Spatial mismatch in diversity facets reveals contrasting protection for New Zealand's cetacean biodiversity

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ABSTRACT

Cetaceans play key roles in the world's ecosystems and provide important economic and social benefits. New Zealand's Exclusive Economic Zone is a global biodiversity hotspot for cetaceans and benefits from a system of marine protected areas (MPAs). However, spatial patterns of cetacean biodiversity and their overlap with MPAs have never been assessed.

We quantify this overlap by using a comprehensive cetacean at-sea sightings database, high-resolution environmental data layers, and information on ecological and evolutionary characteristics of each species to model spatial patterns of taxonomic, functional, and phylogenetic diversity of cetaceans. We examine areas of congruence among hotspots of richness and uniqueness components of biodiversity and measure the contribution of species to biodiversity.

We find that cetacean taxonomic and phylogenetic diversity are spatially mismatched with MPAs, but this is less true for functional diversity. Hotspots of congruence among richness indices are located on the continental shelf break, whereas hotspots of uniqueness indices are located closer to shore on the continental shelf. Seven species have high contributions to biodiversity, with blue whale being the only species being evolutionarily distinct, functionally unique, specialised and globally endangered.

Our results underline the potential of multicomponent biodiversity indices, their spatial congruence, and the contribution of species to biodiversity to be used as guides for a strategic placement and expansion of MPAs to protect biodiversity.

1. Introduction

Biodiversity is facing globally intensifying threats, with multiple potential consequences for ecosystems and human well-being (Cardinale et al., 2012; Hooper et al., 2012; Isbell et al., 2017). Despite increasing effort and investment in the protection of biodiversity globally, there remains a requirement for increased protection (Sala et al., 2021) and accurate identification of biodiversity hotspots (Daru et al., 2015; Brum et al., 2017). In this context, taxonomic diversity remains the most widely used measure of biodiversity, despite growing recognition that it does not account for the ecological functions that species perform within ecosystems, nor represent species evolutionary histories (Devictor et al., 2010; Thuiller et al., 2015; Li et al., 2020). Adopting an integrated view from taxonomic, functional, and phylogenetic standpoints may, however, improve our understanding of biodiversity distribution across large spatial scales (Devictor et al., 2010, Stuart-Smith et al., 2013, Runge et al., 2015, Thuiller et al., 2015, S.L. Maxwell et al., 2020; S.M. Maxwell et al., 2020).

Protected areas are viewed as essential tools to protect biodiversity and ecosystems (Davidson and Dulvy, 2017; Cazalis et al., 2020; Mouillot et al., 2020). Conservation planning, however, has mainly focused on identifying priority areas that protect a proportion of the geographic range of specific biological features, such as species ranges. The assumption underpinning this approach is that maximising the representation of species within protected areas will ensure their persistence. However, planning protected areas in such a way as to capture maximum biodiversity, may not necessarily safeguard important ecological processes mediated by a wide range of functionally important species (Pimiento et al., 2020a, 2020b). Few studies have demonstrated a discrepancy between the design of protected areas and spatial patterns of biodiversity (Daru et al., 2015; Venter et al., 2018; Franke et al., 2020), especially with regards to protecting key functional roles and the diversity of species evolutionary history (Mouillot et al., 2016; Pollock et al., 2017; Daru et al., 2019). In this context, identifying which species contribute the most to measures of taxonomic, functional, and phylogenetic diversity and are threatened at the global scale, is of particular importance for targeting species-based conservation priorities (Isaac et al., 2007, Pool et al., 2014, Pimiento et al., 2020a, 2020b).

The New Zealand Exclusive Economic Zone (EEZ) is a global cetacean biodiversity hotspot (Kaschner et al., 2006; Albouy et al., 2017; Stephenson et al., 2021): in total, 47 cetacean species, subspecies and/or ecotypes including resident, migrant or vagrant taxa are known to occur in New Zealand waters (Baker et al., 2019). All cetaceans in New Zealand's EEZ are protected under national law by the New Zealand Marine Mammals Protection Act (1978). New Zealand has pioneered marine protection with the establishment of the Marine Reserves Act in 1971 and the creation of one of the world's first no-take marine reserves in 1975 (Ballantine and Gordon, 1979). Marine protection has increased in New Zealand's waters since then (Ballantine, 2014; Scott, 2016), with the creation of 44 no-take marine reserves and a network of partly no-take protected areas. These areas were mostly designed to promote recovery of exploited species (e.g., reef fish and benthic invertebrates), and more recently, also include areas of set netting restrictions for the protection of endemic coastal dolphins. Identifying hotspots of congruence among multiple components of cetacean biodiversity and the species that mostly contribute to this biodiversity is necessary to assess the effectiveness of current MPAs at protecting cetacean biodiversity and guide the expansion and placement of future MPAs.

Here, we model spatial patterns of taxonomic, functional, and phylogenetic diversity of cetaceans in New Zealand's EEZ to assess patterns of biodiversity and protection by MPAs to guide conservation planning. We measure overlap among biodiversity indices and their hotspots with MPAs. We assess spatial congruence among multiple components of biodiversity and calculate species contributions to biodiversity coupled with their global IUCN red list threat status. To do so, we used a database of high resolution at-sea sightings of cetaceans collected within the New Zealand EEZ and spanning more than 14,000 sightings occasions. We develop spatial predictions of cetacean species potential geographic distributions across the New Zealand EEZ and calculated measures of taxonomic, functional, and phylogenetic diversity. We then assess the extent to which MPAs overlap cetacean biodiversity. We finally examine the contribution of each species to patterns of functional and phylogenetic cetacean biodiversity coupled with their global IUCN red list status to inform conservation priorities for endangered species contributing much to cetacean biodiversity in New Zealand waters.

2. Methods

2.1. Cetacean at-sea sightings records

We used a comprehensive database of cetacean at-sea sightings records collected within the New Zealand Exclusive Economic Zone (EEZ). New Zealand's EEZ area extends over 4.2 million km^2 of the South Pacific Ocean, between latitude 25 to 57°S and longitude 162 to 172°W (Fig. 1). Sightings data originated from a variety of sources (citizen scientists, seismic vessels, tourist charters, scientific surveys, fishing vessels, aircrafts, and New Zealand ferries) and are described by Stephenson et al. (2020). Following quality control, that is, removing ~6000 records that lacked species identification or location, were located on land or outside the New Zealand EEZ, we used a total of 14,513 at-sea cetacean sightings records for 28 cetacean species (Table S1).

2.2. Environmental data

We used high resolution (1km^2) gridded data for thirteen environmental variables (Table S2) to describe cetacean environmental niches and habitat (i.e., physical processes and oceanographic features that may either influence cetaceans directly, or indirectly such as by influencing prey distribution; Bluhm et al., 2007, Lambert et al., 2014, Mannocci et al., 2020). These included: bathymetry, chlorophyll-a concentration in surface waters, distance to the 500-metre isobath, distance to shore, coloured dissolved organic matter concentration in surface waters, diffuse downwelling attenuation, mixed layer depth, seabed slope, sea surface temperature, tidal current speed, the residuals of a GLM relating temperature to depth using natural splines (positive residual values represent waters "abnormally" warm considering how deep they are, and vice-versa), and estimates of surface water primary productivity (Table S2). Predictor variables were not highly correlated (Pearson's |r| < 0.7; Stephenson et al. (2020)).

