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Hungyen Chen
Department of Agronomy, National Taiwan University, Taipei, Taiwan, R.O.C. Research Center for Bioinformatics and Biosciences, National Research Institute of Fisheries Science, Kanagawa, Japan., chen@lbm.ab.a.u-tokyo.ac.jp

Satoshi Nagai
Research Center for Bioinformatics and Biosciences, National Research Institute of Fisheries Science, Kanagawa, Japan.

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PHYLOGENETICALLY CLUMPED SPECIES COMPOSITION OF MARINE GREEN ALGAE (CHLOROPHYTA) IN THE TEMPERATE ZONE

Hungyen Chen[1, 2] and Satoshi Nagai[2]

Key words: biodiversity, global distribution, phylogenetic diversity, sea surface temperature, species richness.

ABSTRACT

Global patterns of diversity in marine algae have been reported at the genus level but rarely at the species level. In this study, we investigate the global distribution of species diversity for marine green algae and evaluate the effect of water temperature upon the species composition. We calculated and mapped the species richness and phylogenetic diversity of green algae in 5° × 5° latitude-longitude cells. We then compared and grouped the different spatial patterns of phylogenetic species composition of green algae around the world. Finally, we fitted a locally weighted scatterplot smoothing (LOWESS) curve to the sea surface temperature (SST) data to determine how the species diversity varied with SST. We found hotspots of species richness and phylogenetic diversity in green algae in the seas around western Europe and the coasts of India, Brazil, South Africa, and northeastern Australia, and about half of these hotspots were located in the Atlantic Ocean. Both the species richness and the phylogenetic diversity of green algae were found to be higher in warm waters. In the tropics, the greater the species richness, the more the phylogenetic species composition was dispersed over multiple clusters. Conversely, in the temperate zone, the greater the species richness, the higher the phylogenetic clumpedness of the species in a community. The species in a community were evenly distributed on the phylogenetic tree in waters warmer than 23°C. On the other hand, the phylogenetic species composition was clumped in waters cooler than 23°C and this phylogenetic clumpedness increased as SST decreased. Our results indicate that the evolutionary processes of species composition in local communities of green algae have adapted to local environmental conditions, and suggest a phylogenetically clumped species composition of marine green algae in the temperate zones.

I. INTRODUCTION

Understanding the spatial distributions of species and the mechanisms that generate and maintain biodiversity is an important objective in ecology. The global distribution of species richness is one of the most interesting topics in terrestrial and marine ecology (Gaston, 2000). As a result, global patterns of marine species richness have been widely studied in organisms such as phytoplankton (Irigoien et al., 2004; Barton et al., 2010; Boyce et al., 2010), zooplankton (Irigoien et al., 2004; Tittensor et al., 2010), coral species (Hughes et al., 2003; Bellwood et al., 2004), marine mammals (Tittensor et al., 2010), tuna and billfish (Worm et al., 2005; Boyce et al., 2008; Trebilco et al., 2011), and sharks (Lucifora et al., 2011; Chen and Kishino, 2015).

As one of the most diverse and ubiquitous assemblages in aquatic and some terrestrial habitats, green algae play a key role in the global ecosystem (Falkowski et al., 2004; Leliaert et al., 2011). Although green algae have a number of distinct features, they also share many features with land plants (van den Hoek et al., 1995; Graham et al., 2009). The evolution of land plants from green algae initiated the development of terrestrial ecosystems. This led to huge changes in the global environment and was one of the most crucial events in the history of life (Kenrick and Crane, 1997). The Chlorophyta division is a clade of the green chloroplast lineage (Viridiplantae), comprising the early diverging prasinophytes. Species of the Chlorophyta are commonly found in marine, freshwater, and some terrestrial habitats and are morphologically diverse.

The differences in evolutionary history among species within communities should be determined and considered in order to rectify the issues associated with conservation guidelines established using species richness alone (Faith, 1992; Webb et al., 2002). Phylogenetic diversity (PD) was developed to assess the relationship between species diversity and evolutionary processes (Vane-Wright et al., 1991; Cadotte et al., 2008). The PD of an assemblage provides information on the interactions and biogeographic relationships between species with relation to community structure and composition (Webb et al., 2002).

