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Species composition and turnover models provide robust approximations of biodiversity in marine conservation planning

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ABSTRACT

Robust design of Marine Protected Areas in ocean environments is often challenging due to inadequate knowledge of biodiversity patterns, reflecting difficulties in the prediction of species distributions from sampling data that are often sparse or inadequate. Models that combine species and environmental data, such as Gradient Forests (GF), provide one analytical approach to this problem, efficiently combining available information to produce spatial models of species turnover throughout an area of interest. Spatial estimates of species turnover can then be classified to estimate spatial patterns in species composition; however, the performance of GF-based classifications within a conservation planning context has not previously been evaluated. Here we assess the utility for conservation planning (using the software *Zonation*) of a GF-based hierarchical classification that summarises spatial patterns in demersal fish composition in the oceans around New Zealand. Progressively more complex *Zonation* analyses assessed the effects of (i) varying the number of classification groups, (ii) adding information describing species turnover, and (iii) adding information describing spatial variation in demersal fish species richness. The best-performing GF-based conservation ranking used layers describing the distributions of 30 classification groups, demersal fish species turnover between these groups, and species richness. Conservation outcomes from this ranking were only marginally less efficient than those from a more conventional ranking that used 217 individual species distribution layers (7% less efficient). This indicates that GF-based classifications may provide a practical alternative for marine conservation planning. Additional advantages arise from the greater ease with which a single classification layer summarising complex biodiversity patterns can facilitate decision-making in participatory stakeholder processes.

1. Introduction

Robust identification of priority areas for conservation is often hampered by a lack of comprehensive knowledge of biodiversity patterns (Arponen et al., 2008; Ferrier et al., 2007; Hortal et al., 2015). The understanding of biodiversity in marine environments is challenging due to sampling logistics, particularly in deep water, and the large numbers of species that are either poorly described or for which there are too few records to generate robust species distribution models (SDMs) (Anderson et al., 2016; Ellingsen et al., 2007). Although sampling is often most comprehensive for fish species, given their commercial value, SDMs often work well only for more common species. As a consequence, the full complement of biodiversity is typically not represented in marine conservation planning, despite the important roles that less common species can play in the stability and functioning of marine ecosystems (Ellingsen et al., 2007).

One approach used to overcome this difficulty is to summarise biodiversity patterns by classifying readily available environmental data into groups that are likely to have similar biological character (e.g., Dunstan et al. (2012); Gregr and Bodtker (2007); Leathwick et al.

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(2012)). Early environmental classification approaches relied largely on subjective choice of environmental variables likely to drive species distributions (Snelder et al., 2006). However, more recent environmental classification models use species observations to weight and/or transform environmental variables to maximise the correspondence between classification groups and spatial variation in species composition (e.g., Ferrier et al., 2007; Leathwick et al., 2011). These new approaches provide significant improvements over environment-alone approaches (Pitcher et al., 2012) and are more likely to capture information across a full range of species, allowing for representation of both common and rare species when describing spatial variation in species composition and turnover (Stephenson et al., 2018; Sutcliffe et al., 2015).

Gradient Forests (GF – Ellis et al. (2012); Pitcher et al. (2012)) is one analytical approach that uses species distribution data to control the selection, weighting and transformation of environmental predictors to describe species turnover and composition at broad spatial scales. A GF model aggregates results from a collection of Random Forest models (Breiman, 2001), each of which describes the environmental relationships of an individual species. Information from the individual Random Forest models about the relative importance of each environmental predictor, and information on where changes in the presence (or abundance) of the modelled species occur along their ranges is aggregated to generate a transformed set of environmental predictors that have maximal correlation with species turnover. These transformed predictors (representing species compositional turnover) can then be classified to define groups summarising spatial patterns in species composition (Pitcher et al., 2011), including at sites lacking biological samples. For example, Stephenson et al. (2018) used GF models to analyse demersal fish data from an extensive research trawl dataset from New Zealand's marine area to the outer limits of the Extended Continental Shelf (ECS). The transformed predictors from this analysis were then classified and mapped geographically with a classification detail ranging from 10 to 100 groups. Subsequent analysis indicated that a 30-group hierarchical classification was highly effective at summarising spatial patterns in demersal fish composition and turnover, although the hierarchical nature of the classification supports its use at varying levels of classification detail.

GF-based classifications have several key features that could make them particularly useful for resource management and conservation planning. Firstly, they can be created at various hierarchical levels of group-detail, a feature that makes them particularly useful when they need to be applied at differing spatial scales (national to regional to local) (Stephenson et al., 2020). Secondly, because the classification is based on GF (tree-based) models of species turnover functions across environmental gradients, it can readily describe non-linear changes in species composition in relation to environment, e.g., decreases in species turnover at depths >1500 m (Stephenson et al., 2018). Together, these two attributes mean that a single classification can reflect the dynamic environments in inshore areas with a greater number of classes compared to fewer classes in the more homogenous offshore areas. Thirdly, such classifications contain information on inter-group similarities (i.e., estimate of species compositional turnover). Finally, a GF-based classification summarises complex multi-species data to a more manageable number of groups (e.g., <100 groups) which can be more user friendly for participatory processes compared to a greater number of individual species distribution layers (Gleason et al., 2010). However, the performance of using GF-based classifications within a conservation planning context has not yet been evaluated.

