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Marine protected areas are insufficient to conserve global marine plant diversity

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ABSTRACT

Aim Marine plants are only incidentally included in conservation efforts for marine biodiversity. Here, for the first time, we apply phylogenetic methods to marine macrophytes (mangroves and seagrass species) to test for gaps in the current conservation network by identifying global diversity hotspots for these plant groups, and assess the degree to which hotspots are represented within the current network of marine protected areas (MPAs).

Location Global.

Methods We calculated five metrics of marine plant diversity: phylogenetic diversity, species richness, species endemism, phylogenetic endemism and 'evolutionary distinctiveness and global endangerment' (EDGE).

Results Overall, the diversity of marine plants was poorly represented by current MPAs. Different measures of diversity showed spatial mismatch, demonstrating how strategies that maximize one diversity measure may be inefficient at protecting other facets of marine plant biodiversity. However, complementarity analyses revealed that complete representation can be achieved very efficiently with few additional locations.

Main conclusions Our study highlights the need for an integrative approach to conserve both the species diversity and phylogenetic diversity of marine plants. While MPAs are a valuable instrument for conserving marine biodiversity, we now face the challenge of increasing coverage to protect other branches of the marine tree of life.

Keywords
Biodiversity hotspots, complementarity analyses, mangroves, marine plants, phylogenetic diversity, protected areas, seagrasses.

INTRODUCTION

Although the system of marine protected areas (MPAs) remains the most significant instrument for managing and protecting the biological resources of the oceans, MPAs were initially designed for preserving fish stocks, coral reefs and other animal resources (Gaines *et al.*, 2010). This suggests that non-target taxa and their associated habitats are often only incidentally included in current efforts to protect biodiversity in the marine realm. Moreover, the major groups of conservation focus in the marine world, mainly marine mammals, coral reefs and fish, may not fully represent the diversity of other taxa due to their different evolutionary histories (see, e.g., Rodrigues & Brooks, 2007; Mellin *et al.*, 2011). Indeed, there is inconsistent support for the use of cross-taxon surrogates (where well-studied taxonomic groups can effectively serve as surrogates to represent patterns of diversity of more poorly known taxa; Rodrigues & Brooks, 2007) in conservation planning. For example, some studies have suggested that environmental factors may be a more efficient proxy for biodiversity (e.g. Tittensor *et al.*, 2010; Beier & de Albuquerque, 2015), while others have found spatial mismatches between various taxonomic groups (e.g. Zupan *et al.*, 2014), suggesting that usefulness of cross-taxon surrogates may depend on the scale or context of the study (e.g. Ferrier & Watson, 1997; Rodrigues & Brooks, 2007). As a result, explicit examination of the representation of non-target species within

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MPAs is necessary to assess their protection status. Moreover, given that marine species are more prone to extinction than previously thought (McKinney, 1998), due to human pressures (Roberts *et al.*, 2002; McCauley *et al.*, 2015), it is critical to determine the extent to which MPAs conserve species of other distinct evolutionary branches of the marine tree of life (Murdoch *et al.*, 2007).

A common approach to designating areas of conservation priority is via hotspots, i.e. geographical clusters of biodiversity (Myers *et al.*, 2000; see also Orme *et al.*, 2005). In the marine realm, biodiversity hotspots have been defined using taxonomic metrics such as species richness (SR), endemism or risk of extinction (Roberts *et al.*, 2002; Davidson *et al.*, 2012), thereby missing out on the full richness of biodiversity captured by phylogenetic information (Faith, 1994; Williams *et al.*, 1994). Even with simple taxonomic metrics of diversity, spatial mismatches between individual taxonomic metrics have often been reported (Roberts *et al.*, 2002), suggesting that current marine hotspots are insufficient to capture even species-level diversity.

Some lineages differ markedly in the amount of evolutionary history they embody (Vane-Wright *et al.*, 1991; Faith, 1992). As a result, integrating phylogenetic information is an important advance in conservation (Bininda-Emonds *et al.*, 2000), allowing reserve networks to be planned that maximize the amount of unique evolutionary history that is captured (Sechrest *et al.*, 2002; Jetz *et al.*, 2014). For instance, considering phylogenetic metrics in conservation prioritization allows the identification of areas harbouring evolutionarily distinct lineages, i.e. once-diverse lineages that are now reduced due to historical extinctions, or of regions with recently diversified clades that may represent centres of speciation (e.g. Forest *et al.*, 2007). Phylogenetic metrics, including phylogenetic diversity (PD), phylogenetic endemism and evolutionary distinctiveness and global endangerment, all measure different facets of evolutionary diversity (Isaac *et al.*, 2007; Cadotte *et al.*, 2010) and have been used to delineate biodiversity hotspots, but only in the terrestrial realm (Faith, 1992; Rosauer *et al.*, 2009; Safi *et al.*, 2013; Jetz *et al.*, 2014; Zupan *et al.*, 2014; Daru *et al.*, 2015; Guilhaumon *et al.*, 2015). Despite the growing interest in integrating taxonomic and phylogenetic methods for the assessment of biodiversity (Devictor *et al.*, 2010; Mishler *et al.*, 2014; Zupan *et al.*, 2014; Daru *et al.*, 2015), phylogenetic metrics have not been implemented in conservation planning for marine species. While the selection of hotspots based solely on the top grid cells for each metric could ensure protection of certain habitats, this approach may be inefficient (and even ineffective) for maximizing protection of biodiversity (Daru *et al.*, 2015). Complementarity methods, which aim to include the maximum number of unrepresented species or phylogenetic branch lengths with each new location conserved, offer a more powerful and efficient approach for identifying a minimum conservation network that includes all species or phylogenetic branches of interest. Therefore, considerable opportunity exists for improving the representation and efficiency of marine conservation networks, as has previously been advocated (e.g. Justus & Sarkar, 2002; Faith *et al.*, 2004), through the incorporation of phylogenetic information and the application of complementarity methods.

