

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

Barnabas H. Daru^{a,b,*}, Ben G. Holt^c, Jean-Philippe Lessard^{d,e}, Kowiyou Yessoufou^f and T. Jonathan Davies^{g,h}

^aDepartment of Organismic and Evolutionary Biology and Harvard University Herbaria, Harvard University, Cambridge, MA 02138, USA

^bDepartment of Plant Science, University of Pretoria, Private Bag X20, Hatfield 0028, Pretoria, South Africa

^cDepartment of Life Sciences, Imperial College London, Silwood Park Campus, Ascot SL5 7PY, United Kingdom

^dQuebec Centre for Biodiversity Science, Department of Biology, McGill University, Montreal, QC H3A 0G4, Canada

^eDepartment of Biology, Concordia University, Montreal, QC, H4B 1R6, Canada;

^fDepartment of Environmental Sciences, University of South Africa, Florida campus, Florida 1710, South Africa

^gDepartment of Biology, McGill University, Montreal, QC H3A 0G4, Canada

^hAfrican Centre for DNA Barcoding, University of Johannesburg, PO Box 524, Auckland Park, Johannesburg 2006, South Africa

*Corresponding author

Email: barnabas_daru@fas.harvard.edu (B.H. Daru)

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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.

Key-words: Biogeographical regionalization, coastal ecoregions, evolutionary distinctiveness, phylogenetic beta diversity, phyloregions, seagrasses.

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 recognised the value of considering higher taxonomic relationships when delimiting biogeographical regions, and modern biogeographical analyses have attempted to make processes underlying such delimitations transparent and repeatable (Kreft & 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 & 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 & 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 & 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 & 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 & 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 & 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 1.0×1.0 degrees, 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 & 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 & 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 & 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 & 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 $p\beta_{sim}$ 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 ($p\beta_{sim}$) 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 $p\beta_{sim}$ and β_{sim} using cophenetic correlation (Kreft & Jetz 2010). We determined the optimal number of clusters using the elbow method of Salvador & 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 $p\beta_{sim}$ 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 & 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 $p\beta_{sim}$ 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 & 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 $p\beta_{sim}$, respectively; S2 Table), and was thus used to define phyloregions. Based on the elbow criterion, we found 11 phyloregions for $p\beta_{sim}$ (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 $p\beta_{sim}$ 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 $p\beta_{sim}$ 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 (Eiserhard *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 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 & 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 & 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 & 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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Figure