The global diversity gradients for marine algae have been

Paper submitted 12/01/16; revised 03/17/17; accepted 04/14/17. Author for correspondence: Hungyen Chen (e-mail: chen@lbm.ab.a.u-tokyo.ac.jp).
[1] Department of Agronomy, National Taiwan University, Taipei, Taiwan, R.O.C.
[2] Research Center for Bioinformatics and Biosciences, National Research Institute of Fisheries Science, Kanagawa, Japan.

reported at the genus level (Kerswell, 2006; Keith et al., 2014). Keith et al. (2014) also showed that environmental conditions explain more of the observed variation in diversity (of marine macroalgae) at high latitudes than at low latitudes. Our aim is to investigate the global distribution pattern of green algae diversity at the species level. In this study, we mapped the hotspots of green algae species richness. We calculated PD to reveal the global phylogenetic species diversity of green algae. We then compared and grouped the different spatial patterns of phylogenetic species composition of green algae around the world. Finally, we regressed and fitted locally weighted scatterplot smoothing curve to the data point with sea surface temperature to determine how the biodiversity varied among water temperatures.

II. MATERIALS AND METHODS

1. Global Distribution of Green Algae

The global green algae distribution data were retrieved from the Ocean Biogeographic Information System (OBIS) database (OBIS, 2016). The OBIS is a web-based access point to information about the distribution and abundance of living species in the ocean. As of 2017, OBIS contains over 45,000,000 observation from nearly 120,000 species around the world provided by 500 institutions from 56 countries (OBIS, 2016). We retrieved more than 85,000 records of presence (include both sequencing data and morphologic data) of green algae (Chlorophyta division) from OBIS and binned them to 5° × 5° latitude-longitude grid cells. In each grid, we counted the number of species which has been recorded within the area. We found 359 cells containing at least one species (recorded in the OBIS dataset), and we calculated the number of species in each of these cells. These green algae include a wide range of species from macroalgae (visible to naked eyes) to single-cell algae (about 2 to 10 μm in diameter).

2. Construction of Phylogenetic Tree

We constructed the list of green algae species collected from the OBIS records. By searching the species in the list one by one from the National Center for Biotechnology Information (NCBI) database (NCBI, 2016), we obtained the 18S ribosomal RNA gene sequences (linear DNA sequences) for 127 species of green algae. The first appeared data from the result of search engine were used as reference sequences when multiple data were available. We performed sequence alignments (the length of the sequences was 1,566 sites) using MUSCLE (Edgar, 2004) implemented in MEGA 6.0 (Tamura et al., 2013), and then estimated divergence times among species in a Bayesian framework using BEAST 1.8.0 (Drummond et al., 2012). We analyzed our data using the HKY model of nucleotide substitution with gamma-distributed rate heterogeneity among sites (Felsenstein, 1981; Hasegawa et al., 1985; Yang, 1994). We used a random local clock model to account for variable evolutionary rates among lineages (Douzery et al., 2002; Drummond and Suchard, 2010), and we used the Yule process tree prior. We used the default values for the prior distributions of the parameters that specify the substitution process. A log-normal distribution with a location parameter of 1 and a scale parameter of 1.25 was set as the prior for the HKY transition-transversion parameter. We set an exponential distribution with a mean of 0.5 as the prior distribution of the shape parameter to describe the heterogeneity rate among sites. The frequency of change in evolutionary rate followed a Poisson distribution with mean 0.7. We set the mean evolutionary rate to 1, because we only used the relative values of the divergence times in the subsequent step. We set the Markov chain Monte Carlo chain length to 10,000,000. The parameter settings were justified by referring to Chen et al. (2015, 2016), and Chen and Kishino (2015). The topology was fully resolved.

3. Phylogenetic Diversity Indices

Faith's PD, one of the most widely used PD metrics, measures the shared phylogenetic history of the taxa in a sample (Faith, 1992). Mean pairwise distance (MPD) between species pairs, another widely used PD metric, reflects the phylogenetic structure across the entire phylogenetic tree (Webb, 2000). The net relatedness index (NRI), calculated as the standardized MPD, measures community distinctiveness (Webb, 2000). The variation in the phylogenetic diversity of communities may result from differences in their evolutionary histories (Webb et al., 2002; Winter et al., 2009).

PD measures the shared phylogenetic history among taxa in a sample. In this study, we used Faith's PD to estimate the PD of each cell (Faith, 1992). We calculated Faith's PD as the sum of the lengths of all branches in the phylogenetic tree that belonged to a corresponding minimum-spanning path which connected all species recorded in each cell. We used NRI to reflect the phylogenetic clumpedness (PC) of taxa over the phylogenetic pool (Webb, 2000). NRI averages nodes that separate all possible pairs of member species of the community, and is standardized by simulating random sampling. We performed the calculations for Faith's PD and NRI using the package "picante" in R software.

