Multifaceted biodiversity hotspots of marine mammals for conservation priorities

Camille Albouy
Valentine L. Delattre
Bastien Merigot
Christine N. Meynard

Virginia Institute of Marine Science

Follow this and additional works at: https://scholarworks.wm.edu/vimsarticles

Part of the Ecology and Evolutionary Biology Commons, and the Environmental Sciences Commons

Recommended Citation
Albouy, Camille; Delattre, Valentine L.; Merigot, Bastien; Meynard, Christine N.; and Leprieur, Fabien, Multifaceted biodiversity hotspots of marine mammals for conservation priorities (2017). Diversity and Distributions, 23(6), 615-626.
DOI: 10.1111/ddi.12556

This Article is brought to you for free and open access by the Virginia Institute of Marine Science at W&M ScholarWorks. It has been accepted for inclusion in VIMS Articles by an authorized administrator of W&M ScholarWorks. For more information, please contact scholarworks@wm.edu.
Multifaceted biodiversity hotspots of marine mammals for conservation priorities

Camille Albouy1,2,3,*  |  Valentine L. Delattre4,*  |  Bastien Mérigot4  |  Christine N. Meynard5,6  |  Fabien Leprieur4

1Swiss Federal Research Institute WSL, Birmensdorf, Switzerland  
2Landscape Ecology, Institute of Terrestrial Ecosystems, ETH Zürich, Zürich, Switzerland  
3IFREMER, Unité Ecologie et Modèles pour l’Halieutique, Nantes Cedex 3, France  
4Université de Montpellier, UMR 9190 MARBEC (CNRS, IFREMER, IRD, UM), Montpellier Cedex 5, France  
5INRA, UMR CBGP (INRA/IRD/Cirad/ Montpellier SupAgro), Campus International de Baillarguet, Montferrier-sur-Lez Cedex, France  
6Virginia Institute of Marine Science, College of William & Mary, Gloucester Point, VA, USA

Correspondence  
Camille Albouy, Swiss Federal Research Institute WSL, Birmensdorf, Switzerland.  
Email: albouycamille@gmail.com  
and  
Fabien Leprieur, Université de Montpellier, UMR 9190 MARBEC (CNRS, IFREMER, IRD, UM), Montpellier Cedex 5, France.  
Email: fabien.leprieur@umontpellier.fr

Abstract

Aim: Identifying the multifaceted biodiversity hotspots for marine mammals and their spatial overlap with human threats at the global scale. 

Location: World-wide. 

Methods: We compiled a functional trait database for 121 species of marine mammals characterized by 14 functional traits grouped into five categories. We estimated marine mammal species richness (SR) as well as functional (FD) and phylogenetic diversity (PD) per grid cell (1° × 1°) using the FRic index (a measure of trait diversity as the volume of functional space occupied by the species present in an assemblage) and the PD index (the amount of evolutionary history represented by a set of species), respectively. Finally, we assessed the spatial congruence of these three facets of biodiversity hotspots (defined as 2.5% and 5% of the highest values of SR, FD and PD) with human threats at the global scale.

Results: We showed that the FRic index was weakly correlated with both SR and the PD index. Specifically, SR and FRic displayed a triangular relationship, that is, increasing variability in FRic along the species richness gradient. We also observed a striking lack of spatial congruence (<0.1%) between current human threats and the distribution of the multiple facets of biodiversity hotspots.

Main Conclusions: We highlighted that functional diversity calculated using the FRic index is weakly associated with the species richness of marine mammals worldwide. This is one of the most endangered vertebrate groups playing a key ecological role in marine ecosystems. This finding calls for caution when using only species richness as a benchmark for defining marine mammal biodiversity hotspots. The very low level of spatial congruence between hotspots of current threats and those of the multiple facets of marine mammal biodiversity suggests that current biodiversity patterns for this group have already been greatly affected by their history of exploitation.

Keywords  
conservation, functional diversity, marine mammals, phylogenetic diversity
1 | INTRODUCTION

Preventing biodiversity loss under growing anthropogenic pressure is one of the greatest challenges in ecology and conservation biology. Overfishing, bycatch and habitat degradation or loss (e.g., competition with fisheries, pollution and climate change) have caused great declines in marine mammals, 37% of which are currently threatened (Davidson et al., 2012; Schipper et al., 2008). Furthermore, marine mammals play key ecological roles in marine ecosystems world-wide (e.g., Bowen, 1997; Perrin, Wursig, & Thewissen, 2002; Roman & McCarthy, 2010). Because of their large body size (Pauly, Trites, Capuli, & Christensen, 1998) and their major role as production consumers at most trophic levels, marine mammals are often thought of as having a large influence on community structure and composition and on nutrient storage and recycling, among others (Bowen, 1997; Estes et al., 2011). For instance, in south-west Alaska, the decline in populations of sea otters and pinnipeds and the resulting diminution of the kelp ecosystem could be attributed to the increasing number of transient killer whales that shift their diet to smaller prey items (Estes, Doak, Springer, & Williams, 2009; Estes & Duggins, 1995). Their extinction or even their population decay could therefore lead to irreversible consequences for ecosystem functioning (Estes et al., 2011; Heithaus, Frid, Wirsing, & Worm, 2008). To prevent major extinctions, effective conservation efforts (e.g., marine spatial planning) require knowledge of the spatial distribution of the main biodiversity facets (Devictor et al., 2010; Mouillot et al., 2011; Stuart-Smith et al., 2013), particularly in the high seas, where monitoring is difficult and where data gaps obstruct conventional management approaches (Ardron, Gjerde, Pullen, & Tilott, 2008).