Here, we test the utility for conservation planning of the GF-based classifications of demersal fish distributions developed by Stephenson et al. (2020) using the spatial planning software *Zonation* to develop conservation rankings (Moilanen et al., 2014). We first develop a conventional 'baseline' analysis identifying conservation rankings using input layers describing the predicted distributions of 217 individual demersal fish species. We then compare results of the baseline analysis against three separate suites of analyses using GF-based classifications of demersal fish species composition to evaluate: (i) the effect of varying the number of GF classification groups (i.e., 10, 20, 30, 50 or 100 groups) on conservation priorities; (ii) the effect of using both species composition and species turnover layers at a 30-group level; and (iii) the effect of using species richness in addition to using species composition and species turnover at a 30-group level. With the successive addition of different facets of biodiversity represented in our three suites of analyses (demersal fish species compositions, turnover, and richness) we expect to observe an increase in the effectiveness of our spatial conservation planning measures to represent demersal fish biodiversity.

2. Methods

The study area for all analyses comprised New Zealand's marine area to the outer limits of the ECS to depths of 2000 m. All analyses used a large set of data describing the distributions of demersal fish species collected from research bottom-trawl surveys in the study area between 1979 and 2005; this database contained ≈207,000 records of catch for 253 demersal fish species from research trawls at 27,440 unique locations (aggregated to 1 km^2). As changes in trawl sampling methods resulted in difficulties in providing comparable abundance estimates, all catch records were converted into presence/absence for our analyses. Environmental parameters for each trawl were derived by overlaying their location onto fifteen functionally-relevant environmental predictors mapped across the study area on a 1 km resolution grid (for a full list of environment variables see Table 1 in Stephenson et al., 2020). These datasets were used to predict individual species distributions for 217 demersal fish species, a GF-based classifications of species composition and turnover for 253 species of demersal fish, and a spatial estimate of demersal fish species richness.

2.1. Spatial biodiversity estimates

2.1.1. Predicted species distributions

Predicted distributions of species occurrence were produced for 217 demersal fish species with at least 30 records in the dataset (Fig. 1). These predictions were derived from individual logistic BRT models using 15 environmental predictors, and fitted using ten-fold cross-validation to maximise their predictive performance. Individual cross-validated AUC scores, a measure of predictive performance, were calculated during the BRT model fitting process for each species (see Elith et al. (2008)). An example predicted distribution (*Allocyttus niger* – black oreo) is provided in Suppl. Fig. 7.

2.1.2. Gradient forest models of species composition and turnover

Spatial variation in demersal fish species composition and turnover was derived from a GF-based classification using 253 demersal fish species with >10 records in the database (217 species for which SDMs were developed in section 2.1.1, and an additional 36 species with fewer records) (Stephenson et al., 2018). A subset of 13,917 of the research trawl locations (randomly selected from a possible 27,440) and the 15 environmental predictors were analysed with the R package 'gradientForest' (Ellis et al., 2012) and the base package in the statistical computing software R (R Core Team, 2020). Not all research trawl samples were used in the GF model because repeated analyses with

subsamples of the training dataset indicated minimal changes in model stability with expansion of the data beyond ca. 5000–7000 samples (Stephenson et al., 2018). The inclusion of a larger sample number here (13,917 samples) ensured that information from all 253 demersal fish species contributed to the estimates of species compositional turnover. Results from the GF model were used to transform the environmental predictor layers creating a 'transformed environmental space' representing turnover in species composition (Stephenson et al., 2018). A hierarchical numerical classification was then used to transform the environmental layers into varying levels of classification detail (10, 20, 30, 50, and 100 groups; Suppl. Figs. 1–5). A detailed description of the methods for model fitting and evaluation is contained in Stephenson et al. (2018).

2.1.3. Models of species richness

A species richness layer (i.e., the total number of species predicted to occur in any given location) was predicted using an analysis of species count from the research-trawl dataset in a boosted regression tree (BRT) analysis with a Poisson error term (Elith et al., 2008), using the same 15 environmental variables. A ten-fold cross-validation procedure was used to maximise its predictive performance (Suppl. Fig 6).

