
Multifaceted biodiversity hotspots of marine mammals for conservation priorities

Albouy Camille ^{1,2,3,*}, Delattre Valentine L. ⁴, Merigot Bastien ⁴, Meynard Christine N. ^{5,6}, Leprieur Fabien ^{4,*}

¹ Swiss Fed Res Inst WSL, Birmensdorf, Switzerland.

² Swiss Fed Inst Technol, Landscape Ecol, Inst Terr Ecosyst, Zurich, Switzerland.

³ IFREMER, Unite Ecol & Modeles Halieut, Nantes 3, France.

⁴ Univ Montpellier, IFREMER, CNRS, MARBEC,IRD,UM,UMR 9190, Montpellier 5, France.

⁵ Montpellier SupAgro, INRA, UMR CBGP, IRD,Cirad, Campus Int Baillarguet, Montferrier Sur Lez, France.

⁶ Virginia Inst Marine Sci, Coll William & Mary, Gloucester Point, VA 23062 USA.

Corresponding authors : Camille Albouy, email address : albouycamille@gmail.com ; Fabien Leprieur, email address : 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 world-wide. 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

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 (Schipper et al., 2008; Davidson et al., 2012). Furthermore, marine mammals play key ecological roles in marine ecosystems worldwide (e.g., Bowen, 1997; Perrin et al., 2002; Roman & McCarthy, 2010). Because of their large body size (Pauly et al., 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 southwest 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 1995; Estes et al., 2009). Their extinction or even their population decay could therefore lead to irreversible consequences for ecosystem functioning (Heithaus et al., 2008; Estes et al., 2011). 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 et al., 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 et al., 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 et al., 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 (Tilman et al., 1997; Hooper & Dukes, 2004; Petchey et al., 2004, Mokany et al., 2008, Gagic et al., 2015), resilience to perturbations or invasion (Dukes, 2001; Bellwood et al., 2004), and regulation of the flux of matter (Waldbusser et al., 2004). FD is therefore a relevant diversity facet to implement conservation priorities toward for an integrated approach to biodiversity conservation (Devictor et al., 2010; Cadotte et al., 2011; 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 (Webb et al., 2002; Maherali & Klironomos, 2007; D'agata et al., 2014). Whereas SR and PD have been recognized as major components of marine mammal biodiversity (Schipper et al., 2008; Pompa et al., 2011), FD has not yet been considered. Exploring spatial patterns of FD for marine mammals worldwide is therefore urgently needed to (i) assess whether the restrictive use of SR and PD is sufficient for conservation

prioritization in marine mammals, (ii) identify multi-component biodiversity hotspots of marine mammals at a global scale, and (iii) 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, sirenians, 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 behavior, and biology). Mapping the geographical distribution of marine mammals onto a $1^\circ \times 1^\circ$ 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 (Villegger et al., 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 et al., 2009).

METHODS

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 ($1^\circ \times 1^\circ$ grid cells, $\sim 10,000$ 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 behavior) 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, continental slope and offshore, 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 behavior (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 behavior, 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 encyclopedic websites and books, and extant databases (see Supplemental Experimental Procedures). 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.

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 $1^\circ \times 1^\circ$ 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; Vileger 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 et al., 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 (Vileger 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 et al., 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 behavior; 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 et al. 2010), we kept the first four principal axes of this PCoA. Since the FRic index can only be applied to communities containing at least one more species than the number of axes in the PCoA (Vileger 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.

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., 2007) 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 $1^\circ \times 1^\circ$ species richness grid.

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, O_e , corresponding to the independence between the SR and FRic hotspots. O_e was calculated as follows: $O_e = N_i \times N_j / N_T$, where N_i is the number of hotspots for SR, N_j is the number of hotspots for FRic, and N_T is the total number of grid cells. We then conducted a randomization procedure to assess whether the observed number of overlaps (O_o) is significantly different from that obtained by chance (O_e). 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.

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 Fig. 1a). These areas were also characterized by high levels of PD (Fig. 1b), as shown by (i) the significant and positive relationship between SR and PD (Spearman's correlation test: $r_s = 0.669$; $P < 0.001$, Fig. 3a) and (ii) the overall spatial congruence between the hotspots of SR and PD (Fig. 4a and Appendix S3).

High levels of FRic were found along the western coasts of North America (i.e., from Alaska to California) and Peru (Fig. 1c) as well as along the coasts of Argentina and the Falkland Islands. FRic was found to be weakly correlated with SR (Spearman's correlation test: $r_s = 0.179$; $P < 0.001$, Fig. 3b), with these two biodiversity facets displaying a triangular relationship, i.e., increasing variability in FRic values along the SR gradient (Fig. 3b).

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 (Fig. 4b and Appendix S3). For instance, the coastal areas of California, South Africa and southeastern Australia displayed rather similar SR values (34, 38 and 34 species, respectively, Fig 1a) while showing varying levels of FRic (Fig. 1c). The species assemblage of southeastern 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 (Fig. 6). The California hotspot indeed hosted several species with rare combinations of traits, i.e., pinnipeds (northern fur seal (*C. ursinus*), Guadalupe fur seal (*A. townsendi*), harbor 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*).

FRic and PD showed a stronger positive relationship (Spearman's correlation test: $r_s = 0.565$; $P < 0.001$, Fig. 3c), but these two biodiversity facets also displayed a triangular relationship, i.e., increasing variability of FRic values along the PD gradient. This explains the weak spatial congruence between the hotspots of PD and FRic (Fig. 4c 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 (Fig. 2). We identified only 0.5% and 0.8% common grid cells among the three biodiversity facets for the 2.5 and 5% highest values, respectively (see Fig. 2). These areas weakly corresponded to the threat hotspots (see Fig. 5 a, b and 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).

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 et al., 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 Fig. 3) 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.

Since 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 (Fig. 4). 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 et al. 2014). For instance, South Africa harbors 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 (Tilman, 1996; Rosenfeld, 2002; Brookes et al., 2005). 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 (Walker, 1992; Naeem, 1998; Yachi & Loreau, 1999; Elmqvist et al., 2003). 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 (Fig. 2). One possible explanation is that the current patterns of marine mammal biodiversity have already

been greatly affected by their history of exploitation (Reynolds et al., 2007). 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 modelling 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).

Since 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 analyzing 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 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 et al 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., Pio et al., 2011; Tucker & Cadotte, 2013). 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).

ACKNOWLEDGMENTS

CA was supported by an MELS-FQRNT Post-Doctoral 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-CEPL-006)). We thank Sebastien Villeger constructive comments on the MS. This paper is contribution number XXXX of the Virginia Institute of Marine Science, College of William & Mary.

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**, 827–33.
- 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., Cowman P.F., Kronen M., Pinca S., & 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., Ceballos G., & Brown J.H. (2012) Drivers and hotspots of extinction risk in marine mammals. *Proceedings of the National Academy of Sciences*, **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 difference: plant functional diversity matters to

