Phylogenetic regionalization of marine plants reveals close evolutionary affinities among disjunct temperate assemblages

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ABSTRACT

While our knowledge of species distributions and diversity in the terrestrial biosphere has increased sharply over the last decades, we lack equivalent knowledge of the marine world. Here, we use the phylogenetic tree of seagrasses along with their global distributions and a metric of phylogenetic beta diversity to generate a phylogenetically-based delimitation of marine phytoregions (phyloregions). We then evaluate their evolutionary affinities and explore environmental correlates of phylogenetic turnover between them. We identified 11 phyloregions based on the clustering of phylogenetic beta diversity values. Most phyloregions can be classified as either temperate or tropical, and even geographically disjunct temperate regions can harbor closely related species assemblages. Geographic differences in sea surface temperatures account for more phylogenetic turnover than either water salinity or bathymetry. We also found a strong temperate-tropical gradient in evolutionary distinctiveness, with temperate phyloregions being the most evolutionarily unique. Our results highlight differences between the marine and terrestrial worlds, and suggest that the interplay between long-distance dispersal and phylogenetic niche conservatism played a central role in determining the contemporary distributions of seagrasses worldwide.

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1. Introduction

Our knowledge of marine biodiversity lags far behind that of terrestrial regions. For instance, it is estimated that more than 60% of marine species remain undescribed (Appeltans et al., 2012), yet many marine species are affected by human-induced pressures (Roberts et al., 2002). Such threats tend to be highest in coastal areas with lesser impacts in the open oceans (Halpern et al., 2008). There is therefore an urgent need to better understand the distribution and structure of coastal marine biodiversity, and to identify regions harboring unique sets of species (i.e. high species endemism) and evolutionary lineages (i.e. high phylogenetic endemism) if we wish to preserve their taxonomic and phylogenetic diversity. By grouping species assemblages into biogeographic units using information on their shared evolutionary histories (Holt et al., 2013), we can gain insight into the evolutionary and ecological processes shaping species geographical distributions and develop a guide for prioritizing conservation efforts (Winter et al., 2013).

Previous attempts to define marine or oceanic biogeographic regions (e.g. Forbes, 1856; Hayden et al., 1984; Longhurst, 1998) have variously relied on expert opinion, patterns of species richness or endemism, climatic zones, and political boundaries, limiting our ability to infer processes from patterns. A recent synthesis of marine ecoregions by Spalding et al. (2007) represents the most comprehensive biogeographic regionalization of coastal and shelf areas to date. Spalding et al. (2007) divided coastal waters into 12 realms that coincided broadly with the continental plates. In a separate analysis, Short et al. (2007) delimited six phytogeographical zones that separate into temperate and tropical regions. Recent developments in phylogenetic techniques, and the increased availability of genetic data, provide an opportunity to expand upon these efforts by incorporating information on species evolutionary relationships.

Biogeographic regionalizations that treat all species as being equally related fail to account for a substantial amount of the biological variation among different regions. Early biogeographers recognized the value of considering higher taxonomic relationships when delimiting biogeographical regions, and modern biogeographical analyses have

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attempted to make processes underlying such delimitations transparent and repeatable (Kreft and Jetz, 2010). Integrating phylogeny into biogeographic regionalization may reveal the history of diversification and/or dispersal events (Wu et al., 2016) within and between regions (Graham and Fine, 2008; Holt et al., 2013; Daru et al., 2016). Importantly, a phylogenetic approach allows us to quantify similarities among species assemblages even when they share no species in common (Graham and Fine, 2008), helps identify centers of evolutionary radiations (Holt et al., 2013), and provides a guide for prioritizing conservation efforts aimed at preserving evolutionary history (Rosauer et al., 2009; Jetz et al., 2014).