2.2. Conservation rankings

We used the raster-based spatial planning software, *Zonation* (Moilanen et al., 2005, 2014) to develop spatial conservation rankings (Moilanen 2007; Virtanen et al., 2018). Raster layers representing

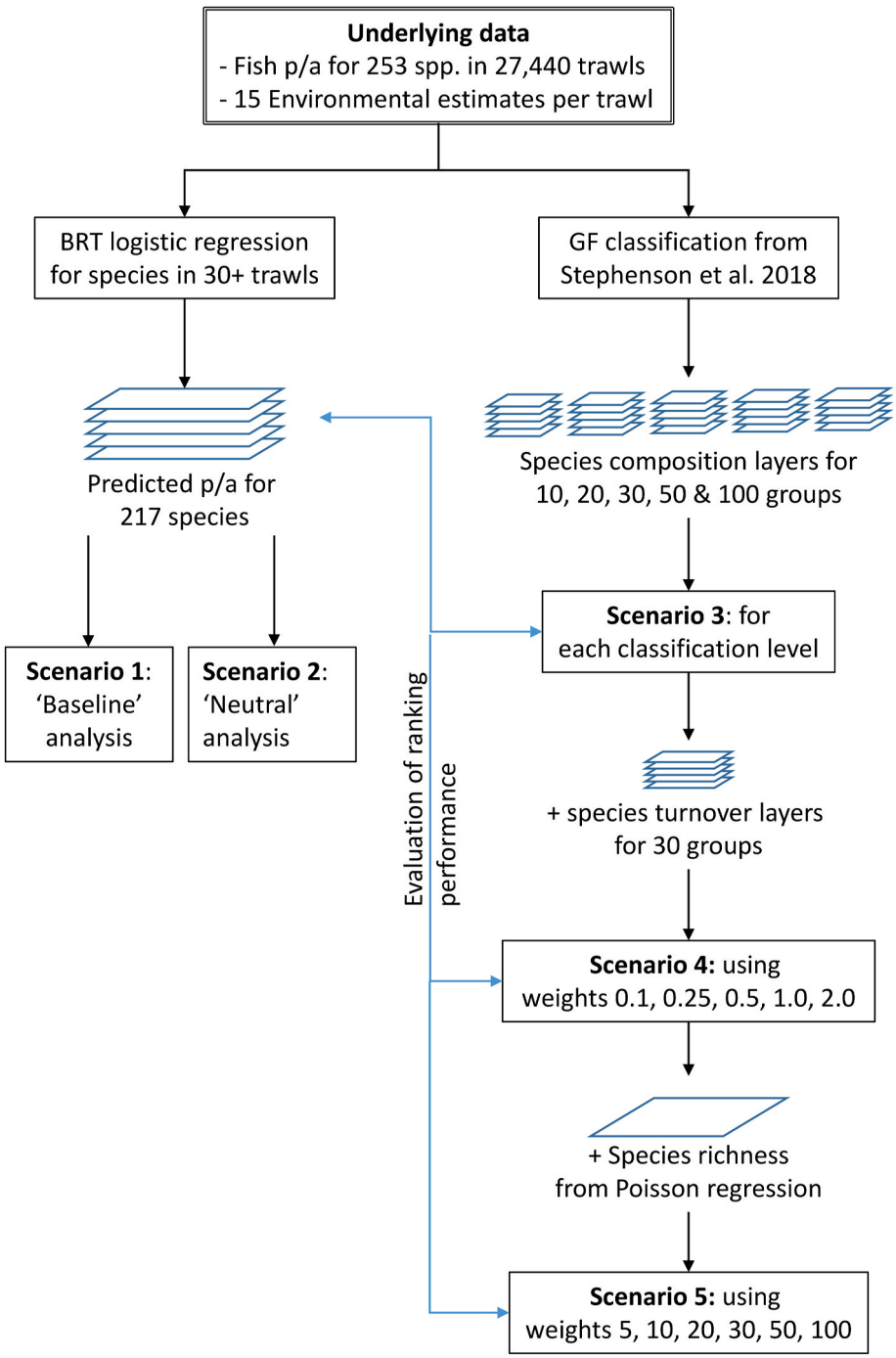

Fig. 1. Key steps in the preparation of spatial data layers and their use in spatial conservation planning analyses.

biodiversity are input into *Zonation* after which an algorithm is run to determine which areas are most valuable for conservation. *Zonation* initially assumes that all cells in a landscape (or seascape) of interest are protected, and then iteratively identifies and removes those cells that generate the smallest marginal losses in the representation of the biodiversity features included in the analysis (Moilanen et al., 2014). Iterative removal produces a nested hierarchical prioritisation of the landscape, allowing identification of relative priority of cells for different protection targets. *Zonation* outputs include maps of conservation ranking, along with tabular summaries of the proportional representation of biodiversity features as a function of landscape protection (Moilanen et al., 2009).

