

Session 8

**Incorporating mechanistic processes in spatial decision science:  
dispersal, movement, functional groups, evolution and range  
shifts**

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# Global biogeography of marine algae with applications for coral reef connectivity

R.T. Etti, T. Schils

**Abstract** Global distribution patterns of marine benthic algae were analyzed according to latitudinal/longitudinal gradients, temperature, spatial scales, taxonomic gradients, and endemism. Global presence/absence records of marine algae from scientific papers, online resources, and gray literature were compiled into a digital database of 131,400 records, with 52,680 unique species-locality records occurring after geographic and taxonomic filters. Records were grouped into 155 unique localities subdivided into three temperature regions (temperate, subtropical, tropical) based on NOAA/NCEP SST data. The Tripartite Similarity Index (TSI) was used to measure similarity between localities, with minimum distances between all pairwise combinations calculated using Dijkstra's algorithm for shortest-path problems along a modeled connectivity network. A graph-theory based dispersal route network proved useful for geographic analyses in the marine realm and should be used in place of geodesic or Euclidean distances to account for land barriers to distribution that are less conspicuous and widespread terrestrially. Analyses of variance/covariance were used to ascertain differences between records regressed along temperature, geographic, and taxonomic gradients. Algal biogeography is complex, with Phaeophyceae, Rhodophyceae, and Ulvophyceae responding differently to temperature gradients and each oceanic basin being statistically distinct. TSI similarity analyses suggest that relatively few algal genera invaded the tropics from cooler waters and rapidly speciated, with more species per genus on average in the tropics compared to cooler regions. Marine algae have distinct diversity patterns compared to corals and reef fishes and different techniques are recommended for biodiversity studies of these organisms. Northern Japan (Honshu and Hokkaido) have the greatest global species (1,504) and generic (459) richness. Endemism metrics were compared between proportions of range-restricted species in each 5-degree latitude-longitude cell and by localities alone, with the current study finding many regions of high range restriction (weighted endemism) that have been ignored previously. Results verify some past findings and speculations, but conflict with others.

**Keywords:** connectivity biogeography algae biodiversity endemism

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## Introduction

Biogeography aims to describe large-scale spatial patterns of biodiversity and the mechanisms driving such patterns. While the biogeography of terrestrial ecosystems has been studied for more than 150 years (see review in Rosenzweig 1995), marine biogeography is much less understood. Many marine organisms have similar patterns of diversity to terrestrial organisms (e.g., higher diversity in the tropics; Koleff et al. 2003), but the mechanisms driving such patterns remain unresolved. Numerous theories have been proposed to explain these patterns, focusing on either historical factors (e.g., center-of-origin hypotheses or climate-induced fragmentation of ranges: McCoy and Heck 1976; Briggs 1999, 2000), physical factors (e.g., oceanic current patterns, tectonic plate movements, or disturbance: Connell 1978; Rotondo et al. 1981; Jokieli and Martinelli 1992; Roberts 1997), or both (Buckley 1982; Wiley 1988; Rohde 1992; Fraser and Currie 1996; Cornell and Karlson 2000; Brooks and McLennan 2001; Mora *et al.* 2003). Also, Hughes et al. (2002) and Price (2002) demonstrated that separate processes govern patterns of endemism and species richness.

The Indo-West Pacific region, centered between the Philippines and Indonesia, has long been described as the center of highest marine biodiversity for corals and shore fishes (e.g., Briggs 1984; Rohde 1992; Stoddart 1992; McAllister *et al.* 1994; Veron 1995; Lieske and Myers 1996; Veron and Stafford-Smith 2000; Hughes et al. 2002; Allen and Adrim 2003; Bellwood et al. 2005; Carpenter and Springer 2005). However, marine algae are known to deviate from this pattern of biodiversity, having peaks in diversity in temperate regions, at least at the genus level (Kerswell 2006).

A major obstacle to describing global biogeographic patterns of marine algae continues to be a lack of uniform, high-resolution spatial data, and the inherent problems of attempting to fit marine algal distributional data into marine biogeographic regions defined previously upon studies of other groups of organisms. Occasionally, comparisons have been made among marine algae from selected regions at selected latitudes (Pielou 1977; Millar 1999; N'Yeurt and Payri 2004). Most algal studies to date are on an oceanic or regional scale (e.g., Taylor 1960; Hollenberg 1968a, b; Pielou 1977; Lawson 1978; Lewis 1990; Cambridge et al. 1991; Silva et al. 1996; Schils 2006). Considerable effort has been given to defining key biogeographic boundaries for algae in temperate waters (e.g., Murray and Littler 1981; Yarish et al. 1984; Novaczek et al. 1989; van den Hoek and Breeman 1989), but only a few attempts have been made to integrate global algal data (van den Hoek 1984; Lüning 1985; Bolton 1994; Adey and Steneck 2001; Kerswell 2006; Santelices et al. 2006). Perhaps

because of a lack of thorough records, past biogeographic studies of algae have classified the entire tropical Indo-West Pacific (IWP) region, from eastern Africa to Easter Island, as one biogeographic region (van den Hoek 1984; Lüning 1985; Adey and Steneck 2001; Kerswell 2006).