We focus our analysis on seagrasses, a major aquatic vegetation type, and the only widespread marine angiosperm taxon. Seagrasses are a group of flowering plants belonging to the monocot order Alismatales, comprising 70 species widely distributed in the estuarine or marine environment, and have a completely submerged life cycle (Hemminga and Duarte, 2000). The group represents an important component of the seascape's natural history, playing a critical role in sediment accumulation and carbon storage. Seagrass meadows also support high rates of secondary productivity; they host algae that support diverse and productive food webs that include fish and birds (Orth et al., 1984), and directly provide food for many marine herbivores including the endangered green sea turtle (*Chelonia mydas*), manatee (*Trichechus* spp.) and dugong (*Dugong dugon*) (Green and Short, 2003; Larkum et al., 2006). Seagrasses also serve as nursery ground for many fish and invertebrate species (Beck et al., 2001). While seagrasses represent only one of the many types of marine coastal ecosystems, we have good data on their spatial distribution and DNA sequences (Daru and Yessoufou, 2016) for reconstructing their phylogenetic relationships. Our analysis thus provides an illustration of the novel insights that can be gained from applying phylogenetic regionalization, but it should be considered as only a first step in generating a comprehensive phylogenetic assessment of coastal marine plant diversity.

Here, we use Simpson's phylogenetic beta dissimilarity metric (Holt et al., 2013) along with data on the global distribution of seagrass species to generate the first phylogenetic regionalization of the coastal regions of the world. First, we group geographical regions into 'phyloregions' based upon phylogenetic similarity among assemblages of seagrass species. We then investigate the effect of oceanographic factors in shaping phylogenetic membership within phyloregions using a suite of environmental variables.

2. Materials and methods

2.1. Taxon sampling and species distributions

We included all 70 currently recognized species of seagrasses worldwide (Green and Short, 2003). Species names were checked for synonyms using The Plant List (www.plantlist.org). Distribution data for all 70 seagrasses are expert-based extent-of-occurrence range maps downloaded from the IUCN Red List website at http://www.iucnredlist.org/technical-documents/spatial-data (accessed June 2014). The IUCN range maps are regularly updated and represent the best current estimate of seagrass distribution. We overlaid the maps onto a Berhmann-projected equal area grid in ArcMap v.10.0 at a resolution of $1.0 \times 1.0°$, totaling 6655 cells. We obtained DNA sequences (*rbcL*, ITS and 18S) for all species that were available from GenBank/EBI (55 of 70 seagrasses). Information on DNA sequences (retrieved from GenBank/EBI) and geographical ranges are presented in S1 Table in Supporting Information in the online version of this paper.

2.2. Phylogenetic reconstruction and divergence time estimation

Sequences were aligned using Multiple Sequence Comparison by the Log-Expectation algorithm (MUSCLE v.3.8.31; Edgar, 2004) and manually edited in PAUP v.4.0b.10 (Swofford, 2003). The combined data set was comprised of 1137, 930, and 1671 base pairs for *rbcL*, ITS and 18S, respectively. We performed a maximum likelihood (ML) analysis on the combined data set using RAxML (Stamatakis et al., 2008) and enforcing a backbone constraint using the DNA-based system of flowering plant classification developed by the Angiosperm Phylogeny Group (APG III, 2009), implemented in Phylomatic v.3 (Webb and Donoghue, 2005; updated on 23 August 2012). In our study, this system provides an initial phylogeny used to constrain the topology of our seagrass phylogeny. Branch lengths were then calibrated in millions of years using a Bayesian Markov chain Monte Carlo (hereafter MCMC) approach implemented in BEAST v.1.7.5 (Drummond and Rambaut, 2007). First, the RAxML starting tree was adjusted so that branch lengths satisfied all secondary calibration points, using PATHd8 v.1.0 (Britton et al., 2007). Second, we used the GTR + G + I substitution model based on the result of AIC from Modeltest v.2.3 (Nylander, 2004) and an uncorrelated lognormal relaxed molecular clock model selected in BEAST v.1.7.5 (Drummond and Rambaut, 2007). We used six calibration points obtained from the literature: Alismatales crown node 128 Ma; Cymodoceae crown node 61 Ma, Zosteraceae crown node 17 Ma, Hydrocharitaceae crown node 75 Ma, and Tofieldiaceae crown node 100 Ma (Janssen and Bremer, 2004); and *Alocasia* crown node 19.28 Ma (Nauheimer et al., 2012). We then ran two replicates of the MCMC analyses in BEAST, each for 100 million generations, sampling every 1000 generations. The MCMC log files were assessed for convergence using the effective sample size (ESS) analysis in Tracer v.1.5 (Rambaut et al., 2013). The resulting tree files were combined in LogCombiner v.1.7.5, discarding the first 25% trees as burn-in. The maximum clade credibility (MCC) tree, with means and 95% highest posterior density (HPD) intervals, was generated with TreeAnnotator v.1.7.5. Fifteen species did not have DNA sequences available and were placed on the MCC tree by grafting them in a multichotomy to the node from which their closest relatives descended based on their taxonomic classification using the R library PASTIS (Thomas et al., 2013). This approach has recently been used, for example, to assemble a complete phylogeny for birds (Jetz et al., 2012) and fruitflies (Yassin et al., 2008). The placement of taxa in the absence of DNA sequences could potentially impact the delineation of phyloregions. To examine sensitivity of our results, we therefore re-ran the analysis of phyloregions (see below) excluding these species. We then compared pβ$_{sim}$ values with those observed when only species with DNA sequences were used and showed a strong correlation with the full dataset ($r = 0.99$, $P = 0.001$; from Mantel test using 999 permutations). We present here results including all species.

