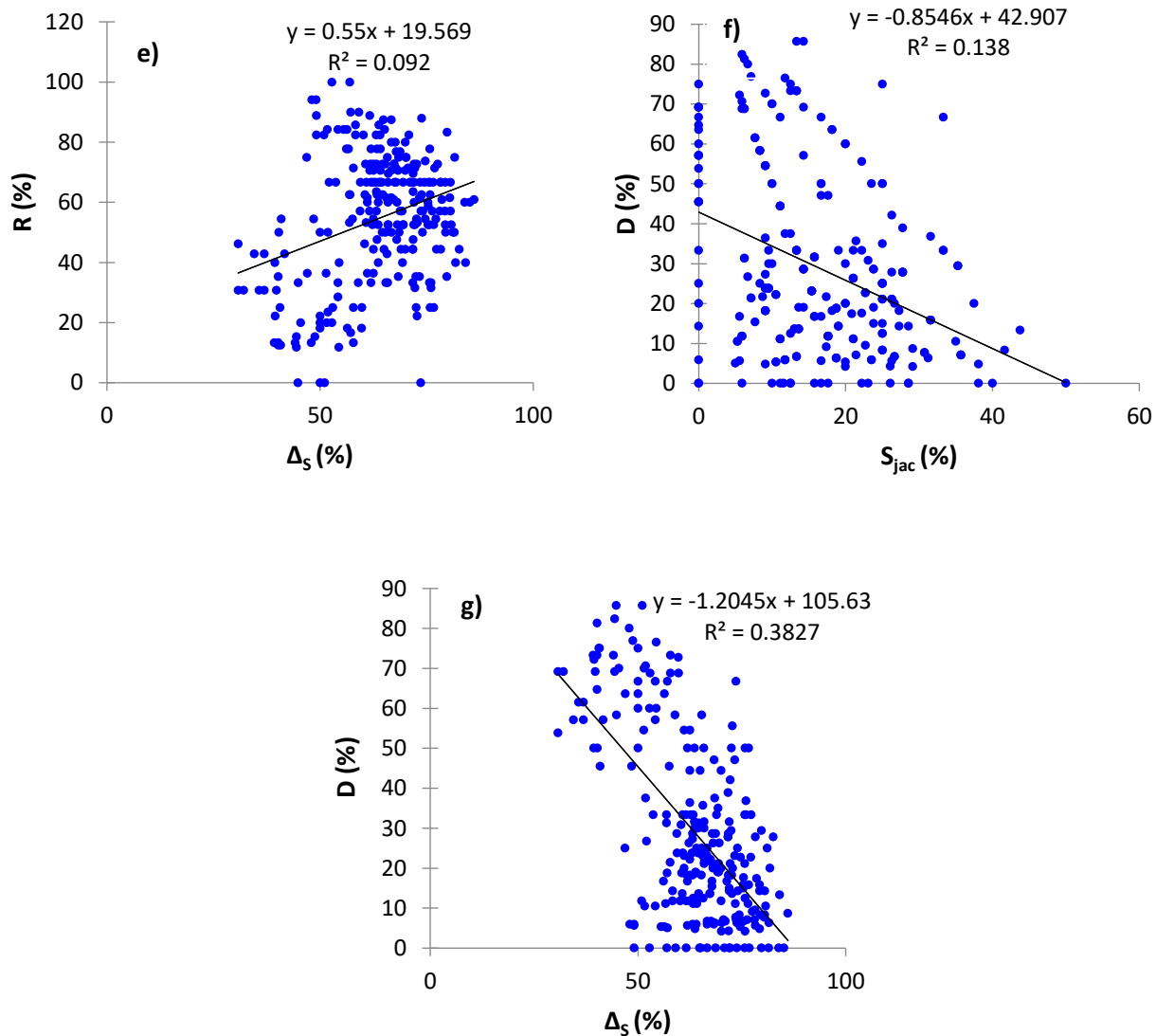
**Figure 1.** Plots of SDR simplex for diatom communities from seaweeds at the Red Sea, Egypt. S, D, and R represent relative similarity, richness difference, and species replacement. (a), and (b) symbols represent pair-wise comparisons using diatom species only and diatom genera, respectively of macroalgal hosts between all different sites and seasons.

The analysis of SDR simplex showed that macroalgae epiphytic diatom species have high values of  $\beta$ -diversity. Therefore multiple pairs are closer to the left (D and R) in the ternary diagram (Figure 1a). This shows that most macroalgal samples have less common species, and several of them have higher values of abundance than the others. The closer the dots to R apex, the more  $\beta$  diversity is resultant from the replacement of species rather than differences in species richness between the two

samples. A slight change from high  $\beta$ -diversity toward similarity was shown when the diatom genera presence/absence data were included in the analysis (Figure 1b). The similarities between the epiphytic diatoms communities associated with the hosts of macroalgae were negligible, based on presence/absence data.