4. Sea Surface Temperature

The sea surface temperature (SST) data were obtained from "IGOSS nmc Reyn_SmithOIv2 monthly SST datasets" downloaded from the IRI/LDEO Climate Data Library website (available online at http://iridl.ldeo.columbia.edu/SOURCES/.IGOSS/.nmc/). Data were retrieved on 22 January 2015. We retrieved the data for each month during 2005-2014 and calculated the 10-year average temperature (°C) for the central point of each 5° × 5° latitude-longitude grid cell.

5. Statistical Analyses

We fitted a natural exponential function to the observed relationships between PD and species number. Letting x be the explanatory variable (horizontal axis) and y be the dependent variable (vertical axis), the exponential regression model can be shown as: $y = ae^{bx} + c$, where $a \neq 0$. We used the function "nls" in R to estimate the exponential function (parameters a, b, and c) and the exponential regression curve that best fit each pair of metrics. We used locally weighted scatterplot smoothing

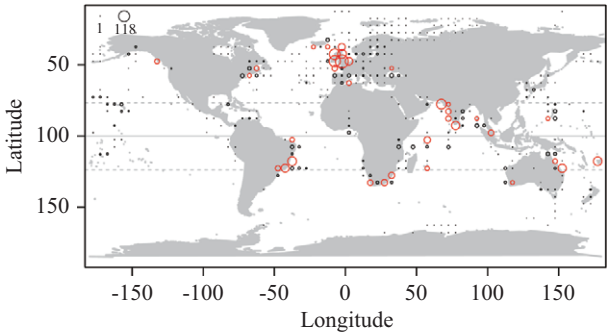

Fig. 1. **Global pattern of species richness of green algae. Each 5° × 5° latitude-longitude cell is indicated by a circle sized based on species richness. The 35 cells with the highest species richness (top 10% of all recorded cells) are indicated by red outlines. Negative numbers indicate southern latitudes and western longitudes.**

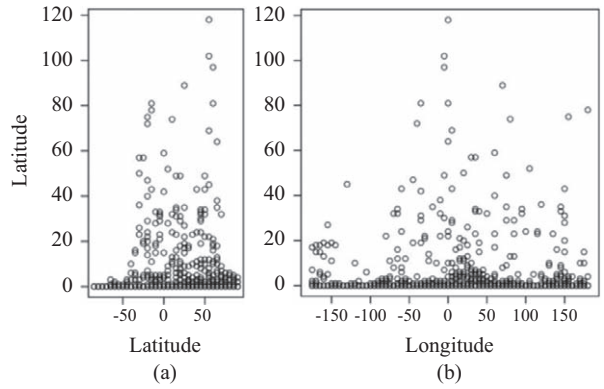

Fig. 2. **Relationship between the species richness of green algae and (a) latitude and (b) longitude. Negative numbers indicate southern latitudes.**

(LOWESS) to fit a smooth curve to the data points. All matrix calculations and statistical analyses were performed, and all maps were created, using statistical software R 3.2.3 (R Core Team, 2015).

III. RESULTS

1. Global Patterns of Diversity in Green Algae

Globally, the species richness of green algae ranged from 1 to 118 species per cell (mean ± standard deviation = 12 ± 18) in the 359 cells of the 5° × 5° latitude-longitude grid in which at least one species was recorded (Fig. 1). Species richness was highest on the green algae in the seas around western Europe and off the coasts of India, Brazil, South Africa, and northeastern Australia. Of the 35 hotspots, or cells with the highest species richness (top 10% of all recorded cells; number of species > 33), 46% (16/35) were located in the Atlantic Ocean, 34% (12/35) in the Indian Ocean, 14% (5/35) in the Pacific Ocean, and one each in the Mediterranean Sea and the Black Sea. The relationships between species and latitude and longitude are shown in Fig. 2. Species richness was highest at latitudes between 20°-30°S and at latitudes around 50°N (Fig. 2(a)), and at longitudes between 50°W-80°E (Fig. 2(b)).