While species richness (SR) has often been the focus of many macroecological studies, a recent interest in the multiple facets of biodiversity has introduced the need to consider phylogenetic and functional facets (Devictor et al., 2010; Mouillot et al., 2011; Stuart-Smith et al., 2013). Phylogenetic diversity (PD) reflects the evolutionary history within a given community and provides additional value to theoretical and applied ecology (Schweiger, Klotz, Durka, & Kühn, 2008). Functional diversity (FD) characterizes the value and range of organismal traits that influence their performance and thus ecosystem functioning (Diaz & Cabido, 2001; Violle et al., 2007). It is therefore critical to know how PD and FD are distributed across the globe for key ecosystem facets, such as marine mammals, if we are aiming to more efficiently protect communities and ecosystems rather than just individual species. Indeed, modification (decline or loss) of the abundance of species presenting distinctive traits or distinctive evolutionary histories may markedly affect community structure and ecosystem functioning (Cadotte, Cardinale, & Oakley, 2008). For example, the amount of PD within a community has been related to ecosystem properties such as productivity (Cadotte et al., 2008) or stability (Cadotte et al., 2010). Some have argued that it is FD, rather than SR, that enhances ecosystem functions such as productivity (Gagic et al., 2015; Hooper & Dukes, 2004; Mokany, Ash, & Roxburgh, 2008; Petchey, Hector, & Gaston, 2004; Tilman et al., 1997), resilience to perturbations or invasion (Bellwood, Hughes, Folke, & Nyström, 2004; Dukes, 2001) and regulation of the flux of matter (Waldbusser, Marinelli, Whitlatch, & Visscher, 2004). FD is therefore a relevant diversity facet to implement conservation priorities towards for an integrated approach to biodiversity conservation (Cadotte, Carscadden, & Miroutchick, 2011; Devictor et al., 2010; Mouillot et al., 2011; Stuart-Smith et al., 2013).

Measuring SR, PD and FD together as complementary biodiversity components is thus necessary to better assess and understand the structure, composition and dynamics of natural communities (D’agata et al., 2014; Maherali & Klironomos, 2007; Webb, Ackerly, McPeek, & Donoghue, 2002). Whereas SR and PD have been recognized as major components of marine mammal biodiversity (Pompa, Ehrlich, & Ceballos, 2011; Schipper et al., 2008), FD has not yet been considered. Exploring spatial patterns of FD for marine mammals world-wide is therefore urgently needed to (1) assess whether the restrictive use of SR and PD is sufficient for conservation prioritization in marine mammals, (2) identify multicomponent biodiversity hotspots of marine mammals at a global scale, and (3) assess their spatial overlap with human threats.

Here, we provided a comprehensive assessment of the spatial overlap among all the facets of marine mammal biodiversity (2.5% of the highest SR, FD and PD index values) as well as with human threats at the global scale. To accomplish this goal, we compiled a functional trait database for 121 species of marine mammals involving pinnipeds, sirensians, cetaceans and two species of otters (see Appendix S1) and representing 94% of the known global SR of marine mammals. Our database consisted of 14 functional traits grouped into five categories (i.e., feeding, habitat, reproduction, social behaviour and biology). Mapping the geographic distribution of marine mammals onto a 1° × 1° grid, we estimated the SR per grid cell and quantified FD as the volume of functional space occupied by the species present in a given grid cell (Villeger, Mason, & Mouillot, 2008). FD represents the extent of the functional differences among species based on the distinction of their morphological, physiological and ecological traits (Petchey & Gaston, 2006). We also calculated PD as the amount of evolutionary history represented by a set of species (Faith, 1992) using a phylogenetic supertree of mammals (Fritz, Bininda-Emond, & Purvis, 2009).