While it is difficult to reconcile evolutionary processes underlying geographic diversity patterns across a wide range of marine taxa (Jablonski et al. 2006), we aimed to determine how algal diversity, on a global scale, differs across latitudinal and longitudinal gradients, temperature, spatial scales, taxonomic gradients, and patterns of endemism. We also sought to create a global marine connectivity network for algae that allows for more accurate estimates of distances between localities for the purposes of similarity analyses and that could inform connectivity of other marine organisms like corals and reef fishes. As algae have the shortest dispersal distance of most marine organisms (Kinlan and Gaines 2003), any connectivity network designed will be a conservative representation of dispersal routes within the marine realm. We feel that understanding the differences in algal diversity patterns compared to corals or reef fishes is integral to defining processes driving coral reef biodiversity as a whole.

## **Materials and methods**

Global presence-absence records of marine algae were collected from online resources, scientific papers, and gray literature and compiled into a digital database of 131,400 records, with 52,680 unique species-locality pairs occurring after treatment with geographic and taxonomic filters. Species were validated for taxonomic accuracy in AlgaeBase (Guiry and Guiry 2006) with invalid or synonymous old names applied to their appropriate synonyms. After all exclusions of groups outside of the study scope and corrections for errors in the genera list were made, approximately 12,200 unique species (varietals, forms, subspecies, ecomorphs, etc. were ignored) were verified taxonomically. The compiled database of over 131,000 algal records had 4,987 original locality records that were then standardized according to modern names and grouped to relatively uniform sizes, yielding 167 distinct localities that were defined as having the finest scale of resolution for use in this study. Of the 167 distinct localities, 12 were excluded from analyses because they either fell outside of the study parameters (algae from terrestrial, freshwater, and landlocked seas) or were too general for any analyses below the regional level.

The remaining 155 localities were further classified into three temperature regions (temperate, subtropical, and tropical) based on NOAA/NCEP sea-surface temperature (SST) data averaged between 1981 and 2005. Tropical localities are defined as having a monthly SST greater than 20°C in both winter and summer and a peak monthly SST above 25°C. Subtropical localities are defined as having a sustained SST greater than 20°C for at least 6 months of the year and only dropping below 15°C on rare occasions (not annually). Portions of the Arabian Sea that have seasonal subtropical upwelling temperatures, but peak SSTs in the range of the tropics were considered subtropical. Temperate localities are all localities that did not fall into either the tropical or subtropical classifications, and include Arctic and Antarctic waters.

Localities were further subdivided into a grid of 5° x 5° mapped on a Plate Carrée Equirectangular Cylindrical Map Projection. Coastline measurements per 5° x 5° cell were not available for all localities at the same spatial resolution were completely unavailable for most Pacific islands. Coastline measurements were not divided by the number of cells a locality occupied due to variations in rugosity and coastline cover per cell. Coastline measurements per 5° bin were taken by assuming full coastline measurements per cell that a locality occurred because richness values per cell were also assumed to represent richness values for an entire locality. The intersection of all localities per 5° latitudinal or longitudinal bin was calculated and all coastline km summed. While this approach overestimated coastline length per bin, the overestimation was of the same kind as assuming all species occurring at all points along an individual locality. To account for the effect of coastline on species richness (and Jarvinen's 1982 proposition that species richness increases mostly as a function of area), the regression of log richness over log coastline for binned data was calculated with respect to latitude and longitude. The residual effect of coastline was removed by determining deviation of actual versus expected (regression) richness values with respect to coastline distance. Residual values were back transformed from log (base 10). Data were scaled to raw richness data with respect to coastline (km) per bin by multiplying all residual values by a constant that would make residual and raw richness data equal at 0° latitude or longitude. Analyses of variance and covariance were used to ascertain differences in patterns revealed by regression analyses between locality records clustered along temperature, geographic, or taxonomic gradients.

The Tripartite Similarity Index (TSI; Tulloss 1997; Schils 2006) was chosen as a measurement of similarity between localities because it overcomes many of the mathematical problems associated with other similarity indices, especially when calculating similarities

between localities with greatly differing numbers of taxa (Tulloss 1997; Schils 2006), as is the case with algae. Separate TSI analyses were performed for genera and species, grouped by oceanic basin and temperature regions. TSI values for pair-wise locality comparisons were accompanied by calculated minimum distances between locality pairs, as determined through implementations of Dijkstra's algorithm (Dijkstra 1959) for shortest-path problems along a modeled connectivity network (Fig. 1). Connectivity networks were used to lessen error in similarity analyses by representing more accurate dispersal route distances compared to basic geodesic distances between locality pairs without considering land masses and other barriers.