2.3. Clustering phyloregions

We evaluated phylogenetic dissimilarity among all possible pairs of grid cells using Simpson's beta dissimilarity metric (β$_{sim}$) and its phylogenetic equivalent (pβ$_{sim}$) following Holt et al. (2013). The phylogenetic Simpson's index reflects the number of shared phylogenetic branch lengths found between two species assemblages and is quantified as the proportion of shared branches in the least diverse assemblage. We define phytogeographic regions based on the phylogenetic similarity between all pairs of grid cells. To identify the best algorithm to cluster grid cells we evaluated the performance of seven hierarchical clustering algorithms on both pβ$_{sim}$ and β$_{sim}$ using cophenetic correlation (Kreft and Jetz, 2010). We determined the optimal number of clusters using the elbow method of Salvador and Chan (2004) implemented in the R package GMD (Zhao et al., 2011). When a phyloregion corresponded closely to a recognized biogeographic region (as defined by Spalding et al., 2007 or Short et al., 2007), we identified this phyloregion using Short et al. (2007) or Spalding et al.'s (2007) terminologies.

We estimated the evolutionary distinctiveness of each phyloregion as the mean pβ$_{sim}$ value between each focal phyloregion and all other phyloregions (see Holt et al., 2013). Broadly speaking, this approach identifies regions that enclose radiations of species that are restricted to a given region. As such, the geographic trend in evolutionary

distinctiveness is not contingent upon the choice of focal phyloregion. We also compared our phylogenetic regionalization to that using information only on species presence/absence. To do this, we generated an equivalent beta diversity (β_{sim}) matrix based on species turnover only.

2.4. Environmental correlates of phylogenetic clustering and turnover

We evaluated the performance of three oceanographic variables (sea surface temperature, sea surface salinity and bathymetry) in differentiating among phyloregions. These variables were obtained from the database of the Ocean Climate Layers for Marine Ecology (Sbrocco and Barber, 2013). We compared differences among phyloregions for each oceanographic variable using analysis of similarity (ANOSIM) with a Monte Carlo randomization test of significance (Clarke, 1993). We then used a partial Mantel test on the distance matrices for each oceanographic variable to test for correlations with global pβ_{sim} values while controlling for geographical non-independence among grid cells.

All statistical analyses were performed in R (R Core Team, 2013) using the following packages: ape (Paradis et al., 2004), gmd (Zhao et al., 2011), mclust (Fraley and Raftery, 2012), clValid (Brock et al., 2008), cluster (Maechler et al., 2013), raster (Hijmans, 2015), picante (Kembel et al., 2010) and vegan (Oksanen et al., 2015). Spatial data were processed in ArcMap v.10.0 (ESRI, 2010).

3. Results

The reconstructed phylogeny (S1 Fig.) is comparable with previous studies (see Coyer et al., 2013), and identifies a major split between *Halodule-Lepilaena-Phyllospadix-Zostera* and other seagrass genera at ~100 Ma.

The unweighted pair group method with arithmetic mean (UPGMA) outperformed all others in terms of cophenetic correlation (cophenetic $r = 0.87$ and 0.74 for β_{sim} and pβ_{sim}, respectively; S2 Table), and was thus used to define phyloregions. Based on the elbow criterion, we found 11 phyloregions for pβ_{sim} (S3 Table; Fig. 1) and 12 (non-phylo) regions for β_{sim} (S2 Fig.).