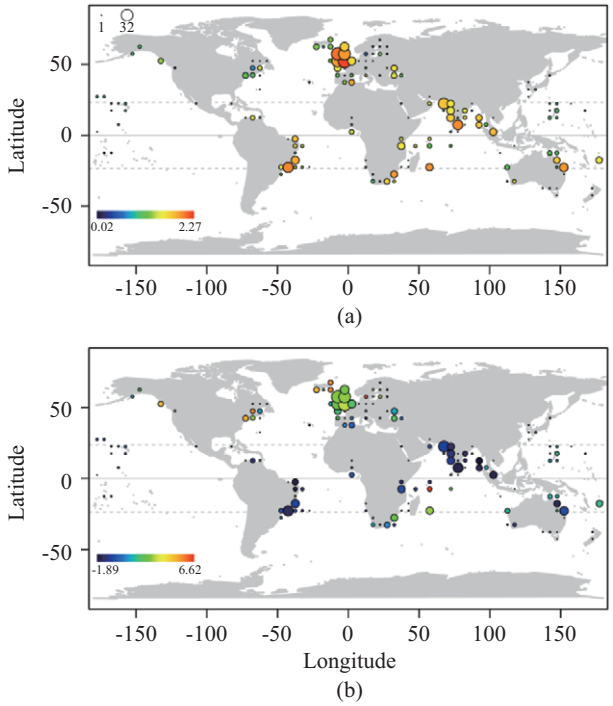

Fig. 3. **Global patterns of (a) phylogenetic diversity and (b) phylogenetic clumpedness of green algae. Each 5° × 5° latitude-longitude cell is colored based on index value and sized based on the number of species in the phylogenetic analysis (species for which RNA sequences were available). Negative numbers indicate southern latitudes and western longitudes.**

2. Spatial Patterns of Phylogenetic Diversity in Green Algae

Maps of the phylogenetic diversity of green algae are shown in Fig. 3. The number of species of green algae for which 18S ribosomal RNA sequences were available ranged from 1 to 32 (mean ± standard deviation = 6 ± 6) in the 220 cells in which at least one such species was recorded. The number of species for which an RNA sequence was available was highly correlated with the number of species from the database worldwide ($r = 0.96$; p-value < 0.001). The global pattern of species richness of green algae can therefore be investigated using only the species for which an RNA sequence was available. PD ranged from 0.02 to 2.77 (mean ± standard deviation = 1.30 ± 0.64), and PD hotspots were found in areas with high species richness (Fig. 3(a)) such as the seas around western Europe and the coasts of India, Brazil, South Africa, and northeastern Australia. PD was modestly negatively correlated with latitude ($r = -0.15$; p-value = 0.06; Fig. 4(a)). PC ranged from -1.89 to 6.62 (mean ± standard deviation = 0.94 ± 1.81) and large PC values were found at latitudes between 45°-70°N (Fig. 3(b)), in areas such as the seas around Iceland, the coasts of the northeastern USA and Alaska, and the Baltic Sea. PC was moderately positively correlated with latitude ($r = 0.54$; p-value = 0.06; Fig. 4(b)).

We compared the PD and PC values for the cells located at latitudes above 30° (in both the northern and southern hemispheres) with those for the cells located at latitudes below 30°.

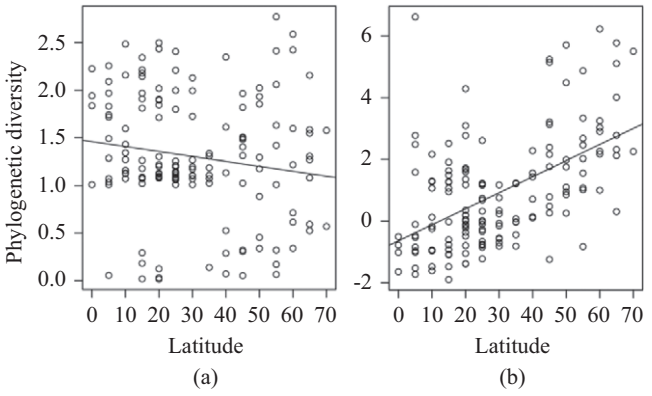

Fig. 4. Scatterplots of relationships between latitude and (a) phylogenetic diversity and (b) phylogenetic clumpedness of green algae. Each scatterplot is fitted with a simple linear regression line.