The TSI value for each pair-wise comparison of localities was calculated using the following formulas, where Min = minimum and Max = maximum:

a = Total # species or genera unique to the most diverse locality

b = Total # species or genera unique to the least diverse locality

c = Total # species or genera shared by both localities

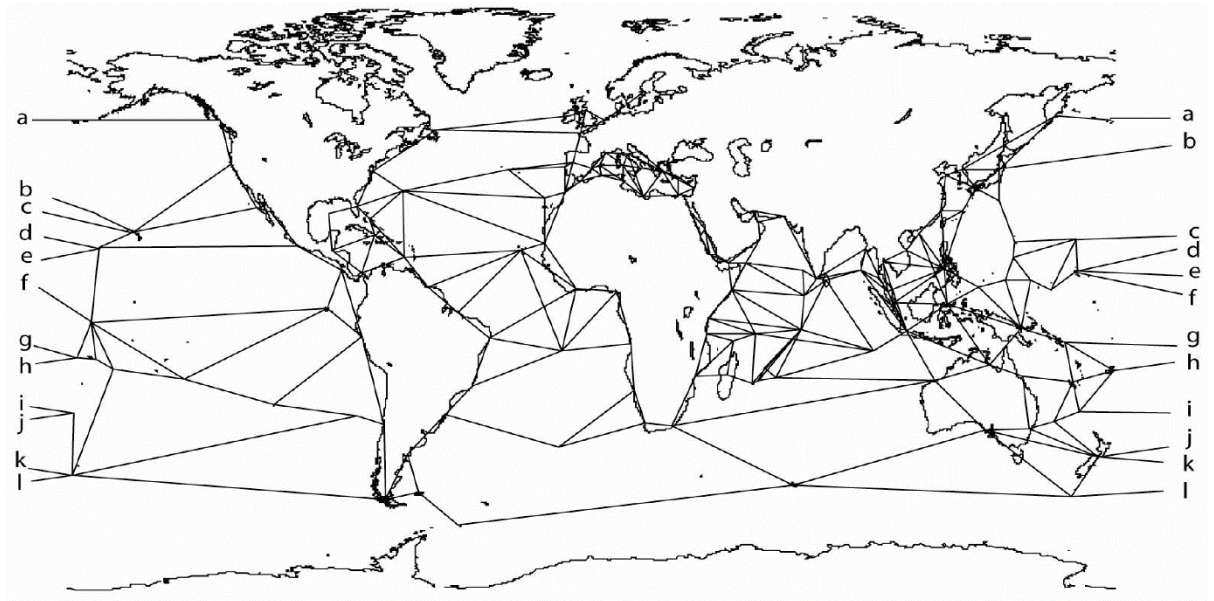
$$U = [\text{Log}[(1 + ((\text{Min}[a,b] + c) \cdot (\text{Max}[a,b] + c))^{-1})] \cdot [\text{Log}[2]]^{-1}]^{-1}$$

$$S = 1 \cdot [\sqrt{(\text{Log}[2 + (\text{Min}[a,b] \cdot ((c + 1)^{-1}))]) \cdot \text{Log}[2]}^{-1}]^{-1}$$

$$R = (\text{Log}[1 + (c \cdot (c + a)^{-1})]) \cdot \text{Log}[1 + (c \cdot (c + b)^{-1})] \cdot (\text{Log}[2]^2)^{-1}$$

$$T = \sqrt{(U \cdot S \cdot R)}$$

Endemism metrics were calculated by a corrected weighted-measure (Linder 2001) using two methods: as the proportion of range-restricted species in each 5° x 5° cell (assuming the same species over the total cells of a given locality), and by localities alone. Endemism was determined through two variations on Linder's (2001) corrected weighted endemism metric, measured as the proportion of range-restricted species in each 5° x 5° cell. When species are assumed to occur over the entire range of a locality (as in the occurrence data used in this study), the ranges of species from large localities may be overestimated. In both methods, because occurrence data were used, species were assumed to occur over the entire coastline of a locality. In the first method, the total number of cells occupied by each species was calculated, whereas in the second method, locality size was ignored and endemism values were calculated based on the number of localities a given species occurred. First, the total



**Fig. 1** Global biogeographic marine connectivity network based on Dijkstra's algorithm for shortest path problems (Dijkstra 1959) and taking into account NOAA/NCEP sea-surface temperature data (1981-2005). Letters represent adjacent pathways across the Pacific, which is divided in this map projection. Crossing of temperature regions (temperate, subtropical, tropical) were only allowed in the model at adjacent localities, generally along continents and not across open water. Antarctic and arctic localities are excluded from pathway calculations. Edge length of pathways were calculated using Geodesic distances. Note that in this Plate Carrée Equiangular Cylindrical Map Projection, while the globe is plotted along a  $5^\circ \times 5^\circ$  latitude-longitude grid, with all degree lengths equal in size, scales are inappropriate

number of grid cells or localities (range) of each species was counted. Then, the summed inverse values of the ranges of all species within a given grid cell or locality were calculated (dividing 1 by the total number of grid cells or localities a species occurred) and divided by the total number of species occurring within each cell or locality. All of the species in a given grid cell or locality contributed to a calculation of endemism by generating an average proportion of range extents for the species found in a given cell or locality. Cells or localities with a higher proportion of range-restricted species have a higher value than cells or localities with a higher proportion of widespread species, and thus can be considered cells or localities with a higher degree of endemism.