2.3. Species distribution models

2.3.1. Ensemble models for highly sighted species

We modelled geographic distributions of species with high sighting frequency (≥50 sightings, Stephenson et al. (2020); n = 13 species) using an ensemble modelling approach (Araújo and New, 2007). To maximise the benefits of competing statistical frameworks with different strengths and weaknesses and reduce the reliance on a single model algorithm, we used seven statistical algorithms of species distribution models (SDMs; generalised linear models (GLM), generalised additive models (GAM), generalised boosted regression tree models (GBM), random forests (RF), multivariate adaptive regression spines (MARS), artificial neural networks (ANN) and support vector machine (SVM)) (using the *ensemble_modelling()* function in the *SSDM* package (Schmitt et al., 2017)).

We generated pseudo-absences for each species following recommendations from Barbet-Massin et al. (2012). This includes the generation of 10,000 equally weighted and randomly distributed pseudo-absences for regression models (GLM, GAM and MARS), and an equal number of absences to the number of presences for each species for machine learning models (GBM, RF, ANN and SVM). This procedure was repeated 10 times for each species to generate 10 pseudo-absence data sets. We also used spatial thinning of species occurrences to deal with potential spatial autocorrelation in sightings records following Aiello-Lammens et al. (2015). The aim of thinning is to remove the fewest possible records needed to reduce the effect of sampling bias, while retaining the greatest possible amount of environmental variability for each species. The relative importance of environmental variables was estimated for each species using a jack-knife approach; i.e. the difference in Area Under the Curve (AUC) between an SDM containing all environmental variables and one with each environmental variable omitted in turn (Phillips et al., 2006).

The performance of each model was evaluated using holdout cross-validation; models were calibrated using 70% of the data and evaluated using the remaining 30%. Model performance was evaluated using AUC. We used Pearson's correlation coefficient to compare performance for each pair of statistical algorithms. Then, we performed an ensemble forecasting approach: if an SDM had an AUC superior or equal to 0.75, it
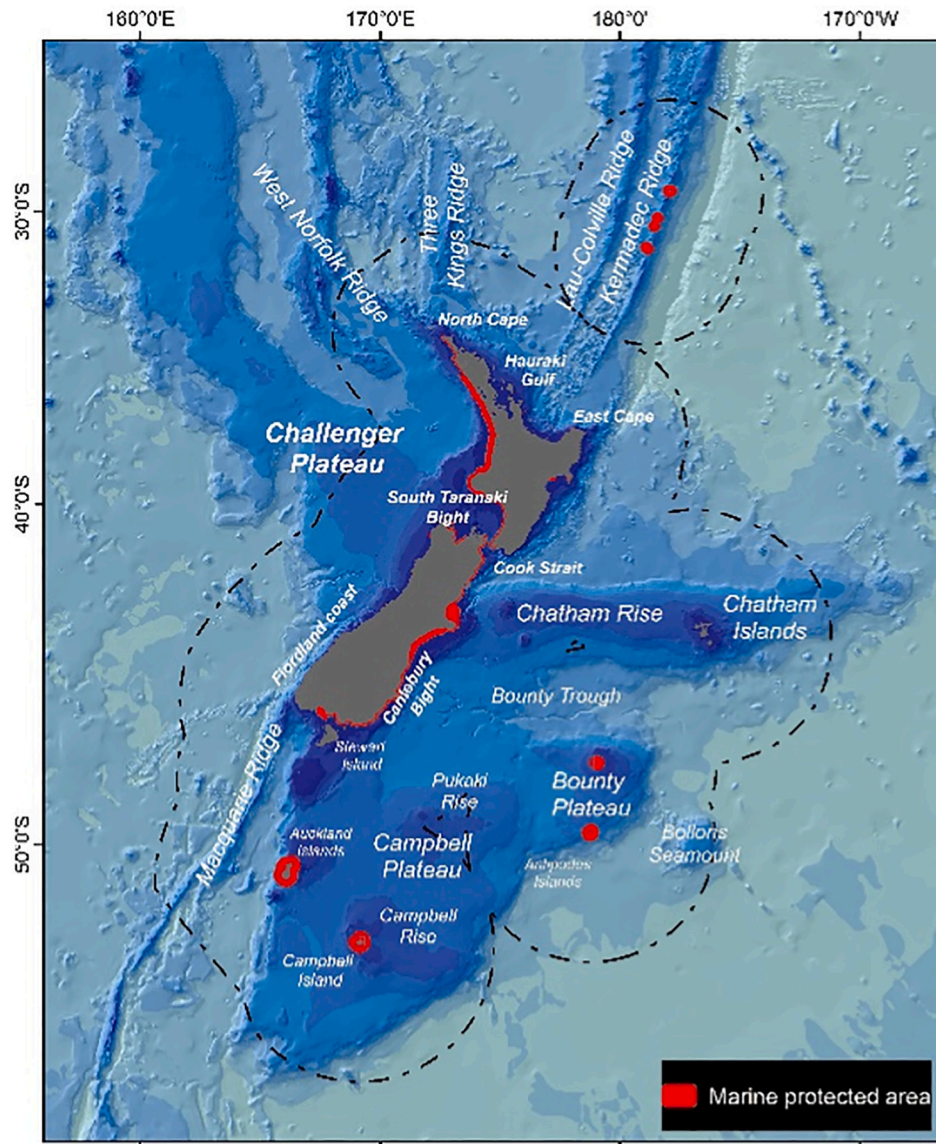
Fig. 1. Map of the New Zealand Exclusive Economic Zone (black dashed line) and surrounding areas. Bathymetry is shown as blue background. Marine protected areas are shown in red. The land is shown in grey colour. Feature names used throughout the text are written in white. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

was used to weight the means of predicted habitat suitability, and to combine ensembles of predicted species distributions (Marmion et al., 2009; Gritti et al., 2013). Finally, we generated binary (presence or absence) outputs of ensemble models using a threshold that maximised the True Skill Statistic (TSS) score (Thuiller et al., 2009).

2.3.2. Relative environmental suitability models for rarely sighted taxa

For species with few sightings (n < 50), we used Relative Environmental Suitability (RES) models from Stephenson et al. (2020). For RES modelling, cetacean sightings data are not used as inputs in the model but as a visual validation only (Stephenson et al., 2020). RES models were built using three environmental variables (sea surface temperature, water depth and distance to shore) to describe species' geographic ranges following methods described in Kaschner et al. (2006). Broadly, the relationships between species and the three environmental variables are described using a trapezoidal response curve based on four parameters: MinA, MinP, MaxP and MaxA. Where MinA and MaxA refer to absolute minimum and maximum variable ranges. While MinP and MaxP describe the "preferred" range of each environmental variable for

each species (Kaschner et al., 2006). While these simplistic models are likely less reliable than those using empirical relationships between species occurrence and habitat, they may be useful for discerning broad geographic distributions of rarely sighted species (Fig. 2).