With this aim, we develop an integrative approach to assess current marine protection efforts by combining spatial analyses with taxonomic and phylogenetic techniques to identify hotspots for two important aquatic and semi-aquatic plant groups: seagrasses and mangroves. These two groups are the only vascular plants inhabiting coastal environments and estuaries world-wide that can live exclusively in the marine environment without any freshwater input; they present an excellent opportunity to explore the degree of protection of a (usually) non-target group in the current marine conservation network. Both seagrasses and mangroves are keystone species, having a disproportionately strong influence on co-occurring species, largely via ecosystem engineering effects. Seagrasses (72 species; Hemminga & Duarte, 2000) and mangroves (70 species; Spalding *et al.*, 1997) play critical roles in sediment accumulation, carbon sequestration and nutrient cycling, act as a nursery for many fish and invertebrates and anchor several foodwebs (Beck *et al.*, 2001; Green & Short, 2003). Cumulatively, their ecosystem services are valued at *c.* USD 2 trillion annually (Costanza *et al.*, 1997; Field *et al.*, 1998; Waycott *et al.*, 2009). We refer to these two ecological groups collectively as 'macrophytes'.

Here, for the first time, we apply phylogenetic methods to marine macrophytes to test for gaps in the current conservation network. Specifically, we address three objectives. First, we map patterns and hotspots (defined as the top 2.5% of cells) of SR, PD, corrected weighted endemism (CWE), phylogenetic endemism (PE) and evolutionary distinctiveness and global endangerment (EDGE) for each taxonomic group. Second, we explore the complementarity of macrophyte SR and PD in representing all species/branch lengths in as small an area as possible. Finally, we evaluate the degree to which the current global network of MPAs covers macrophyte hotspots.

METHODS

Distribution data and phylogenetic reconstruction

We compiled data on the global distribution of all 72 seagrass species and 55 (of 70) mangrove species from the IUCN Red List database extent of occurrence maps (EOO) (http://www.iucnredlist.org/technical-documents/spatial-data). These maps have been extensively assessed and updated, providing accurate presence/absence data at the scale of $1° \times 1°$ grids (*c.* 110 km × 110 km), a resolution commonly used in global-scale macroecological studies (e.g. Storch *et al.*, 2012).

Phylogenetic reconstruction and divergence time estimation for seagrass species

DNA sequences (*rbcL*, ITS and 18S) for 55 (of 72) seagrass species were obtained from GenBank/EBI. The sequences were aligned using SEAVIEW v.4 (Gouy *et al.*, 2010) and manually adjusted using MESQUITE v.2.5 (Maddison & Maddison, 2008). The combined data set comprised 1137, 930 and 1671 base pairs

for *rbcL*, ITS and 18S, respectively. Information on DNA sequences retrieved from GenBank/EBI is presented in Table S1 in Appendix S1 in the Supporting Information.

Phylogenetic relationships were reconstructed on the combined dataset using maximum likelihood (ML; Stamatakis *et al.*, 2008) on the CIPRES cluster (Miller *et al.*, 2009), transforming branch lengths to millions of years by enforcing topological constraints assuming the APG III backbone from Phylomatic v.3 (Webb & Donoghue, 2005). An XML file generated in the software BEAUti v.1.7.5 (Drummond & Rambaut, 2007) was used for the reconstruction of the dated phylogenetic tree using a Bayesian Markov chain Monte Carlo (hereafter MCMC) approach implemented in the software beast v.1.7.5 (Drummond & Rambaut, 2007). Branch lengths were then calibrated in millions of years using a Bayesian MCMC approach in beast v.1.7.5 (Drummond & Rambaut, 2007). A RAxML tree was used as a starting tree, but branch lengths were adjusted to match secondary fossil calibrations using PATHd8 v.1.0 to ensure topological constraints were satisfied (Britton *et al.*, 2007). It is possible that differences in tree reconstruction approaches (e.g. r8s versus PATHd8) might provide additional information on diversity patterns and may merit further investigation. We then used the GTR+G+I model, corresponding to general time-reversible model with rate variation among sites and proportion of invariant sites, as the best model of sequence evolution based on the result of the Akaike information criterion evaluated using Modeltest v.2.3 (Nylander, 2004). In addition, a Yule process was selected as the tree prior, along with an uncorrelated lognormal relaxed molecular clock model selected in beast v.1.7.5 (Drummond & Rambaut, 2007) for rate variation among branches. Next, we applied a normal prior distribution and a total of six calibration points, representing lineages at various phylogenetic depths: 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 independent runs of MCMC analyses in beast, each for 100 million generations, sampling every thousandth iteration. The adequacy of sampling and run convergence was assessed using the effective sample size (ESS) diagnostic in tracer (Rambaut & Drummond, 2007). The ESS values ranged from 296 to 29,217 for the age estimates (Table S2 in Appendix S1), confirming stationarity. The posterior tree distributions from the different chains were then summarized into a maximum clade credibility (MCC) tree using TreeAnotator v.1.7.5 (Drummond & Rambaut, 2007) after removal of 25% trees as burn-in. The following species were used as outgroups: *Alocasia cucullata*, *Alocasia macrorrhizos*, *Alocasia odora*, *Alocasia sanderiana*, *Harperocallis flava* and *Tofieldia furusei* (Table S1 in Appendix S1).