## Results

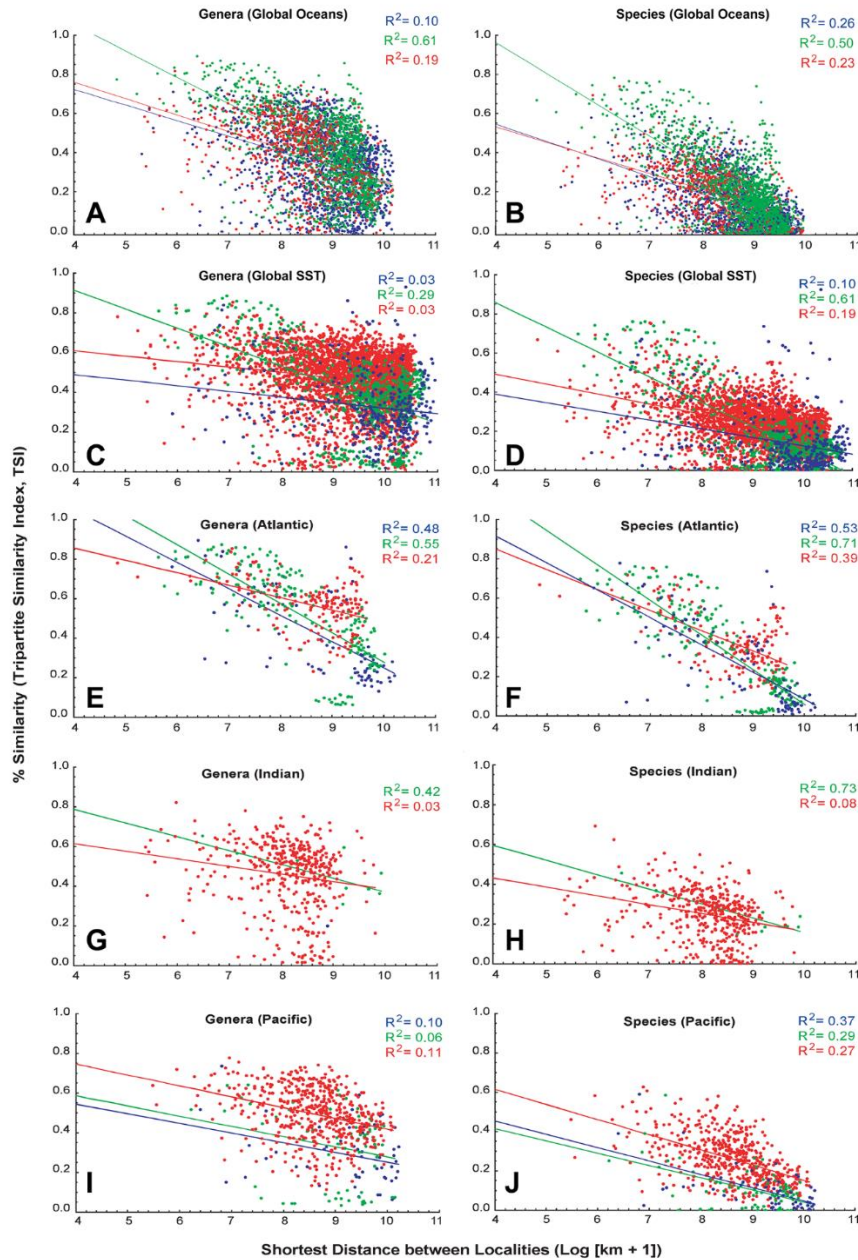
The biogeography of marine algae is extremely complex, with multiple diversity patterns depending upon how data were filtered and analyzed. Tripartite Similarity Index (TSI) analyses revealed that algae behaved statistically different (Fig. 2) based upon taxonomic level (genus, species), algal group (Phaeophyceae, Rhodophyta, Ulvophyceae), oceanic basin (Atlantic, Indian, Pacific), and temperature (temperate, subtropical, tropical). Algae have small, patchy range distributions with bimodal peaks in generic and species richness at mid-latitudes (Fig. 3A,B). Longitudinal diversity gradients are complex, with at least four peaks in diversity globally (Fig. 3A,B; western Pacific, Mediterranean, Caribbean, and the eastern Pacific). The Japanese islands of Honshu and Hokkaido have the greatest individual species (1,504) and generic (459) richness globally of all localities analyzed.

Algal diversity was measured with three metrics: species richness, generic richness, and the ratio of species to genera (SGR). Both generic richness patterns (Fig. 3A) and species richness patterns (Fig. 3B) had clear bimodal richness patterns (whether scaled with area or unscaled), with peaks between 30-40° in both northern and southern hemispheres. In algae, when the diversity of genera is considered, three localities stand out as the most diverse: Honshu and Hokkaido (459 genera), southern Australia (424), and western Australia (395). However, localities that were very diverse generically were not necessarily as diverse at the species level (and vice versa) when relative richness was compared to all locations globally (Figs. 3A,B). This algal pattern is different from corals and fishes, in which localities retain the same relative level of richness across taxonomic levels (Springer 1982; Coudray and Montaggioni 1983; Rohde 1992; Veron and Stafford-Smith 2000; Wilkinson 2004).