- ecosystem processes. *Trends in Ecology & Evolution*, **16**, 646–655.
- Dukes 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. & 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., 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**, 1647–58
- Estes J.A., Terborgh J., Brashares J.S., Power M.E., Berger J., Bond W.J., Carpenter S.R., Essington T.E., Holt R.D., Jackson J.B.C., Marquis R.J., Oksanen L., Oksanen T., Paine R.T., Pickett E.K., Ripple W.J., Sandin S.A., Scheffer M., Schoener T.W., Shurin J.B., Sinclair A.R.E., Soulé M.E., Virtanen R., & Wardle D.A. (2011) Trophic downgrading of planet Earth. *Science*, **333**, 301–6
- 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., Slade E.M., Steffan-Dewenter I., Emmerson M., Potts S.G., Tscharrntke T., Weisser W. & Bommarco 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**, 2014–2620.
- Game E.T., Grantham H.S., Hobday A.J., Pressey R.L., Lombard A.T., Beckley L.E., Gjerde K., Bustamante R., Possingham H.P., & Richardson A.J. (2009) Pelagic protected areas: the missing dimension in ocean conservation. *Trends in ecology & evolution*, **24**, 360–9.
- 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., Tomasini J.A., Douzery E.J.P., Meynard C.N., Mouquet N., Araújo M.B. and 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., Agrosa C., Bruno J.F., Casey K.S., Ebert C., Fox H.E., Fujita R., Heinemann D., Lenihan H.S., Madin E.M.P., Perry M.T., Selig E.R., Spalding M., Steneck R., & 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*. Earthscan, New York.
- 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. 853pp. Developments in Environmental Modelling, 20, Elsevier, New York.
- 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., & Villéger 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.
- Merigot 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 M.G., Smith T.D., Reeves R.R., 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., Meynard C.N., Pauly D., Tomasini J.A., Troussellier M., Velez L., Watson R., Douzery E.J.P., & Mouquet N. (2011) Protected and threatened components of fish biodiversity in the Mediterranean sea. *Current biology : CB*, **21**, 1044–50.
- Mouillot D., Graham N.A.J., Villéger 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., Parravicini V., Bellwood D.R., Leprieur F., Huang D., Cowman P.F., Albouy C., Hughes T.P., Thuiller W., & 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., Whittock 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*. Academic Press, San Diego.
- Petchey O.L. & Gaston K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters*, **9**, 741–758.
- Petchey O.L., Hector A., & Gaston K.J. (2004) How do different measures of functional diversity perform? *Ecology*, **85**, 847–857.
- Pio, D.V., Broennimann, O., Barraclough, T.G., Reeves, G., Rebelo, A.G., Thuiller, W., Guisan, A. & Salamin, N. (2011) Spatial Predictions of Phylogenetic Diversity in Conservation Decision Making. *Conservation Biology*, **25**, 1229–1239.
- Pompa S., Ehrlich P.R., & Ceballos G. (2011) Global distribution and conservation of marine mammals. *Proceedings of the National Academy of Sciences*, **108**, 13600–13605.
- Reynolds J., Marsh H., & Ragen T. (2009) Marine mammal conservation. *Endangered Species Research*, **7**, 23–28.
- R Core Team (2015) Available at: <http://www.r-project.org/>.
- 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**, 2536–44.
- Schipper J., Chanson J.S., Chiozza F., Cox N.A., Hoffmann M., Katariya V., Lamoreux J., Rodrigues A.S.L., Stuart S.N., Temple H.J., Baillie J., Boitani L., Lacher T.E., Mittermeier R.A., Smith A.T., Absolon D., Aguiar J.M., Amori G., Bakkour N., Baldi R., Berridge R.J., Bielby J., Black P.A., Blanc J.J., Brooks T.M., Burton J.A., Butynski T.M., Catullo G., Chapman R., Cokeliss Z., Collen B., Conroy J., Cooke J.G., da Fonseca G.A.B., Derocher A.E., Dublin H.T., Duckworth J.W., Emmons L., Emslie R.H., Festa-Bianchet M., Foster M., Foster S., Garshelis D.L., Gates C., Gimenez-Dixon M., Gonzalez S., Gonzalez-Maya J.F., Good T.C., Hammerson G., Hammond P.S., Happold D., Happold M., Hare J., Harris R.B., Hawkins C.E., Haywood M., Heaney L.R., Hedges S., Helgen K.M., Hilton-Taylor C., Hussain S.A., Ishii N., Jefferson T.A., Jenkins R.K.B., Johnston C.H., Keith M., Kingdon J., Knox D.H., Kovacs K.M., Langhammer P., Leus K., Lewison R., Lichtenstein G., Lowry L.F., Macavoy Z., Mace G.M., Mallon D.P., Masi M., McKnight M.W., Medellín R.A., Medici P., Mills G., Moehlman P.D., Molur S., Mora A., Nowell K., Oates J.F., Olech W., Oliver W.R.L., Oprea M., Patterson B.D., Perrin W.F., Polidoro B.A., Pollock C., Powel A., Protas Y., Racey P., Ragle J., Ramani P., Rathbun G., Reeves R.R., Reilly S.B., Reynolds J.E., Rondinini C., Rosell-Ambal R.G., Rulli M., Rylands A.B., Savini S., Schank C.J., Sechrest W., Self-Sullivan C., Shoemaker A., Sillero-Zubiri C., De Silva N., Smith D.E., Srinivasulu C., Stephenson P.J., van Strien N., Talukdar B.K., Taylor B.L., Timmins R., Tirira D.G., Tognelli M.F., Tsytsulina K., Veiga L.M., Vié J.-C., Williamson E.A., Wyatt S.A., Xie Y., & 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**, 485–95.
- 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.
- Spitz J., Mourocq E., Leauté J.-P., Quéro J.-C., & Ridoux V. (2010) Prey selection by the common dolphin: Fulfilling high energy requirements with high quality food. *Journal of Experimental Marine Biology and Ecology*, **390**, 73–77.
- Steman M.E., Hebsgaard M.B., Fordyce R.E., Ho S.Y.W., Rabosky D.L., Nielsen R., Rahbek C., Glenner H., Sørensen M. V., & Willerslev E. (2009) Radiation of Extant Cetaceans Driven by Restructuring of the Oceans. *Systematic Biology*, **58**, 573–585.
- Stuart-Smith R.D., Bates A.E., Lefcheck J.S., Duffy J.E., Baker S.C., Thomson R.J., Stuart-Smith J.F., Hill N.A., Kininmonth S.J., Airoidi L., Becerro M.A., Campbell S.J., Dawson T.P., Navarrete S.A., Soler G.A., Strain E.M.A., Willis T.J., & Edgar G.J. (2013) Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature*, **501**, 539–542.
- Storå J. & Ericson P.G.P. (2004) A prehistoric breeding population of Harp Seals (*Phoca Groenlandica*) in the Baltic Sea. *Marine Mammal Science*, **20**, 115–133.
- Tilman D. (1996) EcologyBiodiversity: Population versus ecosystem stability. *Ecology*, **77**, 350–363.
- Tilman D., Knops J., Weldin 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.
- Villegger S., Mason N.W.H., & Mouillot D. (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, **89**, 2290–2301.
- Violle 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.
- Wada S., Oishi M., & Yamada T.K. (2003) A newly discovered species of living baleen whale. *Nature*, **426**, 278–281.
- Waldbusser G.G., Marinelli R.L., Whitlatch R.B., & Visscher P.T. (2004) The effects of infaunal 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., McPeck 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-Bracho L., Sandilands D., & Kaschner K. (2014) Prioritizing global marine mammal habitats using

- density maps in place of range maps. *Ecography*, **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.

SUPPORTING INFORMATION

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

Appendix S1 Description of ecological and biological traits.

Appendix S2 Histograms of selected functional traits for quantifying the functional diversity of marine mammals.

Appendix S3 Congruence hotspots (i.e., the highest 5% values) for pairwise combinations of the three biodiversity (SR, PD index, FRic index).

Appendix S4 Congruence hotspots (i.e., the highest 5% values) between the three biodiversity facets (SR, PD index, FRic index) and threats.

Appendix S5 Congruence hotspots (i.e., the highest 2.5 and 5% values) among functional richness (FRic index), phylogenetic diversity (PD index), species richness (SR) and human threats.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

BIOSKETCHES

Camille Albouy is a post-doctoral 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.

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.

Tables

Table 1: Description of the functional traits database used to measure the functional diversity of marine mammals.

<i>Function</i>	<i>Trait</i>	<i>Modalities/unit</i>	<i>Nature</i>		
Feeding	Main diet*	A zooplankton	nominal		
		B invertebrates (w/o squid)			
		C high vertebrates			
		D fish			
		E squid			
		F seagrass			
	Foraging depth range*	A epipelagic	nominal		
		B mesopelagic			
		C benthic			
		D all depths			
		Foraging location*		A continental shelf	nominal
				B cont. shelf and slope	
C continental slope					
D cont. slope and offshore					
E offshore					
F all					
	Fasting strategy*	1 yes	binomial		
		0 no			
Habitat	Terrestriality*	1 yes	binomial		
		0 no			
Reproduction	Female sexual maturity**	years	quantitative		
	Weaning**	months	quantitative		
	Gestation length*	months	quantitative		
	Inter-litter interval**	months	quantitative		
	Breeding site*	A ice and/or land	ordered		
B coastal water					
C oceanic water					
Social	Social group size* ^a	individuals/school	quantitative		
	Social behavior*	A mostly social	ordered		
		B social and solitary			
Biology	Adult max body mass* ^a	kg	quantitative		
	Sexual dimorphism*	0 none	ordered		
		1 moderate (10 to 30%) 2 strong (above 30%)			

* > 90% filled (less than 10% missing values)

** from 80 to 90% filled (10 to 20% missing values)

^a log-transformed traits in order to attenuate the effect of strong values on the results.

List of Figures

Figure 1. Global maps of (a) species richness (SR), (b) phylogenetic diversity (PD index), and (c) functional richness (FRic index) for marine mammals. The PD index and FRic index for each grid cell are expressed as the percentage of the PD index and FRic index for the global pool of species.