We performed two suites of conservation rankings using gridded data layers with a spatial resolution of 1 km: (1) 'baseline' and 'neutral' analyses against which subsequent GF-based analyses could be evaluated; and (2) a GF-based analyses examining the effect of (i) varying the number of GF classification groups on conservation priorities; (ii) incorporating metrics of species turnover in conjunction with species composition; and (iii) incorporating species richness in addition to using species composition and species turnover at a 30-group level. For each analysis, we specified the additive benefit function as the cell removal rule, which considers all biodiversity features within a location and gives more weight to locations with greater numbers of biodiversity features, maximizing average performance over all biodiversity features. To maximise processing speed, *Zonation's* default workflow uses an 'Edge Removal' option, which preferentially targets for removal cells at the edges of a landscape. In initial trial rankings, this penalised the rankings assigned to classification groups occurring around the periphery of the study area (e.g., shallow- and deep-water groups), while those away from the study area margins (e.g., intermediate depth groups) received inflated rankings. To avoid this bias, we inserted 'edge' cells randomly on a regular 100 km grid throughout the study area, maintaining processing speed without unduly penalising groups located around the periphery of the study area.

2.2.1. *'Baseline' and 'neutral' zonation analyses*

We initially developed 'baseline' and 'neutral' analyses against which the performance of all GF-based analyses could be assessed. Scenario 1 (representing a conventional 'baseline' analysis) used input layers describing predicted distributions of the 217 demersal fish species. Species layers were weighted using their individual cross-validated AUC scores. Given their relatively narrow range (0.75–0.99), AUC scores were squared to give greater weighting to well predicted species and less weight to less well predicted species (AUC scores used as weights varied between 0.56 and 0.99). Scenario 2 (a 'neutral' or unweighted analysis) used a cell removal rule in *Zonation* that removes cells at random, i.e., without any consideration of their contribution to conservation outcomes. This random analysis was repeated ten times, with rankings averaged to ensure that results were not affected by the random nature of a single iteration of the cell removal rule.

2.2.2. *GF-classification based zonation analyses*

Three sets of *Zonation* analyses of progressively increasing complexity were performed using data input layers derived predominantly from the GF-based classification. Scenario 3 only considered spatial variation in demersal fish composition (as represented by the GF classification groups); Scenario 4 considered demersal fish composition and turnover (as represented by the by the GF classification groups and layers describing their inter-group similarities); and Scenario 5 considered demersal fish composition, turnover and species richness. Analyses in Scenarios 4 and 5 extended the best-performing variant from the previous set.

Scenario 3 tested the effect of variation in the number of GF classification groups used as input layers (i.e., 10, 20, 30, 50 and 100 groups) on conservation rankings (upper right of Fig. 1). Each of these analyses used a set of spatial data layers comprising one layer for each of its classification groups (i.e., 10 layers representing the 10 classification groups were used in the first analysis, 20 layers for the 20 groups in the second analysis, etc). Occupied cells within each of these classification group layers were assigned a value indicating their similarity to their group centroid (1 – Manhattan distance) within the transformed environmental space; values typically ranged between 0.95 and one. This approach favoured the selection during ranking of those cells with the strongest similarities to the group centroid, preferring cells with highest within group similarity over cells that were transitional between two related classification groups. These sets of layers represent the distributions of groups that summarise spatial variation in demersal fish species composition (referred to herein as 'species composition layers'). Given the hierarchical nature of the classification, we expect that a wider range of species will be represented in our spatial conservation rankings with increasing number of classification groups. However, increases in species representation may be minimal past a certain number of classification groups.

Scenario 4 tested the effect of using both species composition and species turnover layers at a 30-group level of classification on conservation outcomes (Fig. 1). The 30-group level of classification was selected because it represented a moderate number of groups while carrying little penalty in conservation planning outcomes (see results). During these analyses, ranking favoured the selection of groups differing strongly in their composition from all other groups (i.e., accounting for intra-group similarity), indicating a likelihood of groups supporting distinct species not represented elsewhere. Five different weightings were applied to the species turnover layers (0.1, 0.25, 0.5, 1.0, 2.0) to vary their influence on ranking outcomes relative to that of the species composition layers, which were all set to a weight of 1. These layers represent intra-group similarity of demersal fish composition (i.e., demersal fish turnover) and are referred to herein as 'turnover layers'). The addition of demersal fish turnover will favour the selection of groups differing strongly in their composition from all other groups. We expect that a wider range of species will be represented in our spatial conservation rankings with increasing weighting of this layer. However, similarly to the analysis using only species composition, increases in species representation may be minimal past a mid-range weighting of these layers.

Scenario 5 tested the effect of adding a species richness layer to the analysis using equal weighting of species composition and turnover layers (Fig. 1). During analysis, ranking favoured the selection of cells with higher species richness indicating the likelihood of them supporting more species. Five different weights were applied to the species richness layer (5, 10, 20, 50, 100) to vary its influence relative to the species composition and turnover layers. While the rate of species turnover between sites may determine the optimal spatial arrangement of a set of conservation areas (Scenarios 3 and 4), the total number of species (alpha diversity) contributes to the relative local importance of an area for conservation (Arponen et al., 2008). In scenario 5, we expect a further gain in the representation of a wider range of species with increasing weighting of the layer representing variation in species richness when combined with layers representing demersal fish species composition and turnover.