2 | METHODS

2.1 | Database

We compiled geographic range maps from the IUCN database (http://www.iucnredlist.org) for 128 species. We then established a presence/absence matrix and derived SR by overlapping the geographic ranges and counting how many species occur in each grid cell (1° × 1° grid cells, ~10,000 km²). We built a functional trait database for 121 marine mammal species for which we had sufficient data (i.e., only seven species were not considered from the initial IUCN database). The data covered five functions of marine mammals (i.e., biology, feeding, reproduction, habitat and social behaviour) reflecting trade-offs in resource allocation. Our database included the following 14 functional quantitative and qualitative traits: main diet (zooplankton, invertebrates, high vertebrates, fish, squid, seagrass), foraging depth range (epipelagic,
mesopelagic, benthic, all depths), foraging location (continental shelf, continental shelf and slope, continental slope, offshore, any distance to shore), fasting strategy (presence, absence), female sexual maturity, weaning, gestation length, inter-litter interval, breeding site (ice and/or land, coastal water, oceanic water), social group size, social behaviour (mostly social, social and solitary, mostly solitary), terrestriality (yes/no), adult maximum body mass and sexual dimorphism (none, moderate, strong; Table 1). These variables reflected the behaviour, life-history biology and ecology of marine mammals and were used for their intrinsic value or as a proxy of hard-to-measure traits (Lavorel & Garnier, 2002). Data were gathered from a survey of the scientific literature, reliable encyclopaedic websites and books, and extant databases (see Appendix S1). Except for the adult maximum body mass, the reported values for the quantitative traits reflect the average of the entire population studied for each species. However, when a single value for the maximum body mass was not available and we had a range of maximum body mass values, the mean maximum body mass was used instead. For this latter trait, missing
values were extrapolated from data on the maximum body length using an allometric relationship. More precise information on functional traits and their modalities used in this study is available in Appendices S1 and S2.

2.2 | Species richness and functional and phylogenetic diversity

SR was estimated as the number of species of marine mammals found in a given cell in a 1° × 1° grid. PD was measured from a phylogenetic supertree of mammals (Fritz et al., 2009) using the PD index (Faith, 1992), which represents the minimum total length of all the phylogenetic branches required to span a given set of species on the phylogenetic tree (Faith, 1992). FD was quantified using a functional richness index (FRic; Villeger et al., 2008). The FRic index relies on a multidimensional Euclidean space, where the axes are functional traits (or factorial axes from a principal coordinates analysis (PCoA) computed using these traits) along which species are placed according to their trait values (Mouillot, Graham, Villéger, Mason, & Bellwood, 2013). This index measures the volume of functional space occupied by a given species assemblage by calculating the convex hull volume, defined by the species at the vertices of the functional space, that encompasses the entire trait space filled by all species in this assemblage (Villeger et al., 2008). We preferred to use the FRic index instead of the well-known FD index based on a functional dendrogram (Petchey & Gaston, 2006), as a recent study showed that the FD index may lead to a biased assessment of functional diversity and inaccurate ecological conclusions (Maire, Grenouillet, Brosse, & Villéger, 2015). We computed the pairwise functional distances between species using the Gower dissimilarity index to build the functional space. This distance allows mixing different types of variables while weighting functional traits in order to give equal weight to each function (i.e., biology (feeding, habitat), reproduction, social behaviour; Legendre & Legendre, 1998). Then, a PCoA was performed using this distance matrix to build a multidimensional functional space (Legendre & Legendre, 1998). According to the 2-norm, which quantifies the proximity between two matrices (Mérigot, Durbec, & Gaertner, 2010), we kept the first four principal axes of this PCoA. As the FRic index can only be applied to communities containing at least one more species than the number of axes in the PCoA (Villeger et al., 2008), we did not consider cells in which only five or fewer species occurred (mostly located in the Arctic region). We expressed the FRic index for each assemblage as the percentage of the total functional space filled by all the marine mammals. We did the same with the PD index by dividing the total sum of branch lengths for each assemblage by the total sum of branch lengths for the global pool of species.

2.3 | Human threats

To characterize the congruence between human threats and marine mammal biodiversity facets, we used the global map of marine impact. This map, provided by Halpern et al. (2008), was obtained by listing 38 categories of anthropogenic drivers of change in marine ecosystems based on expert judgment. They limited their analyses to anthropogenic drivers with global coverage or those for which they could develop global coverage. As a consequence, they excluded many regional-scale and incomplete data. They quantified the vulnerability (Halpern et al., 2008) of 20 distinct marine ecosystems to 17 anthropogenic drivers of ecological change such as fishing, shipping or climate change. Finally, they created the cumulative impact map by overlaying the anthropogenic drivers’ maps onto the ecosystems and using the vulnerability scores to translate the threats into a metric of ecological impact. The global map by Halpern et al. (2008) was re-projected to fit with our 1° × 1° species richness grid.

2.4 | Spatial congruence analysis

To map the spatial congruence between all marine mammal biodiversity facets and human threats, we performed an analysis of the spatial overlap between hotspots (Mouillot et al., 2011), focusing on pairwise hotspot comparisons. This analysis allows the identification of whether two biodiversity facets present similar spatial repartition of high values, which is not straightforward using a correlation coefficient that only evaluates the degree of dispersion between two quantitative variables. We defined as hotspots all grid cells with values in the upper 2.5% and 5% of the biodiversity facet and human threat value distributions. For example, for a pairwise comparison between SR and FRic, we calculated the observed number of overlaps, which corresponds to the number of cells recorded as a hotspot for SR and the FRic index, expressed as percentage. Then, we evaluated the expected number of overlaps, Oe, corresponding to the independence between the SR and FRic hotspots. Oe was calculated as follows: 

\[ O_e = N_i \times N_j / N \]

where Ni is the number of hotspots for SR, Nj is the number of hotspots for FRic and N is the total number of grid cells.