Figure 2. Map showing hotspot (i.e., the highest 2.5% and 5% values) congruence among functional richness (FRic index), phylogenetic diversity (PD index) and species richness (SR).

Figure 3. 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.

Figure 4. 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.

Figure 5. 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.

Figure 6. 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 gray 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.

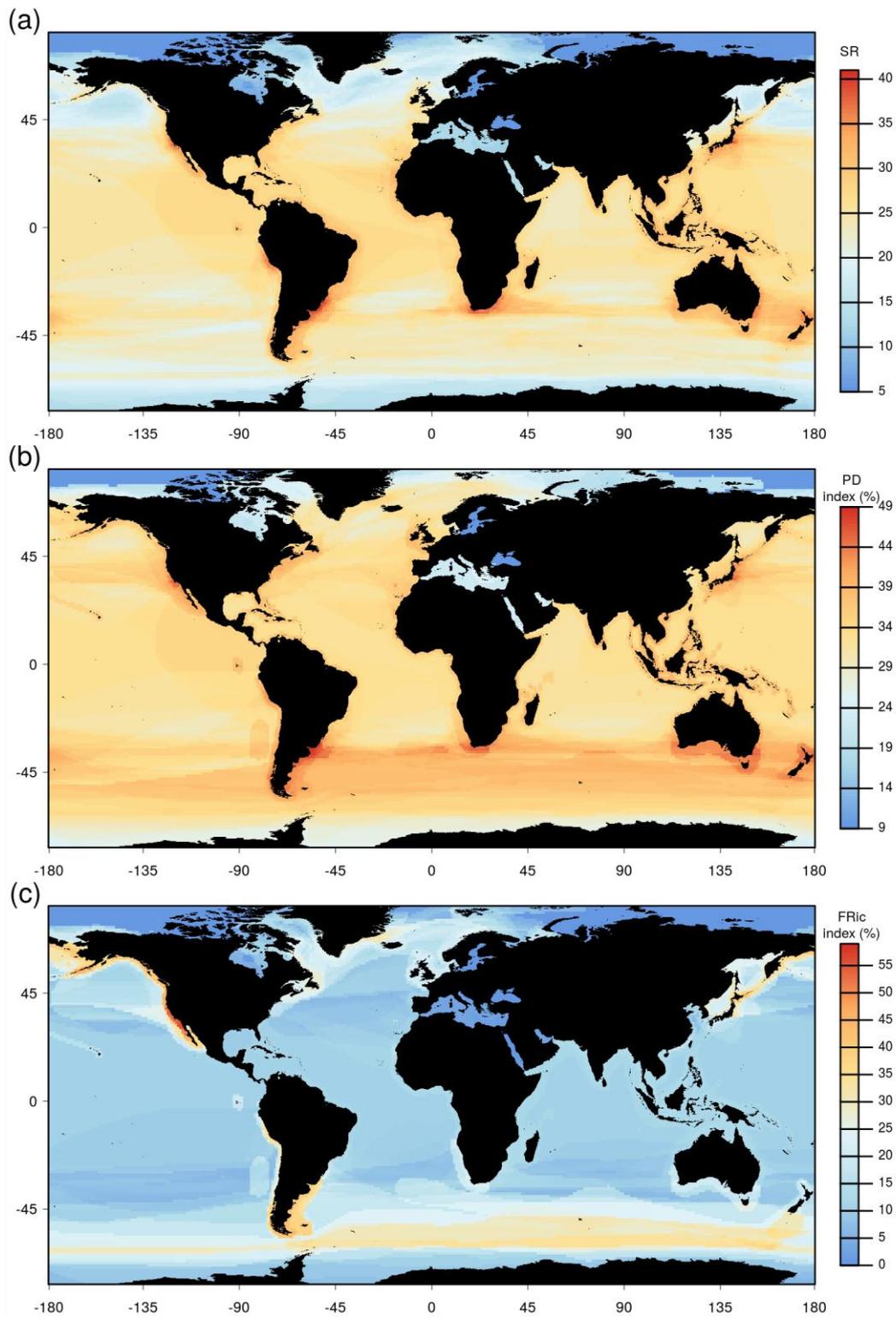


Figure 1

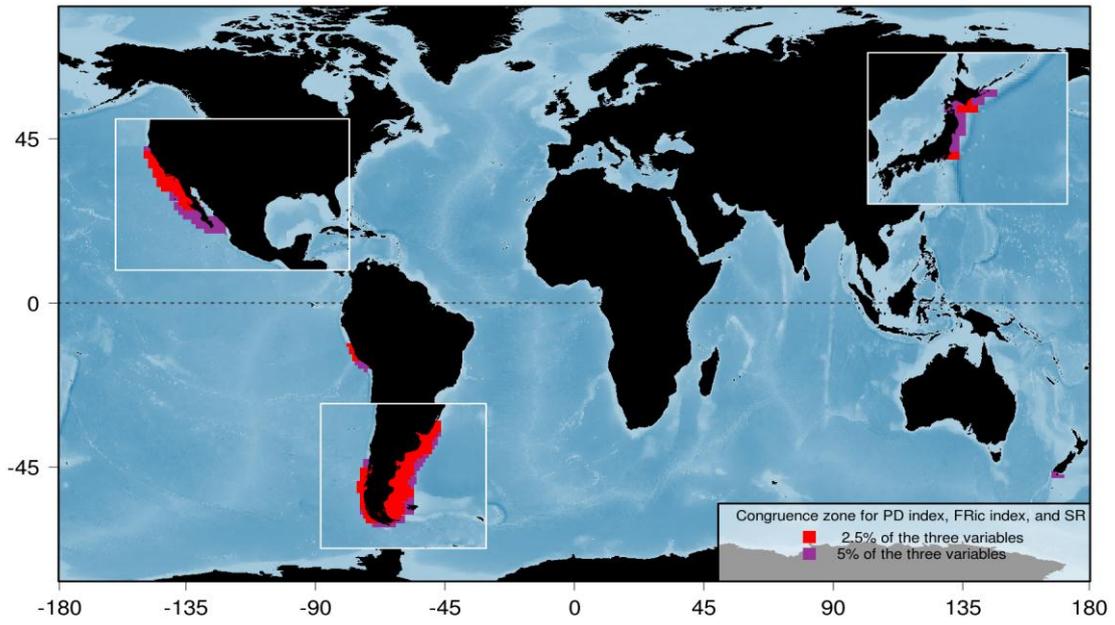


Figure 2

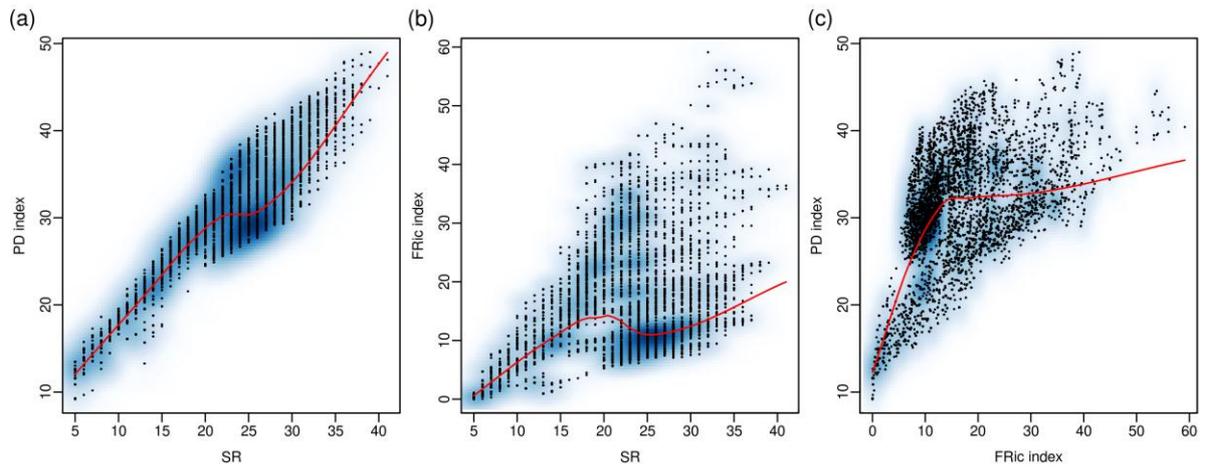


Figure 3

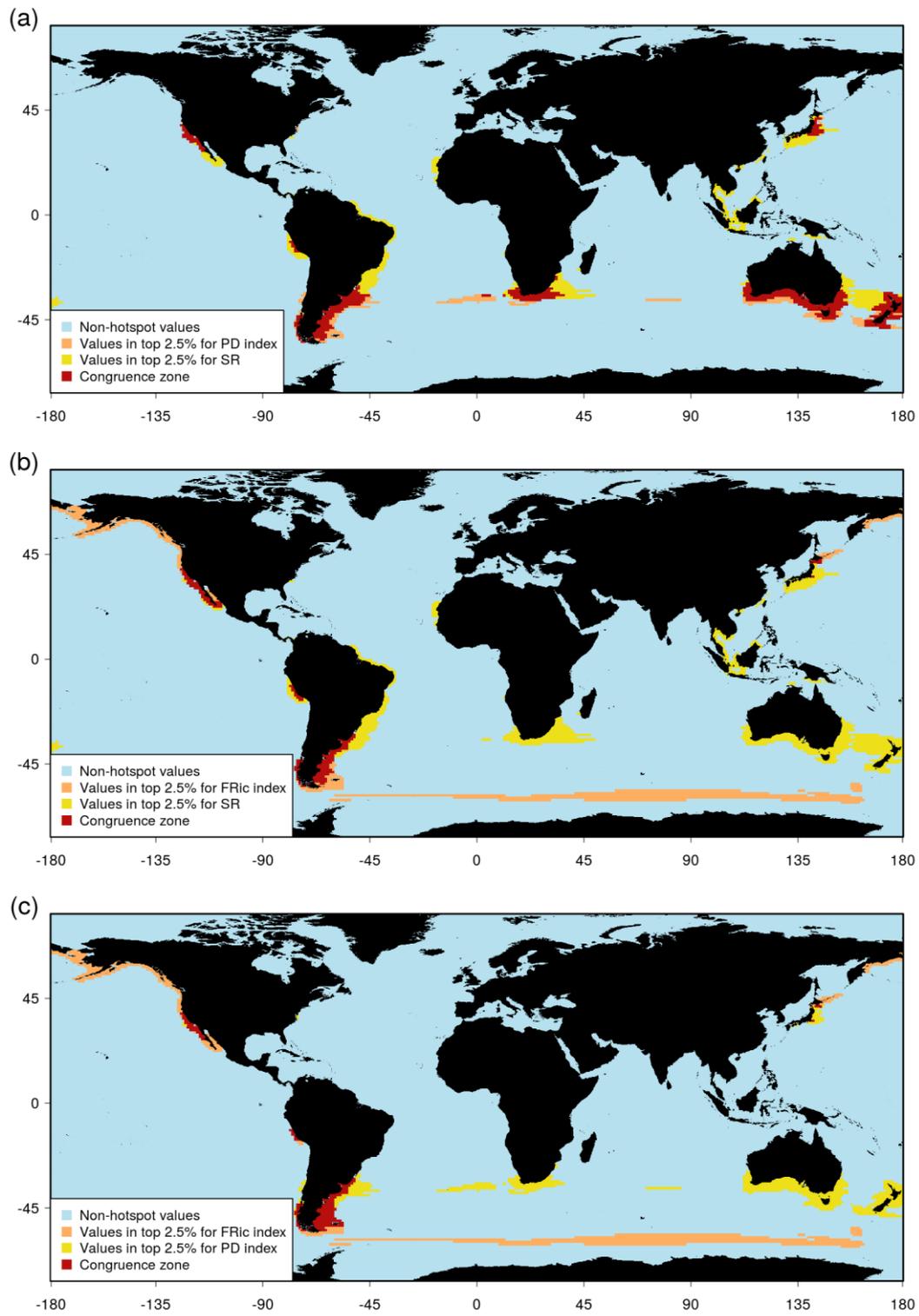


Figure 4

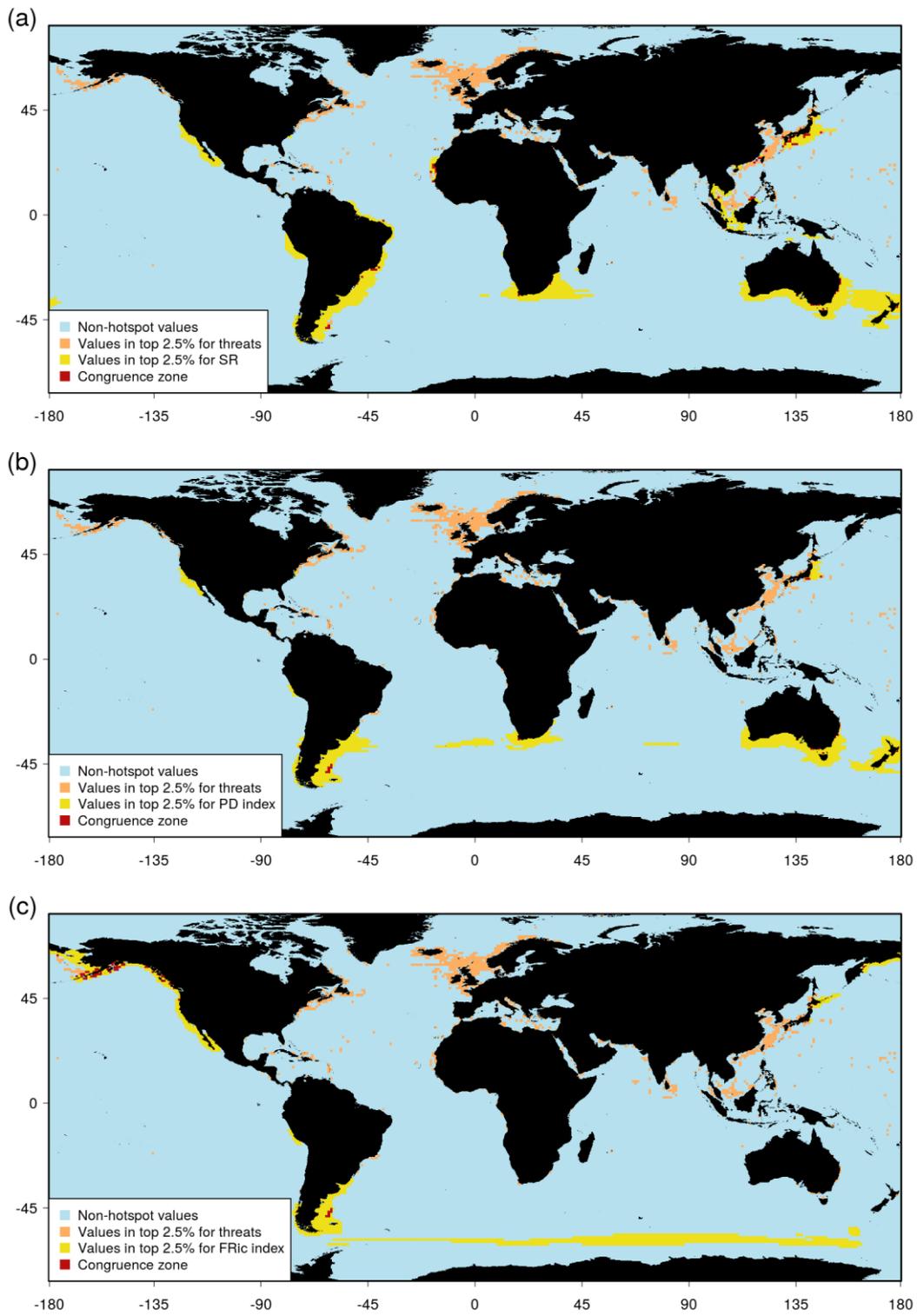


Figure 5

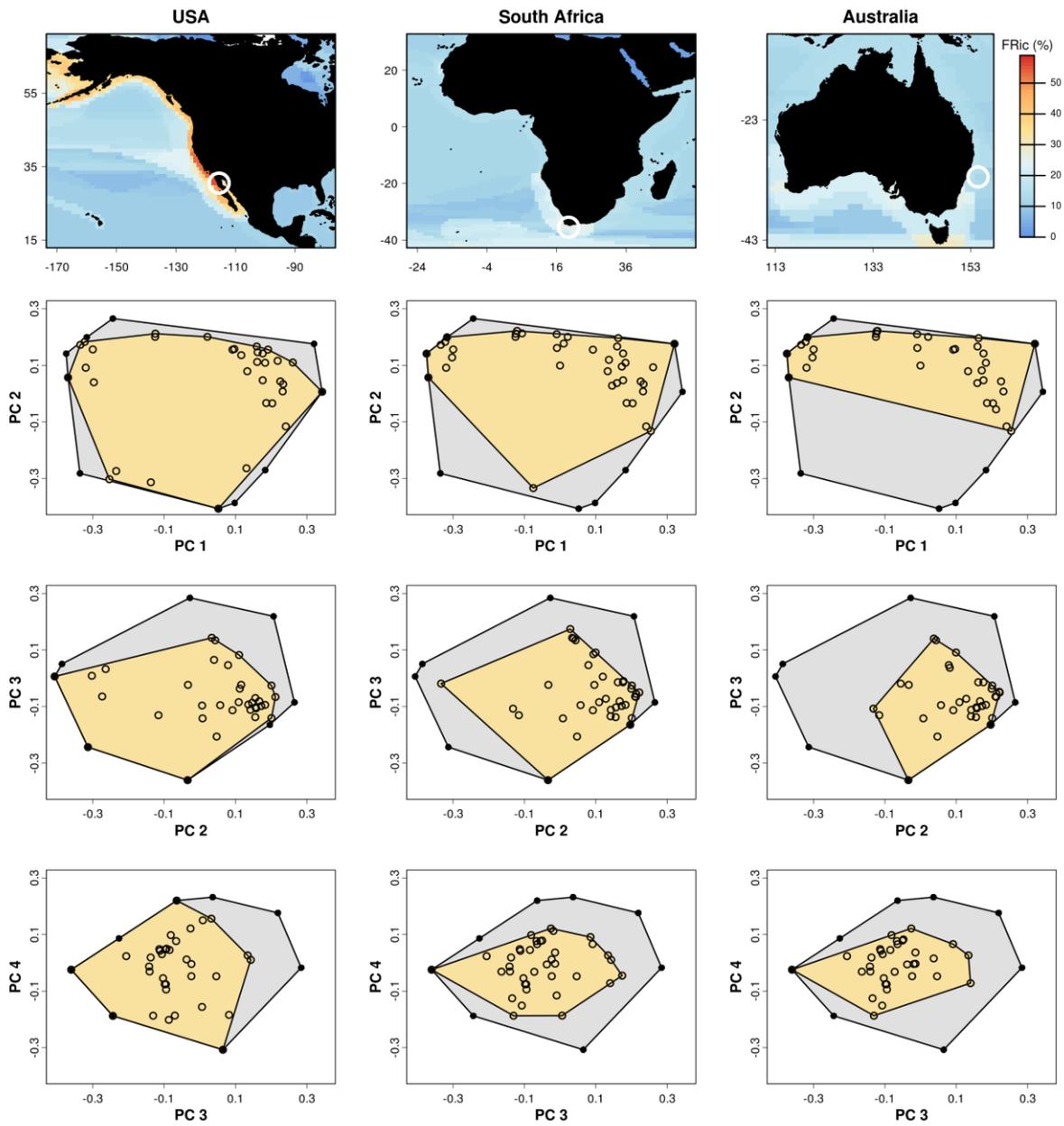


Figure 6

Supplemental Materials: Albouy et al. *Multifaceted biodiversity hotspots of marine mammals for conservation priorities*

Appendix S1. Description of ecological and biological traits

Diet composition

For each species, their main diet was determined using a Hierarchical Cluster Analysis upon standardized diet composition available for 97 species of marine mammals (Pauly et al., 1998). The Hierarchical Cluster Analysis was based on the Bray Curtis distance and the unweighted pair-group method using arithmetic averages (UPGMA) linkage method, which provided a more faithful representation of the initial distance matrix than other linkage methods [unweighted pair-group method using centroids (UPGMC), weighted pair-group method using arithmetic averages (WPGMA), Ward's method, single linkage, complete linkage] according to a goodness-of-fit measure (the 2-norm; Merigot et al., 2010). We used the Kelley-Gardner-Sutcliffe penalty function (KGS) to identify distinct groups of species (Kelley et al., 1996). This method maximizes differences between groups and cohesiveness within groups based on the distance matrix. The minimum of the KGS function corresponds to the optimal number of groups. According to the KGS method we discriminate 6 groups of species according to their main diet i.e. zooplankton, invertebrates (without squid), high vertebrates, fish, squid and seagrass (see below). For the species not included in Pauly et al., (1998), we classified in each group based on a literature survey.

Functional traits

Main Diet

Species were split into five groups according to their main diet (see above and Figure. S1a), i.e., zooplankton (A), invertebrates (squid excepted) (B), high vertebrates (C), fish (D)