Geographic ranges for each taxon were obtained by converting predicted relative environmental suitability into strict presence or absence. We use a probabilistic approach (the *convertToPA* function in the virtualspecies package v.1.5.1; Leroy et al., 2016), in which the probability of getting a presence of the species in each grid cell is dependent on its suitability in this grid cell. We defined the probability of presence as a logistic transformation of environmental suitability (Meynard and Kaplan, 2012; Meynard and Kaplan, 2013). Using this approach, the only parameter that can be customised is the parameter that determines the threshold of suitability above which the species is present and below which the species is absent (β). We randomly simulated β for each species 999 times and used the mean value of simulations as a cut-off to define presence or absence (Meynard and Kaplan, 2013).
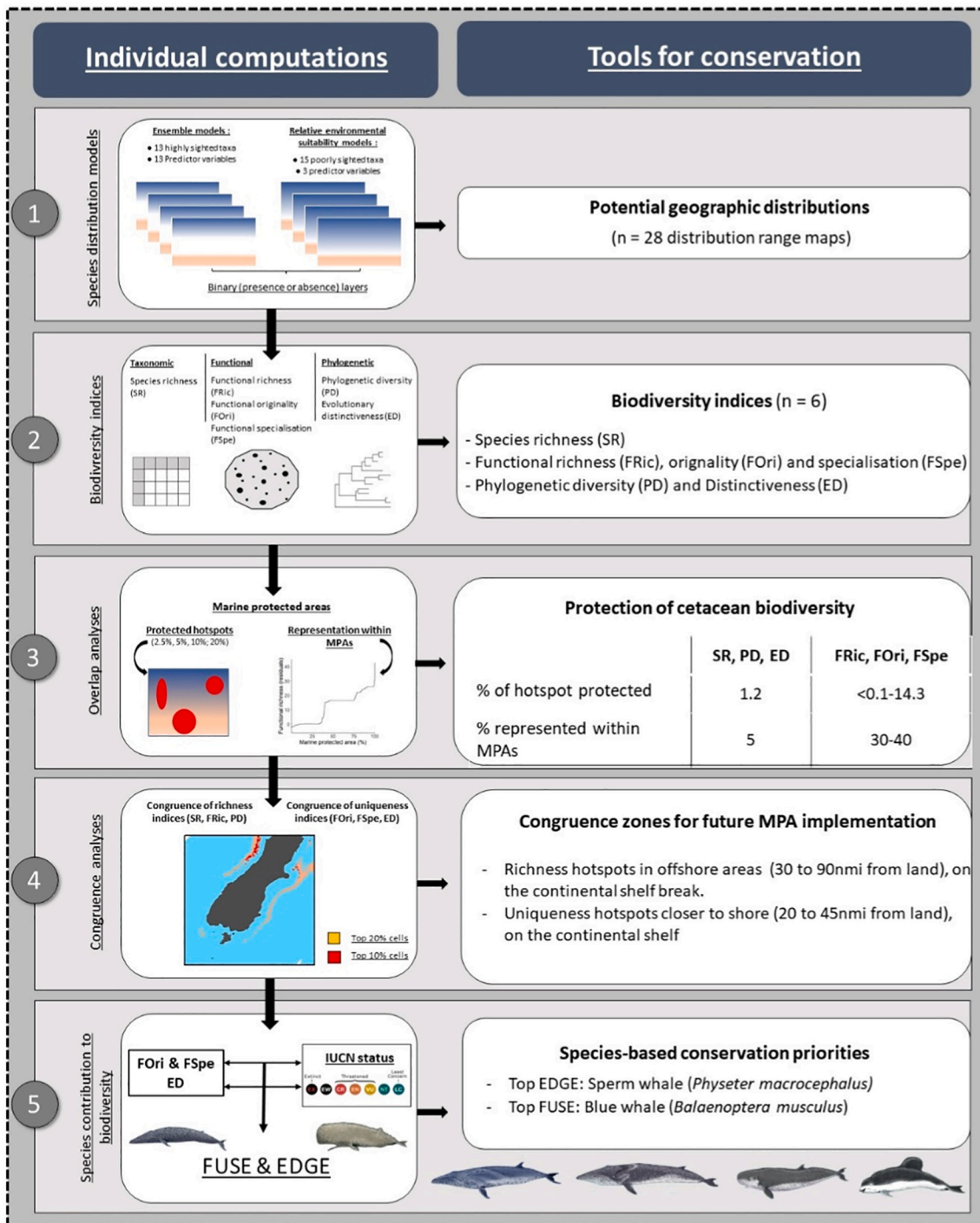
Fig. 2. Workflow diagram depicting each step of the individual computations performed in this study and their expected output for cetacean conservation in New Zealand. **(1)** Species distribution models were developed using two different methods: ensemble species distribution models were performed using thirteen environmental predictor variables for highly sighted species (≥50 at-sea sightings). Relative environmental suitability models were developed using three environmental predictor variables for poorly sighted species (<50 at-sea sightings). Both models were then transformed into binary layers of presence or absence for each species and used for further analyses. **(2)** A complementary set of biodiversity indices were measured at the scale of the Exclusive Economic Zone for the taxonomic (species richness, SR), functional (functional richness, FRic; functional originality, FOri; and functional specialisation, FSpe) and phylogenetic (phylogenetic diversity, PD; and evolutionary distinctiveness, ED) diversity components of biodiversity. **(3)** Overlap with marine protected areas (MPA) was measured using two complementary methods: the percentage of hotspots (i.e. the top 2.5, 5, 10 and 20% cells of each biodiversity index) overlapping MPAs; and the values of each biodiversity index represented within MPAs. **(4)** Congruence analyses were developed to identify areas of importance for biodiversity for future MPA implementation. For this purpose, indices were grouped into two sets, those that represent richness (species richness, functional richness, and taxonomic diversity) and those that represent uniqueness (functional originality, functional specialisation, and evolutionary distinctiveness) facets of biodiversity. Congruence was measured for pairwise combinations of two indices within each group and for three indices simultaneously. **(5)** Species contribution to biodiversity was measured to classify species for conservation priorities. We measured the contribution of species to (a) FOri and FSpe, (b) ED. We then coupled these contributions with their global degree of endangerment (IUCN red list status) to identify Functional Unique, Specialised and Endangered species (FUSE) and Evolutionary Distinct and Globally Endangered species (EDGE).

2.4. Functional traits

We built a database of thirteen functional traits following Albouy et al. (2017) for all at-sea sighted cetacean species contained in our database. These fourteen traits spanned five categories: resource acquisition, life-history, reproduction, social behaviour, and morphology; and included: diet composition, foraging depth range, foraging location, fasting, female sexual maturity, weaning, gestation length, inter-litter interval, breeding site, social group size, social behaviour, adult maximum body mass and sexual dimorphism (Table S3). We coded all traits following a quantitative, semi-quantitative or binomial coding framework (Table S3). Most values (>85%) were retrieved from the literature (encyclopaedias, books, scientific literature, and the grey literature), but expert knowledge (LT, WR, TB) was also used to parameterise a subset (c. 5%) of values.

There was a total of 28 trait values (7.1%) for which information was unavailable. We imputed these values to the trait database using a regularised iterative Principal Component Analysis algorithm (the *imputePCA* function in the missMDA package v.1.17; Josse and Husson, 2016). However, we used the original functional trait matrix for further analyses as it was highly correlated with the imputed matrix (Mantel test; r = 0.97, p < 0.001).