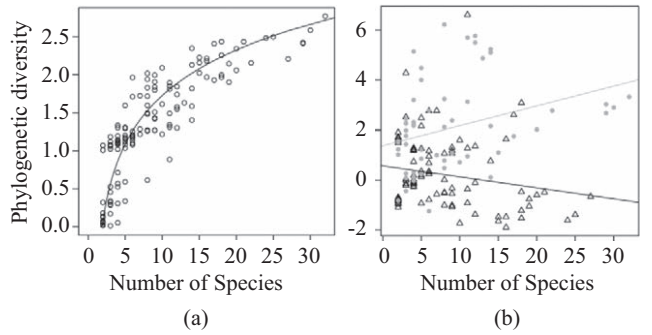

Fig. 5. Scatterplots of relationships between number of species in the phylogenetic analysis (species for which RNA sequences were available) and (a) phylogenetic diversity and (b) phylogenetic clumpedness of green algae. (a) is fitted with an exponential regression curve in (b), the gray filled circle and black open triangle represent the cells located at latitudes above and below 30° (in both the northern and southern hemispheres), respectively (b) is fitted with two simple linear regression lines. The gray and black lines apply to the cells located at latitudes above and below 30°, respectively.

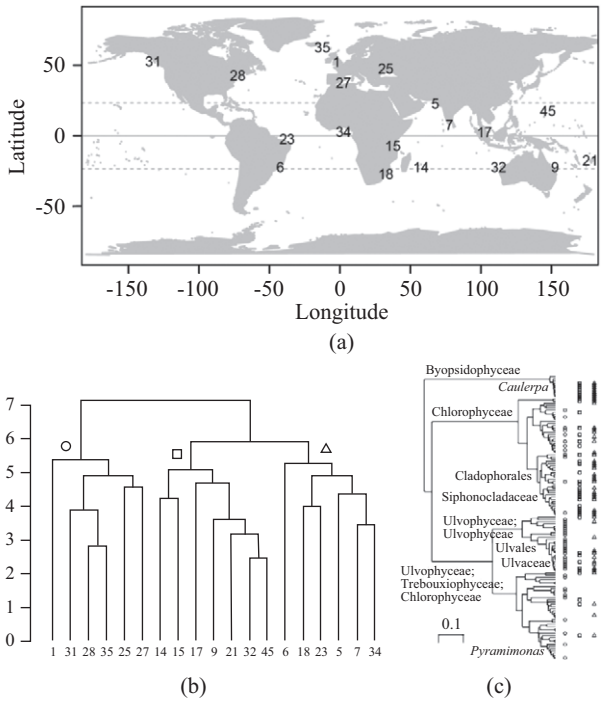

Fig. 6. Global patterns of phylogenetic composition of green algae. (a) Map showing the distribution of the cells with the largest numbers of species in the phylogenetic analysis (species for which RNA sequences are available). The number represents the rank of the number of species for each cell worldwide. Negative numbers indicate southern latitudes and western longitudes. (b) Dendrogram based on cluster analysis of the species compositions of the cells shown in (a). (c) Species compositions of the three main clusters of cells in (b). The tree shows the phylogenetic relationships of between species derived from Bayesian analysis of RNA sequences.

The PD means were 1.16 (s.d. = 0.71) and 1.39 (s.d. = 0.59) for the cells located at latitudes above and below 30°, respectively. The PC means were 2.06 (s.d. = 1.80) and 0.22 (s.d. = 1.43) for the cells located at latitudes above and below 30°, respectively. PD was significantly smaller for the cells located at latitudes above 30° (t = -2.05; p-value = 0.02). PC, however, was significantly larger for the cells located at latitudes above 30° (t = 6.67; p-value < 0.001).

3. Correlation between Phylogenetic Diversity and Number of Species

We found that PD was highly positively correlated with the species number (r = 0.81; p-value < 0.001; Fig. 5(a)). The relationship was non-linear (Fig. 5(a)). We therefore fitted the relationships between PD and species number to a natural exponential function. The equation of the exponential function ($y = a\, e^{bx} + c$) was estimated as $y = 1.1\, e^{1.2x} + 0.8$ (p-values < 0.001 for a and b, and p-value = 0.38 for c), and the exponential regression curve that best fit the data is shown in Fig. 5(a).

PC was modestly positively correlated with species number (r = 0.29; p-value = 0.09; Fig. 5(b)). However, the patterns of PC differ between the cells located in the latitudes above 30° and those located at latitudes below 30°. PC was modestly negatively correlated with low (< 30°) latitudes (r = -0.19; p-value = 0.07; Fig. 5(b)) and modestly positively correlated with high (> 30°) latitudes (r = 0.33; p-value = 0.01; Fig. 5(b)).