Temperate regions had fewer species per genus than other temperature zones. The tropics generally had the highest average number of species per genus for any given locality (Fig. 2A,B), as indicated by its lower slope. For all algal classes, the Y-intercepts of temperate algae were always the highest, while Y-intercepts of subtropical algae always the lowest (Fig. 2C,D). Subtropical algal slopes were almost always steeper than those of tropical algae (except for the Ulvophyceae).

When algae are grouped regardless of temperature, the Indian and Pacific Oceans are very similar in their response to increasing distance between localities (Fig. 2C,D), but respond differently when temperature is accounted for (Fig. 2G-J). The results of the temperature analyses show that temperature has an effect on how florae turnover as distance increases (Fig. 2C,D) and that information is lost when localities are lumped into larger

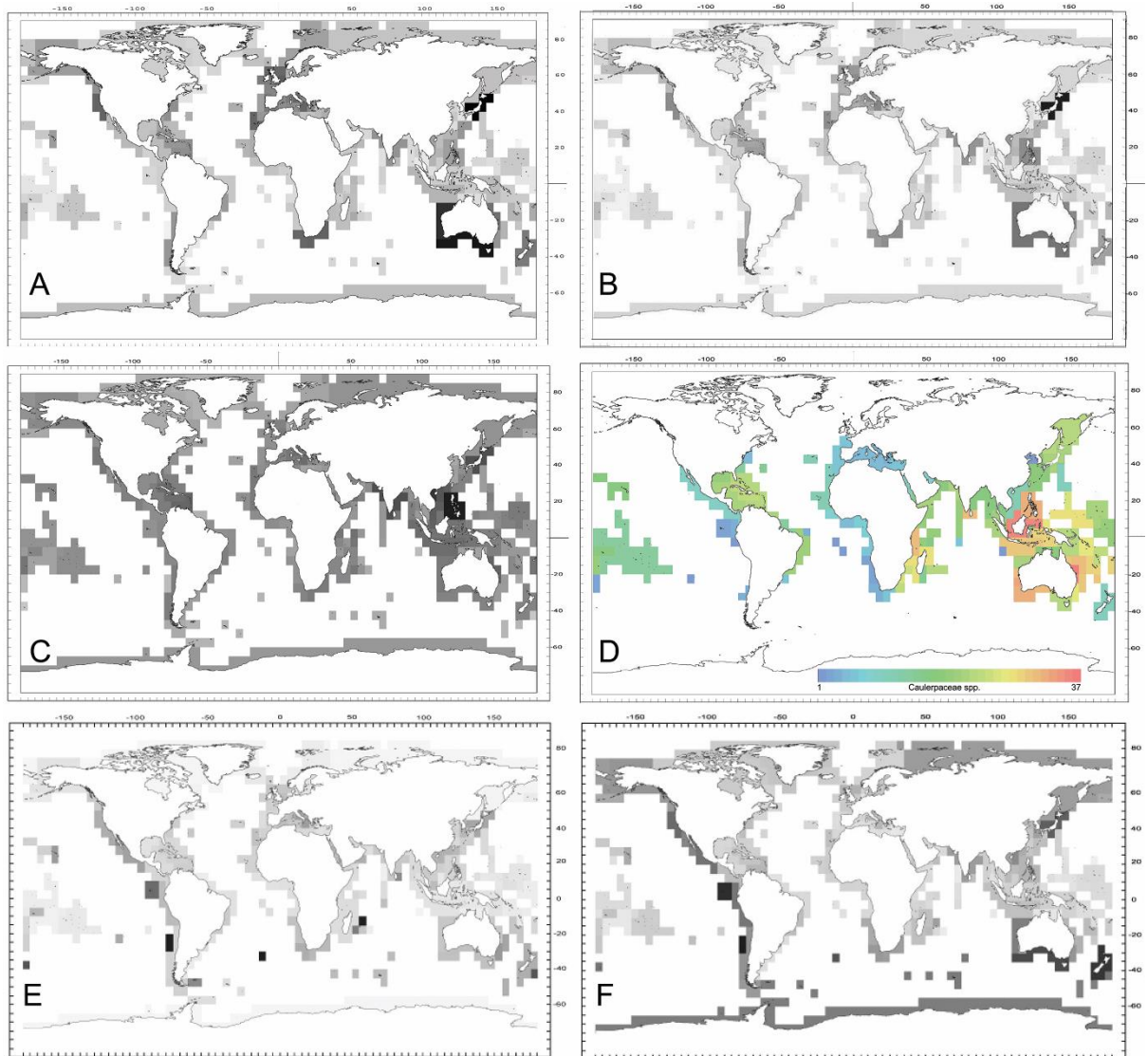




**Fig. 2** Similarity versus distance of algae according to various metrics. X-Axis values represent minimum distances between pairwise locality comparisons in Ln [km + 1] and are calculated using Dijkstra's algorithm for shortest paths (Dijkstra 1959). Y-axes represent percent similarity between locality pairs within a temperature region, and are calculated according to the Tripartite Similarity Index (Tulloss 1997; Schils 2006). Corresponding R-squared values are color-coded according to individual regressions. (A) Genus-level and (B) species-level similarity versus distance between localities of three oceanic basins. Pacific Ocean = blue; Atlantic Ocean = green; Indian Ocean = red. (C) Genus-level and (D) species-level similarity versus distance between localities of three temperature regions. Temperate localities = blue; Subtropics = green; Tropics = red. E-J represent labeled genus-level and species-level similarity versus distance between localities of three temperature regions subdivided into individual oceanic basins. Note that for Indian Ocean graphs, no regression line exists for temperate localities because there are only 2 temperate localities in the Indian Ocean as defined in this study, resulting in only a single pairwise comparison