Seventeen species did not have available DNA sequences and were placed on the MCC phylogeny 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) or fruitflies (Yassin *et al.*, 2008). The reconstructed phylogeny is available in Fig. S1 in Appendix S1.

Phylogenetic reconstruction and divergence time estimation for mangrove species

The mangrove phylogeny is a fully dated molecular phylogenetic tree for 55 (of 70) mangrove species based on *rbcL*, ITS and 18S from Daru *et al.* (2013), reconstructed using Bayesian inference and five independent fossil calibrations with normal prior distributions as follows: Vitaceae crown node (43 Ma, SD 9 Ma), Moraceae crown node (31 Ma, SD 4 Ma), Oleaceae crown node (41 Ma, SD 6 Ma), Malvaceae crown node (39 Ma, SD 4 Ma) and angiosperm crown (Amborellaceae; 149 Ma, SD 3 Ma) (see Daru *et al.*, 2013, for a full description of tree reconstruction, Table S3 in Appendix S1 for GenBank accession numbers and Fig. S2 in Appendix S1 for the mangrove phylogenetic tree). We recognize that our phylogenetic reconstruction may introduce some error into the data, but given that all 15 missing mangrove species are represented by sister relatives it is unlikely that the incomplete sampling of the macrophytes will alter any results here.

Diversity metrics

We calculated five metrics commonly used in quantifying biodiversity at various organizational scales: SR, PD, CWE, PE and EDGE (Safi *et al.*, 2013; Jetz *et al.*, 2014; Daru *et al.*, 2015).

PD estimates the amount of evolutionary history captured by a set of taxa by summing the branch lengths that connect species from the tip to the root of a dated phylogenetic tree (Faith, 1992). It has gained recognition from its use in prioritizing terrestrial conservation areas (e.g. Forest *et al.*, 2007; Jetz *et al.*, 2014). The range-weighted variant of PD, phylogenetic endemism (PE), identifies geographical concentrations of phylogenetically and geographically restricted species (Rosauer *et al.*, 2009). PE not only estimates the degree to which PD is captured by a clade, but also how much of the clade is restricted to a geographical location. PE was measured by multiplying each branch length by the fraction of its range found within a given area (Rosauer *et al.*, 2009). Species endemism was calculated using Crisp *et al.*'s (2001) CWE which represents endemism as counts of species in a grid cell by the inverse of their range size, weighted over total richness.

The EDGE metric was measured by calculating the evolutionary distinctiveness (ED) score of each species, i.e. the degree of phylogenetic isolation, and combining it with global endangerment (GE) from IUCN conservation threat categories (Isaac *et al.*, 2007). The EDGE metric is expressed as:

$$\mathrm{EDGE} = \ln(1+\mathrm{ED}) + \mathrm{GE} \times \ln(2)$$

where GE is the probability of extinction based on the following IUCN threat categories: least concern = 0, near threatened and

conservation dependent = 1, vulnerable = 2, endangered = 3 and critically endangered = 4 (Purvis *et al.*, 2005).

As phylogenetic metrics are often expressed in units of time, and SR and endemism in space, we standardized all metrics by representing their attributes across grid cells where they occur to identify hotspots. CWE, PD, PE and SR were calculated using BIODIVERSE (Laffan *et al.*, 2010). All other analyses were performed using R (R Core Team, 2013).

Statistical analysis

For each metric, we defined hotspots as the top 2.5% of grid cells, following a commonly used method in the geographical assessment of biodiversity (Orme *et al.*, 2005; Ceballos & Ehrlich, 2006; Daru *et al.*, 2015). Relationships among the diversity measures were tested by applying spatial autoregressive models using Moran's *I* statistic to correct for geographical dependence of the variables, computed using SAM v.4.0 software (Rangel *et al.*, 2010).

Complementary sites for SR were selected by choosing the richest cell, and subsequently adding cells based on richness of the unrepresented cells until all species were captured at least once (Vane-Wright *et al.*, 1991). Complementary PD sites were chosen in a similar manner, capturing all branch lengths at least once in as small a subset of sites as possible (Faith *et al.*, 2004).