squid (E) and seagrass (F). Each group induces typical effects onto life-history and biology of prey populations (Perrin et al., 2002). Main diet also reflects trophic level of species. Most species (Odontocetes and Pinnipeds) feed on fish (46%, cat. D) or squid (34%, cat. E). Zooplankton (cat. A) is the main diet of 13% of species including most baleen whales, Crabeater seal *L. carcinophaga* and Kerguelen fur seal *A. gazella*. The remaining Gray whale *E. robustus* feeds on invertebrates (cat. B) as well as otters, walrus *O. rosmarus* and Bearded seal *E. barbatus*. Apex-predators of marine ecosystems Orca *O. orca* and leopard seal *H. leptonyx* mainly feed on high vertebrates (cat. C). Odontocetes and Pinnipeds being present in every group reflects highly diversified feeding strategies and might originate from an intense competition for resources. Essentially, Odontocetes often travel in large groups of several co-occurrent species (Jefferson et al., 2011). Diversification of foraging strategies could allow optimization of foraging efforts without reaching deleterious threshold. Nevertheless, diet might only reflect prey availability rather than ecological preference (Perrin et al., 2002).

Foraging depth range

Foraging depth range was coded as epipelagic, mesopelagic, benthic, and all depths. Most species (42%) have generalist preferences (cat. D) regarding foraging depth range (*Fig. S1B*). One third is specialized in benthic and benthic-demersal feeding and therefore might contribute to sediment bioturbation (cat. C). The proportions of species feeding in either epipelagic or mesopelagic layers are barely equal. Epipelagic feeders (cat. A) are mostly Mysticetes (i.e., baleen whales filtering zooplankton in the upper water layer) whereas mesopelagic-specialized species mostly feed in the deep scattering layer at night, particularly at dawn and dusk when preys vertically migrate. This foraging strategy minimizes energetic cost of feeding and enables species with low diving capacity to feed (Perrin et al., 2002).

Foraging location

This functional trait included 6 modalities i.e. continental shelf, continental shelf and slope, continental slope, continental slope and offshore, offshore, any distance to shore. According to this classification, 46% of marine mammals are found in the coastal ocean (cat. A in Figure S1c). The continental shelf is characterized by both specific hydrodynamic conditions and nutrients entries from the continent. These features create a suitable habitat for biology by generating phytoplanktonic blooms and consequently high concentrations of potential preys. Coastal habitat preferences could also reflect a predator avoidance strategy since orcas *O. orca* (i.e., ubiquitous apex predators) do not usually enter coastal areas (Perrin et al., 2002). Furthermore, land-using species (e.g., Pinnipeds) usually forage near shore (Jefferson et al., 2011). 