We then conducted a randomization procedure to assess whether the observed number of overlaps (Oe) is significantly different from that obtained by chance (O*). The values contained in the cells for one of the two variables considered were randomly permuted 999 times, and the number of overlaps was estimated for each. All index calculations, statistical analyses and graphical representations were performed with R statistical software (R Core Team, 2015) using the cluster, ade4, stats, clue and vegan packages.

3 | RESULTS

Our results showed that SR was concentrated in temperate and tropical coastal waters, particularly along the coasts of the western USA, Peru, Argentina, South Africa, eastern Japan, New Zealand and southeastern Australia (i.e., more than 30 species per cell, see Figure 1a). These areas were also characterized by high levels of PD (Figure 1b), as shown by (1) the significant and positive relationship between SR and PD (Spearman’s correlation test: \( r_s = .669; \ p < .001 \), Figure 2a), and (2) the overall spatial congruence between the hotspots of SR and PD (Figure 3a and Appendix S3).

High levels of FRic were found along the western coasts of North America (i.e., from Alaska to California) and Peru (Figure 1c) as well as...
FRIC was found to be weakly correlated with SR (Spearman’s correlation test: \( r_s = .179; p < .001, \) Figure 2b), with these two biodiversity facets displaying a triangular relationship, that is, increasing variability in FRIC values along the SR gradient (Figure 2b). Indeed, both high and low values of FRIC were found in hotspots of SR, explaining the weak spatial congruence between hotspots of SR and FRIC (Figure 3b). For instance, the coastal areas of California, South Africa and south-eastern Australia displayed rather similar SR values (34, 38 and 34 species, respectively, Figure 1a) while showing varying levels of FRIC (Figure 1c). The species assemblage of south-eastern Australia only occupied 10% of the global functional volume of marine mammals, whereas the species assemblage of California filled 56% of the global functional volume (Figure 4). The California hotspot indeed hosted several species with rare combinations of traits, that is, pinnipeds (northern fur seal (C. ursinus), Guadalupe fur seal (A. townsendi), harbour seal (P. vitulina), Californian sea lion (Z. californianus) and northern elephant seal (M. angustirostris)), baleen whales (Bryde’s whale (B. edeni), humpback whale (M. novaeangliae), fin whale (B. physalus) and blue whale (B. musculus)) and other cetacean species (short-finned pilot whale (G. macrorhynchus), Indo-Pacific beaked whale (I. pacificus), melon-headed whale (P. electra) and northern right whale dolphin (L. borealis)). South Africa appears to be a hotspot of SR but with low values of FRIC, which can be related to the occurrence of only one pinniped species, the brown fur seal (A. pusillus).

Functional richness index and PD showed a stronger positive relationship (Spearman’s correlation test: \( r_s = .565; p < .001, \) Figure 2c), but these two biodiversity facets also displayed a triangular relationship, that is, increasing variability of FRIC values along the PD gradient. This explains the weak spatial congruence between the hotspots of PD and FRIC (Figure 3c and Appendix S3). Overall, multifaceted hotspots (congruence areas among SR, PD and FRIC) of marine mammal biodiversity only covered small areas in California, Japan and South America (Figure 5). We identified only 0.5% and 0.8% common
FIGURE 2 Plot showing the relationships among species richness (SR), phylogenetic diversity (PD index) and functional richness (FRic index). The red line is a smooth curve computed by the loess method. [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 3 Maps showing hotspot (i.e., the highest 2.5% values) congruence between (a) functional richness (FRic index) and species richness (SR), (b) FRic index and PD index, and (c) SR and PD index. [Colour figure can be viewed at wileyonlinelibrary.com]
grid cells among the three biodiversity facets for the 2.5 and 5% highest values, respectively (see Figure 5). These areas weakly corresponded to the threat hotspots (see Figure 6a–c as well as Appendix S4, 0.03% and 0.07% for the 2.5 and 5% highest values, respectively). This spatial matching occurred along the Pacific Japanese coast and in the Magellan Strait between the Falkland Islands and the Argentina coast (see Appendix S5). We identified 0.1%, 0.19% and 0.21% common grid cells between human threats and PD, FRic and SR, respectively, for 2.5% of the highest values. For 5% of the highest values, the percentages of common grid cells between human threats and each biodiversity facet reached the values of 0.31% (PD), 0.3% (FRic) and 0.61% (SR).