The performance of the current MPA network was assessed by overlaying hotspots and complementary areas onto GIS base maps of MPAs from the World Database on Protected Areas (IUCN & UNEP-WCMC, 2015); all grid cells included within MPAs were identified. A cell was considered protected when at least 50% of its area was within an MPA.

RESULTS

The SR for both groups of coastal macrophytes is unevenly distributed across the globe, revealing the classic latitudinal gradient with higher richness in the tropics than temperate regions (Fig. S3 in Appendix S1). The central Indo-Pacific region is particularly species rich, with a maximum richness of 22 seagrass and 37 mangrove species per 1° × 1° grid cell (Fig. S3 in Appendix S1).

The five types of hotspots for each aquatic macrophyte showed varying degrees of spatial congruence (Figs S4 & S5 in Appendix S1). Seagrasses shared only 6% (26 out of 430) of hotspot cells among all five metrics (Fig. 1a), and no grid cells were identified by all five diversity metrics as hotspots for mangroves. All diversity measures were positively correlated, but with variation in the strength of the positive relationship ranging from $r = 0.44$ (for CWE versus SR) to 0.99 (PD versus EDGE) in the spatial autoregressive models for seagrasses (Table 1), and from 0.61 for EDGE versus SR, to 0.99 for EDGE versus PD in mangroves (Table 2). Cumulatively, marine macrophytes occurred in 16 hotspots covering 606 grid cells (*c.* 7,500,000 km^2, Fig. 2 and Table S4 in Appendix S1) for all five metrics combined. Separately, seagrass hotspots occupied 5,329,000 km^2 (6.5% of the global distribution of seagrass species; Fig. 3a), while mangrove hotspots covered 2,379,000 km^2 (6% of the total mangrove area; Fig. 3b).

The effectiveness of the current MPA network at representing the hotspots differs between diversity metrics and the two macrophyte groups (Fig. 4). In general, seagrass hotspots and complementary areas are better protected than those of mangroves. For example, whereas hotspots and complementary

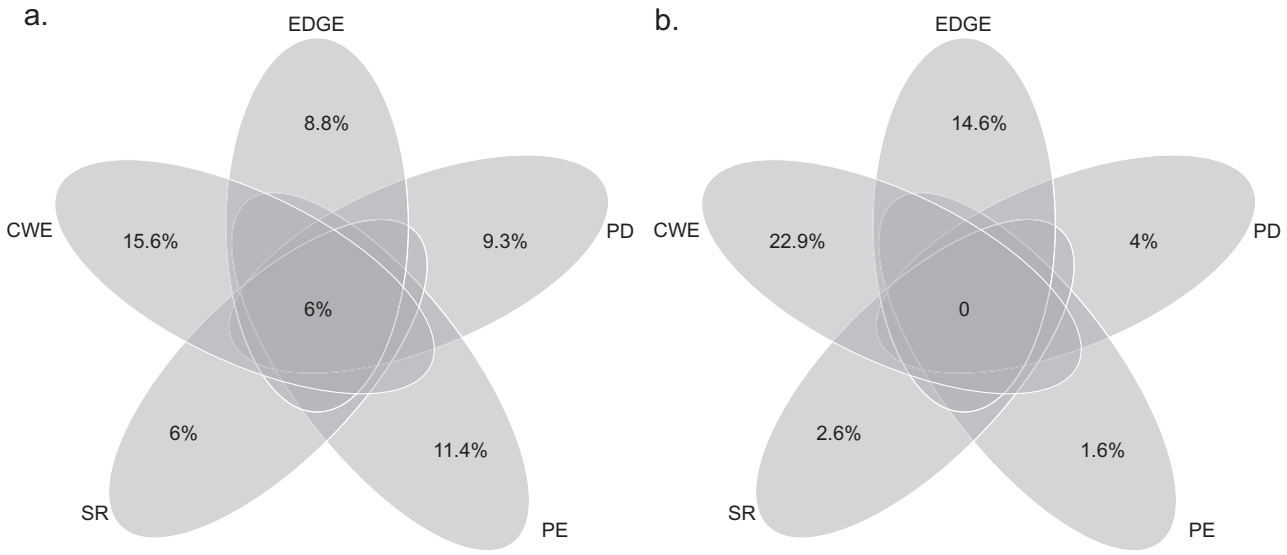

Figure 1 Venn diagram of spatial overlap among five types of hotspots, indicating the proportion of hotspot cells shared by all five metrics and the proportion of hotspot cells unique to each metric: (a) seagrasses, (b) mangroves. SR, species richness; PD, phylogenetic diversity; CWE, corrected weighted endemism; PE, phylogenetic endemism; EDGE, evolutionary distinctiveness and global endangerment. The phylogenetic trees used for computing the evolutionary metrics are derived from BEAST analysis and represent the 50% majority rule consensus tree for mangroves and maximum clade credibility tree for seagrasses.

Table 1 Pairwise correlation of seagrass diversity metrics after accounting for spatial autocorrelation using spatial autoregressive models. The correlation coefficients (r) are indicated.