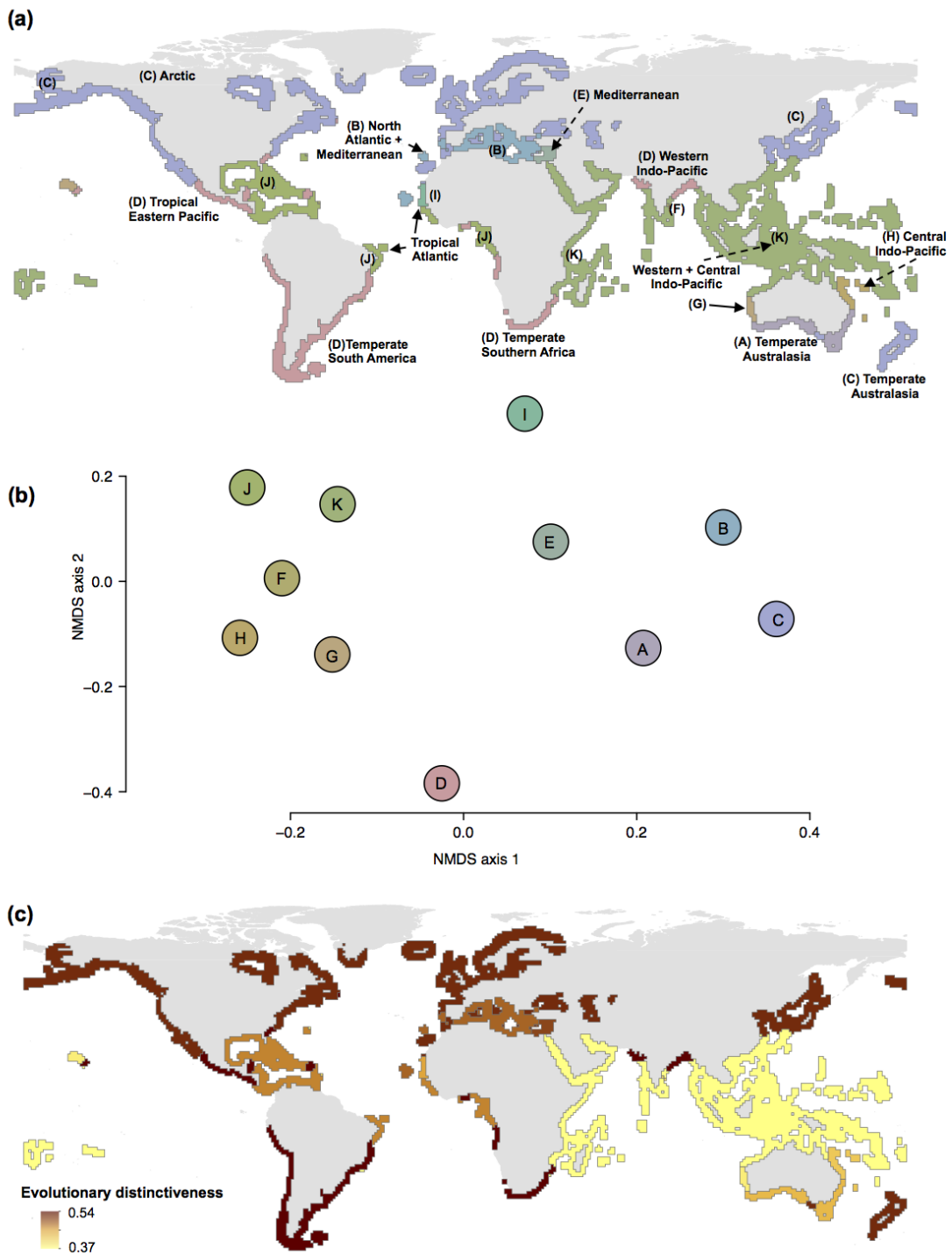


Fig 1. Relationships among marine phyloreions based on phylogenetic turnover ($p\beta_{sim}$) of seagrass species worldwide (a) in geographic space, (b) in NMDS ordination space (two-dimensional solution, stress = 0.158), and (c) as map of evolutionary distinctiveness per phyloreion. Colors differentiating between phyloreions in the map (a), and NMDS (b) are identical, and depict the amount of phylogenetic turnover among phyloreions. Darker colors for the evolutionary distinctiveness (c) indicate phyloreions of high evolutionary distinctiveness.

Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1. List of taxa included in phylogeny with GenBank accession numbers.

Table S2. Performance of clustering algorithms for phylogenetic beta diversity ($p\beta_{sim}$) and beta diversity (β_{sim}) of seagrass assemblages based on cophenetic correlation.

Table S3. Summary information for clustering phytogeographic zones of seagrasses based on phylogenetic beta diversity.

S1 Fig. Results from divergence dating with BEAST for seagrass species obtained from a combined plastid and nuclear dataset.

S2 Fig. Threshold of explained variances to identify the optimal number of clusters for (A) phylogenetic beta diversity ($p\beta_{sim}$), and (B) beta diversity (β_{sim}), for seagrass species of the world.

S3 Fig. Relationships among marine regions based on species presence/absence data (A) in geographic space, (B) NMDS ordination space (stress = 0.109), and (C) as dendrogram.

S4 Fig. Analysis of similarity (ANOSIM) results for comparison among marine phyloregions based on oceanographic variables. (A) Sea surface temperature ($^{\circ}\text{C}$), (B) Sea surface salinity (psu), and (C) Bathymetry (m). The ANOSIM boxplot gives the R statistics and statistical significance between the variables by computing the grouping vector to obtain the empirical distribution of correlation coefficients under a null-model. The values on the y-axes are cell rank scores between and within the phyloregions. Colours of boxplots correspond to phyloregions represented in Fig. 1. Comparisons between phyloregions represent compositional dissimilarities. Phyloregions with very different species composition would have greater compositional dissimilarities between than within phyloregions; R = correlation strength; p = statistical significance

TABLE S1. List of taxa included in phylogeny with GenBank accession numbers. Missing sequences are indicated with a dash in the relevant position.

Taxon Author	Order	Family APG	Species geographic range (km ²)	GenBank ITS	GenBank 18S	GenBank <i>rbcL</i>
<i>Amphibolis antarctica</i> (Labill.) Asch.	Alismatales	Cymodoceaceae	757 920	–	–	U80686
<i>Amphibolis griffithii</i> (J.M.Black) Hartog	Alismatales	Cymodoceaceae	482 430	–	–	HQ901574
<i>Cymodocea nodosa</i> (Ucria) Asch.	Alismatales	Cymodoceaceae	2 264 000	AF102272	–	U80688
<i>Cymodocea rotundata</i> Asch. & Schweinf.	Alismatales	Cymodoceaceae	14 105 610	–	JN034102	JQ031763
<i>Cymodocea serrulata</i> (R.Br.) Asch. & Magnus	Alismatales	Cymodoceaceae	13 224 620	–	–	U80687
<i>Enhalus acoroides</i> (L.f.) Royle	Alismatales	Hydrocharitaceae	11 985 350	AY870347	AY95240 3	AB004889
<i>Halodule beaudettei</i> (Hartog) Hartog	Alismatales	Cymodoceaceae	6 067 650	–	–	U80689
<i>Halodule pinifolia</i> (Miki) Hartog	Alismatales	Cymodoceaceae	11 546 650	–	–	U80690
<i>Halodule uninervis</i> (Forssk.) Boiss.	Alismatales	Cymodoceaceae	15 119 330	–	AY95240 1	AB571210
<i>Halodule wrightii</i> Asch.	Alismatales	Cymodoceaceae	6 068 000	–	–	HQ901575
<i>Halophila australis</i> Doty & B.C.Stone	Alismatales	Hydrocharitaceae	656 800	AF366414	–	–
<i>Halophila beccarii</i> Asch.	Alismatales	Hydrocharitaceae	1 850 540	AF366441	–	JN225339
<i>Halophila decipiens</i> Ostenf.	Alismatales	Hydrocharitaceae	15 367 760	AF395673	–	U80698
<i>Halophila euphlebica</i> Makino	Alismatales	Hydrocharitaceae	31 910	AB243968	–	–
<i>Halophila hawaiiiana</i> Doty & B.C.Stone	Alismatales	Hydrocharitaceae	130 630	AF366426	–	–
<i>Halophila johnsonii</i> Eiseman	Alismatales	Hydrocharitaceae	16 901 460	AF366425	–	–
<i>Halophila minor</i> (Zoll.) Hartog	Alismatales	Hydrocharitaceae	8 396 000	AF366406	–	JN225347
<i>Halophila nipponica</i> J.Kuo	Alismatales	Hydrocharitaceae	554 630	HQ687164	–	–
<i>Halophila ovalis</i> (R.Br.) Hook.f.	Alismatales	Hydrocharitaceae	16 901 458	AF366434	AY95240 0	AB004890
<i>Halophila spinulosa</i> (R.Br.) Asch.	Alismatales	Hydrocharitaceae	5 719 350	AF366440	–	–