geographic regions like oceanic basins (Fig. 2A,B). In the Atlantic Ocean, similarities between tropical localities sharply decreased with distance (especially for species), with the temperate and subtropical localities showing similar patterns (regression slopes) compared to tropical localities (Fig. 2E,F). This pattern can be attributed to most tropical localities in the Atlantic occurring in the Caribbean, and thus, similarities are much higher for longer distances in the tropics compared to other temperature regions because of geographical characteristics. Globally, the subtropics revealed a distinct pattern compared to other temperature regions (Fig. 2), with very high similarities among geographically close localities and sharply decreasing similarities with distance. The Rhodophyta contribute disproportionately to overall richness within higher diversity localities because the Rhodophyta have more total genera (752) and species (5,251) than the other algal groups combined.

ANOVA of algae within different temperature zones revealed that there was a significant difference among the regressions of data for all three temperatures. Post-hoc Tukey tests revealed that all temperature zones were significantly different from each other. Additional ANCOVA tests to ascertain differences between regression equations for each temperature region revealed that the slopes of all temperature zones were significantly different from each other (i.e., not parallel). Multiple comparisons among slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.6) revealed that only the regression lines of the temperate (TE) and tropical (TR) algae were parallel. Multiple comparisons among slopes using an ANCOVA-modified Tukey analysis (after Zar 1999 Section 18.7) revealed that the parallel slopes of the temperate and tropics had significantly different Y-intercepts. When all algal classes were grouped, ANOVA and ANCOVA revealed that significant differences existed among algae in each temperature region. These could be explained by the different



**Fig. 3** Global richness of marine algae represented on a continuous gradient from white (no genera present or open ocean) to black (highest richness) across a variety of taxonomic levels (A) genera, (B) species, (C) species-to-genus ratios, (D) Chlorophyceae species diversity in color to emphasize contrast, (E) endemism as the proportion of range-restricted species within each grid cell, (F) endemism as the proportion of range-restricted species within each locality). Richness was binned per 5° bin of latitude or longitude after removing the residual effects of coastline distance. All figures lack scales as they are Plate Carrée Equirectangular

slopes (or species-to-genus ratios, SGRs) found between pair-wise comparisons of TE x ST and ST x TR. Algae within the subtropics have a closer relationship to algae within the tropics for low-diversity localities and algae within the temperate region for higher-diversity localities (Fig. 2C,D). Only TR x TE had significantly different Y-intercepts. ANOVA tests for the Ulvophyceae and Phaeophyceae distributions in different temperature zones revealed no significant difference among all three temperatures. However, ANOVA and ANCOVA of

the Rhodophyta revealed a difference between the subtropics and other temperature zones, but not between the temperate and tropical zones with each other.

Comparisons of distribution ranges by algal class revealed that the genera of the Ulvophyceae had significantly longer distribution ranges (as percent coastline) than the Phaeophyceae and the Rhodophyta. While the Phaeophyceae had a larger mean generic distribution range than the Rhodophyta, the overall ranges of each were not significantly different. When species ranges were examined, all three algal groups were significantly different from each other, with the Ulvophyceae having the largest ranges, followed by the Phaeophyceae and Rhodophyta. Generic distribution ranges were remarkably similar for temperature regions and for algal groups, with mean ranges between 13-23% of global coastline kilometers. Species ranges were also similar between temperature regions and algal groups, with mean ranges between 4-7% of global coastline.

When the ratios of species-to-genus are analyzed, a unimodal peak in diversity occurs centered on the Philippines and India, with secondary peaks in Honshu-Hokkaido (Japan), the Caribbean, the Great Barrier Reef (Australia), and Indonesia (Fig. 3C), meaning the tropics had more species per genus compared to temperate regions, which appears to be a result of relatively few algal genera invading the tropics and speciating (e.g., the Chlorophyceae are an algal group with highest biodiversity in the tropics, Fig. 3D). Unlike what would be expected if the species-to-genus ratio (SGR) of algae did not represent a valid metric (Jarvinen 1982 suggested SGR was a mathematical artifact, as species always increase with higher generic diversity), an extremely tight relationship existed between species and genera of different algal groups and temperature regions, with most regression equations being significantly different from each other (Fig. 2). This finding contrasts with Enquist et al.'s (2002) results, where the SGR of tree populations did not vary significantly with geography or habitat. could be explained by the different

Endemism patterns vary widely between traditional methods and range-restriction methods (Fig. 3E, F), with the current study finding many regions of high range restrictions (weighted endemism) that have been ignored previously (e.g., the eastern Pacific). Results verify some past findings and speculations, but conflict with others.