	PD	CWE	PE	EDGE
SR	0.93**	0.44*	0.65**	0.99**
PD		0.41$^{n.s.}$	0.71**	0.99**
CWE			0.73**	0.42$^{n.s.}$
PE				0.61**

SR, species richness; PD, phylogenetic diversity; CWE, corrected weighted endemism; PE, phylogenetic endemism; EDGE, evolutionary distinctiveness and global endangerment.
**$P < 0.001$; *$P < 0.01$; n.s., $P > 0.05$.

Table 2 Pairwise correlation of mangrove diversity metrics after accounting for spatial autocorrelation using spatial autoregressive models. The correlation coefficients (r) are indicated.

	PD	CWE	PE	EDGE
SR	0.95*	0.89$^{n.s.}$	0.95**	0.61**
PD		0.89$^{n.s.}$	0.95**	0.99**
CWE			0.67**	0.41$^{n.s.}$
PE				0.86**

SR, species richness; PD, phylogenetic diversity; CWE, corrected weighted endemism; PE, phylogenetic endemism; EDGE, evolutionary distinctiveness and global endangerment.
**$P < 0.001$; *$P < 0.01$; n.s., $P > 0.05$.

areas of seagrass diversity measures have protection exceeding 60%, mangrove hotspots of SR, PD and SR complementarity do not have any protection in the current network of MPAs (Fig. 4).

Complementarity analysis of PD and SR showed that all seagrass species could be represented at least once in a selection of 19 grid cells (235,000 km^2; Fig. 5a), and complementary PD in 13 cells (161,000 km^2; Fig. 5b). Complementary SR cells of mangrove species could be represented in five cells (61,000 km^2; Fig. 5c), and all their complementary phylogenetic branch lengths were captured in only three cells (37,000 km^2; Fig. 5d). Several locations are identified repeatedly by these analyses, suggesting their greater conservation priority; for example south-western Australia, north-western America and southern Japan. In all cases, complementary selection of cells performed significantly more efficiently than random selection of sites (Fig. S6 in Appendix S1).

DISCUSSION

Marine plant SR and PD are inadequately protected by current MPAs, a conservation challenge that is aggravated because the different diversity metrics show little spatial congruence. As a result, conserving additional sites might, for example, improve the representation of species within the MPA network but have little benefit for the conservation of evolutionary distinctiveness or PD. However, by incorporating phylogenetic information in hotspot analyses and using complementarity techniques, gaps at the species and phylogenetic levels in the conservation network can be identified and efficiently addressed. Improved conserva-

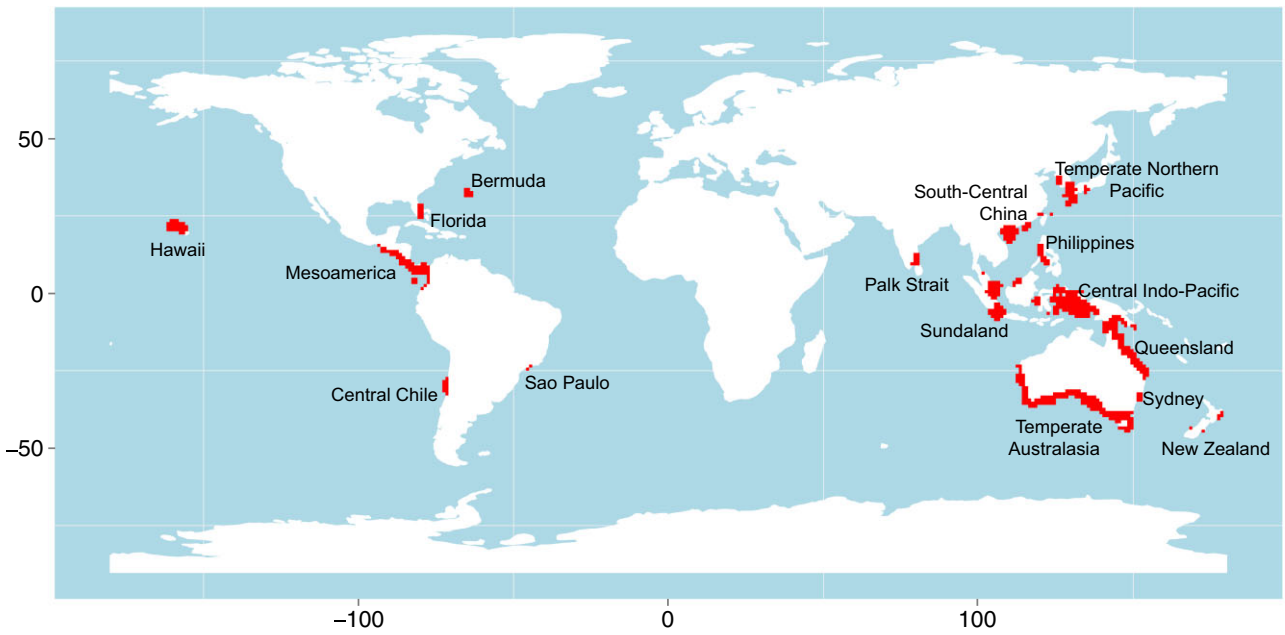

Figure 2 Global marine plant diversity hotspots across 1° × 1° grid cells. The hotspots are the top 2.5% grid cells (dark grey) derived from a combination of five measures of diversity – species richness, phylogenetic diversity, species endemism, phylogenetic endemism and evolutionary distinctiveness and global endangerment – for seagrass and mangrove species combined. The map was generated using the equal Behrmann projection. The phylogenetic trees used for computing the evolutionary metrics are derived from BEAST analysis and represent the 50% majority rule consensus tree for mangroves and maximum clade credibility tree for seagrasses.