<i>Halophila stipulacea</i> (Forssk.) Asch.	Alismatales	Hydrocharitaceae	2 981 250	AY352637	–	JN225356
<i>Halophila tricostata</i> M.Greenway	Alismatales	Hydrocharitaceae	296 650	AF366438	–	–
<i>Lepilaena australis</i> J.Drumm. ex Harv.	Alismatales	Potamogetonaceae	796 130	–	–	U80729
<i>Phyllospadix iwatensis</i> Makino	Alismatales	Zosteraceae	663 410	JQ766110	HQ66059 5	–
<i>Phyllospadix scouleri</i> Hook.	Alismatales	Zosteraceae	671 690	–	–	DQ859172
<i>Phyllospadix torreyi</i> S.Watson	Alismatales	Zosteraceae	465 630	AY077985	–	U80731
<i>Posidonia angustifolia</i> Cambridge & J.Kuo	Alismatales	Posidoniaceae	731 380	GQ927719	–	–
<i>Posidonia australis</i> Hook.f.	Alismatales	Posidoniaceae	869 490	GQ927720	–	HQ901573
<i>Posidonia coriacea</i> Cambridge & J.Kuo	Alismatales	Posidoniaceae	566 390	GQ927721	–	–
<i>Posidonia denhartogii</i> J.Kuo & Cambridge	Alismatales	Posidoniaceae	426 370	GQ927722	–	–
<i>Posidonia kirkmanii</i> J.Kuo & Cambridge	Alismatales	Posidoniaceae	149 930	GQ927724	–	–
<i>Posidonia oceanica</i> (L.) Delile	Alismatales	Posidoniaceae	1 721 360	GQ927725	AY49194 2	U80719
<i>Posidonia ostenfeldii</i> Hartog	Alismatales	Posidoniaceae	149 930	GQ927726	–	–
<i>Posidonia sinuosa</i> Cambridge & J.Kuo	Alismatales	Posidoniaceae	431 660	GQ927727	–	–
<i>Ruppia cirrhosa</i> (Petagna) Grande	Alismatales	Ruppiaceae	419 790	JQ034335	–	JN113277
<i>Ruppia maritima</i> L.	Alismatales	Ruppiaceae	5 847 640	JN034094	JN034103	HQ901576
<i>Ruppia megacarpa</i> R.Mason	Alismatales	Ruppiaceae	209 720	JQ034337	–	JQ034324
<i>Ruppia polycarpa</i> R.Mason	Alismatales	Ruppiaceae	174 960	–	–	AB507898
<i>Ruppia tuberosa</i> J.S.Davis & Toml.	Alismatales	Ruppiaceae	154 150	–	–	AB507899
<i>Syringodium filiforme</i> Kütz.	Alismatales	Cymodoceaceae	2 785 590	–	AF168876	U03727
<i>Syringodium isoetifolium</i> (Asch.) Dandy	Alismatales	Cymodoceaceae	14 939 340	–	–	U80691
<i>Thalassia hemprichii</i> (Ehrenb. ex Solms) Asch.	Alismatales	Hydrocharitaceae	14 381 540	–	AY95238 6	AB004897
<i>Thalassia testudinum</i> Banks & Sol. ex K.D.Koenig	Alismatales	Hydrocharitaceae	2 771 500	AY870348	AF168878	HQ901568
<i>Thalassodendron ciliatum</i> (Forssk.)	Alismatales	Cymodoceaceae	10 585 660	–	–	U80692

Hartog							
<i>Thalassodendron pachyrhizum</i>	Alismatales	Cymodoceaceae	186 780	–	–	U80692	
<i>Zostera asiatica</i> Hartog	Alismatales	Zosteraceae	1 366 410	EF198347	–	AB125352	
<i>Zostera caespitosa</i> Miki	Alismatales	Zosteraceae	715 850	JQ937100	–	AB125351	
<i>Zostera capensis</i> Setch.	Alismatales	Zosteraceae	624 180	JQ937097	–	AM235166	
<i>Zostera caulescens</i> Miki	Alismatales	Zosteraceae	572 260	JQ937099	–	AB125350	
<i>Zostera japonica</i> Asch. & Graebn.	Alismatales	Zosteraceae	2 462 920	JQ766111	–	AB125353	
<i>Zostera marina</i> L.	Alismatales	Zosteraceae	9 768 880	JN034095	HQ44594 0	AB125349	
<i>Zostera muelleri</i> Irmisch ex Asch.	Alismatales	Zosteraceae	1 416 170	AY078004	–	AY077962	
<i>Zostera noltii</i> Hornem.	Alismatales	Zosteraceae	2 963 360	AY077992	AF207058	U80733	
<i>Zostera pacifica</i> S.Watson	Alismatales	Zosteraceae	9 768 880	EF198348	–	–	
<i>Zostera tasmanica</i> M.Martens ex Asch.	Alismatales	Zosteraceae	151 360	AY077990	–	U80730	
Outgroups							
<i>Alocasia cucullata</i> (Lour.) G.Don	Alismatales	Araceae		AB429340	–	JQ237188	
<i>Alocasia macrorrhizos</i> (L.) G.Don	Alismatales	Araceae		–	–	JF828103	
<i>Alocasia odora</i> (Lindl.) K.Koch	Alismatales	Araceae		AF469030	–	JQ933213	
<i>Alocasia sandariana</i> W.Bull	Alismatales	Araceae		–	–	EU193192	
<i>Harperocallis flava</i> McDaniel	Alismatales	Tofieldiaceae		AB541108	–	HQ901586	
<i>Tofieldia furusei</i> (Hiyama) M.N.Tamura & Fuse	Alismatales	Tofieldiaceae		AB561187	–	–	

TABLE S2. Performance of clustering algorithms for phylogenetic beta diversity ($p\beta_{sim}$) and beta diversity (β_{sim}) of seagrass assemblages based on cophenetic correlation.