18% of species are generalists regarding foraging location (cat. F), meaning horizontal habitat flexibility is less common than vertical habitat flexibility (42%, Figure S1c, cat. D). 14% of marine mammals forage both above the continental slope and offshore (cat. D), where particular hydrogeological features generate upwellings, inducing high primary productivity and thus high concentrations of preys for marine mammals. The surprisingly low number of species favoring this prey-rich habitat could originate from a high predation pressure from orcas. Finally, very few species use offshore waters as habitat (cat. E; mainly ice-breeding Pinnipeds), perhaps because of the low productivity of these waters.

Fasting Strategy

The binomial ‘fasting strategy’ trait was coded according to the presence of an obligatory fast in the life cycle of a given species. One third of marine mammals fast during their life cycle (cat. 1 in Figure S1d). Fasting is used both by migrating baleen whales during the reproductive season, and by some Pinniped species. Fasting Pinnipeds are usually territorial; males fast in order to keep their territory and optimize their chances of

reproduction in a context of high male-to-male sexual competition (Riedman, 1990). Furthermore, some Pinnipeds' females also fast for several days when nursing their pups (Jefferson et al., 2011). The fasting strategy usually follows a period of increased feeding, inducing a thicker layer of blubber as well as higher lipid rate in the milk and higher growing rate of pups (Perrin et al., 2002; Berta, 2012).

Terrestriality

Terrestriality applies to 29% of marine mammals (Fig. S1E), as an example Pinnipeds and otters using land or ice for various activities e.g., social activities, reproduction, thermogenesis, predation of seabirds, and avoiding strategy from orcas' high predation pressure (Perrin et al., 2002). These kind of species frequent alternatively marine and terrestrial ecosystems and might be affected by habitat degradation of both environments. On the other hand, strictly aquatic species have a continuous effect on marine ecosystems, in which they satisfy all their needs including social activities, reproduction and feeding.