2.5. Biodiversity indices

We measured cetacean biodiversity for each grid cell of the EEZ using species richness as an indicator of taxonomic diversity, three indices of functional diversity and two indices of phylogenetic diversity. Species richness (SR) was measured by summing the individual probability of presence or absence of each species in each grid cell. Functional diversity was measured using the mean value of the following multidimensional indices in each grid cell (Villéger et al. (2008); using the R function *multidimFD* downloaded in December 2020 from: http://villeger.sebastien.free.fr/): functional richness (FRic), functional originality (FOri) and functional specialisation (FSpe). For these, we first produced a multidimensional functional space, using Principal Coordinates Analysis (PCoA) based on a Gower's distance dissimilarity matrix of each pairwise combination of all 28 species according to their 14 functional traits. Gower's distance was used as it allows the use of both binary and semi-quantitative values and can also deal with missing trait values. We ensured that equal weights were given to each of the trait categories (e.g. for the resource acquisition category which contained 3 traits, each trait was given a weighting of 1/3; Table S3). We

then synthesised functional traits using the first four axes of the functional space (as determined, using the R function *quality_funct_space*; Maire et al. (2015); Fig. 3). We built our functional space using four dimensions because the difference between mean squared deviations of a five-dimensional space and a four-dimensional space was negligible (0.0000001). Then, we calculated FRic as the total convex hull volume occupied by the species pool in the functional space (Villéger et al., 2008). FOri was calculated as the mean distance between each species and its closest neighbour in the functional space (Villéger et al., 2008). FOri increases as species contained in a community share fewer traits with other species. It may therefore be seen as equivalent to the inverse functional redundancy of a community (Mouillot et al., 2013a, 2013b). Finally, we calculated FSpe as the mean distance of each species to the centroid of the functional space (Villéger et al., 2008). Increases in functional specialisation show how specialist species (i.e., having extreme trait combinations) tend to increase in occurrence (Mouillot et al., 2013a, 2013b).

For phylogenetic diversity, we retrieved cetacean phylogeny from a molecular phylogenetic tree of cetaceans (Steeman et al., 2009). First, we used Faith's index (PD; using the *pd* function in the *picante* package v.1.8.2; Kembel et al., 2010), 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). Second, we measured evolutionary distinctiveness (ED; Isaac et al. (2007); using the *evol.distinct* function in *picante*), which is a measure of phylogenetic isolation of a species in the species pool. It is calculated as the ratio between total branch length and the number of species within a clade. ED increases as species have a long unshared branch length with all other species.

PD is mathematically correlated to SR (Tucker and Cadotte, 2013). Thus, we calculated the standardized effect size of phylogenetic diversity (ses.pd, using the *ses.pd* function in *picante*), which is the difference between the observed phylogenetic diversity in an assemblage and the mean phylogenetic diversity obtained with null assemblages generated by randomizing species from the regional pool 999 times, divided by the standard deviation of phylogenetic diversity in the null model (Gotelli and Graves, 1996). Positive ses.pd values indicate higher phylogenetic diversity than expected given SR, and vice-versa.

FRic is also mathematically correlated to species richness (Laliberté and Legendre, 2010). Thus, we calculated the residuals from a local regression model (frequently referred to as a loess curve) with SR as predictor variable and PD as response variable (res.pd). We then tested for a relationship between ses.pd and res.pd using Pearson's correlation coefficient (r). We found a high correlation (r = 0.77) among ses.pd and
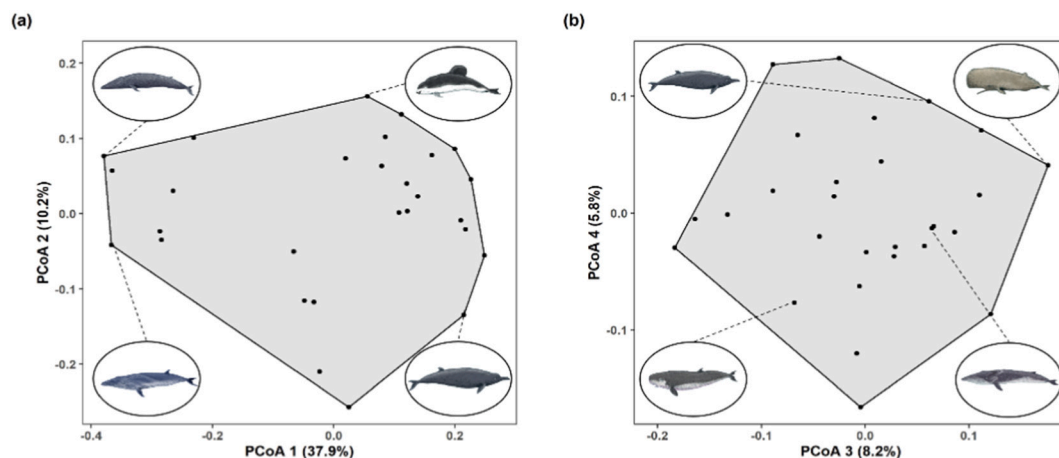

Fig. 3. Functional space of cetacean species considered in this study. Functional space was generated using the first four axes of a Principal Coordinates Analysis (PCoA) of 13 functional traits, based on dissimilarities among trait modalities. (a) Axis 1 versus axis 2; (b) axis 3 versus axis 4. Silhouettes illustrate the position of key species in the functional space, from top, right, bottom to left: (a) Blue whale (*Balaenoptera musculus*), spectacled porpoise (*Phocoena dioptrica*), Arnoux's beaked whale (*Berardius arnuxii*) and sei whale (*Balaenoptera borealis*); (b) Arnoux's beaked whale (*Berardius arnuxii*), sperm whale (*Physeter catodon*), fin whale (*Balaenoptera physalus*) and pygmy sperm whale (*Kogia breviceps*).

res.pd. For all analyses, we therefore replaced PD and FRic by the residuals from a loess model involving SR as predictor variable and PD or FRic as response variable, respectively. A negative PD or FRic index indicates lower diversity than expected given SR, and vice-versa.

2.6. Congruence analyses

To map the spatial congruence between all cetacean biodiversity indices themselves we used spatial congruence analyses. Spatial congruence analyses were undertaken between hotspots of complementary biodiversity indices. That is, indices that describe richness (SR, PD and FRic) and those that describe distinctiveness (ED, FOri and FSpe). Congruence analysis allows the identification of whether two biodiversity indices present similar spatial patterns of high values, which may not be visible if only correlations among indices are displayed (Albouy et al., 2017). 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 FRic. We then performed a randomization procedure, to assess whether the observed number of overlaps (Oo) was significantly different from that obtained by chance (Oe; Mouillot et al., 2011). The values contained in the cells for one of the two variables considered were randomly permuted 9999 times, and the number of overlaps was estimated for each. We tested for congruence among all pairwise of combinations of indices within these two sets. We then tested for overall congruence among the three indices for each set of index individually (Albouy et al., 2017).

2.7. Marine protected areas

We aggregated grided layers (1km^2) containing detailed polygons of a set of MPAs (n = 135) for New Zealand's EEZ, covering a total of 74,373 km^2 (1.8%) of the EEZ. We considered all MPAs that restrict set-net and/or trawl fishing year-round. That is, we considered (1) New Zealand's 44 no-take marine reserves (https://koordinates.com/layer/6026-doc-marine-reserves/), (2) 26 partly no-take MPAs and (3) 59 areas of set netting restrictions designed to protect endemic coastal dolphins (Set netting prohibitions | Ministry for Primary Industries Open Data Site (arcgis.com)).

2.8. Overlap analyses

We measured overlap between cetacean biodiversity hotspots and MPAs. We defined hotspots as all grid cells with values in the upper 2.5, 5, 10 and 20% of cells of each biodiversity index for comparison. Overlap analyses were performed: (1) between hotspots of the different biodiversity indices and MPAs, (2) for the biodiversity represented in each protected grid cell of the EEZ. First, we overlaid gridded MPA locations with the hotspots of each biodiversity index. We then measured the percentage of hotspots overlapped by MPAs, considering that even if a subset of a cell overlapped a protected area, the value of the index belonging to this cell potentially benefits from a protection effect. Second, we measured the diversity represented within each protected grid cell, following Mouillot et al. (2011). This approach provides a synthesised and continuous assessment of whether MPAs overlap areas of high biodiversity. For each biodiversity index, we extracted all grid cells overlapping MPAs, which we ranked from the least to the most diverse. We then plotted these ranked values of protected biodiversity against the cumulative percentage of protected area.