Cluster algorithm	Phylogenetic beta diversity ($p\beta_{sim}$)	Beta diversity (β_{sim})
Complete linkage agglomerative clustering method = "complete"	0.51	0.53
UPGMA agglomerative clustering method = "average"	0.74	0.87
WPGMA agglomerative clustering method = "mcquitty"	0.68	0.80
UPGMC agglomerative clustering method = "centroid"	0.73	0.85
WPGMC agglomerative clustering method = "median"	0.35	0.77
Ward's minimum variance clustering method = "ward"	0.72	0.82
DIANA	0.50	0.56

Cophenetic correlation values represent the correlation (using Spearman's) between the original pairwise distances between the grid cells and the new pairwise distances between the grid cells based on the dendrogram produced by the clustering algorithm. Cluster algorithms are tested by grouping grid cell assemblages for seagrass species of the world. Values in bold correspond to best performing algorithm.

TABLE S3. Summary information for clustering phytogeographic zones of seagrasses based on phylogenetic beta diversity.

Phyloregion (common name)	Area in km ² (number of grid cells)	Mean $p\beta_{sim}$ (number of species)	Cluster composition
(A) Temperate Australasia	1,995,000 (161)	0.414 (26)	Cymodoceaceae (<i>Amphibolis antarctica</i> , <i>Amphibolis griffithii</i> , <i>Halodule uninervis</i> , <i>Syringodium isoetifolium</i> , <i>Thalassodendron pachyrhizum</i>); Hydrocharitaceae (<i>Halophila australis</i> , <i>Halophila decipiens</i> , <i>Halophila ovalis</i> , <i>Halophila spinulosa</i>); Potamogetonaceae (<i>Lepilaena australis</i> , <i>Lepilaena marina</i>); Posidoniaceae (<i>Posidonia angustifolia</i> , <i>Posidonia australis</i> , <i>Posidonia coriacea</i> , <i>Posidonia denhartogii</i> , <i>Posidonia kirkmanii</i> , <i>Posidonia ostenfeldii</i> , <i>Posidonia sinuosa</i>); Ruppiceae (<i>Ruppia maritima</i> , <i>Ruppia megacarpa</i> , <i>Ruppia polycarpa</i> , <i>Ruppia tuberosa</i>); Zosteraceae (<i>Zostera muelleri</i> , <i>Zostera nigricaulis</i> , <i>Zostera polychlamys</i> , <i>Zostera tasmanica</i>).
(B) North Atlantic + Mediterranean	3,656,000 (295)	0.436 (7)	Cymodoceaceae (<i>Cymodocea nodosa</i>); Hydrocharitaceae (<i>Halophila stipulacea</i>); Posidoniaceae (<i>Posidonia oceanica</i>); Ruppiceae (<i>Ruppia cirrhosa</i> , <i>Ruppia maritima</i>); Zosteraceae (<i>Zostera marina</i> , <i>Zostera noltii</i>).
(C) Arctic + Temperate Australasia	28,502,000 (2300)	0.503 (44)	Cymodoceaceae (<i>Amphibolis antarctica</i> , <i>Cymodocea nodosa</i> , <i>Cymodocea rotundata</i> , <i>Cymodocea serrulata</i> , <i>Enhalus acoroides</i> , <i>Halodule pinifolia</i> , <i>Halodule uninervis</i> , <i>Halodule wrightii</i> , <i>Syringodium isoetifolium</i>); Hydrocharitaceae (<i>Halophila australis</i> , <i>Halophila decipiens</i> , <i>Halophila major</i> , <i>Halophila minor</i> , <i>Halophila nipponica</i> , <i>Halophila ovalis</i> , <i>Halophila stipulacea</i> , <i>Thalassia hemprichii</i>); Potamogetonaceae (<i>Lepilaena australis</i> , <i>Lepilaena marina</i>); Posidoniaceae (<i>Posidonia</i>