The increasing similarity in epiphytic diatom structure was necessarily correlated with the existence of taxonomically close species (increasing taxonomic similarity; Mantel's  $r = 0.76$ ,  $p \leq 0.0001$ ; Figure 2a). Patterns of beta-diversity were negatively correlated with both similarity of species,  $S_{jac}$  ( $r = -0.999$ ,  $p \leq 0.0001$ ; Figure 2b), and taxonomic similarity,  $\Delta_s$  ( $r = -0.763$ ,  $p \leq 0.0001$ ; Figure 2c). In other words, a rise in species dissimilarity leads to an increase in beta diversity. The correlations were measured separately for R and D to measure which variable of beta diversity (species replacement, R, or species richness differences, D) was responsible for those results. There was no significant correlation between species replacement and Jaccard similarity,  $S_{jac}$  ( $r = -0.074$ ,  $p = 0.235$ ; Figure 2d). On the other hand, there was a strong positive correlation between species replacement and taxonomic similarity,  $\Delta_s$  ( $r = 0.303$ ,  $p \leq 0.0001$ ; Figure 2e). There was also a strong negative correlation between richness differences and both  $S_{jac}$  ( $r = -0.371$ ,  $p \leq 0.0001$ ; Figure 2f) and  $\Delta_s$  ( $r = -0.619$ ,  $p \leq 0.0001$ ; Figure 2g). So, the differences in species richness between spatial or temporal scales and algal hosts were the most significant beta diversity variable responsible for the observed difference in epiphytic diatoms in terms of species composition dissimilarity and taxonomic pattern dissimilarity.





**Figure 2.** Correlation and regression between various  $\beta$ -diversity measures of macroalgae (%) at the Red Sea, Egypt. (a) Correlation between Jaccard similarity (% S<sub>jac</sub>) and taxonomic similarity (% Δ<sub>s</sub>). (b) Correlation between  $\beta$ -diversity (%) and Jaccard similarity (% S<sub>jac</sub>). (c) Correlation between  $\beta$ -diversity (%) and taxonomic similarity (% Δ<sub>s</sub>). (d) Correlation between species replacement (% R) and Jaccard similarity (% S<sub>jac</sub>). (e) Correlation between species replacement (% R) and taxonomic similarity (% Δ<sub>s</sub>). (f) Correlation between richness difference (% D) and Jaccard similarity (% S<sub>jac</sub>). (g) Correlation between richness difference (% D) and taxonomic similarity (% Δ<sub>s</sub>). Points represent the comparisons of pair-wise of diatom communities of macroalgal hosts between all sites and seasons.

#### 4. Discussion

In this study, the distribution of epiphytic diatoms on various macroalgae species is remarkably variable, with 30.7% of the total diatom taxa recorded primarily from Safaga during the spring season on *Palisada perforata*. Few species were epiphytic on *Sargassum* sp. present in Hurghada, and *Palisada perforata* in Al-Quseir and Safaga during winter. The macroalgae-associated epiphytic diatoms in Egypt's Red Sea were dominated by *Fragilarioforma virescens*, *Licmophora ehrenbergii*, *Licmophora flabellata*, *Nitzschia gracilis*, and *Nitzschia* sp.1. Garrison et al. (1987) suggested the sea-ice would most likely be a shelter for benthic and planktonic diatoms. Five epiphytic diatoms from Potter Cove are related to the marine-ice (*Fragilariopsis rhombica*,

*Actinocyclus actinochilus*, *Nitzschia hybrid*, *Navicula directa*, and *Thalassiosira lentiginosa* (Crosta et al., 2008). This low number of sea ice species within the community of epiphytic diatom shows that it is not common to exchange epiphytic diatoms with the sea-ice substratum. The current results indicate the level of diatom species and genera influenced by temporal variation based on Jaccard and taxonomic similarity as described by analysis of PERMANOVA. Schmidt et al. (2007) stated that temporal variation affects the rate of microbial variability, as microorganisms may process resources on a much faster time scale than macroorganisms and adapt to the variations in natural environments. For example, in autumn and winter, the rhodophyte *Palisada perforata* was collected from Al-Quseir, but the algae present in the former season hosted 10 diatom taxa while only 3 diatom species were found on the algae present in the later season. The other conditions that may affect the diatoms or other group distribution are the environmental factors such as nutrients, salinity, hydrodynamic regime, and light availability (Frankovich et al., 2006; Fawzy, 2016), as well as physiological responses (Ruesink, 1998), biological processes such as grazing (Hillebrand et al., 2000) and chemical interactions with the host (Amsler et al., 2005).