Female Sexual Maturity (F)

Sexual maturity was filled in for females rather than males because of the delay between sexual and social maturity in most Pinnipeds, rendering female sexual maturity more reliable as a proxy for age at first reproduction. For 60% of marine mammals, females become sexually mature in less than 8 years. In 30% of species, females become sexually mature at 8-10 years old. 10% of species have a sexual maturity higher than 10 years, which could induce a low resilience in ecosystems where these species occur. This life-history trait reflects a trade-off between costs and benefits of various reproduction strategies. Age of female sexual maturity is also a proxy of both life expectancy (lowest for otters, highest for baleen whales) and mean growth rate (Perrin et al., 2002).

Weaning (G)

For this trait we considered that the weaning is the mean duration of lactation. In two thirds of marine mammals, weaning occurs early (in less than 20 months). However, lactating length is very variable between species and is up to 60 months for Atlantic spotted dolphins (*S. frontalis*). Early weaning strategy being common reflects an usually high predation pressure. The high range of weaning age enlightens the great variability of life expectancy and pups growth rate between species and is also a proxy of juveniles' habitat [4]. Essentially, the lower is the lactating length, the faster the pups need to develop proper diving capacities. In the end, lactating length affects the feeding strategies of juveniles (i.e. foraging layer) (Perrin et al., 2002).

Gestation length (H)

Gestation length stands for the actual duration between mating and calving, including diapause of Pinnipeds. The 10-12 months gestation shared by nearly 60 % of marine mammals reflects a typical lifecycle driven by seasonal variations of abiotic parameters, conditioning both prey availability and migrations. Gestation length ranges from 2 months for the sea otter (*L. felina*) to 18 months for the Australian sea lion (*N. cinerea*). This high variability suggests that the intensity of predation pressure fluctuates from one species to the other.

Inter-litter interval (I)

Inter-litter interval is the duration between two successive calving events. 45% of species calve every 10-15 months (e.g. most Pinnipeds and some Odontocets), in accordance with an annual rythm of life cycle. For remaining species, duration between two calves is greater and

up to 60 months for orcas and sperm whales *P.macrocephalus*, suggesting a particularly low ecosystem resilience.

Breeding site (J)

The breeding site' trait was coded according to three categories, ice and/or land, coastal water, oceanic water). Nearly two thirds of marine mammals mate offshore (cat. C), while 27% breed on ice or land (cat. A, e.g. otters and most of Pinnipeds), and 8 % in coastal waters (cat. B, including Sirenians, some Pinnipeds and several baleen whales, e.g. Bowhead whale *B. mysticetus* and Right whales *Eubalaena spp.*). This trait discriminates two groups of Pinnipeds according to their life-history strategies, with mating occurring either on land and ice or offshore. Usually, mating on land or ice suggests territoriality and thus a high male-to-male sexual competition, leading to high sexual dimorphism and obligatory fasting during life cycle (Perrin et al., 2002). Secondly, land and ice breeding species (cat. A) might be particularly affected by climate change, e.g. through ice melting.

Social group size (K)

Social group size stands for the harem size of Pinnipeds, size of the migration group of Mysticetes, and the smallest stable group size of Odontocetes. Most of marine mammals travel in schools comprised of 10 individuals or less, such as Pinnipeds, Mysticetes, Sirenians and large Odontocetes. However, *Delphinidae* are highly sociable and usually travel in large pods containing up to 400 individuals or more (Jefferson et al., 2011). A very high predation pressure on lower trophic levels might be induced by those large foraging pods (Perrin et al., 2002).

Social behaviour (L)

The social behaviour trait was divided into 4 modalities: mostly social, social and solitary, mostly solitary. Nearly 60% of species (e.g. Odontocetes and half of Pinnipeds) are sociable and thus frequently spotted in groups. Solitary species include baleen whales, some large Odontocetes and the remaining Pinnipeds. When associated with “social group size” trait, this variable allows to grasp social behaviour through both frequency and magnitude. Both traits reflect a trade-off between benefits of sociality (e.g. higher resource acquisition and protection, reproduction, parental care and thermogenesis) and its drawbacks (e.g. increased predation, competition and diseases spreading, Perrin et al., 2002).

Adult max body mass (M)

This highly variable trait ranges from 25.6 kg (marine otter, *E. lutris*) to $1.8 \cdot 10^8$ kg (Blue whale, *B. musculus*). 83% of marine mammals weigh less than 5 tons. Body mass is an indicator of ecological niche and a proxy of numerous traits reflecting ecological processes, e.g. distance of dispersion, competition abilities, metabolic rate, life expectancy and resource availability and distribution (Allen et al., 1999; Lambert, 2006; McGill et al., 2006; Bremner, 2008; Philpott et al., 2009; Sundstrom et al., 2012). For instance, high body mass allows marine mammals to make deep long dives (e.g. Sperm whale, *P. macrocephalus*) because body mass is indirectly correlated with oxygen rate in muscles and inversely correlated with specific metabolic rate (Hoelzel, 2009).

Sexual dimorphism (N)

Dimorphism trait tells whether there are none, low or high differences in size or body mass between individuals of opposite sexes within the same species. A third of marine mammals (mostly Pinnipeds) show sexual dimorphism of length or body mass (at a lower degree for 15% of species, and a higher degree for the remaining 18%). Dimorphism reflects

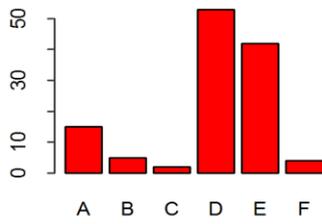
polygamy associated with high sexual competition and intersexual variability of life expectancy, weaning body mass and age at sexual maturity (Perrin et al., 2002; Jefferson et al., 2011). Moreover, dimorphism might be also linked to sexual habitat segregation and variation of foraging strategy between sexes, such as for Sperm whales and Grey seal *H. gripus* (Lyrholm et al., 1999; Breed et al., 2009). Sexual dimorphism of length or body mass has not been noticed in two thirds of marine mammals, suggesting low sexual competition. However, actual sexual competition might be underestimated given poor knowledge on some species (e.g. beaked whales) and since other neglected features may play an important role in sexual selection (e.g. narvals' *M. monoceros* tusks, beaked whales' teeth, Mysticetes' spermatic competition).

Dealing with missing data

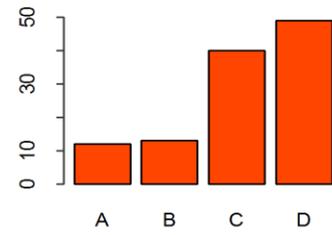
Functional information was not available for all species, so we had to make some assumptions in order to complete our database as much as possible. For example, Beaked whales share a great number of functional characteristics including diet, habitat depth, behavior, and skull morphoanatomy. Because of Mesoplodon's late evolutionary divergence (-13 Ma; Steeman et al., 2009) and high traits conservatism, we assumed that the value of traits could be extrapolated from available fragmented data. Another example is the recently described Omura's whale *Balaenoptera omurai* (Wada et al., 2003), in this case, functional data were mostly assumed from other *Balaenoptera* whales since they have many biological and morpho-anatomical characteristics in common (e.g., baleen plates suggesting specialized zooplankton diet Spitz et al., 2010). Traits were selected if at least 80% of values were filled in (i.e., less than 20% of missing values).