2.2.3. Assessing ranking performance

We assessed the performance of all GF-based analyses using two measures of conservation performance, both of which were calculated using the predicted distributions of the 217 demersal fish species. The first measured the overall mean species representation throughout the removal process (herein referred to as "mean species representation"), providing an integrated measure of performance that is averaged both across all species and across a full range of protection options (i.e., 0–100% of the landscape); this can be seen as broadly analogous to the commonly used Area Under the Curve (AUC) statistic. The second measured the number of species with more than 20% of their predicted distribution protected in the top-ranked 20% of cells (herein referred to as "highly protected species"). This measure assesses the proportion of species with high representation, providing a complementary metric to average representation, for which high values might conceal very low levels of representation for some species.

3. Results

3.1. Scenario 1 and 2: baseline and neutral ranking

Scenario 1 (baseline *Zonation* analysis using the predicted distributions of 217 individual demersal fish species) identified high-ranking cells throughout New Zealand's marine area to the outer limits of the ECS (Fig. 2), with highest concentrations in shallower, inshore waters, often in northern regions. Overall mean species representation was 0.667 when averaged across all species and throughout the ranking removal sequence (Table 1a). Protection of the top-ranked 20% of cells from this ranking would provide 20% or greater representation for 179 of the 217 demersal fish species (82%) (Fig. 3). By contrast, Scenario 2 in which cells were randomly selected delivered overall average species representation of 0.437 (±0.001 across ten iterations). Only 64 of the 217 demersal fish species were highly protected from this random ranking (Fig. 3).

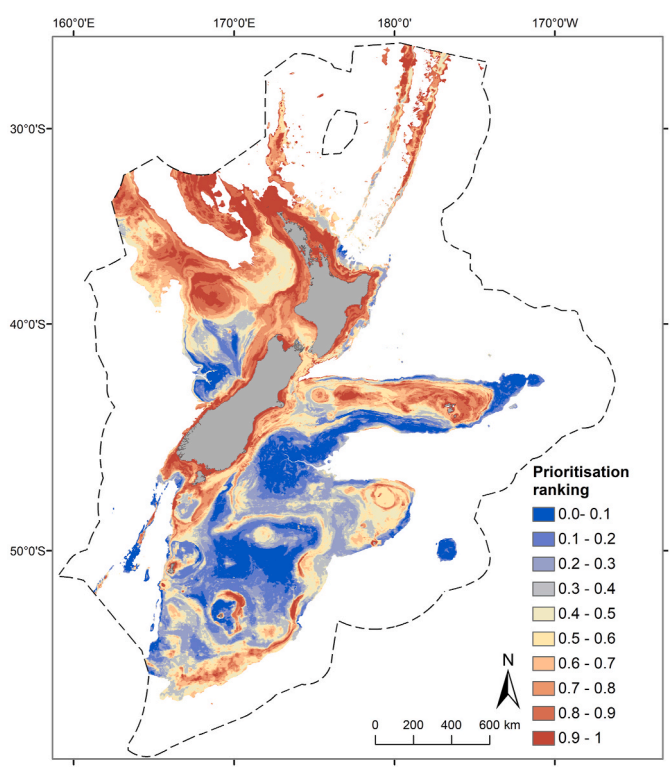

Fig. 2. Conservation priority for 1 km grid cells in New Zealand's marine area to the outer limits of the ECS to depths of 2000 m, based on a Zonation analysis of maps predicting the distributions of 217 demersal fish species. Prioritisation ranking values ranging from 0 to 1 where low values indicate low conservation priority and high values indicate high conservation priority.

Table 1
Performance of Scenarios using various combinations of input layers. Values indicate the overall average representation of 217 species throughout the ranking process, and the number of species with more than 20% of their predicted distribution protected in the top-ranked 20% of cells. Numbers in brackets for all but the first line in (a) indicate the relative performance of each ranking compared to the performance achieved by the baseline ranking of species layers, expressed as a percentage.

a) Scenarios 1 and 2: 217 species distribution layers

Analysis option	Representation	No. species >20%
Scenario 1: Baseline	0.667	179
Scenario 2: Neutral	0.437 (65.5)	64 (35.8)

b) Scenario suite 3: GF-classification using species composition layers. Bolded numbers are those used in subsequent scenarios.

Number of groups	Representation	No. species >20%
10	0.561 (84.1)	107 (59.8)
20	0.565 (84.7)	103 (57.5)
30	**0.576 (86.5)**	**101 (56.4)**
50	0.577 (86.4)	107 (59.8)
100	0.578 (86.7)	112 (62.6)

c) Scenario suite 4: adding species turnover layers to 30-group GF-classification. Bolded numbers are those used in subsequent scenarios.

Relative weight ofspecies turnover layers	Representation	No. species >20%
0.10	0.595 (89.2)	104 (58.1)
0.25	0.604 (90.6)	104 (58.1)
0.50	0.609 (91.3)	105 (58.7)
1.00	**0.610 (91.4)**	**105 (58.7)**
2.00	0.605 (90.6)	107 (59.8)

d) Scenario suite 5: Adding species richness layers to 30 group GF-classification and equal weighted species turnover layers.