## Discussion

Algal biodiversity patterns differ depending upon which method is considered or which taxonomic group is examined. According to our analyses, temperate waters have higher numbers of uniquely temperate genera than the tropics, but the majority of genera are found throughout all temperature regions. Generic richness is used sometimes as a proxy for species richness (Kerswell 2006). For organisms that show the same richness pattern across taxonomic levels (e.g., reef fishes and corals; Springer 1982; Coudray and Montaggioni 1983; Rohde 1992; Veron and Stafford-Smith 2000; Wilkinson 2004), this approach avoids the taxonomic problem associated with solely examining species richness (i.e., genera are more monophyletically robust to phylogenetic studies than species).

If the world is merely divided into three broad temperature zones, the temperate region has highest overall algal diversity at both the species and genus level. Algal diversity is highest at latitudinal midpoints (30°S and 40°N), but only when total taxon richness is considered. Overall algal richness peaks at 130°E like corals and shore fishes (Hughes et al. 2002; Mora *et al.* 2003), but much more variability occurs elsewhere and richness plots for algae are not unimodal (Fig. 2) as they are for corals and fishes (Mora et al. 2003). Generic diversity increases as latitude increases (up to the Arctic and Antarctic border regions, where diversity decreases). Since speciation at a generic level is slower than speciation at species level, more genera in temperate regions may be the result of greater evolutionary ages for temperate algae compared to tropical algae. Considering that temperate algae are more than twice as diverse as tropical algae (Fig. 3A,B), and that relatively few genera have high species diversity in the tropics, a possible explanation is that most algal genera evolved in temperate regions. At the oceanic scale, the Pacific has the highest diversity with just below 75% of all global genera occurring there. The Antarctic is the least diverse with only 17.5% of all global genera (and while many species are restricted to the Antarctic, Fig. 3F, few genera are), followed by the Arctic Ocean. Of 1,137 unique genera, 388 (34.1%) are specific to a single ocean, while only 91 genera (8%) occur in all oceans.

No locality is a single hotspot of algal richness, unlike corals and shore fishes, which have a single hotspot of richness in the Indo-West Pacific (IWP) triangle (Springer 1982, Coudray and Montaggioni 1983, Rohde 1992, Veron and Stafford-Smith 2000, Wilkinson 2004). Reef fish richness increases with increasing coral reef area (Komyakova et al. 2013), with reef fish richness peaking where coral habitat peaks in the IWP (Ormond and Roberts 1997).

Localities of highest algal diversity are usually widespread (though several adjacent localities

have very high diversity; Fig. 2). However, at smaller spatial scales algal diversity also increases with increasing coral reef area (Schils et al. 2013). When individual algal classes are considered, hotspots vary for each algal group compared to hotspots for overall algal diversity. Only four localities have species richness peaks both latitudinally and longitudinally: Honshu-Hokkaido, southern Australia, the Atlantic coast of South Africa, and the two adjacent localities of Italy and the eastern coast of the Adriatic Sea (Fig. 3B). These four localities of latitude and longitude intersections might be considered regional centers of algal diversity.

Despite differences in richness patterns between algae and other marine groups, the SGR diversity pattern for algae (Fig. 3C) mimics closely the latitudinal richness patterns of corals, shore fishes, snails, and lobsters (Roberts et al. 2002). While the metrics are different, it may be possible that an unknown mechanism responsible for increased richness of many marine groups in the tropics may also be affecting algal diversity. Differences in SGR do not appear to be merely the result of sampling effort or correlated with geographic area, as suggested by Jarvinen (1982). Jarvinen (1982) reviewed the use of SGR in biogeography and outlined strong evidence that patterns in the SGR are a statistical artifact. In Jarvinen's (1982) argument, SGR increased as species richness increased, which in turn increased directly with increasing area. Interestingly, the SGR diversity pattern for algae (Fig. 3C) is distinct from the species richness pattern (Fig. 3B) only latitudinally, but mimics closely the genus and species richness patterns longitudinally (Fig. 3A, B). If SGR was a mathematical artifact, then the same transformation in diversity pattern would be seen latitudinally and longitudinally. However, Jarvinen's (1982) position that more species occur per genus (higher SGR) in larger areas compared to smaller areas does not hold true uniformly for algae. Regions of high species richness are not uniformly regions of high SGR (Fig. 3B, C).

The high SGR of algae in the tropics might be considered a comparatively more recent event than speciation in temperate regions, which has progressed from the evolution of separate species into multiple genera. It is hypothesized that the tropics have a higher overall SGR compared to other regions as a result of relatively few genera invading the tropics from cooler waters, where algae likely originated (noted by lower generic diversity in the tropics compared to other temperature regions of similar species richness; Fig. 2), but speciating to a higher degree than the floras of cooler waters. Each taxonomic group has evolved differently, suggesting that different algal groups have different capacities for speciation in different temperature regimes. Broad examination of individual algal classes suggests contributions to SGR on a global scale. Tropical algae have the smallest mean species range, but the longest

generic range of all temperature populations (Fig. 3C). If relatively few genera invaded the tropics from colder temperature regions and then speciated at a high rate, this would result in a comparatively constant but high similarity at the generic level. Because of the short dispersal capacity of algae (Kinlan and Gaines 2003), species were not able to spread widely. The SGR values for algae are highest in the tropics, while generic diversity is highest in the temperate zone. As a result, the proposition that number of species merely increases with generic age (Jokiel and Martinelli 1992) might not hold true for algae.