**FIGURE 4** Functional diversity as measured by the FRic index for coastal regions of (a) California (USA), (b) South Africa and (c) South America. FRic values are, respectively, 56%, 23.3% and 10.9%, and the assemblages contain, respectively, 34, 38 and 34 species. Below each map, the projection of species in multidimensional space (PCoA) in terms of axis 1/2 (first column), 2/3 (second column) and 3/4 (third column) is shown. The grey polygon represents the functional volume of the global species pool, while yellow polygons stand for specific regional assemblages. Filled black circles represent the species of the global pool shaping the functional convex hull. Open circles represent species within each regional assemblage and are hence useful for an overview of functional dispersion. [Colour figure can be viewed at wileyonlinelibrary.com]
DISCUSSION

The spatial patterns in the species richness of marine mammals are consistent with those reported in Schipper et al. (2008) based on the same IUCN data, who suggested that the number of marine mammals might be associated with primary productivity. Indeed, the SR peaks at approximately 40° N and S, corresponding to belts of high oceanic productivity (Field, Behrenfeld, Randerson, & Falkowski, 1998) and coastal areas corresponding to upwelling systems. The low SR in the highly productive North Atlantic Ocean (Field et al., 1998) contradicts this hypothesis, but it could reflect historical anthropogenic depletion of SR in that region (Storå & Ericson, 2004). The high correlation between SR and PD was expected because of the richness dependence of the PD index used here, defined as the sum of all branches on the phylogenetic tree that span a given assemblage of species (Faith, 1992). The observed triangular relationship between SR and FRic (see Figure 2) suggests that the higher the SR within an assemblage, the more variable, and thus unpredictable, the FD. Indeed, two communities containing the same number of species can have very different levels of FD depending on the functional redundancy of the co-occurring species.

As FD and SR were weakly related, the latter cannot be used effectively as a proxy for functional diversity in a conservation framework. However, the correlation between FD and PD still leaves much room for error if SR is used as a proxy for conservation purposes. Proof of this is the little spatial overlap between PD and FD hotspots (Figure 3). Subsequently, unexpectedly low FD compared to PD is predicted when species are more functionally similar than expected given their phylogenetic divergence (Safi et al., 2011). This may indicate that species are “packed” in the functional niche space due to a suite of potentially non-mutually exclusive processes such as environmental filtering and relaxed competition (Safi et al., 2011). A good way to quantitatively assess whether functional (and phylogenetic) diversity is greater or lower than expected based on the species richness would be the use of null models or regression techniques (Winter, Devictor, & Schweiger, 2013). For instance, South Africa harbours numerous and phylogenetically distant species but presents low FRic index values due to the high functional redundancy of the component species and the scarce occurrence of pinnipeds in temperate and tropical regions (Pompa et al., 2011). Functional redundancy may help communities cope with disturbances by allowing them to bounce back to pre-existing levels following a given ecosystem process, therefore providing insurance for ecosystem resilience (Brookes, Aldridge, Wallace, Linden, & Ganf, 2005; Rosenfeld, 2002; Tilman, 1996). When perturbations cause local species extinctions, ecosystem processes would be maintained by species that are functionally similar but differ in their responses to changes in environmental factors or disturbances (Elmqvist et al., 2003; Naeem, 1998; Walker, 1992; Yachi & Loreau, 1999). However, this also means that some functional groups are not represented in these areas. On the other hand, the Californian assemblage presents higher FRic values but might be less functionally redundant and therefore might have lower resilience to ecosystem perturbations, which should be taken into account for future conservation actions.

Our results also showed a striking lack of spatial congruence between hotspots of current threats and those of the multiple facets of marine mammal biodiversity (Figure 5). One possible explanation is that the current patterns of marine mammal biodiversity have already been greatly affected by their history of exploitation (Reynolds, Marsh, & Ragen, 2009). Indeed, threats are concentrated in the North Atlantic and in the Pacific Ocean around Japan, both regions that have historically been known for their whaling and fishing. Some recent modeling efforts encompassing both current occurrence records as well as historical and fossil data have suggested that this exploitation history has had large consequences on species distributions and may significantly bias our perception of baseline expectations for conservation purposes (Monsarrat et al., 2015).

As the League of Nations recognized that whales were overexploited and that there was a need to regulate whaling activities in 1925, many actions have been conducted to protect marine mammals (e.g., the Marine Mammal Protection Act of 1972 amended by the United States Congress). Nevertheless, conservation actions have not been fully investigated for this threatened group. For instance, the most effective solution for protecting marine mammals is the establishment...
of marine-protected areas (MPAs, see Gormley et al., 2012). There are many MPAs around the globe, but their effectiveness in securing the function and evolutionary history of marine mammals is still difficult to demonstrate (but see Mouillot et al., 2016 for corals and fishes), and they are difficult to implement in the open ocean. Currently, few conservation solutions have been proposed for marine mammals at a global scale (see Pompa et al., 2011) and these solutions have never integrated a systematic approach in conservation planning (e.g., Sobral et al., 2014) by accounting for the multiple facets of biodiversity and species abundance. Furthermore, these propositions have not begun by analysing the already installed MPA system or proposed a solution to optimize it. Moreover, these solutions have been based on range maps, which are not appropriate for conservation planning in the same way in terrestrial and marine environments (Williams et al., 2014) and may inadvertently lead to protecting largely marginal habitat. Indeed, as Williams et al. (2014) showed, range maps assume uniform distributions and therefore oversimplify the spatial variability in species distributions and abundance.