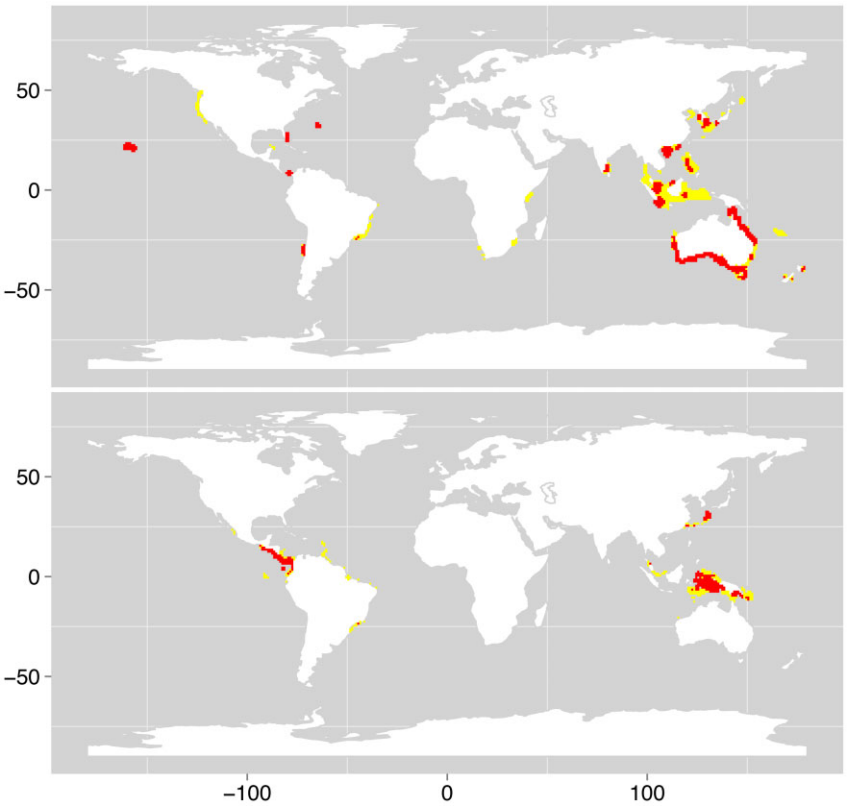

Figure 3 Union map of hotspots across 1° × 1° grid cells, derived from the combination of species richness, phylogenetic endemism, species endemism, phylogenetic endemism and evolutionary distinctiveness and global endangerment: (a) seagrass species (b) mangrove species. The richest 2.5% hotspots cells are shown in red and the 5.0% hotspots in yellow.