Appendix S2. Histograms of selected functional traits for quantifying the marine mammals functional diversity

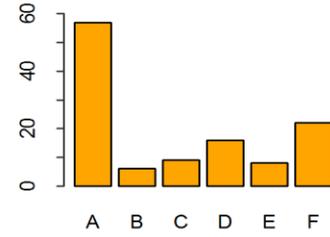
a) Main Diet



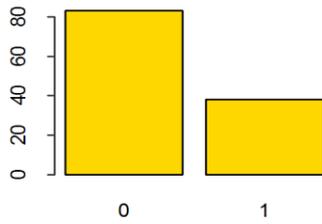
b) Foraging Depth Range



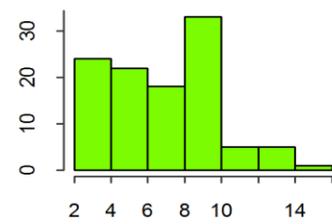
c) Foraging Location



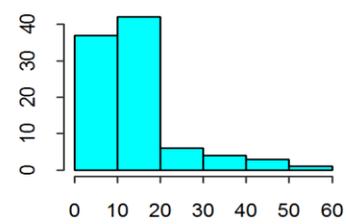
d) Fasting Strategy



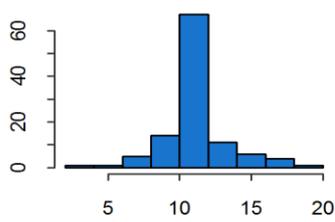
e) Female Sexual Maturity



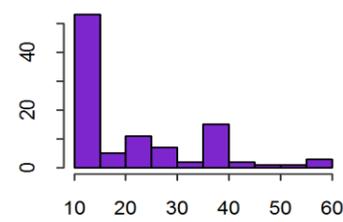
f) Weaning



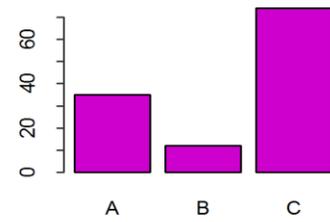
g) Gestation



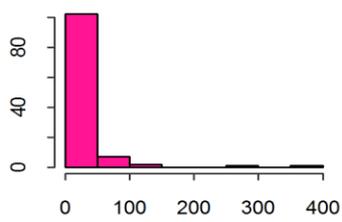
h) Inter-Litter Interval



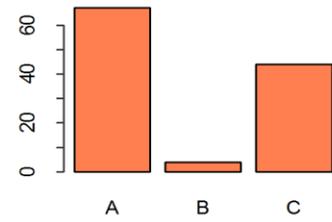
i) Breeding Site



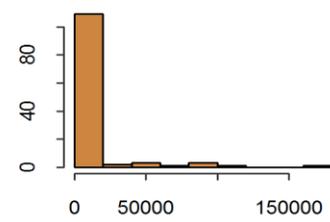
j) Social Group Size



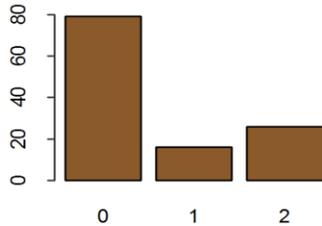
k) Social Behavior



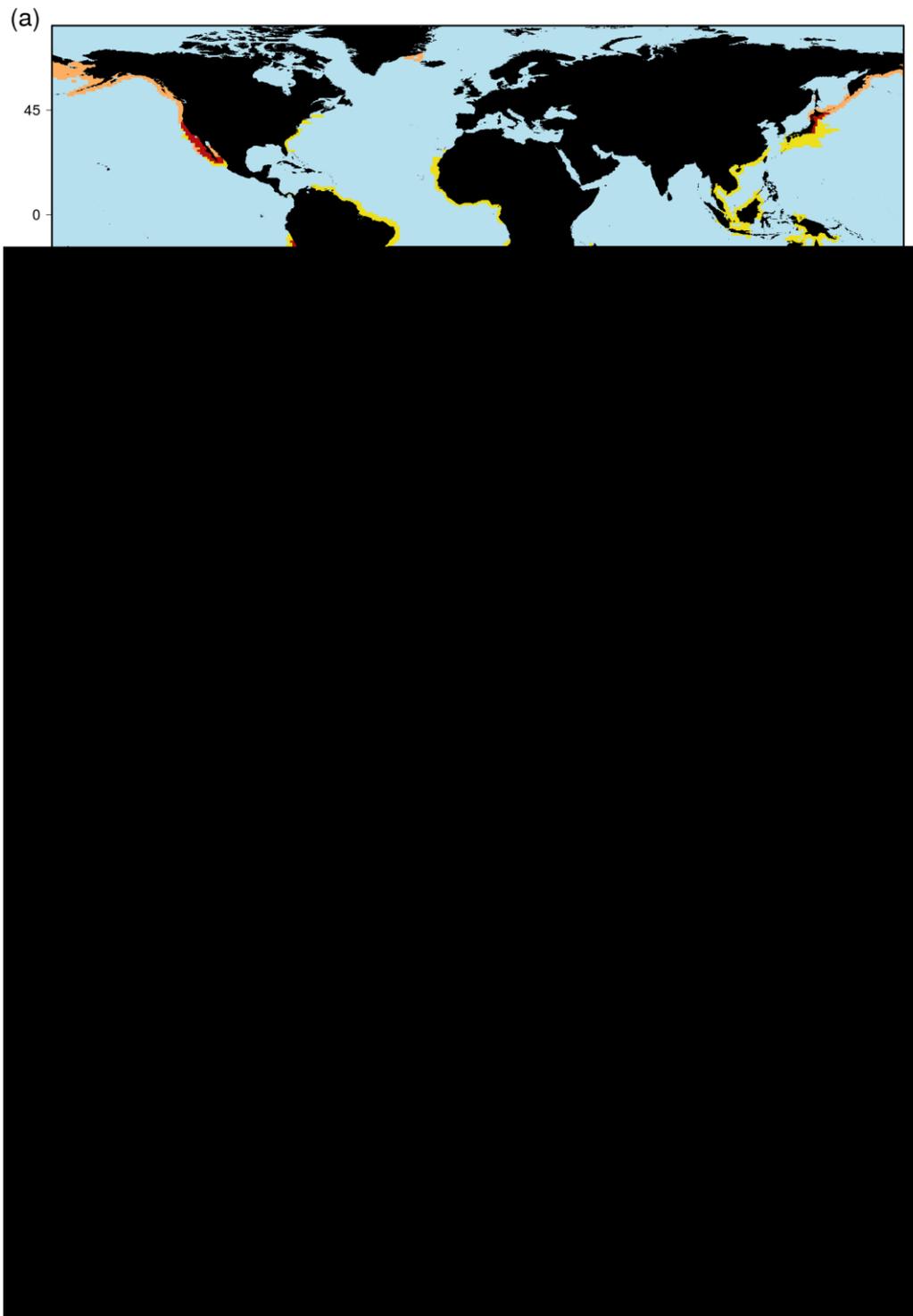
l) Adult Max Body Mass



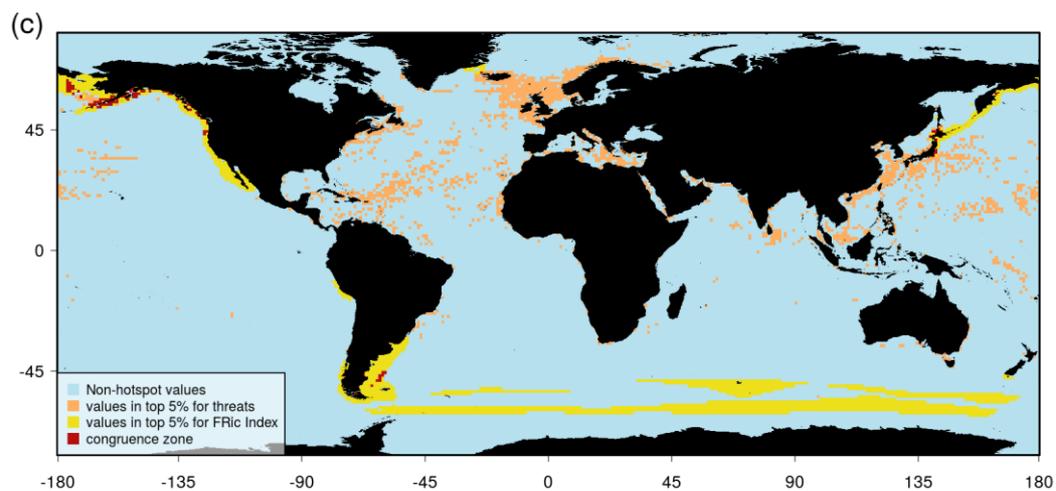
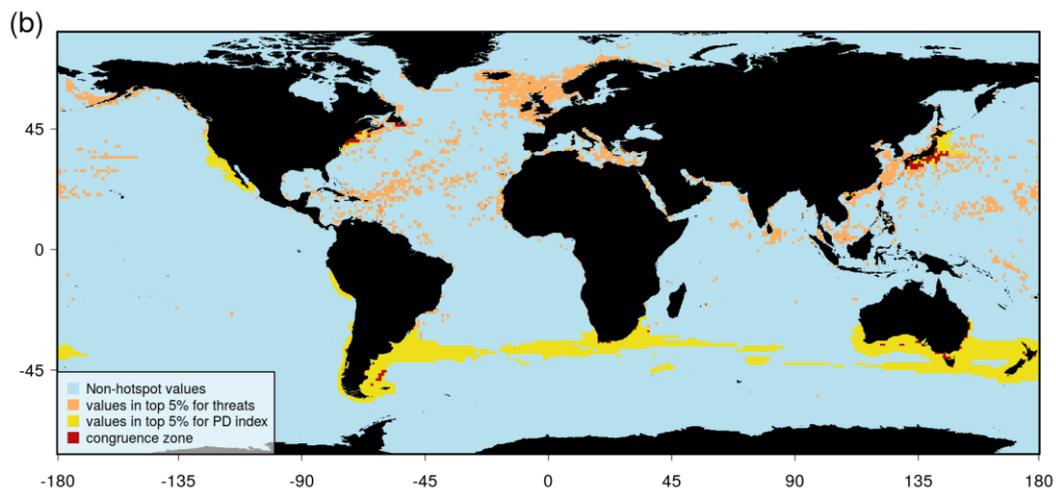
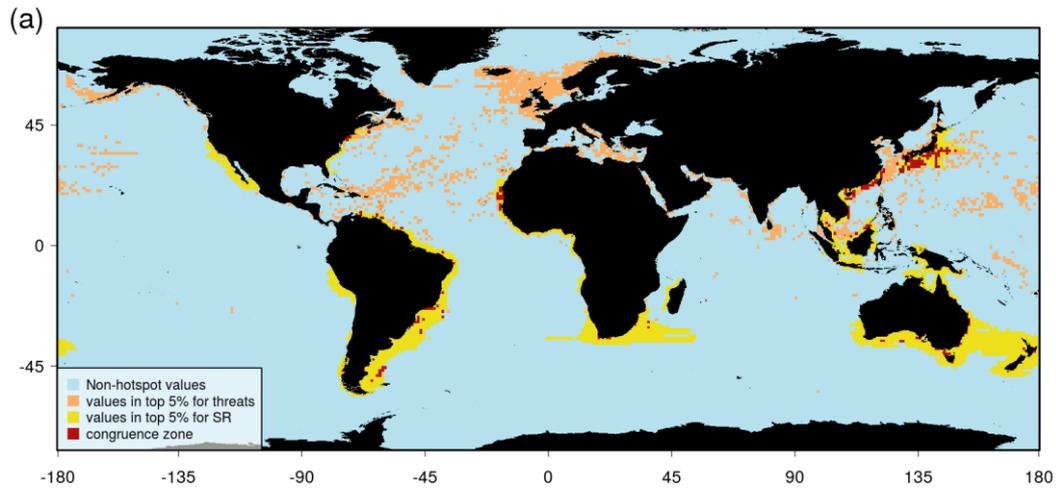
m) Dimorphism