In addition to these drawbacks, the conservation of marine mammals imposes a number of challenges. Numerous marine mammals are indeed wide-ranging species, spanning several degrees of latitude, multiple countries and even across hemispheres (e.g., the blue whale (*Balaenoptera musculus*), which covers both the Northern and Southern Hemispheres). In such large areas for both coastal and open ocean areas, economic activities and environmental threats will vary significantly, and species are therefore not equally vulnerable throughout their ranges. These features of the marine mammal life cycle imply that no system of MPAs is able to protect them across their entire spatial range (Hoyt, 2005). Future conservation planning suggestions should therefore identify which part of the species range is crucial to protect, such as feeding, calving, breeding areas and migration routes (Game et al., 2009), and once these areas are identified, the protection strategy needs to be implemented in consultation with several countries. Many marine mammal species migrate and have feeding grounds that are distant from their calving grounds, and they must therefore be protected during migration. Establishing protection

---

**FIGURE 6** Maps showing hotspot (i.e., the highest 2.5% values) congruence between (a) threats (cumulative human threats extracted from Halpern et al., 2008) and SR, (b) threats and PD index, and (c) threats and FRic index. [Colour figure can be viewed at wileyonlinelibrary.com]
corridors and pelagic MPAs seems to be a way forward even if it may require the design of very large MPAs, which may make the monitoring and management of such areas difficult (Pendoley, Schofield, Whittuck, Ierodiaconou, & Hays, 2014). Overall, to produce a realistic conservation plan for marine mammals at large spatial scales, this plan should be based on the existing MPAs system, which needs to be extended by including appropriate pelagic areas and connecting them through corridors.

To conclude, this study provides new insights into the functional and phylogenetic diversity facets of marine mammals, which is a prerequisite when establishing conservation area networks (e.g., Plo et al., 2011; Tucker, Cadotte, Davies, & Rebelo, 2012). Species are not all equivalent, with some clades carrying more evolutionary history or performing more singular functions in the ecosystem than others (e.g., Guilhaumon et al., 2015). To implement a conservation plan at a global scale, it is essential to evaluate the effectiveness with which protected areas cover the multiple facets of marine mammal biodiversity (e.g., Sobral et al., 2014).

ACKNOWLEDGEMENTS

CA was supported by an MELS-FQRNT Postdoctoral Fellowship during the conception and writing of this manuscript. This work was funded by the French National Research Agency (ANR MORSE (CEP&S 2011-Project ANR-11-CERP-006)). We thank Sebastien Villeger for these constructive comments on the MS.

AUTHOR CONTRIBUTIONS

All the authors contributed to the design of the study; V.D. compiled all the data; C.A., V.D. and F.L. conducted the analyses; C.A. made the figures; and C.A., V.D. and F.L. wrote the first draft with substantial input from B.M. and C.M.