Our results show a separate grouping of phyloregions within tropical and temperate regions (Fig. 1). Notably, tropical phyloregions F, G and H in the Indo-Pacific group together as do temperate phyloregions A, B and C (Arctic + Temperate Australasia, and Temperate North Atlantic + Mediterranean), emphasizing the tropical-temperate distinction (Fig. 1b). The two largest temperate phyloregions (C & D) are found in both northern and southern temperate latitudes (Fig. 1a). Our phyloregions correspond broadly to assemblages delineated using only species composition data ($r = 0.753$, $P = 0.001$, Pearson's product–moment correlation from Mantel test of pβ_{sim} and β_{sim}; S3 Fig.).

We also investigated the evolutionary distinctiveness (ED) of phyloregions, and found a strong temperate-tropical gradient (Fig. 1c). We show that phyloregion D (including temperate South America, and temperate Southern Africa) represents the most evolutionarily distinct phyloregions (mean p$\beta_{sim} = 0.54$), followed by phyloregion C (Arctic and Temperate Australasia, mean p$\beta_{sim} = 0.50$). In contrast, the Indo-Pacific phyloregions have the lowest evolutionary distinctiveness (mean p$\beta_{sim} = 0.37$).

Finally, we explored whether different phyloregions were characterized by different oceanographic factors. We found that turnover in the environmental variables examined was generally greater among than within phyloregions, and this trend was more pronounced for sea surface temperature (ANOSIM, $r = 0.52$, $P < 0.001$), than for sea surface salinity (ANOSIM $r = 0.17$, $P < 0.001$) or bathymetry (ANOSIM $r = 0.071$, $P < 0.001$) (S4 Fig.). Further, we found a stronger correlation between the global pβ_{sim} values for seagrasses and the distance matrix of sea surface temperature (partial Mantel test, $r = 0.372$, $P = 0.001$) than between distance matrices of sea surface salinity (partial Mantel test, $r = 0.005$, $P = 0.18$) or bathymetry (partial Mantel test, $r = 0.058$, $P = 0.001$).

4. Discussion

We used a metric of phylogenetic beta diversity to classify assemblages of seagrasses into biogeographic regions (phyloregions). Our results differ to previous delineations based on species composition data (Short et al., 2007; Spalding et al., 2007), with phyloregions falling within distinct temperate and tropical groupings, despite the geographic disjunct between temperate regions in the southern and northern hemispheres. Moreover, we show that temperate phyloregions are more evolutionarily distinct than tropical phyloregions, contrasting with patterns observed for terrestrial vertebrates (Holt et al., 2013). We find that sea surface temperature is more strongly correlated with the global turnover in phylogenetic beta diversity and the classification of seagrass assemblages into distinct phyloregions than salinity or bathymetry. Our results point to the importance of long-distance dispersal (Wu et al., 2016) and phylogenetic niche conservatism in shaping the contemporary distributions of seagrasses. Nevertheless, we cannot exclude the potential role of convergent diversification of taxa between geographically disjunct areas, leading to such areas harboring phylogenetically close taxa.

The grouping of many temperate assemblages into a few large phyloregions despite their geographical separation is notable. For example, phyloregion C is circumpolar (Fig. 1a), and both phyloregions C and D, which are recognized as distinct in our analysis, bridge the tropics. Our study shows that geographically disjunct assemblages within these phyloregions (C and D) harbor different species from the same few, largely temperate, clades such as the genus *Zostera*. The close phylogenetic affinities among disjunct temperate assemblages may reflect frequent long distance migration mediated by various dispersal mechanisms including birds (Wu et al., 2016). The high dispersal capacity of seagrass taxa is reflected in the wide distribution of several species, for example, *Zostera marina* L. (eelgrass), which has a circumpolar distribution in the northern hemisphere. However, despite the apparent lack of dispersal barriers, only a subset of lineages from the global phylogeny have successfully diversified and established in temperate regions. We therefore suggest that phylogenetic niche conservatism (Wiens et al., 2010) may have constrained the evolution of temperate climate niches in seagrasses.