TSI similarity analyses suggest that relatively few algal genera invaded the tropics from cooler waters but that these speciated rapidly, with more species per genus on average in the tropics compared to cooler regions. Marine algae have distinct diversity patterns compared to corals and shore fishes and separate techniques should be used for analyzing algae. Distinct differences between temperature regions and oceanic basins and differences between algal groups suggest that different algal phyla should not be grouped for analyses. The implementation of a connectivity network proves useful for geographic analyses in the marine realm (especially over large geographic regions) and should be used in place of geodesic or Euclidean distances to account for land barriers to distribution that are less conspicuous and widespread terrestrially.

In contrast to the Jablonski et al. (2006) "Out of the Tropics" (OTT) model, an alternative might apply for algae, tentatively referred to as the "Into the Tropics" (ITT) model. In the ITT model, it is proposed that algae originated in temperate regions and not only invaded into the tropics, but taxa were retained in temperate regions because of lower extinction rates there (Weir and Schluter 2007). Molecular phylogenetic analyses to determine whether tropical algal taxa were derived from temperate taxa could be used to evaluate such a model. Additionally, the determination of extinction rates for algae based on extant taxa compared to fossilized taxa could also be used to evaluate the ITT model. Jablonski et al. (2006) found that taxa limited to the tropics had different extinction rates from both temperate and cosmopolitan taxa. The current range distributions of algae (Fig. 3C) can also be explained by an ITT model, as can the disparity of high tropical SGR as a result of relatively few speciose genera in the tropics.

Several possibilities are proposed to explain why our findings for endemism (Fig. 3E,F) deviate from past results. Endemism analyses reveal amphitropical peaks in range-restricted species and along the entire west coast of the Americas, regardless of temperature. In both endemism analyses, several isolated islands and archipelagoes had the highest proportion of range-restricted species: the Galapagos; San Juan and Felix islands in the eastern Pacific; the

Chatham, Bounty, and Antipodes islands in the southwestern Pacific; the Cargados Carajos Shoals and Saya de Malha Banks in the Indian Ocean; and Tristan da Cunha in the Atlantic. Oceanic endemism is highest in the Pacific Ocean (19.7% of all Pacific genera are only found in the Pacific). Of 8,091 total algal species analyzed, 2,726 (over one-third) were found in only a single locality. While Honshu-Hokkaido had the greatest overall numbers of total species and single-locality endemics (362 out of 1,504 total species), species richness was not a linear predictor of high endemism values. Localities with high species richness (Fig. 3B) do not uniformly have high endemism richness (Fig. 3E,F), although as total numbers of species increase, some increase in the proportion of range-restricted species is expected. Given the high number of species only found in Honshu-Hokkaido, it is possible that the Japanese flora is singularly large and isolated. Honshu-Hokkaido had the highest species richness of any locality, with nearly one-quarter of all species found being restricted there.

In a variation of Linder's (2001) original weighted endemism approach, locality size was ignored. The same endemism hotspots found with the original Linder (2001) methodology were found again with the modified methodology (Fig. 3F) but many localities missed previously by the first methodology (Fig. 3E) proved to have a much higher proportion of range-restricted species, especially toward the poles. Given current data limitations (occurrence data for geographic entities as opposed to uniform cells), the second method is more applicable for algae.

Toward the poles, endemism is elevated (Fig. 3F), which might suggest that increased speciation rates coupled with low dispersal capacities for algae lead to a young, unique flora that will slowly radiate and invade toward the equator. The poles are the areas of the lowest richness (Fig. 3A, B), showing that richness and endemism are not concordant in marine polar algae. The entire western coast of the Americas (including tropical regions) had high endemism (Fig. 3F). When locality size was ignored, amphitropical localities had a much higher proportion of range-restricted species, as did the entire western coast of the Americas (Fig. 3F). Many, but not all, upwelling regions had a high proportion of range-restricted species (Fig. 3F). The only localities where corals, fishes, and algae all have high endemism are Easter Island, the main Hawaiian Islands, the Mascarene Islands (especially Mauritius), the Sea of Cortez, Sri Lanka, South Africa, and Western Australia (Fig. 3F).

The results of this study provide many building blocks for future work. Many of its methodologies are generally applicable for all marine environments, such that similar approaches to coral and reef fish data can be taken thus creating a uniform approach to studying coastal marine communities. To date, many studies have compared shore fish



diversity with coral diversity, but few have added algal diversity to the equation. By comparing corals and algae uniformly in the same manner as the present study, new insights into coral reef dynamics are likely to be revealed.

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