REFERENCES

Ardron, J., Gjerde, K., Pullen, S., & Tilot, V. (2008). Marine spatial planning in the high seas. Marine Policy, 32, 832–839.
Bellwood, D. R., Hughes, T. P., Folke, C., & Nyström, M. (2004). Confronting the coral reef crisis. Nature, 429, 827–833.
Bowen, W. D. (1997). Role of marine mammals in aquatic ecosystems. Marine Ecology Progress Series, 158, 267–274.
Brookes, J., Aldridge, K., Wallace, T., Linden, L., & Ganf, G. (2005). Multiple interception pathways for resource utilisation and increased ecosystem resilience. Hydrobiologia, 552, 135–146.
Cadotte, M. W., Cardinale, B. J., & Oakley, T. H. (2008). Evolutionary history and the effect of biodiversity on plant productivity. Proceedings of the National Academy of Sciences of the United States of America, 105, 17012–17017.
Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology, 48, 1079–1087.
Cadotte, M. W., Jonathan Davies, T., Regetz, J., Kembel, S. W., Cleland, E., & Oakley, T. H. (2010). Phylogenetic diversity metrics for ecological communities: Integrating species richness, abundance and evolutionary history. Ecology Letters, 13, 96–105.
D’agata, S., Mouillot, D., Kulbicki, M., Andréfouët, S., Bellwood, D. R., Cinner, J. E., … Vigliola, L. (2014). Human-mediated loss of phylogenetic and functional diversity in coral reef fishes. Current Biology, 24, 555–560.
Davidson, A. D., Boyer, A. G., Kim, H., Pompa-Mansilla, S., Hamilton, M. J., Costa, D. P., … Brown, J. H. (2012). Drivers and hotspots of extinction risk in marine mammals. Proceedings of the National Academy of Sciences of the United States of America, 109, 3395–3400.
Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., & Mouquet, N. (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: ‘The need for integrative conservation strategies in a changing world. Ecology Letters, 13, 1030–1040.
Diaz, S., & Cabido, M. (2001). Vive la différence: Plant functional diversity and the maintenance of ecological processes and services. Functional diversity and the maintenance of ecological processes and services. 48, 1079–1087.
Duke, J. S. (2001). Oikos Productivity and complementarity in grassland microcosms of varying diversity. Oikos, 94, 468–480.
Elmqvist, T., Folke, C., Nystrom, M., Peterson, G., Bengtsson, J., Walker, B., & Norberg, J. (2003). Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment, 1, 488–494.
Estes, J. A., Doak, D. F., Springer, A. M., & Williams, T. M. (2009). Causes and consequences of marine mammal population declines in southwest Alaska: A food-web perspective. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 364, 1647–1658.
Estes, J. A., & Duggins, D. O. (1995). Sea otters and kelp forests in Alaska: Generality and variation in a community ecological paradigm. Ecological Monographs, 65, 75–100.
Estes, J. A., Terborgh, J., Brashears, J. S., Power, M. E., Berger, J., Bond, W. J., … Wardle, D. A. (2011). Trophic downgrading of planet Earth. Science, 333, 301–306.
Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. Biological Conservation, 61, 1–10.
Field, C. B., Behrenfeld, M. J., Randerson, J. T., & Falkowski, P. (1998). Primary production of the biosphere: Integrating terrestrial and oceanic components. Science, 281, 237–240.
Fritz, S. A., Bininda-Emonds, O. R. P., & Purvis, A. (2009). Geographical variation in predictors of mammalian extinction risk: Big is bad, but only in the tropics. Ecology Letters, 12, 538–549.
Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., … Bommaroco, R. (2015). Functional identity and diversity predict ecosystem functioning better than species-based indices. Proceedings of the Royal Society of London B: Biological Sciences, 282, 2014–2062.
Gane, E. T., Grantham, H. S., Hobday, A. J., Pressley, R. L., Lombard, A. T., Beckley, L. E., … Richardson, A. J. (2009). Pelagic protected areas: The missing dimension in ocean conservation. Trends in Ecology & Evolution, 24, 360–369.
Gormley, A. M., Slooten, E., Dawson, S., Barker, R. J., Rayment, W., du Fresne, S., & Bräger, S. (2012). First evidence that marine protected areas can work for marine mammals. Journal of Applied Ecology, 49(2), 474–480.
Guilhaumon, F., Albouy, C., Claudet, J., Velez, L., Ben Rais Lasram, F., Tomasinia, J. A., Mouillot, D. (2015). Representing taxonomic, phylogenetic, and functional diversity: New challenges for Mediterranean marine protected area. Diversity and Distribution, 21, 175–187.
Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., Agosta, C., … Watson, R. (2008). A global map of human impact on marine ecosystems. Science, 319, 948–952.
Heithaus, M. R., Frid, A., Wirsing, A. J., & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. Trends in Ecology and Evolution, 23, 202–210.
Hooper, D. U., & Dukes, J. S. (2004). Overyielding among plant functional groups in a long-term experiment. Ecology Letters, 7, 95–105.
Hoyt, E. (2005). Marine protected areas for whales, dolphins, and porpoises: A world handbook for cetacean habitat conservation. New York, NY: Eatthescan.
Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. Functional Ecology, 16, 545–556.

Legendre, P., & Legendre, L. (1998). Numerical ecology, 2nd English edition. 853 pp. Developments in Environmental Modelling, 20. New York, NY: Elsevier.

Maherali, H., & Klironomos, J. N. (2007). Influence of phylogeny on fungal community assembly and ecosystem functioning. Science, 316, 1746–1748.

Maire, E., Grenouillet, G., Brosse, S., & Villeger, S. (2015). How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. Global Ecology and Biogeography, 24, 728–740.

Mérigot, B., Durbec, J.-P., & Gaertner, J.-C. (2010). On goodness-of-fit measure for dendrogram-based analyses. Ecology, 91, 1850–1859.

Mokany, K., Ash, J., & Roxburgh, S. (2008). Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. Journal of Ecology, 96, 884–893.

Monsarrat, S., Pennino, D. G., Smith, T. D., Reeves, R. T., Meynard, C. N., Kaplan, D. M., & Rodrigues, A. S. L. (2015). Historical summer distribution of the endangered North Atlantic right whale (Eubalaena glacialis): A hypothesis based on environmental preferences of a congeneric species. Diversity and Distributions, 21, 925–937.

Mouillot, D., Albouy, C., Guilhaumon, F., Ben Rais Lasram, F., Coll, M., Devictor, V., ... Mouquet, N. (2011). Protected and threatened components of fish biodiversity in the Mediterranean sea. Current Biology: CB, 21, 1044–1050.

Mouillot, D., Graham, N. A. J., Villeger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. Trends in Ecology & Evolution, 28, 167–177.

Mouillot, D., Parraïvici, V., Bellwood, D. R., Leprieur, F., Huang, D., Cowman, P. F., ... Guilhaumon, F. (2016). Global marine protected areas do not secure the evolutionary history of tropical corals and fishes. Nature Communications, 7, 10359.