			<i>angustifolia</i> , <i>Posidonia australis</i> , <i>Posidonia coriacea</i> , <i>Posidonia denhartogii</i> , <i>Posidonia oceanica</i>); Ruppiales (<i>Ruppia cirrhosa</i> , <i>Ruppia maritima</i> , <i>Ruppia megacarpa</i> , <i>Ruppia polycarpa</i> , <i>Ruppia tuberosa</i>); Zosteraceae (<i>Zostera asiatica</i> , <i>Zostera caespitosa</i> , <i>Zostera caulescens</i> , <i>Zostera geojeensis</i> , <i>Zostera japonica</i> , <i>Zostera marina</i> , <i>Zostera muelleri</i> , <i>Zostera nigricaulis</i> , <i>Zostera noltii</i> , <i>Zostera tasmanica</i> , <i>Phyllospadix iwatensis</i> , <i>Phyllospadix japonicus</i> , <i>Phyllospadix scouleri</i> , <i>Phyllospadix serrulatus</i> , <i>Phyllospadix torreyi</i>).
(D) Temperate South America + Temperate Southern Africa	7,819,000 (631)	0.539 (24)	Cymodoceaceae (<i>Cymodocea rotundata</i> , <i>Cymodocea serrulata</i> , <i>Halodule emarginata</i> , <i>Halodule pinifolia</i> , <i>Halodule uninervis</i> , <i>Halodule wrightii</i> , <i>Syringodium filiforme</i> , <i>Syringodium isoetifolium</i> , <i>Thalassodendron ciliatum</i>); Hydrocharitaceae (<i>Enhalus acoroides</i> , <i>Halophila baillonis</i> , <i>Halophila beccarii</i> , <i>Halophila decipiens</i> , <i>Halophila engelmannii</i> , <i>Halophila gaudichaudii</i> , <i>Halophila ovalis</i> , <i>Halophila stipulacea</i> , <i>Thalassia hemprichii</i> , <i>Thalassia testudinum</i>); Ruppiales (<i>Ruppia cirrhosa</i> , <i>Ruppia filifolia</i> , <i>Ruppia maritima</i>); Zosteraceae (<i>Zostera capensis</i> , <i>Zostera chilensis</i>).
(E) Mediterranean	533,000 (43)	0.459 (4)	Cymodoceaceae (<i>Cymodocea nodosa</i>); Hydrocharitaceae (<i>Halophila stipulacea</i>); Posidoniaceae (<i>Posidonia oceanica</i>); Zosteraceae (<i>Zostera noltii</i>).
(F) Western Indo-Pacific	37,000 (3)	0.396 (10)	Cymodoceaceae (<i>Cymodocea rotundata</i> , <i>Cymodocea serrulata</i> , <i>Halodule pinifolia</i> , <i>Halodule uninervis</i> , <i>Halodule wrightii</i>); Hydrocharitaceae (<i>Halophila beccarii</i> , <i>Halophila decipiens</i> , <i>Halophila gaudichaudii</i> , <i>Halophila ovalis</i> , <i>Halophila stipulacea</i>).

(G) Western + Central Indo-Pacific	632,000 (51)	0.372 (28)	Cymodoceaceae (<i>Amphibolis antarctica</i> , <i>Amphibolis griffithii</i> , <i>Cymodocea angustata</i> , <i>Cymodocea serrulata</i> , <i>Halodule pinifolia</i> , <i>Halodule uninervis</i> , <i>Syringodium isoetifolium</i> , <i>Thalassodendron ciliatum</i> , <i>Thalassodendron pachyrhizum</i>); Hydrocharitaceae (<i>Halophila australis</i> , <i>Halophila decipiens</i> , <i>Halophila gaudichaudii</i> , <i>Halophila hawaiiiana</i> , <i>Halophila ovalis</i> , <i>Halophila spinulosa</i>); Potamogetonaceae (<i>Lepilaena australis</i>); Posidoniaceae (<i>Posidonia angustifolia</i> , <i>Posidonia australis</i> , <i>Posidonia coriacea</i> , <i>Posidonia denhartogii</i> , <i>Posidonia sinuosa</i>); Ruppiaceae (<i>Ruppia maritima</i> , <i>Ruppia megacarpa</i> , <i>Ruppia polycarpa</i> , <i>Ruppia tuberosa</i>); Zosteraceae (<i>Zostera muelleri</i> , <i>Zostera nigricaulis</i> , <i>Zostera polychlamys</i>).
(H) Central Indo-Pacific	880,000 (71)	0.410 (15)	Cymodoceaceae (<i>Cymodocea rotundata</i> , <i>Cymodocea serrulata</i> , <i>Halodule pinifolia</i> , <i>Halodule uninervis</i> , <i>Syringodium isoetifolium</i>); Hydrocharitaceae (<i>Halophila capricorni</i> , <i>Halophila decipiens</i> , <i>Halophila minor</i> , <i>Halophila ovalis</i> , <i>Halophila spinulosa</i> , <i>Halophila tricostata</i> , <i>Thalassia hemprichii</i>); Potamogetonaceae (<i>Lepilaena australis</i>); Ruppiaceae (<i>Ruppia maritima</i>); Zosteraceae (<i>Zostera muelleri</i>).
(I) Tropical Atlantic (West African coast)	285,000 (23)	0.425 (3)	Cymodoceaceae (<i>Cymodocea nodosa</i> , <i>Halodule wrightii</i>); Zosteraceae (<i>Zostera noltii</i>).
(J) Tropical Atlantic	6,791,000 (548)	0.433 (11)	Cymodoceaceae (<i>Halodule bermudensis</i> , <i>Halodule ciliata</i> , <i>Halodule emarginata</i> , <i>Halodule wrightii</i> , <i>Syringodium filiforme</i>); Hydrocharitaceae (<i>Halophila baillonis</i> , <i>Halophila decipiens</i> , <i>Halophila engelmannii</i> , <i>Halophila stipulacea</i> , <i>Thalassia testudinum</i>); Ruppiaceae (<i>Ruppia maritima</i>).