2.9. Species contribution to biodiversity

We measured the contribution of each species to biodiversity using a range of evolutionary and functional metrics. Globally, many species that are evolutionarily and/or functionally distinct, and globally endangered do not benefit from existing conservation projects or protected areas (Isaac et al., 2007; Pimiento et al., 2020a, 2020b). However, species contribution to biodiversity has been suggested as an effective tool to guide species-based conservation priority (Redding and Mooers, 2006, Isaac et al., 2007, Pimiento et al., 2020a, 2020b). We retrieved up-to-date IUCN red list status for all species of the database from the IUCN website (IUCN, 2021).

For phylogenetic diversity, we used the evolutionary distinctiveness of each species as described above (Isaac et al., 2007). We then combined evolutionary distinctiveness with the IUCN red list status of each species, to define evolutionarily distinct and globally endangered species (EDGE species; Isaac et al. (2007)). The EDGE index is defined as:

$$EDGE = ln(1 + ED) + GE*ln(2)$$

where ED is the evolutionary distinctiveness of each species, and GE is the IUCN red list category weight (Least Concern = 0, Near Threatened and Conservation Dependent = 1, Vulnerable = 2, Endangered = 3, Critically Endangered = 4; Butchart et al. (2004)).

For functional diversity, we measured the functional originality and specialisation of each species from our functional space, as described above (Villéger et al., 2008). These contributions were then integrated and combined with extinction risk to identify species that are both important contributors to functional diversity and endangered (FUSE species; (Pimiento et al., 2020a, 2020b)). To measure the FUSE index, we used the following formula:

$$FUSE = FUGE + FSGE$$

where

$$FUGE = ln(1 + (FOri \times GE))$$

and

$$FSGE = ln(1 + (FSpe \times GE))$$

where FOri is the standardized functional originality (also referred to as functional uniqueness by Pimiento et al. (2020a, 2020b)) of each species and FSpe the standardized functional specialisation. GE is the IUCN red list scores, from LC = 0 to CR = 4 (see above).

3. Results

3.1. Species distribution models

Ensemble modelling of species distribution for highly sighted taxa (n = 13) performed well across species and algorithms (mean AUC = 0.89 ± 0.06; sensitivity = 0.89 ± 0.07; specificity = 0.90 ± 0.05; Table S4). Across all species, environmental variables having the highest relative influence were distance to shore (% relative influence = 19.2 ± 10.5), temperature residuals (10.3 ± 8.5); mixed layer depth = 9.00 ± 9.90; bathymetry (9.35 ± 4.3), VGPM (7.6 ± 3.1) and sea surface temperature (7.2 ± 3.11; Table S5).

3.2. Functional trait space of cetaceans

The first axis of the trait space (37.9%, Fig. 3(a)) was strongly related to diet composition, foraging depth range and foraging location but strongly negatively related to fasting (Table S6). Southern right whale dolphin (*Lissodelphis peronii*) scored the highest value along the first axis, whereas blue whale (*Balaenoptera musculus*) scored the lowest value. The second axis (10.2%; Fig. 3(a)) was negatively related to foraging location, social behaviour and sexual dimorphism (Table S6). Sperm whale (*Physeter catodon*) scored the lowest value on the second axis, whereas dusky dolphin (*Lagenorhynchus obscurus*) scored the highest. The third axis (8.2%; Fig. 3(b)) of the trait space was negatively correlated to gestation length, weaning and female sexual maturity but positively related to breeding site and foraging location (Table S6).

Killer whale (*Orcinus orca*) scored the lowest value on the third axis, and hourglass dolphin (*Lagenorhynchus cruciger*) scored the highest value. Lastly, the fourth axis of the functional space (5.8%; Fig. 3(b)) was positively correlated to female sexual maturity and adult maximum body mass, but negatively correlated to diet composition (Table S6). Spectacle porpoise (*Phocoena dioptrica*) scored the lowest value on the fourth axis and blue whale (*Balaenoptera musculus*) scored the highest.

3.3. Spatial patterns of cetacean diversity

Species richness, phylogenetic diversity and evolutionary distinctiveness reached their highest values offshore (i.e. at a distance of 40 to 100 nautical miles from the land, Fig. 4(a)–(c)). In contrast, functional richness, originality and specialisation were highest in areas closer to shore (i.e. 0 to 40 nmi from the land, Fig. 4(d)–(e)).

Species richness ranged from 0 to 21 species (Fig. 4(a)). The highest values (>16 species) were in offshore areas along the west and east coasts of both mainland islands, the Chatham Islands, the eastern margins of the Challenger Plateau and the western margins of Chatham Rise. Predicted phylogenetic diversity was also highest in offshore areas (Fig. 4(b)). The highest values of phylogenetic diversity were located off the west and east coasts of both mainland islands, Chatham Rise and Islands, Steward Island, the Kermadec Ridge and the Auckland Islands.

Northern waters of the EEZ had greater phylogenetic diversity than southern waters (Fig. 4(b)). Evolutionary distinctiveness showed similar broad-scale spatial patterns to species richness (Fig. 4(c)).

Functional richness peaked along the edge of the continental shelf (i.e. 25–35 nmi from the land; Fig. 4(d)), on the Canterbury Bight, East Cape and the Hauraki Gulf (Fig. 4(d)). Finally, functional originality and functional specialisation were high along most of the continental shelf close to shore (0 to 25 nmi from the land) of both mainland islands and Chatham Island (Fig. 4(d) & (f)).

3.4. Spatial congruence among diversity indices

Congruence analyses using two indices, showed that the most congruent indices were SR and FRic (Fig. S1a, b, c & d; SR/FRic). In contrast, SR and PD, and PD and FRic were poorly congruent for the 2.5, 5% and 10% top cells (Fig. S1a, b & c; SR/PD & PD/FRic). ED & FOri and ED & FSpe, were not congruent for the 2.5% top cells (Fig. S1a), nor were ED and FSpe for the 5% top cells (Fig. S1b).