Weight of species richness layer	Representation	No. species >20%
5	0.621 (93.2)	116 (64.8)
10	0.623 (93.4)	125 (69.8)
20	0.619 (92.8)	130 (72.6)
30	0.616 (92.3)	139 (77.7)
50	0.610 (91.4)	143 (79.9)
100	0.600 (90.0)	146 (81.6)

3.2. Scenario 3: GF-based groups

The suite of Scenario 3 analyses (varying number of GF-based groups) delivered overall average species representation that ranged between 0.561 (10 groups) and 0.578 (100 groups) (Table 1b; Fig. 3; Suppl. Fig. 8). This was equivalent to 84.1–86.7% of the performance delivered by the baseline ranking. Numbers of highly protected species varied between 101 (30 groups) and 112 species (100 groups), equivalent to 56.4–62.6% of the value from the baseline ranking (Table 1b; Fig. 3). Examination of the characteristics of groups in the top-ranked 20% of cells at a 30-group level of classification (Table 2) indicated a trend whereby spatially extensive groups generally received lower representation than those of more limited geographic extent. Given the relatively low sensitivity of our ranking outcomes to the number of classification groups, a classification with a moderate number of groups (30-group classification) was selected for further analyses.

3.3. Scenario 4: inclusion of species turnover

The suite of Scenario 4 analyses added species turnover layers (with varying weights) to the 30-group classification. Increases in conservation performance varied depending on the relative weighting of the classification groups and turnover layers respectively (Table 1). Overall average species representation increased from 0.576 (no species turnover layers – 30 groups in Table 1b) to 0.610 when species composition and species turnover layers were equally weighted (Suppl. Fig. 9, Table 1c; Fig. 3); this latter value corresponded to 91.4% of the

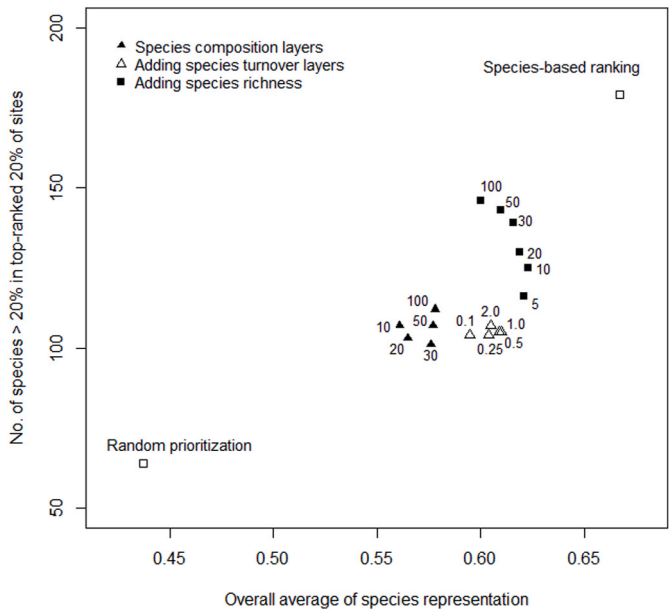

Fig. 3. Performance of rankings using various sets of input layers in comparison to the baseline (species-based) ranking (open square, top right) and random removal of species layers (open square, bottom left). Rankings are compared against the overall average of species representation throughout the ranking process, and the number of species with >20% representation within the top-ranked 20% of cells. For the ranking using species composition (solid triangles), values indicate the number of classification groups used; for the ranking using species composition and turnover layers at a 30-group GF (open triangles), values indicate the relative weighting applied to turnover layers; for the ranking using equally weighted species composition and turnover layers, and a species richness layer (solid squares), values indicate the weighting applied to the richness layer.

performance delivered by the baseline ranking. Ranking performance declined slightly when weights for the turnover layers were increased beyond this point (Fig. 3). By contrast, there was only a small increase in numbers of highly protected species when turnover layers were added; this increase showed minimal variation as the relative weighting of the turnover layers was increased (Fig. 3).

Including turnover layers changed the representation of individual classification groups in the top-ranked 20% of cells (Table 2; Suppl. Fig. 9). Sixteen groups, mostly of limited spatial extent, showed no change, receiving 100% protection in both sets of analyses. Three extensive groups (1–3) with limited similarity to other groups (i.e., groups which strongly different to most other groups), received increased representation, whereas several groups (4, 8–11, 13, 21, 22, 25 & 26) that were closely related to several other groups showed decreases in representation. Consequently, there was a significant positive relationship between the change in representation of individual classification groups and their average dissimilarity to all other groups (correlation = 0.438, p = 0.022).