(K) Western + Central Indo-Pacific II	31,340,000 (2529)	0.370 (29)	<p>Cymodoceaceae (<i>Cymodocea angustata</i>, <i>Cymodocea rotundata</i>, <i>Cymodocea serrulata</i>, <i>Enhalus acoroides</i>, <i>Halodule pinifolia</i>, <i>Halodule uninervis</i>, <i>Halodule wrightii</i>, <i>Syringodium isoetifolium</i>, <i>Thalassodendron ciliatum</i>); Hydrocharitaceae (<i>Halophila beccarii</i>, <i>Halophila capricorni</i>, <i>Halophila decipiens</i>, <i>Halophila gaudichaudii</i>, <i>Halophila major</i>, <i>Halophila minor</i>, <i>Halophila nipponica</i>, <i>Halophila ovalis</i>, <i>Halophila spinulosa</i>, <i>Halophila stipulacea</i>, <i>Halophila sulawesii</i>, <i>Halophila tricostata</i>, <i>Thalassia hemprichii</i>); Posidoniaceae (<i>Posidonia coriacea</i>); Ruppiaceae (<i>Ruppia maritima</i>); Zosteraceae (<i>Zostera asiatica</i>, <i>Zostera capensis</i>, <i>Zostera japonica</i>, <i>Zostera marina</i>, <i>Zostera muelleri</i>).</p>
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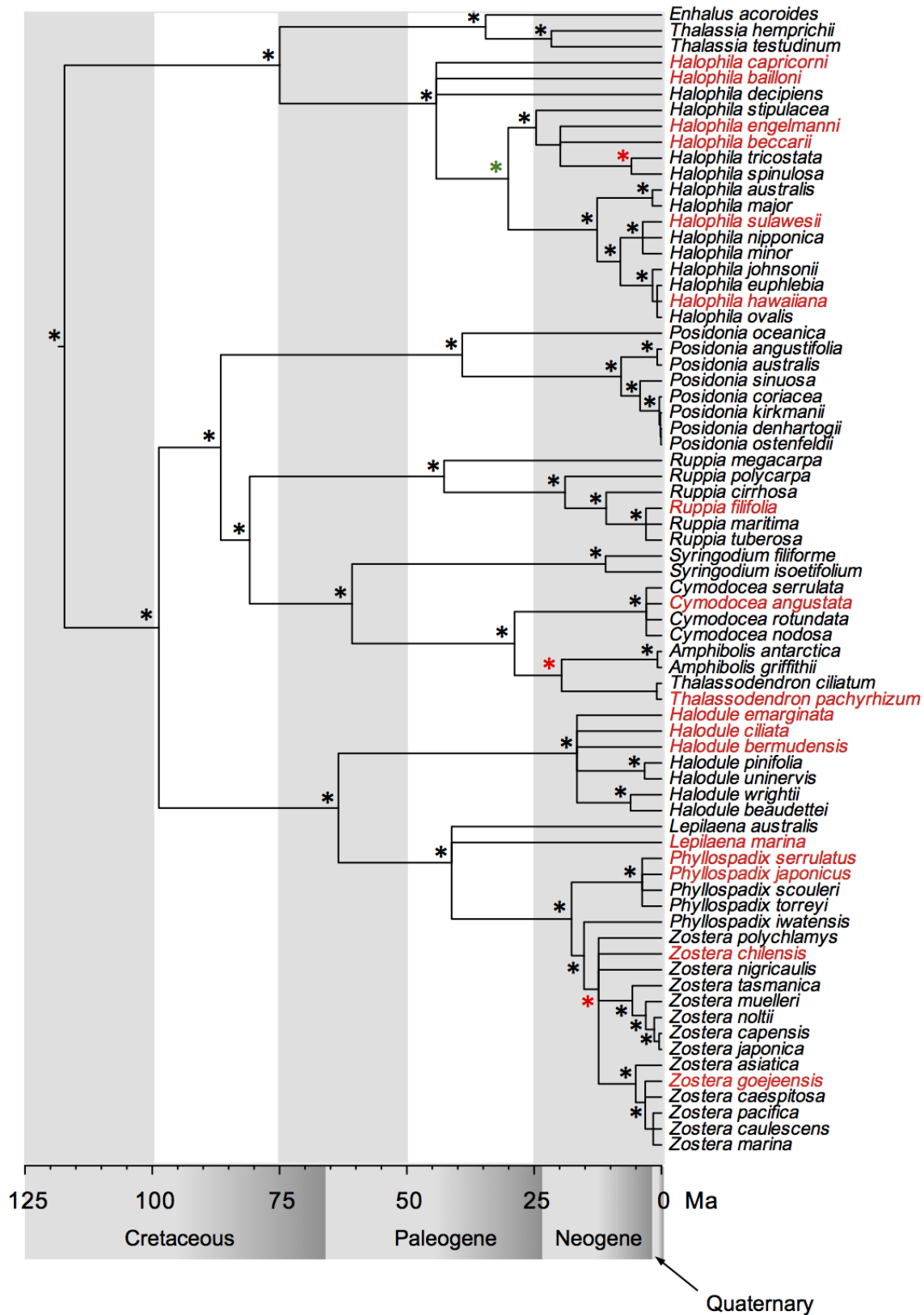


FIG. S1. Results from divergence dating with BEAST for seagrass species obtained from a combined plastid and nuclear dataset. Stars at nodes indicate levels of support; black:

PP > 0.99, green PP > 0.95, red: PP < 0.9. Tip labels indicated in red are those with missing DNA sequences.