Congruence using three indices (SR, FRic and PD, ED, FOri and FSpe) was extremely low for the top 2.5 and 5% top cells (data not shown). Congruence of SR, FRic and PD was however apparent for the 10% and 20% top cells (Fig. S2(a)). Areas of congruence were in offshore areas (30 to 90 nmi from land), on the continental shelf break, especially in the
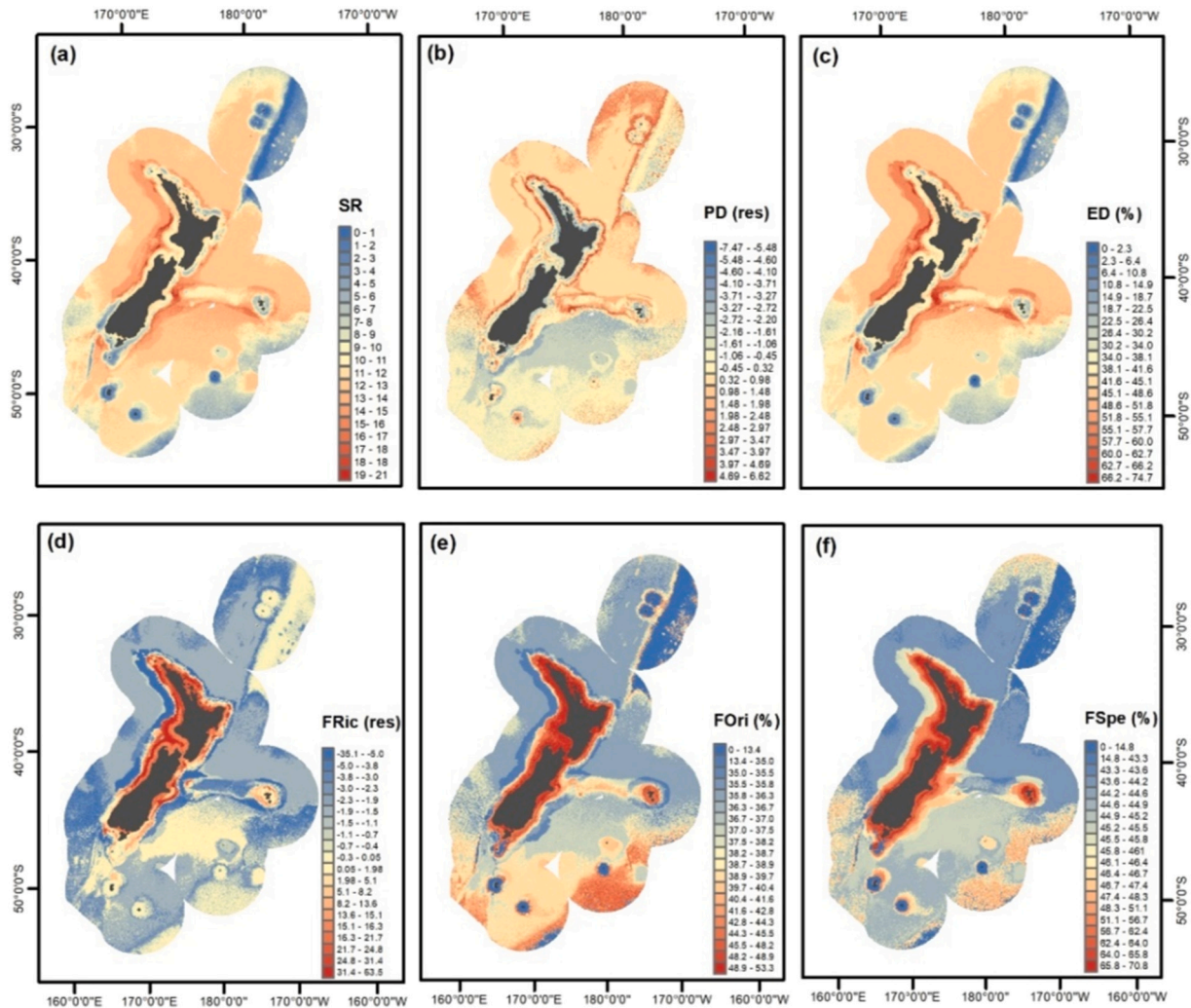

Fig. 4. Modelled spatial patterns of cetacean biodiversity in New Zealand's Exclusive Economic Zone as measured and predicted using six indices. (a) SR: species richness; (b) PD: phylogenetic diversity; (c) ED: evolutionary distinctiveness; (d) FRic: functional richness; (e) FOri: functional originality; (f) FSpe: functional specialisation. Res: residuals from relationships with species richness using local regression models. ED, FOri, and FSpe are represented as the percentage of their maximum possible value.

outer Hauraki Gulf, East Cape, Chatham Islands, the north-west of the North Island, the South Taranaki Bight and the Canterbury Bight (Fig. S2 (a)).

There was a higher congruence among ED, FOri and FSpe indices (Fig. S2(b)). Most congruence zones were located closer to shore (20 to 45 nmi from land), especially on the continental shelf around the South Taranaki Bight and Challenger Plateau, but also the West Coast of the South Island, Canterbury Bight and the northernmost part of the North Island (Fig. S2(b)).

3.5. Biodiversity overlaps with marine protected areas

There was little overlap (<1.2%) between species richness, phylogenetic diversity, and evolutionary distinctiveness hotspots with MPAs (Fig. 5(a) & (b)). In contrast, hotspots of functional richness, originality and specialisation had a greater amount of overlap with MPAs, yet this overlap was still relatively low (% of overlap ≤ 0.1–14.3%; Fig. 5(a) & (b)).

Regarding the representation of diversity indices within MPAs (Fig. 5 (c) & (d)): values within the top 10% hotspots of species richness, phylogenetic diversity and evolutionary distinctiveness were represented in only c. 5% of MPAs. In contrast, values within the top 10% hotspots of functional richness, originality and specialisation were represented in c. 60–70% of MPAs (Fig. 5(c) & (d)).
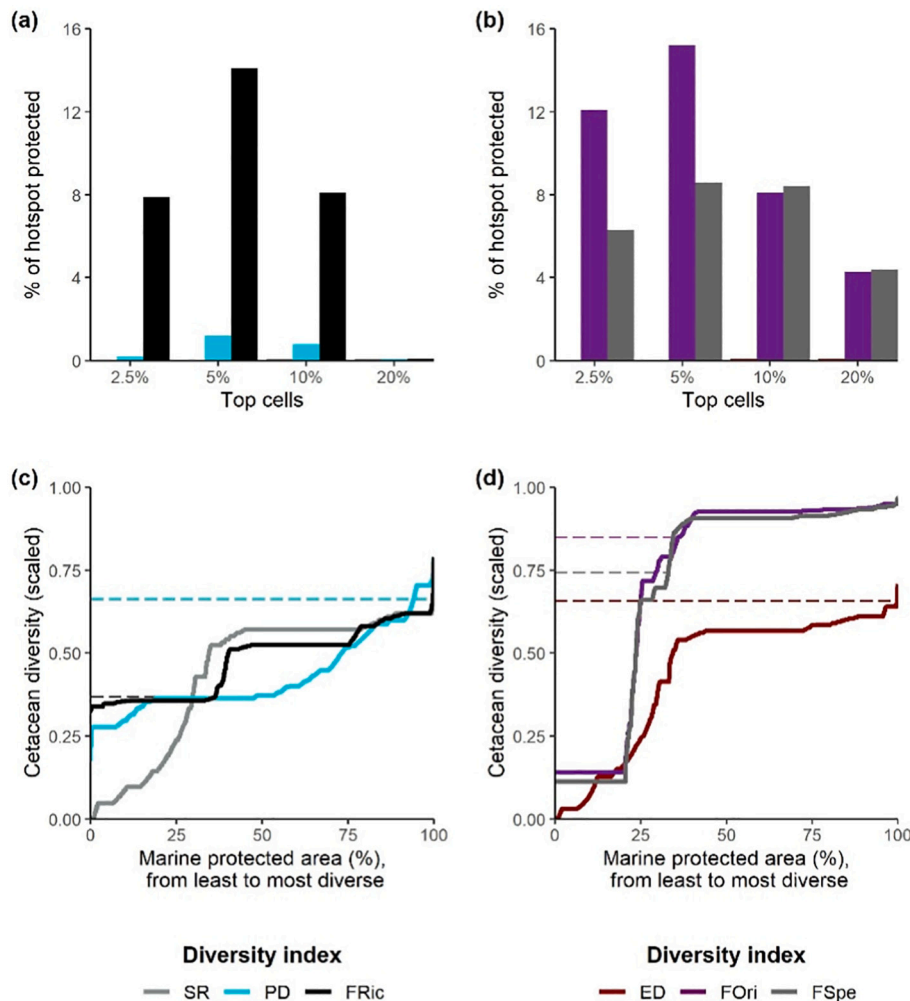
3.6. Species' contribution to biodiversity