4. Phylogenetic Compositions of Global Green Algae

To obtain further insight into green algae PD, we examined the phylogenetic species compositions of the cells with the highest species richness (Fig. 6). Fig. 6(a) shows the global distribution of the 19 areas with the highest number of species. We compared the species compositions in all cells using the presence/absence data for each species in each cell. We performed hierarchical cluster analysis on the species composition data, using Euclidean distances and average linkage clustering, and generated a dendrogram from the results (Fig. 6(b)). There was a clear distinction between the clusters of cells located at latitudes above 30° and those located at latitudes below 30° (Figs. 6(b) and (c)).

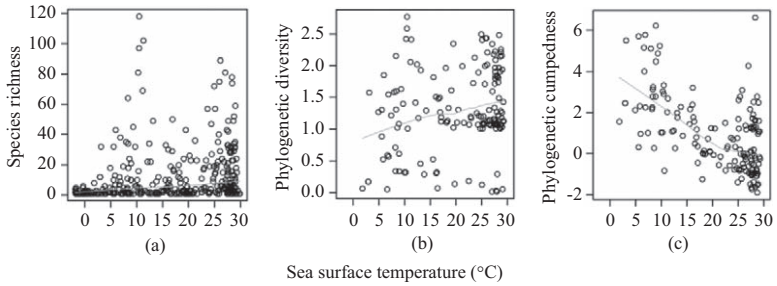

Fig. 7. Relationship between of sea surface temperature and (a) species richness, (b) phylogenetic diversity and (c) phylogenetic clumpedness of green algae. Each panel is fitted with a locally weighted scatterplot smoothing (LOWESS) curve.

In the clusters of cells located at latitudes above 30° (denoted by circle marks in Figs. 6(b) and (c)) most of the species belonged to the genus *Cladophora*, some species belonged to the order Ulvales and some of the other species also belonged to the classes Ulvophyceae and Chlorophyceae. Conversely, in the clusters of cells located at latitudes below 30° (denoted by square and triangle marks in Fig. 6(b) and (c)), most of the species belonged to the genus *Caulerpa*, some species belonged to the families Siphonocladaceae and Ulvaceae and some species belonged to the class Chlorophyceae.

2. Correlation Between Biodiversity and Temperature

Green algae are present at SSTs ranging from -2 to 30°C (Fig. 7). Globally, species richness was found to increase slightly with SST, although the two variables were only weakly correlated ($r = 0.256$; p-value < 0.001), (Fig. 7(a)). PD showed a similar global pattern. The LOWESS curve shows that PD also increased with SST although they were only weakly correlated ($r = 0.201$; p-value $= 0.01$; Fig. 7(b)). Conversely, PC was negatively correlated with SST ($r = -0.577$; p-value < 0.001; Fig. 7(c)). The LOWESS curve shows that PC decreased sharply with increasing SST until SST reached ~22°C. However, the trend was much weaker at temperatures between 23 and 30°C.

IV. DISCUSSION

Green algae (Chlorophyta) species inhabit a diverse range of marine, freshwater and terrestrial environments (Graham et al., 2009; Leliaert et al., 2012), and some have adapted to extreme environments, such as deserts, arctic and hypersaline habitats, deep oceanic waters and deep-sea hydrothermal vents (Lewis and Lewis, 2005; De Wever et al., 2009; Leliaert et al., 2011). Nearly half of the hotspots of green algae were found in the Atlantic Ocean, and most of them were located in the seas around western Europe. The high species diversity and wide species distribution in Europe may result from the cold ocean currents flowing from polar and sub-polar regions which bring in plenty of plankton. The hotspots located in the Indian Ocean may be related with the Coral Triangle, an area extending from the Philippines to the Solomon Islands, and contains 76% of the world's total complement of coral species (Veron et al., 2009). The algae can benefit from a safe place to live and consume the polyp's carbon dioxide and nitrogenous waste.