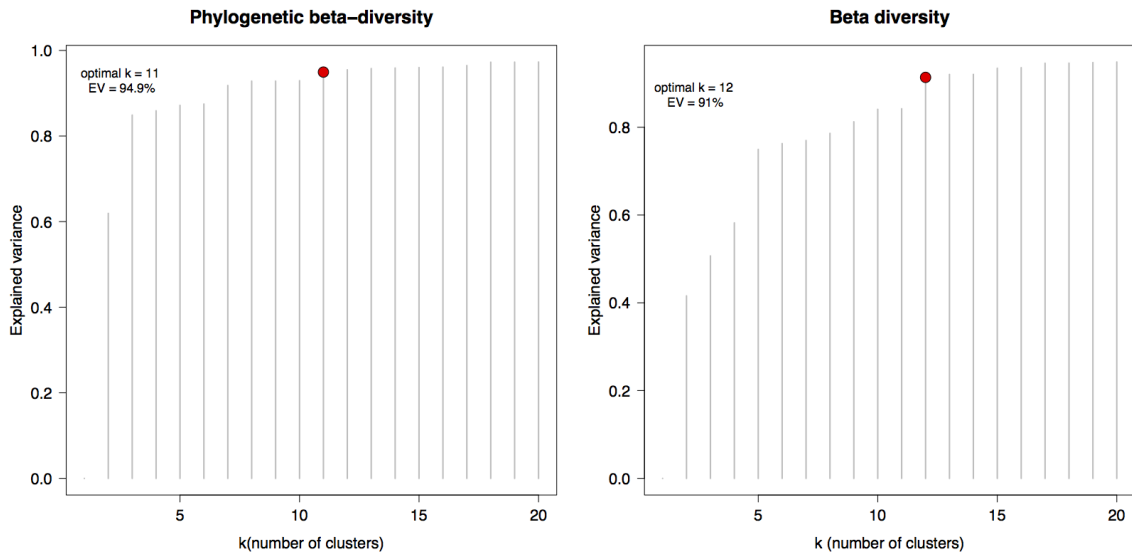


FIG. S2. Threshold of explained variances to identify the optimal number of clusters for (A) phylogenetic beta diversity ($p\beta_{sim}$), and (B) beta diversity (β_{sim}), for seagrass species of the world. The "elbow" (optimal cluster) of the graph is indicated by the red circle.

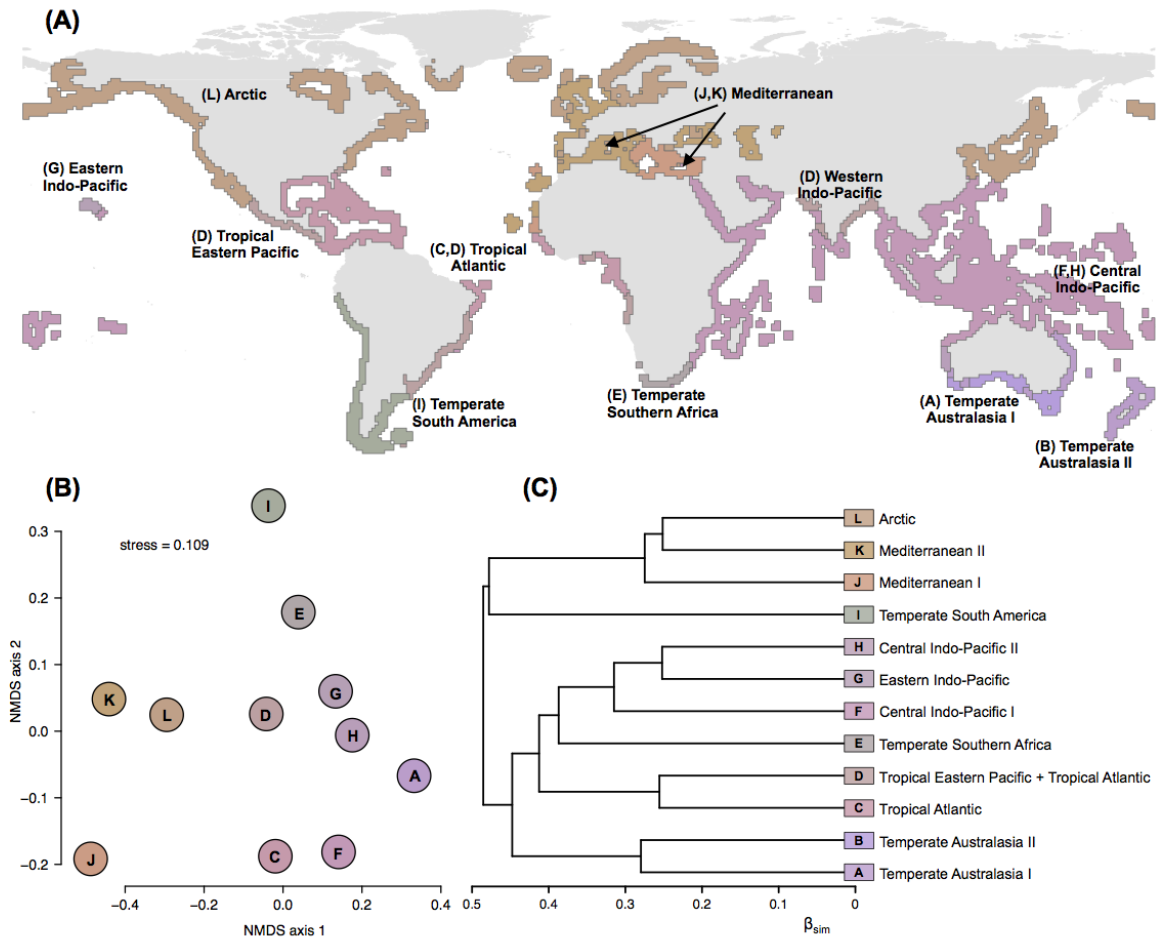


FIG. S3. Relationships among marine regions based on species presence/absence data (A) in geographic space, (B) NMDS ordination space (stress = 0.109), and (C) as dendrogram. Relationships are obtained based on UPGMA clustering of beta diversity (β_{sim}) values for species assemblages in $1.0^\circ \times 1.0^\circ$ grid cells. Grid cells cluster into 12 regions based upon the ‘L method’ of Salvador & Chan (2004). Colors differentiating between phyloregions in the map, dendrogram and NMDS are identical, and depict the amount of species turnover among regions. The map is plotted using Berhmann projection.