The current study considered water temperature, pH, magnesium, chloride, and salinity as the primary sources of variability of diatom assemblages based on Jaccard and taxonomic similarity as described in DistLM analysis. Lepoint et al. (2000) stated that the seasonal studies indicate indirect evidence that the biomass of epiphytic algae rises as temperature and light increase. pH may directly affect the assemblages of epiphytes or may be indirectly connected with the noticed changes by several environmental factors (e.g., characteristics of organic carbon and availability of nutrients). Krause et al. (2012) found that pH ranged from 7.1 to 7.67, preferring distinguished group at the community level, and likely leading to changes in composition and causing essential effects on the communities of marine microorganisms. Salinity is considered the main environmental factor restricting the diatom community structure along the gradients of estuarine (Snoeijs, 1999). Huvane (2002) studied the valves of diatom in Florida Bay sediment cores and sediments of the surface. They confirmed that diatoms were the best indicators of salinity conditions in history. Changes in nutrient availability are reflected in the species composition and structure of algal communities (Snoeijs, 1999). Sundbäck and Snoeijs (1991) reported that the addition of nutrients resulted in particular changes in the diatoms dominance, while shifts were more apparent at the macroscopic level, in other words, an increase of the filamentous Chlorophyta than in the microflora.

The proposed measure of taxonomic beta diversity includes species richness and details on the degree of taxonomic higher-order structure between species plots. The patterns of beta diversity are estimated by two processes, the species replacement and differences in species richness. An essential task in ecology, conservation, and biogeography is to determine the relative function of each component in evaluating beta diversity (Baselga, 2007). Nevertheless, species replacement and differences in species richness led to the high beta diversity values (some points were close to R apex, but the others were close to D apex in SDR simplex graph, Figure 1). Based on the presence/absence results, the similarities between the communities of epiphytic diatoms associated with algal hosts were minor. This means that the epiphytic diatoms differ among the algal host. Differences in species richness were more critical in the current study than the replacement of species in structuring beta diversity patterns of epiphytic diatoms, as observed similarity patterns (Sjac,  $\Delta s$ ) were negatively related to the richness differences and not to the replacement of species (Figure 2d,e,f,g). For most benthic diatoms and other epiphytes the vegetated ecosystem is the ideal habitat (Frankovich et al., 2006). The algae's thallus can display the order of magnitude of a larger surface area relative to the sediments for diatoms growth and colonization (Zieman et al., 1989). But, the effective behavior of the epiphytic diatoms for attachment themselves to macroalgal host is the major factor for this mutualistic relationship (Romagnoli et al., 2007). Considering the composition of the species of epiphytic microalgae, the species enumerated displayed various preference patterns.

In this study, some epiphytic diatoms have shown host specificity on a few algal hosts, giving specific epiphytic flora. Certain ones did not reflect the preceding pattern of preference and occurred on most macroalgae, reflecting the absence of selectivity. Our results are consistent with the Madkour and El-Shoubaky (2007) findings. Actually, there is no rule for the epiphytes selectivity, and there is a major argument about the cause of one species preference for a certain host. Numerous authors stated different results. For example, Adam et al. (2017) found differences in species composition as a function of substrate representing selectivity between algal species and substrate, while Sullivan (1984) found similarities in the communities of epiphytic diatoms, representing non-selectivity between the algal hosts and epiphytes. Ismael (2012) found that Oscillatoriales favored Chlorophyta to Rhodophyta and on species level; for each host of Chlorophyta they displayed selectivity.

## 5. Conclusion

In this investigation, we suggested that the temporal variations, environmental variables, and algal hosts may affect the diversity and taxonomic composition of the communities of epiphytic diatoms. On a few hosts, some epiphytic diatoms display host specificity, resulting in a unialgal epiphytic flora. Other diatoms did not represent the preceding pattern of preference and existed on most macroalgae, indicating a lack of selectivity. Any host effect on epiphytic communities identified in the ecological studies may be clarified, invoking several reasons, such as different life cycles of the hosts and chemical interactions as well as the various environmental conditions that the host may have encountered, making it challenging to identify a single major factor. Therefore, these conclusions were based on correlation data and must be confirmed through future experiments.

**Conflict of interest.** The author declares that there are no conflicts of interest regarding the publication of this paper.

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