The patterns in the species composition of local communities of interacting species and the processes that affect the phylogenetic relationships within those communities have been widely studied in evolutionary ecology (Webb, 2000; 2002; Chen et al., 2016). The taxonomic diversity (Simberloff, 1970) of communities has been used to compare observed species-to-genus ratios to a priori expectations (Elton, 1946; Moreau, 1948) or to explicit null models (Simberloff, 1970). NRI and the phylogenetic nearest taxa index (NTI) were proposed as methods of measuring phylogenetic relatedness using the number of nodes that separate the taxa of a phylogeny (Webb, 2000). Phylogenetic skew (PS) was proposed as a measure of the species composition of a community that takes into account the species composition of a set of target communities, known as meta-communities (Chen et al., 2015). It compares the distribution of divergence times in a community with the distribution expected when the species composition is obtained by random sampling from the meta-community. If the species of a community have diverged recently, they will be aggregated in the species tree. On the other hand, if the species diverged a long time ago, they will be dispersed over multiple clusters. Therefore, a large PS value suggests that a species composition is phylogenetically clumped.

PD and PC are summary statistics for tree topologies and branch lengths. PD quantifies the phylogenetic richness of a community and is mathematically positively correlated with species richness (Schweiger et al., 2008). Our results showed that PD was highly positively correlated with global species richness in green algae. However, the relationship between PC and species richness was not consistent across latitudes. In the tropics (the areas at latitudes below 30), the greater the species richness, the more dispersed the phylogenetic species composition was over multiple clusters. In the temperate zone (the areas at latitudes above 30°), the greater the species richness, the higher the phylogenetic clumpedness of the species of a community. That is, the species in the temperate zone were aggregated in specific phylogenetic clusters on the species tree. On a global scale, warm water allows higher species richness and phylogenetic diversity. Water temperature also has an important effect on the phylogenetic species composition for marine green algae. Our PC results showed that the species of a community in waters warmer

than 23°C were distributed evenly on the phylogenetic tree. In waters cooler than 23°C, species composition was phylogenetically clumped, and phylogenetic clumpedness increased as SST decreased. This result may indicate that the evolutionary processes of species composition in local communities of green algae have adapted to the local environmental conditions, and that the species composition of marine green algae in the temperate zones is phylogenetically clumped. It may also suggest that phylogenetically close species tend to occur in similar environmental conditions.

In our study, the cells located at latitudes above and below 30° had distinct species compositions. In the areas at latitudes above 30° we found many *Cladophora* species. *Cladophora* is a genus of reticulated filamentous Ulvophyceae, and it contains many species that are very hard to tell apart and classify. This is due to the great variation in their appearances, which are affected by habitat, age, and environmental conditions (Gestinari et al., 2010). The Ulvophyceae are a class of green algae, distinguished on the basis of ultrastructural morphology, life cycle, and molecular phylogenetic data (Graham et al., 2009). Sea lettuce, of genus *Ulva* and class Ulvophyceae, is a type of edible green algae that is widely distributed along the world's coastlines. Some species belonging to the class Chlorophyceae were also found at latitudes above 30°. They are usually green due to the dominance of pigments chlorophyll a and chlorophyll b. On the other hand, many *Caulerpa* species were found at latitudes below 30°. *Caulerpa* organisms consist of only one cell with many nuclei, and are one of the biggest single cells in the world. Some species (especially *Caulerpa lentillifera* and *C. racemosa*) are a commonly-eaten and famous delicacy in Okinawa, Japan (and are called sea-grapes). Some species belonging to the families Siphonocladaceae and Ulvaceae, and some species belonging to the class Chlorophyceae were also found in at latitudes below 30°.

In conclusion, we showed that water temperature is a determining factor for phylogenetic species composition in marine green algae. The species of a community were evenly distributed on the phylogenetic tree in waters warmer than 23°C. On the other hand, species composition was phylogenetically clumped in waters cooler than 23°C, and phylogenetic clumpedness increased as SST decreased. The species composition of marine green algae in the temperate zones was phylogenetically clumped. Conversely, phylogenetic species compositions were dispersed over multiple clusters in the tropics. However, although hotspots of phylogenetic diversity were found in both areas, species compositions were more phylogenetically clumped in the temperate zones. This result suggests that, for marine green algae, phylogenetically close species tend to occur in similar environmental conditions. As a result, it is important to consider both the species diversity and the species composition phylogenetically when establishing conservation practices. Besides protecting hotspots, it is necessary to take full account of phylogenetic patterns of species composition to conserve species diversity. Evolutionary history as well as species richness should be conserved to maintain ecosystem processes and evolutionarily distinct species (Trindade-Filho et al., 2012).

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