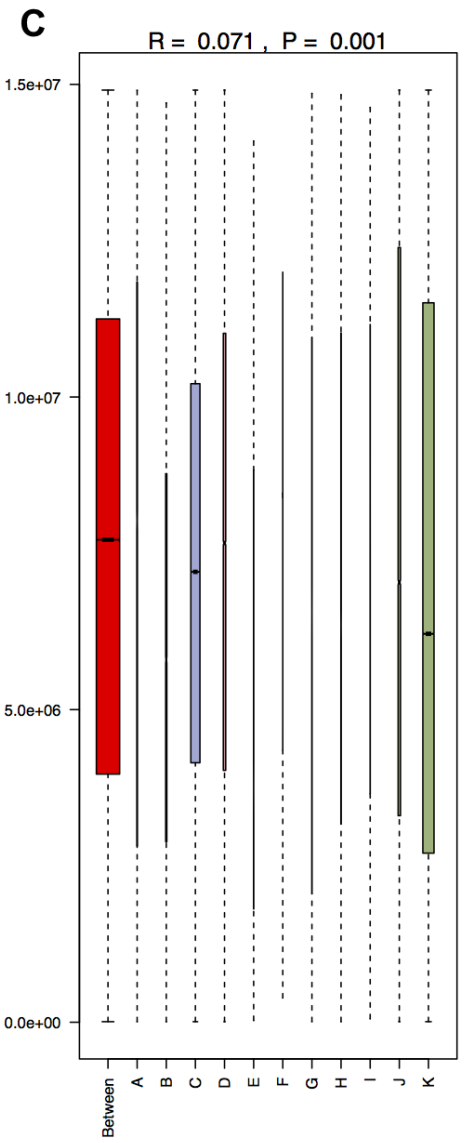
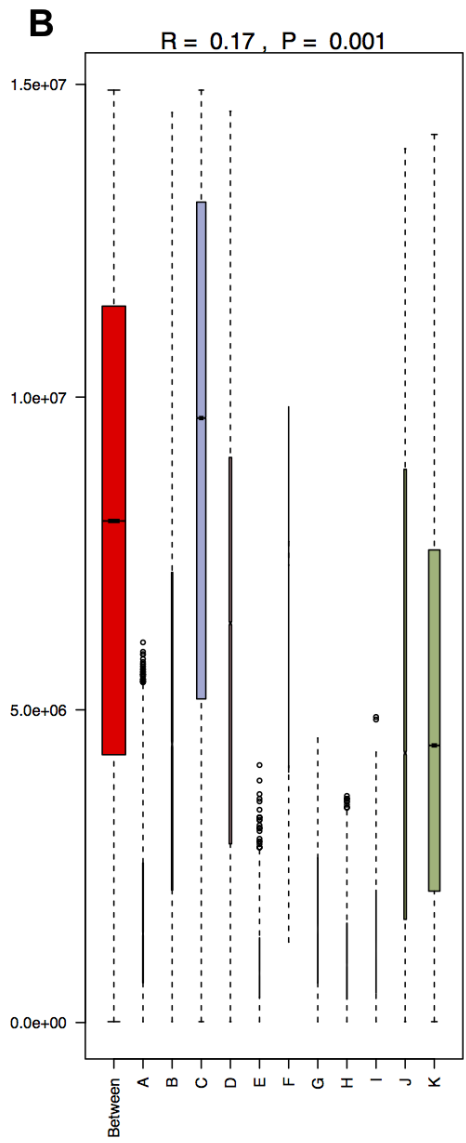
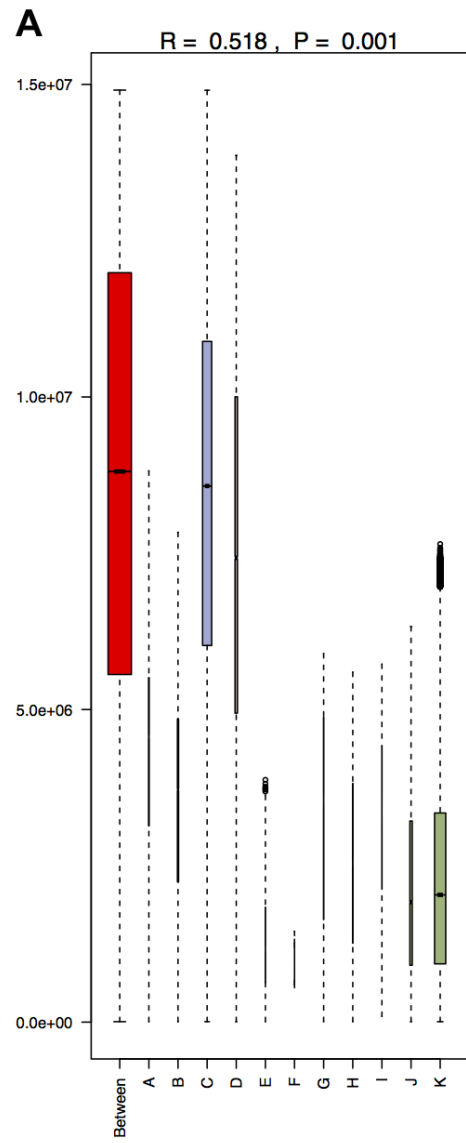


FIG. S4. Analysis of similarity (ANOSIM) results for comparison among marine phyloregions based on oceanographic variables. (A) Sea surface temperature ($^{\circ}\text{C}$), (B) Sea surface salinity (psu), and (C) Bathymetry (m). The ANOSIM boxplot gives the R statistics and statistical significance between the variables by computing the grouping vector to obtain the empirical distribution of correlation coefficients under a null-model. The values on the y-axes are cell rank scores between and within the phyloregions. Colours of boxplots correspond to phyloregions represented in Fig. 1. Comparisons between phyloregions represent compositional dissimilarities. Phyloregions with very different species composition would have greater compositional dissimilarities between than within phyloregions; R = correlation strength; p = statistical significance