3.4. Scenario 5: adding species richness

Adding the species richness layer in Scenario 5 using equal weighted 30-group species composition and turnover layers provided further improvements in ranking performance. The gain in overall average representation was greatest when the richness layer was given a relatively low weighting (10), with the average species representation increasing from 0.610 (no richness) to 0.623 (Table 1d; Fig. 3). This equated to 93.4% of the species representation delivered by the baseline ranking. Further increases in the weight of the species richness layer beyond a value of 10 gradually reduced the overall species representation. By contrast, numbers of highly protected species increased steadily as increasing weight was applied to the species richness layer (Table 1d; Fig. 3), from 105 (without including richness) to 143 species (weight = 50), but only small further gains to 146 with a weighting of 100. This ranking equated to increases in performance from 58.7% (without including richness) to 81.6% (weight = 100) of that delivered by the baseline ranking.

Adding the species richness layer changed in the proportion of classification groups that represented within the top-ranked 20% of grid cells. For example, when using a weight of 50 for the richness layer (Table 2) there was a strong positive relationship between the average species richness of a group and the proportion of a group that occurred within the top 20% of cells within the conservation ranking (correlation = 0.673, p-value = 0.0001). A number of groups with high average species richness had more of their spatial distribution protected within the top 20% of cells when species richness was included, including several that were spatially extensive (e.g., groups 3, 4, 6, 10 & 11, Table 2). By contrast, several groups that had below average species richness (groups 2, 9, 17, 21, 22, 24, 25, 26, Table 2) had less of their spatial distribution protected in the top 20% of cells when species richness was included in the analysis.

Comparison of Scenario 5 (Fig. 4) with the baseline ranking (Fig. 1) indicated that, while they deliver similar levels of performance for biodiversity, they exhibited some marked differences in the spatial distribution of high ranked cells. In particular, a high proportion of high ranked cells from Scenario 1 occurred in northern areas, while a greater proportion of those for Scenario 5 occurred along the Chatham Rise and around the margins of the Campbell Plateau (east and south east of the study area).

4. Discussion

Description of spatial variation in community composition and species turnover is central both to our understanding of the scaling of diversity, and the consequent robust identification of priority sites for conservation (McKnight et al., 2007). Here, a Gradient Forest based analysis that summarised a large and complex species distribution dataset into a single classification layer effectively captured the information required for robust spatial conservation planning for demersal fish. In our analyses, a classification consisting of as few as thirty groups provided an adequate summary of spatial variation in demersal fish composition across New Zealand's marine area to the outer limits of the ECS to depths of 2000 m, an area encompassing nearly 2.5 million km^2. The strongest conservation outcomes were delivered when *Zonation* analyses were conducted using layers describing species composition, species turnover, and species richness.

At a more practical level, we were surprised by the relatively low sensitivity of our conservation ranking outcomes to the number of classification groups used as inputs in our first set of analyses. Given this initial result, we chose a 30-group level of classification for our subsequent analyses, largely because of practical considerations. A classification containing a moderate number of groups may be more likely to be understood and used by broad groups of resource managers, stakeholders and scientists with varying technical expertise, while carrying little penalty in conservation planning outcomes. This ability to effectively summarise complex biodiversity patterns has strong relevance in conservation planning (e.g., defining networks of marine protected areas (MPA)) because the reduced number of groups provides an accessible description and common currency for discussions among different resource users (Gleason et al., 2010; Stephenson et al., 2020). Classifications are more likely to be adopted for management purposes if they can demonstrate integration of true patterns in habitats or biotic assemblages, rather than solely environmental clustering. A description of the biotic and environmental characteristics of a 30-group demersal fish GF classification has been recently developed (e.g., see Stephenson et al., 2020) to facilitate the communication of biodiversity information in stakeholder and engagement processes.

Table 2
Comparison of proportion of individual groups occurring in the top-ranked 20% of grid cells from rankings using GF analysis 1 (30 species composition layers), GF analysis 2 (30 equal-weighted species composition and species turnover layers), and GF analysis 3 (as per GF analysis 2 with a species richness layer with a weighting of 50). Values include each group's spatial extent, mean inter-group similarity (mean distance) to all other groups, and mean species richness. For the 3 analyses, further values presented are the proportion of each group's total extent represented within the top-ranked 20% of cells, and percentage change between GF analysis 1 and 2, and 2 and 3, respectively.