The three most evolutionarily distinct species were southern right whale (*Eubalaena australis*; 7.2%), sperm whale (*Physeter macrocephalus*; 6.9%) and pygmy sperm whale (*Kogia breviceps*; 6.9%; Fig. 6, Table S5), while the three most evolutionary distinct and endangered species were sperm whale (EDGE = 3.44), southern right whale (EDGE = 3.41) and blue whale (*Balaenoptera musculus*; 3.36; Fig. 6, Table S5). In contrast, species contributing the most to functional originality were pygmy sperm whale (5.47%), spectacled porpoise (*Phocoena dioptrica*; 5.6%) and Arnoux's beaked whale (*Berardius arnuxii*; 5.1%; Fig. 6, Table S5), while the three most functionally specialised species were blue whale (6.7%), sei whale (*Balaenoptera borealis*; 5.8%) and fin whale (*Balaenoptera physalus*; 5.7%; Fig. 6, Table S5). Finally, the most functionally unique, specialised, and endangered species were blue whale (FUSE = 2.31), sei whale (2.19) and fin whale (1.67; Fig. 6, Table S5).

4. Discussion

Our analyses identified a spatial mismatch between hotspots of taxonomic, functional, and phylogenetic cetacean diversity and MPAs in New Zealand's Exclusive Economic Zone. Our results suggest that current MPAs poorly overlap hotspots of richness and uniqueness of cetacean diversity. We further show that New Zealand's MPAs are not representative of cetacean biodiversity for at least 30% of MPAs. Finally, we identify hotspots of congruence among multiple components of biodiversity and rank species contributions to biodiversity, revealing

Fig. 5. (a) & (b): Percentage of cetacean biodiversity hotspots (top cells) overlapped by MPAs in the New Zealand Exclusive Economic Zone. (c) & (d) Cetacean biodiversity represented in New Zealand's MPAs. Each plot gives the values of the corresponding diversity index represented within protected grid cells of the New Zealand Exclusive Economic Zone. To produce these plots, we first scaled each of the six indices to their range values (0 to 1). Then, we extracted the values of each index within each protected grid cell and ranked values from the lowest to the highest. Finally, we plotted the cumulative percentage of protected cells in New Zealand's Exclusive Economic Zone (horizontal axis) against the ranked diversity values (vertical axes). The coloured bands indicate values within the top 10% cells of each index. (a) & (c) SR: species richness; PD: phylogenetic diversity; FRic: functional richness; (b) & (d) ED: evolutionary distinctiveness; FOri: functional originality; FSpe: functional specialisation.
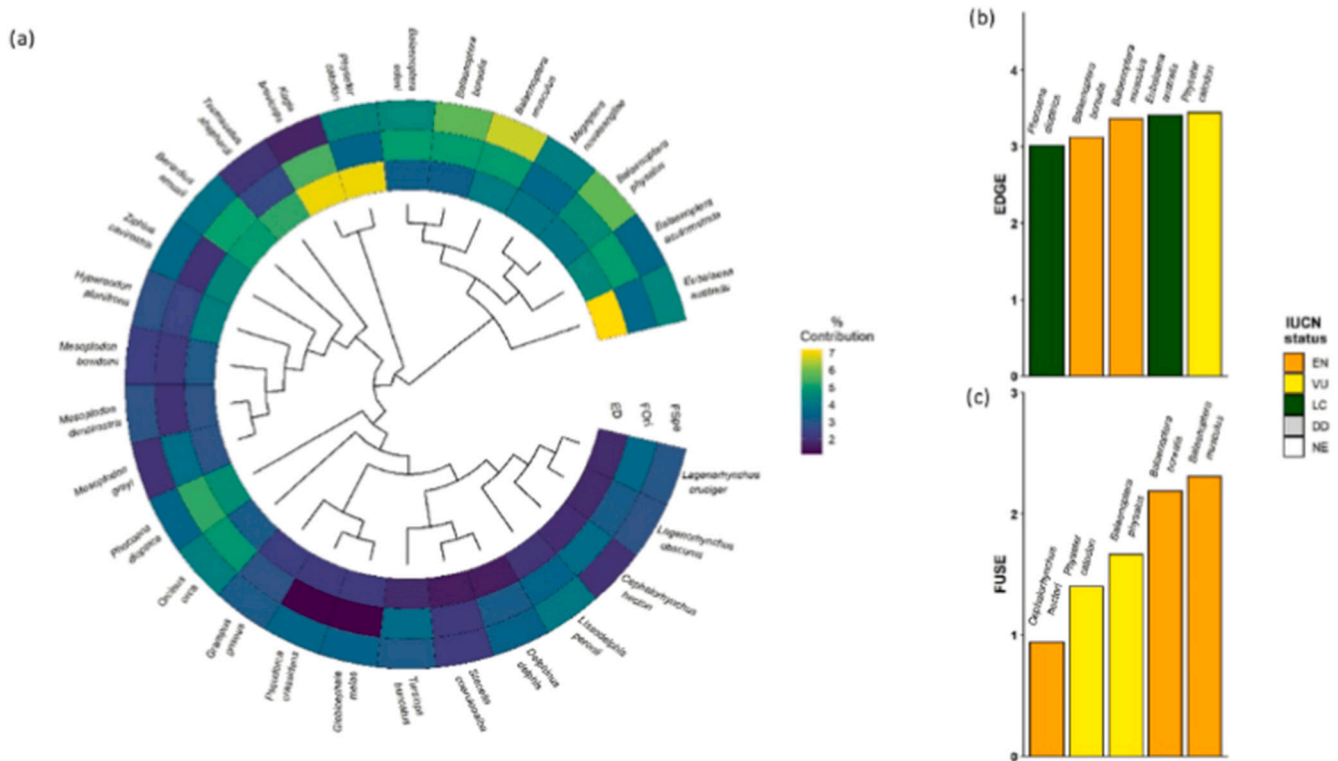
Fig. 6. Species contribution to biodiversity. (a) Phylogenetic tree of cetacean species used in this study showing values of Evolutionary distinctiveness (ED), functional originality (FOri) and specialisation (FSpe) (b). Top five scoring Evolutionary Distinct and Globally Endangered (EDGE) species. (c) Top five scoring = Functionally Unique Specialised and Endangered (FUSE) species. IUCN (red list) status: EN = endangered; VU = vulnerable; LC = least concern; NE: not evaluated; DD = data deficient. All values of species contribution to biodiversity are given in Table S6.

priorities and guidance for future cetacean distribution hotspots and species-based conservation efforts.

Our results revealed that species richness, phylogenetic diversity and evolutionary distinctiveness reached their highest values in areas 40 to 100 nautical miles from the coast. The location of these hotspots represent overlap areas between the ranges of species inhabiting inshore waters and those favouring offshore waters (Stephenson et al., 2020). Species distribution models of cetacean distributions at the scale of New Zealand's EEZ, have suggested that many of the cetacean species accounted for here (e.g., common dolphin, Māui dolphin, blue whale, fin whale, bottlenose dolphin and Bryde's whales) display preferences for northern, warmer, and high salinity, nutrient poor subtropical waters located to the west and north of New Zealand (Stephenson et al., 2020; but see Derville et al. (2016) and Barlow et al. (2020)). This result reflects the greater phylogenetic diversity found in northern areas of the EEZ. However, it is unclear whether preferences for northern waters are an indication of the environmental niches of these species or those of their prey. Nevertheless, we show that these areas have high conservation value for New Zealand's cetacean species evolutionary history.