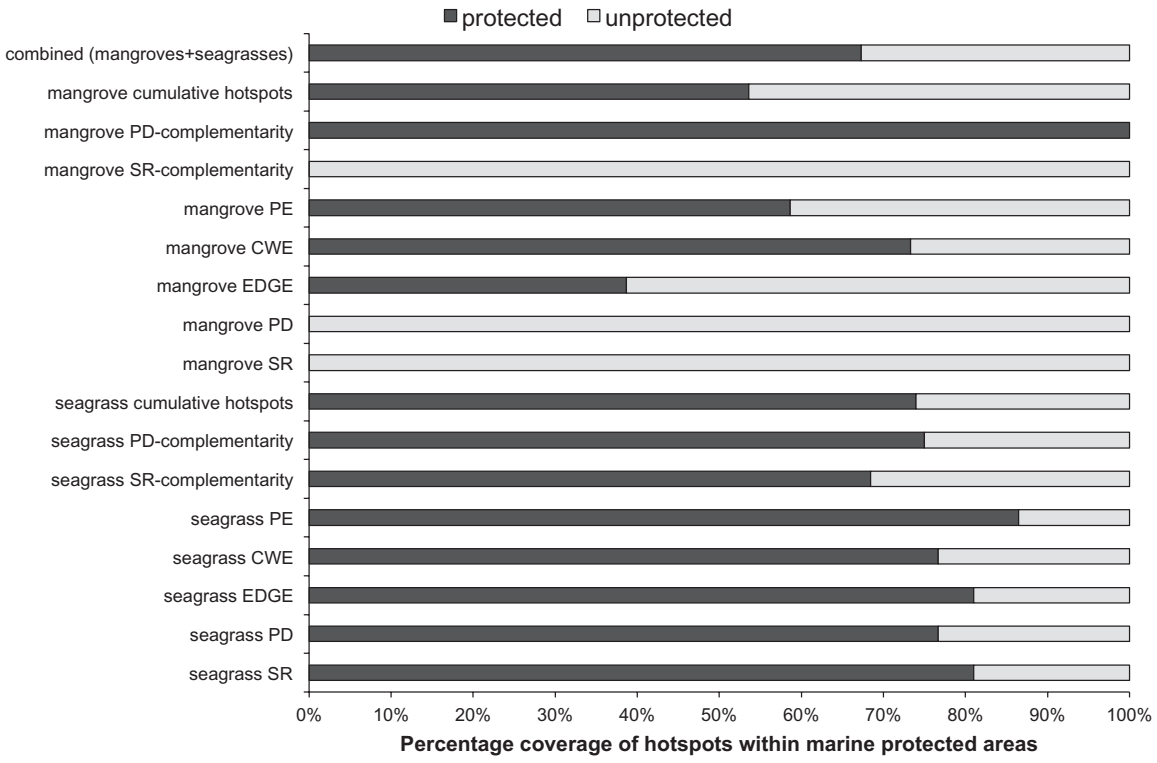

Figure 4 Degree of *in situ* protection of marine plants diversity measures within existing marine protected areas (dark grey represents proportion of hotspot cells represented within marine protected areas). SR, species richness; PD, phylogenetic diversity; CWE, corrected weighted endemism; PE, phylogenetic endemism; EDGE, evolutionary distinctiveness and global endangerment.

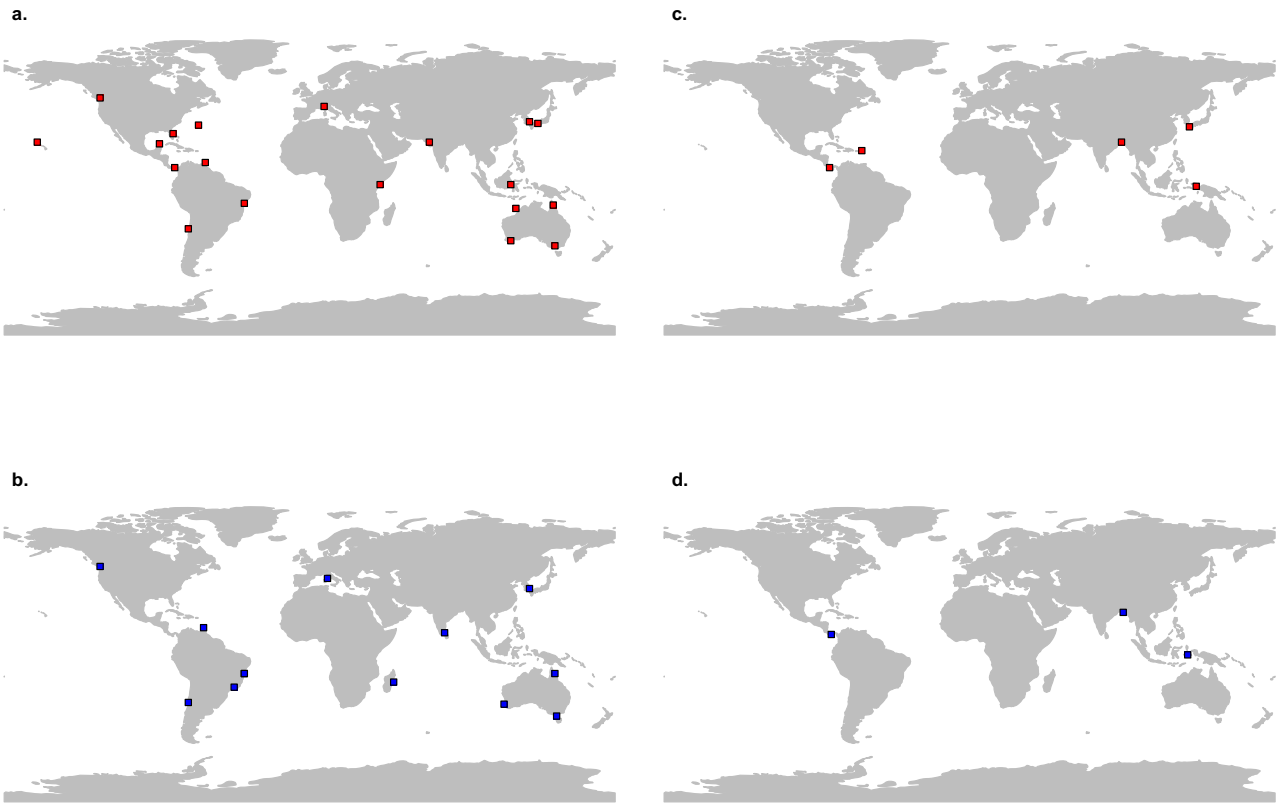

Figure 5 Distribution of complementarity in 1° × 1° grid cells using a greedy algorithm that maximally represents species richness (red cells) and phylogenetic diversity (blue cells) in as few grid cells as possible: (a), (b) seagrasses; (c), (d) mangroves. The phylogenetic trees used for computing the evolutionary metrics are derived from BEAST analysis and represent the 50% majority rule consensus tree for mangroves and maximum clade credibility tree for seagrasses.

tion of these marine plants must be a priority given their keystone roles in the marine realm (Costanza *et al.*, 1997), along with their impacts extending far beyond their spatial extent (e.g. acting as nursery grounds for fish populations, supporting fisheries beyond their geographical boundaries; Beck *et al.*, 2001; Green & Short, 2003).