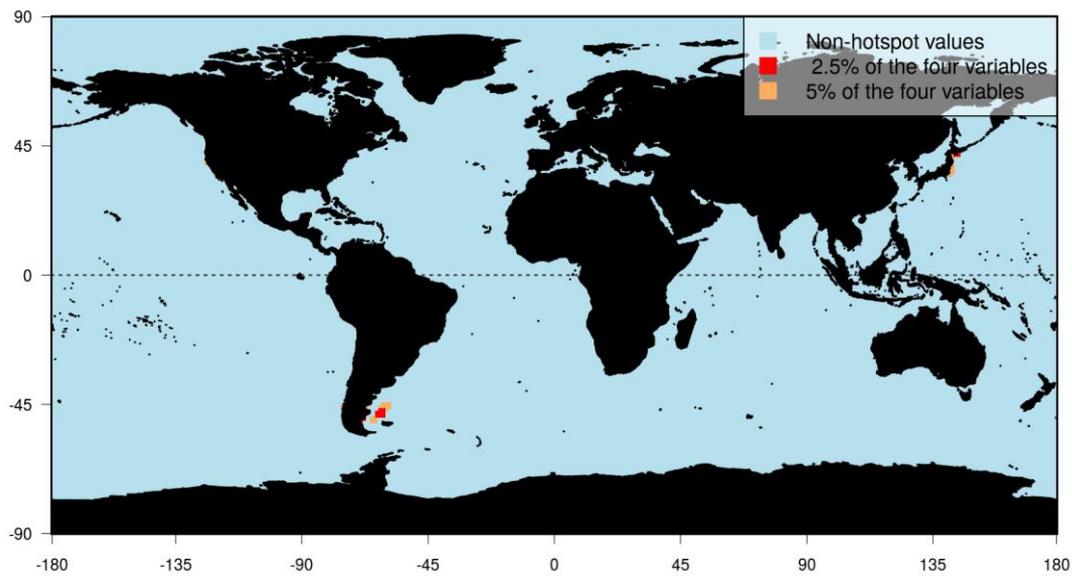
Appendix S3. Maps showing hotspots (i.e. the highest 5% values) congruence between (a) functional richness (FRic index) and species richness (SR), (b) FRic and phylogenetic diversity index (PD index), (c) SR and PD index.



Appendix S4. Maps showing hotspots (i.e. the highest 5% values) congruence between (a) threats (cumulative human impacts extracted from Halpern et al., 2008) and SR, (b) threats and PD index and (c) threats and FRic index.



Appendix S5. Map showing hotspots (i.e. the highest 2.5% and 5% values) congruence between functional diversity (FD), phylogenetic diversity (PD) species richness (SR) and human threats.



Supplemental References

- Allen C.R., Forsyth E.A., & Holling C.S. (1999) Body Mass Patterns Predict Invasions and Extinctions in Transforming Landscapes. *Ecosystems*, **2**, 114–121.
- Berta A. (2012) *Return to the Sea: The Life and Evolutionary Times of Marine Mammals*. University of California Press,
- Breed G.A., Jonsen I.D., Myers R.A., Bowen W.D., & Leonard M.L. (2009) Sex-specific, seasonal foraging tactics of adult grey seals (*Halichoerus grypus*) revealed by state–space analysis. *Ecology*, **90**, 3209–3221.
- Bremner J. (2008) Species' traits and ecological functioning in marine conservation and management. *Journal of Experimental Marine Biology and Ecology*, **366**, 37–47.
- Halpern B.S., Walbridge S., Selkoe K.A., Kappel C. V., Micheli F., Agrosa C., Bruno J.F., Casey K.S., Ebert C., Fox H.E., Fujita R., Heinemann D., Lenihan H.S., Madin E.M.P., Perry M.T., Selig E.R., Spalding M., Steneck R., & Watson R. (2008) A global map of human impact on marine ecosystems. *Science*, **319**, 948–952.
- Hoelzel A.. (2009) *Marine Mammal Biology: An Evolutionary Approach*. John Wiley & Sons,
- Jefferson T.A., Webber M.A., & Pitman R.L. (2011) *Marine Mammals of the World: A Comprehensive Guide to Their Identification*.
- Kelley L.A., Gardner S.P., & Sutcliffe M.J. (1996) An automated approach for clustering an ensemble of NMR-derived protein structures into conformationally related subfamilies. *Protein engineering*, **9**, 1063–5.
- Lambert W.D. (2006) Functional Convergence of Ecosystems: Evidence from Body Mass Distributions of North American Late Miocene Mammal Faunas. *Ecosystems*, **9**, 97–118.
- Lyrholm T., Leimar O., Johanneson B., & Gyllenstein U. (1999) Sex-biased dispersal in sperm whales: contrasting mitochondrial and nuclear genetic structure of global populations. *Proceedings. Biological sciences / The Royal Society*, **266**, 347–54.
- McGill B.J., Enquist B.J., Weiher E., & Westoby M. (2006) Rebuilding community ecology from functional traits. *Trends in ecology & evolution*, **21**, 178–85.
- Merigot B., Durbec J.-P., & Gaertner J.-C. (2010) On goodness-of-fit measure for dendrogram-based analyses. *Ecology*, **91**, 1850–1859.
- Pauly D., Christensen V., Dalsgaard J., Froese R., & Torres F. (1998) Fishing down marine food webs. *Science*, **279** %W <Go, 860–863.
- Perrin W.F., Würsig B., & Thewissen J.G.M. (2002) *Encyclopedia of marine mammals*. Academic Press, San Diego.
- Philpott S.M., Soong O., Lowenstein J.H., Pulido A.L., Lopez D.T., Flynn D.F.B., & DeClerck F. (2009) Functional richness and ecosystem services: bird predation on arthropods in tropical agroecosystems. *Ecological Applications*, **19**, 1858–1867.
- Riedman M. (1990) *The Pinnipeds: Seals, Sea Lions, and Walruses*. University of California Press,
- Sundstrom S.M., Allen C.R., & Barichiev C. (2012) Species, functional groups, and thresholds in ecological resilience. *Conservation biology : the journal of the Society for Conservation Biology*, **26**, 305–14.