There are several explanations for why temperate seagrass phyloregions are particularly evolutionarily distinct. First, whilst there may be few geographic barriers to dispersal, ecological and climatic barriers including oceanographic factors might limit the exchange of taxa between phyloregions (Eiserhardt et al., 2013). Second, tropical species with temperate origins may have been lost through extinction. For example, during the closure of the Isthmus of Panama c. 3.1 Ma, a major glaciation took place in the northern continents (Barry, 1989), which resulted in the extinction or southward migration of lineages to adjoining oceans (Jackson, 1994). Briggs (2003) suggested that several lineages that originated in the northern hemisphere including *Zostera* (eelgrass), *Laminaria* (kelp), and *Phycodrys* (red algae) have either gone extinct or were exported to the southern hemisphere, often bypassing the tropics by means of isothermic submergence.

Oceanographic variables are important in structuring marine biotas (Tittensor et al., 2010; Belanger et al., 2012). Here we show that sea surface temperature, and to a lesser extent, sea surface salinity and bathymetry, explain phylogenetic turnover of seagrass assemblages and the grouping of these assemblages into phyloregions. Although our indices of the marine environment are, by necessity, coarse, these results together with the clear division of global seagrass assemblages into temperate and tropical phyloregions, further emphasize the importance of niche conservatism, and suggest that water temperature may impose a strong abiotic filter on seagrass species. In addition, we note the much greater variance in both temperature and sea surface salinity among temperate phyloregions in comparison to tropical phyloregions. We thus suggest that the steeper environmental
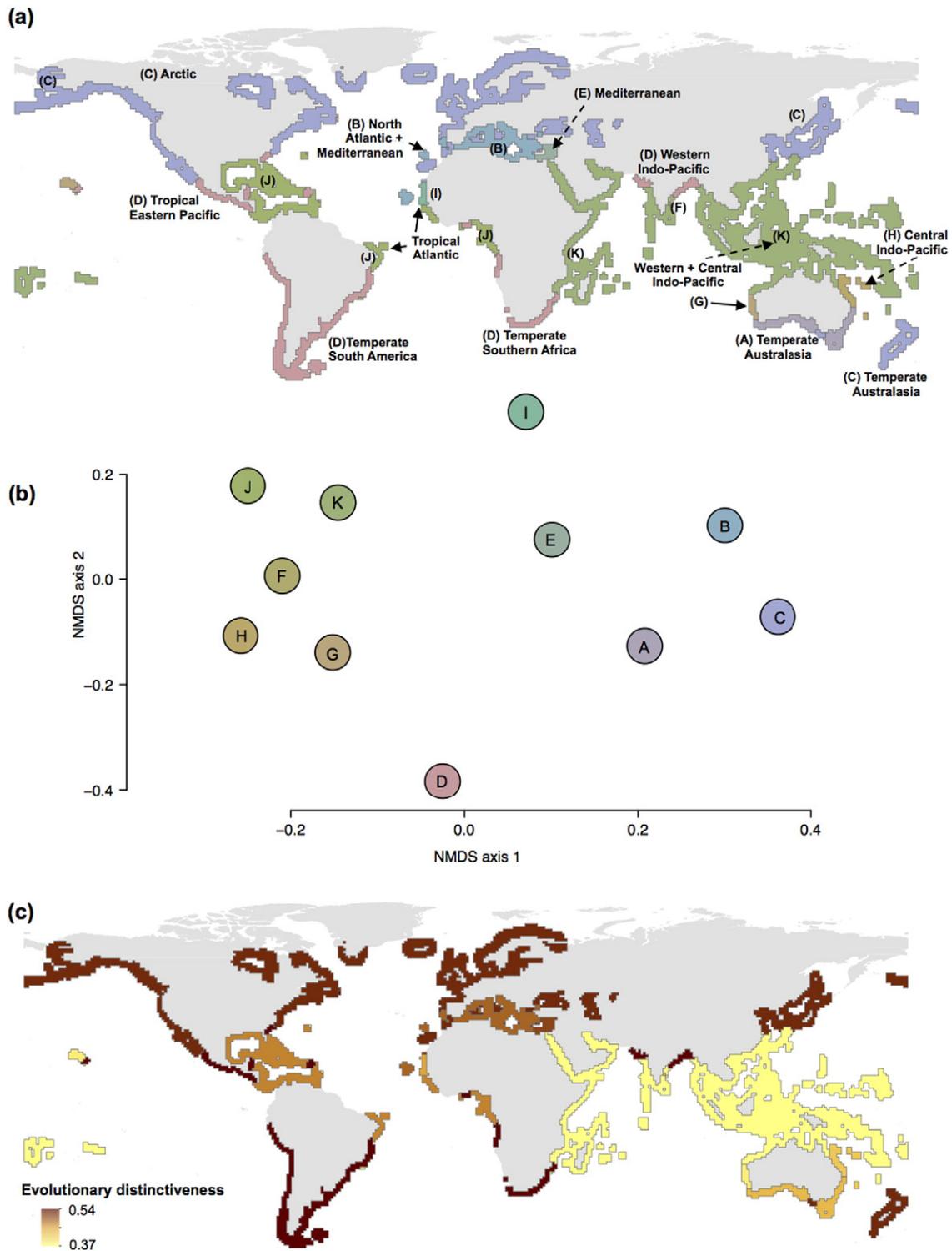
Fig. 1. Relationships among marine phyloregions based on phylogenetic turnover ($p\beta_{sim}$) of seagrass species worldwide (a) in geographic space, (b) in NMDS ordination space (two-dimensional solution, stress = 0.158), and (c) as map of evolutionary distinctiveness per phyloregion. Colors differentiating between phyloregions in the map (a), and NMDS (b) are identical, and depict the amount of phylogenetic turnover among phyloregions. Darker colors for the evolutionary distinctiveness (c) indicate phyloregions of high evolutionary distinctiveness.