While PD has been incorporated into terrestrial biodiversity conservation planning (e.g. Jetz *et al.*, 2014; Zupan *et al.*, 2014), this study represents the first integrative application of recently developed diversity metrics in the marine realm. The five diversity measures examined here showed a high degree of spatial incongruence for seagrasses and mangroves, with very few hotspots shared among all (or even most) diversity metrics, reflecting similar patterns to those observed for terrestrial species (e.g. Devictor *et al.*, 2010; Zupan *et al.*, 2014), particularly terrestrial plants (e.g. Daru *et al.*, 2015). Thus, if the conservation goal is the protection of centres of seagrass species endemism, efforts should be focused in Hawaii, central Chile and temperate Australasia. However, these efforts would do little to improve the protection of mangrove species endemism (highest in Mesoamerica) or phylogenetic endemism (focused in the central Indo-Pacific for mangroves and temperate Australasia for seagrasses). Therefore, conservation planning cannot assume that one diversity metric can act as a surrogate for the others, necessitating an integrative approach to maximize protection of both PD and species diversity.

Complementarity methods for PD and SR are efficient in capturing diversity, ensuring maximum representation of all species or branch lengths within the smallest possible area. For instance, mangroves species are completely captured in only five complementary cells (< 1% of mangrove area), and PD in three complementary cells, matching findings from terrestrial systems that careful selection of additional conservation areas can greatly improve the representativeness of conservation networks (e.g. Pollock *et al.*, 2015). Although complementary methods have drawbacks, for example that sites are often distant from existing protected areas, potentially reducing connectivity among reserve networks, representing all species and/or branch lengths in a small area is a pragmatic conservation priority given high rates of loss of coastal marine habitats (Waycott *et al.*, 2009). We therefore propose a two-pronged strategy when selecting protected areas: using complementarity analyses to ensure complete representation in tandem with the identification of hotspot cells that improve the connectivity of conservation areas.

We show that analysing evolutionary diversity (including PD, PE and EDGE) provides additional information about the evolutionary history of taxa and the feature diversity (traits) they

comprise. This information is not adequately captured by species-level metrics (although see Li *et al.*, 2015) and is relevant to policy makers (Laity *et al.*, 2015). Indeed, the conservation of the PD of marine macrophytes maximizes future options (*sensu* Forest *et al.*, 2007), contributing to ensuring the long-term provisioning of ecosystem services (e.g. medicinal compounds for humans and nursery grounds for fisheries). In addition, identifying areas with higher or lower PD than expected could reveal theatres of unusual evolutionary events, highlighting regions of particular conservation value with evolutionarily old or young lineages or centres of speciation (Winter *et al.*, 2013; Laity *et al.*, 2015). Thus, the spatial incongruence observed among the macrophytes evolutionary metrics and species-level metrics illustrates the opportunities available to conservation planners and policy makers to protect both species diversity and PD. While the addition of phylogenetic information into conservation planning may complicate some prioritization decisions (e.g. how to weight PD relative to SR), we believe that the explicit consideration of the evolutionary history (and adaptive potential) of lineages allows for more informed and, potentially, more comprehensive planning.

Our approach identified global conservation priorities for macrophytes, a group that is only incidentally included within MPAs, and has highlighted the need to incorporate other phylogenetic branches of the marine tree of life when designating future MPAs. Specifically, taxa that are abundant and rich in cold waters (as opposed to macrophytes and coral reef species) and with functional traits different from taxa already considered (e.g. benthic and/or decomposer taxa) are likely to provide the most unique data, and should therefore be targeted as a priority for inclusion in subsequent analyses. Because the marine macrophytes examined in this study occur in the coastal regions of the world, our results indicate near-shore conservation priorities. Off-shore conservation planning would also benefit from the consideration of widely distributed taxa using these integrative methods, including marine mammals (Pompa *et al.*, 2011) and lobsters (Williams, 1986).

Our approach incorporates traditional taxonomic metrics such as CWE and SR, along with evolutionary metrics such as PD, PE and EDGE, and offers a powerful means of identifying conservation areas in need of protection which lie outside the existing MPA network. Conservation decision making can be guided by such integrative approach when designing marine reserves to ensure maximum protection of areas of high diversity and a unique evolutionary history.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supporting tables (Table S1–S4) and figures (Figs S1–S6).

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

Figure S2 The 50% majority rule consensus tree of mangrove species obtained from a Bayesian analysis of the combined dataset (*rbcL* + ITS +18S).

Figure S3 Maps of global distribution of species richness for aquatic macrophytes.

Figure S4 Diversity hotspots for five measures of seagrasses diversity.

Figure S5 Diversity hotspots for five measures of mangroves diversity.

Figure S6 Gains in phylogenetic diversity and species richness complementarity.

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

Table S2 Summary of priors and uncorrelated lognormal relaxed molecular clock BEAST analysis of seagrass species.
Table S3 List of mangrove taxa included in phylogeny with GenBank accession numbers.
Table S4 Characteristics of global diversity hotspots of marine plants.

BIOSKETCHES

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