Naeem, S. (1998). Species redundancy and ecosystem reliability. Conservation Biology, 12, 39–45.

Pauly, D., Trites, A. W., Capuli, E., & Christensen, V. (1998). Diet composition and trophic levels of marine mammals. ICES Journal of Marine Science, 55, 467–481.

Pendoley, K. L., Schofield, G., Whittick, P. A., Ierodiaconou, D., & Hays, G. C. (2014). Protected species use of a coastal marine migratory corridor connecting marine protected areas. Marine Biology, 161, 1455–1466.

Perrin, W. F., Würsig, B., & Thewissen, J. G. M. (2002). Encyclopedia of marine mammals. San Diego: Academic Press.

Petchey, O. L., & Gaston, K. J. (2006). Functional diversity: Back to basics Encyclopedia of marine biology. San Diego: Academic Press.

Pompa, S., Ehrlich, P. R., & Ceballos, G. (2011). Global distribution and conservation of marine mammals. Proceedings of the National Academy of Sciences of the United States of America, 108, 13600–13605.

R Development Core Team (2015). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reynolds, J., Marsh, H., & Ragen, T. (2009). Marine mammal conservation. Endangered Species Research, 7, 23–28.

Roman, J., & McCarthy, J. J. (2010). The Whale pump: Marine mammals enhance primary productivity in a coastal basin. PLoS ONE, 5, e13255.

Rosenfeld, J. S. (2002). Functional redundancy in ecology and conservation. Oikos, 98, 156–162.

Safi, K., Cianciaruso, M. V., Loyola, R. D., Brito, D., Armour-Marshall, K., & Diniz-Filho, J. A. F. (2011). Understanding global patterns of mammalian functional and phylogenetic diversity. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 366, 2536–2544.

Schipper, J., Chanson, J. S., Chiozza, F., Cox, N. A., Hoffmann, M., Katariva, V., ... Young, B. E. (2008). The status of the world’s land and marine mammals: Diversity, threat, and knowledge. Science, 322, 225–230.

Schweiger, O., Klotz, S., Durka, W., & Kühn, I. (2008). A comparative test of phylogenetic diversity indices. Oecologia, 157, 485–495.

Sobral, F. L., Jardim, L., Lemes, P., Machado, N., Loyola, R., & Cianciaruso, M. V. (2014). Spatial conservation priorities for top predators reveal mismatches among taxonomic, phylogenetic and functional diversity. Natureza & Conservação, 12, 150–155.

Storà, J., & Ericson, P. G. P. (2004). A prehistoric breeding ground of Harp Seals (Phoca Groenlandica) in the Baltic Sea. Marine Mammal Science, 20, 115–133.

Stuart-Smith, R. D., Bates, A. E., Lefcheck, J. S., Duffy, J. E., Baker, S. C., Thomson, R. J., ... Edgar, G. J. (2013). Integrating abundance and functional traits reveals new global hotspots of fish diversity. Nature, 501, 539–542.

Tilman, D. (1996). EcologyBiodiversity: Population versus ecosystem stability. Ecology, 77, 350–363.

Tilman, D., Knops, J., Weldon, D., Reich, P., Ritchie, M., & Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. Science, 277, 1300–1302.

Tucker, C. M., Cadotte, M. W., Davies, T. J., & Rebelo, T. G. (2012). Incorporating geographical and evolutionary rarity into conservation prioritization. Conservation Biology, 26, 593–601.

Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology, 89, 2290–2301.

Viole, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional!. Oikos, 116, 882–892.

Waldbusser, G. G., Marinelli, R. L., Whitlatch, R. B., & Visscher, P. T. (2004). The effects of faunal biodiversity on biogeochemistry of coastal marine sediments. Limnology and Oceanography, 49, 1482–1492.

Walker, B. H. (1992). Biodiversity and ecological redundancy. Conservation Biology, 6, 18–23.

Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. Annual Review of Ecology and Systematics, 33, 475–505.

Williams, R., Grand, J., Hooker, S. K., Buckland, S. T., Reeves, R. R., Rojas-Brago, L., ... Kaschner, K. (2014). Prioritizing global marine mammal habitats using density maps in place of range maps. Ecology, 37, 212–220.

Winter, M., Devictor, V., & Schweiger, O. (2013). Phylogenetic diversity and nature conservation: Where are we? Trends in Ecology & Evolution, 28, 199–204.

Yachi, S., & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proceedings of the National Academy of Sciences of the United States of America, 96, 1463–1468.

**BIOSKETCH**

Camille Albouy is a postdoctoral researcher in marine ecology at the Swiss Federal Institute of Technology in Zurich. His research is mainly focused on large-scale patterns and processes of marine biodiversity.
He is particularly interested in forecasting changes in marine fish food webs under climatic constraints.

**SUPPORTING INFORMATION**

Additional Supporting Information may be found online in the supporting information tab for this article.