gradients separating temperate phyloregions might translate to greater ecological barriers to dispersal between them, despite the apparent ease with which species seem to be able to move through the marine realm, contributing to their evolutionary distinctiveness.

The evolutionary and biogeographic histories of species in the marine realm remains obscure; our work here sheds new light on global distribution patterns of seagrasses, and highlights distinct geographic

assemblages of seagrass species that might represent targets for conservation. Low diversity seagrass communities might still provide high ecosystem functioning (keystone effect; Smith et al., 2014); however, we suggest that conservation efforts should not focus only on ecosystem properties. Phylogenetic diversity, like taxonomic richness, may be considered an important conservation target in its own right (e.g. Redding and Mooers, 2006). Bowen et al. (2013) suggested that previous

paradigms relating to the origins of marine biodiversity have been recently overturned, with phylogeographic evidence showing that (1) speciation can occur without geographic barriers, (2) peripheral regions can be a source of new species, and (3) species are exchanged among hotspots and peripheral areas (the biotic exchange hypotheses). Such patterns suggest extensive species migration across the marine realm. We might therefore have predicted little or no phylogenetic structure in species regional assemblages. However, our analysis reveals distinct regional clusters with strong phylogenetic structure (i.e. evolutionary distinctiveness), and indicates that the radiation of several seagrass clades may have been restricted geographically.

5. Conclusions

Our regionalization of seagrass assemblages provides new insights into the mechanisms structuring coastal biodiversity, and support for previously recognized divisions, such as the tropical-temperate split (Short et al., 2007). However, by additionally considering phylogeny, we also highlight that temperate seagrass assemblages bridge the tropics. In addition, our approach has allowed us to identify regions that harbor evolutionarily distinct lineages, such as Temperate South America, Temperate Southern Africa, the east coast of USA, and parts of Europe. Several of these regions are hotspots of marine plant diversity (Daru and le Roux, 2016), have already been experiencing high rates of habitat modification, disturbance and destruction (Orth et al., 2006; Short et al., 2011), and loss of evolutionarily distinct lineages, such as in mangrove forests (Daru et al., 2013; Yessoufou and Stoffberg, 2016), and thus represent conservation priorities.

Although our study focused only on seagrasses (soft-bottom phytoregions), it provides an important step towards a better understanding of phylogenetic structure of coastal marine diversity. However, our phylogenetic knowledge of off-shore marine biodiversity made up of hard-bottom phytoregions, which are dominated by macroalgae, represents a significant research gap that will require new data on species distributions and phylogenetic relationships.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.08.022.

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