Functional diversity measures increased toward near-shore zones of New Zealand. The New Zealand cetacean fauna comprises a diverse array of species, including endemic species that inhabit nearshore habitats only and other resident, migratory or vagrant taxa (Baker et al., 2019). An increase in functional originality toward near shore zones suggests a decrease in functional redundancy, which may reflect increased vulnerability and sensitivity of functions to environmental change in near-shore areas of the EEZ, as has been reported for other coastal areas worldwide (Mouillot et al., 2014; McLean et al., 2019). Increasing functional specialisation suggests that species inhabiting near-shore areas are also specialist species, performing unique functional roles (Mouillot et al., 2013a, 2013b). Here, the use of these two indices simultaneously was necessary to fully describe ecological

patterns, which was also the case for other studies (e.g., Colin et al., 2018 and Pimiento et al., 2020b). Together these two patterns of functional originality and specialisation suggest that the loss of a single species in near shore areas may destabilize ecological processes (Pimiento et al., 2020a, 2020b). Given that taxonomic and phylogenetic diversity measures were lowest in nearshore areas, the spatial patterns of functional diversity that were observed here, have important implications for conservation planning.

New Zealand is considered a global biodiversity hotspot for cetaceans, encompassing exceptional taxonomic, functional, and phylogenetic diversity (Kaschner et al., 2006; Albouy et al., 2017; Stephenson et al., 2021). Given this status, making well-informed decisions is crucial at both national and international scales to promote the long-term conservation of this biodiversity. Our study provides fruitful results in this sense, including that around 30% of MPAs in New Zealand are currently located in areas of low cetacean biodiversity. This indicates that despite the recent increase in MPA coverage over the last decade in New Zealand's EEZ, one third are generally not located in the most suitable or important sites to protect cetacean biodiversity. This lack of congruence between cetacean biodiversity and existing MPAs likely reflects a lack of consideration for this aspect of marine biodiversity within the current network. For example, most no-take marine reserves are established in relatively small areas in coastal habitat to promote recovery of exploited species (e.g., reef fish, invertebrates). Additionally, historical MPA planning processes were unlikely to have detailed information available on cetacean biodiversity to draw upon, and instead, designation for protection of cetaceans has been targeted at single species such as Hector's and Maui dolphins (Derville et al., 2016). Expanding MPAs with large and/or offshore MPAs and Important Marine Mammal Areas appears to be necessary for cetacean conservation in New Zealand, as was also suggested for other ecosystems worldwide (Singleton and Roberts, 2014, Davies et al., 2017, Agardy et al., 2019, S.

L. Maxwell et al., 2020; S.M. Maxwell et al., 2020).

We identified congruent areas among indices of both richness and distinctiveness. Areas of congruence among richness indices were mostly located along the edge of the continental shelf. In contrast, areas of congruence among indices of distinctiveness were located closer to shore, on the continental shelf. Shelf-break areas may function as transition zones where both coastal and offshore species overlap within a narrow band of highly variable habitat characteristics. The New Zealand continental slope environment is punctuated by diverse topographical features (e.g., submarine canyons, seamounts, plateaus) and this diversity in habitat types may be reflected by the high diversity of species that use this area. The western boundary currents that define New Zealand's broad oceanographic setting are steered by seafloor topography at approximately the depth of the continental shelf break (Smith et al., 2013), which likely promotes mesoscale features (e.g., eddies, fronts) that may provide foraging opportunities for diverse cetacean species. Mobile species such as cetaceans may provide different functions in different areas, particularly those that use certain habitats for different life-history stages (e.g., breeding/calving areas for baleen whales; Rayment et al., 2015). Protecting these areas may represent strategic investment to increase conservation gains by MPAs in New Zealand's waters.

The fact that functional diversity indices spatially differed from our estimates of phylogenetic diversity suggests that our set of traits are not phylogenetically conserved; i.e. that closely related species do not necessarily share similar traits (Thuiller et al., 2015). This discrepancy supports the notion that prioritizing phylogenetic diversity for conservation does not capture functional diversity reliably (Mazel et al., 2018). Thus, this study highlights the need to integrate multiple components of biodiversity in conservation frameworks (Devictor et al., 2010; Mazel et al., 2018). The relationship between evolutionary and functional distinctiveness depends on the mode of trait evolution, the rates of speciation and extinction in a clade, and the interaction between these processes (Grenié et al., 2018). The influence of factors such as convergent evolution and niche conservatism on the relationship between evolution and functional strategies at the assemblage level is still poorly explored (Mazel et al., 2017; McLean et al., 2021). A comprehensive perspective on how functional and evolutionary distinctiveness relate across different taxa, is necessary to further guide conservation prioritization.

We found that the most evolutionarily distinct, functionally original and/or specialised species differed from those being threatened at the global scale. As functionally original and specialised species differ in trait composition from the rest of the species pool, these may support unique ecosystem functions (Mouillot et al., 2013a, 2013b), yet do not seem to be considered by conservation strategies as species needing prioritized protection. Sperm whales and pygmy sperm whales are deep diving specialists, that contribute to the recycling of nutrients stored in the deep ocean and enhance carbon sequestration (Lavery et al., 2010). Southern right whales are also ecological specialists that forage on dense aggregations of zooplankton consisting largely of euphausiids and copepods (Tormosov et al., 1998). The significant spatial separation between foraging and breeding grounds promotes large scale transport of micronutrients that enhance productivity in the micronutrient poor southern ocean (Wing et al., 2014). The mismatch between red list status and functional traits validates the use of functional diversity metrics as an important component to identify species that are not threatened at the global scale, but likely support unique functions in ecosystems, such as the New Zealand Exclusive Economic Zone.

Our study provides novel results and highlights conservation gaps for cetaceans in New Zealand's waters, that can be used to improve MPA planning. However, we recognise that it may represent a starting point. Further research effort should be focused in improving fine-scale knowledge on cetacean ecology and distribution, such as, increasing sampling effort and diversifying sampling methods, for example, using targeted eDNA (Juhel et al., 2021) or tracking data (Hays et al., 2019).

Comparing mapping approaches among different distribution maps and modelling approaches (Albouy et al., 2017; Herkt et al., 2017; Derville et al., 2018), will further strengthen our capacity to protect this biodiversity.

New Zealand waters are among the most diverse areas for cetaceans on Earth and face increasing environmental changes. Given the increasingly recognised link between biodiversity, its protection and human well-being (Ban et al., 2019), protecting such biodiversity should therefore be a priority (Sala et al., 2021). Thus, it is important to establish systematic conservation planning for the multiple components and facets of biodiversity (Brum et al., 2017), as a key process within government agencies responsible for conservation and development planning. Our results can be used by managers to identify areas that should be considered for cetacean conservation planning in New Zealand waters. Priorities for conservation should be continuously updated as solutions are implemented when knowledge of changes in species contribution to biodiversity and degree of endangerment changes. Our study identifies novel, yet important, challenges for increasing the protection of cetacean biodiversity in New Zealand's marine environment.

CRediT authorship contribution statement

Théophile L. Mouton, Fabien Leprieur, Fabrice Stephenson and Camille Albouy: Conceptualization. Fabrice Stephenson, Théophile L. Mouton, Leigh Torres, Will Rayment and Tom Brough: Data curation. Théophile L. Mouton: Formal analysis, Writing - original draft. All authors: Writing - review & editing.

Declaration of competing interest

Authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109484.

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