				GF analysis 1	GF analysis 2		GF analysis 3	
Group	Extent (km^2)	Mean distance	Mean richness	Proportion in top 20%	Proportion in top 20%	% change relative to GF 1	Proportion in top 20%	% change relative to GF 2
1	444,083	0.181	7.1	0.030	0.090	200.0	0.084	−6.7
2	526,900	0.165	6.5	0.031	0.062	100.0	0.042	−32.3
3	128,496	0.142	12.1	0.249	0.275	10.4	0.316	14.9
4	252,919	0.122	14.6	0.143	0.128	−10.5	0.294	129.7
5	10,519	0.132	12.1	1.000	1.000	0.0	1.000	0.0
6	73,390	0.143	10.7	0.086	0.107	24.4	0.130	21.5
7	69,446	0.156	13.3	1.000	1.000	0.0	1.000	0.0
8	56,071	0.117	9.5	0.050	0.041	−18.0	0.039	−4.9
9	1211	0.117	5.7	0.424	0.349	−17.7	0.166	−52.4
10	2522	0.109	16.3	0.559	0.403	−27.9	0.703	74.4
11	120,759	0.102	15.6	0.266	0.183	−31.2	0.442	141.5
12	39,024	0.104	14.7	1.000	1.000	0.0	1.000	0.0
13	354,744	0.108	12.1	0.383	0.276	−27.9	0.313	13.4
14	96,679	0.120	10.0	1.000	1.000	0.0	1.000	0.0
15	1120	0.127	5.8	1.000	1.000	0.0	1.000	0.0
16	1605	0.129	6.7	1.000	1.000	0.0	1.000	0.0
17	35,186	0.130	8.7	1.000	1.000	0.0	0.684	−31.6
18	3831	0.138	9.5	1.000	1.000	0.0	0.998	−0.2
19	30,854	0.117	8.6	1.000	1.000	0.0	1.000	0.0
20	10,689	0.114	10.7	1.000	1.000	0.0	0.905	−9.5
21	42,989	0.103	10.6	1.000	0.874	−12.6	0.598	−31.6
22	71,305	0.106	9.3	0.456	0.347	−23.9	0.262	−24.5
23	3261	0.119	13.1	1.000	1.000	0.0	1.000	0.0
24	5468	0.118	9.9	1.000	1.000	0.0	0.897	−10.3
25	7021	0.120	5.9	0.873	0.740	−15.2	0.321	−56.6
26	30,396	0.115	9.6	0.818	0.654	−20.0	0.415	−36.5
27	16,234	0.134	5.4	1.000	1.000	0.0	1.000	0.0
28	6345	0.140	10.9	1.000	1.000	0.0	1.000	0.0
29	500	0.147	11.6	1.000	1.000	0.0	1.000	0.0
30	18,344	0.189	7.9	1.000	1.000	0.0	1.000	0.0
Overall	2,461,911	0.129	10.1	0.712	0.684		0.654	

Further improvements in conservation ranking efficiency were achieved when adding species turnover layers. While the initial analyses using species composition groups effectively treated all groups as equally different from each other (as has been the case in the few studies that have used less complex environmental classifications, e.g., Ferrari et al. (2018); Sutcliffe et al. (2015)) adding species turnover layers gave greater emphasis to those groups with high compositional differences to all other groups (i.e., low intra-group similarity). These locations are likely to support distinctive species assemblages, providing small but valuable gains in overall average species representation. The further inclusion of the species richness layer improved the performance of the ranking analyses, encouraging the allocation of high rankings to sites supporting large numbers of species (Arponen et al., 2008), irrespective of their group membership. While the total number of species (alpha diversity) contributes to the relative local importance of an area for conservation, it is the rate of species turnover between sites that largely determines the optimal spatial arrangement of a set of conservation areas (Arponen et al., 2008; McKnight et al., 2007; Nekola and White, 1999, 2002).

Despite the practical advantages of using a single biologically informed environment-based spatial classification layer, none of the analyses of GF-based layers performed quite as effectively as the baseline ranking analysis (i.e., using 217 individual species distribution layers). The higher performance of the baseline ranking most likely reflects, at least in part, the comprehensive dataset available here (>27,000 unique trawl samples versus ~ 13,000 trawl samples used to construction the GF-based classification). Unfortunately such datasets are typically rare, and generally only sample fish species; other taxa are rarely sampled with this intensity (Costello et al., 2017).

Our results suggest that GF-based classifications provide important advantages in settings where data may be inadequate to develop individual species models for conservation planning. Previous analyses have demonstrated that species turnover rates derived by GF models were relatively robust with smaller datasets (Stephenson et al., 2018). In particular, repeated GF analyses with sub-samples of our entire dataset exhibited minimal variation in model outcomes once ca. 5000–7000 samples were used to define the model (Stephenson et al., 2018). By contrast, fewer individual species distribution layers could be generated with this lower number of samples than represented in the GF models. In addition, conservation planning with a lower number of species distribution models would require an assumption of taxonomic surrogacy, i.e., that one species captures variation in another (Arponen et al., 2008), an unlikely assumption since relationships between environmental variables and species can vary between taxonomic groups (Hortal and Lobo, 2005; Sutcliffe et al., 2012). By contrast, the use in GF models of information describing species turnover makes them more likely to function robustly as surrogates for a full complement of biodiversity, even when lower numbers of species records are used (Aroponen et al., 2008).

Conservation outcomes differed depending on the measure used to assess performance. When using average representation through the ranking process as a measure, use of just the species composition and species turnover layers achieved average representation close to that achieved by the full set of individual species distribution layers. By contrast, when using numbers of highly protected species as a measure, addition of the species richness layer was required to deliver adequate performance. Careful consideration should therefore be given to the overall planning goals when choosing between these two measures, and

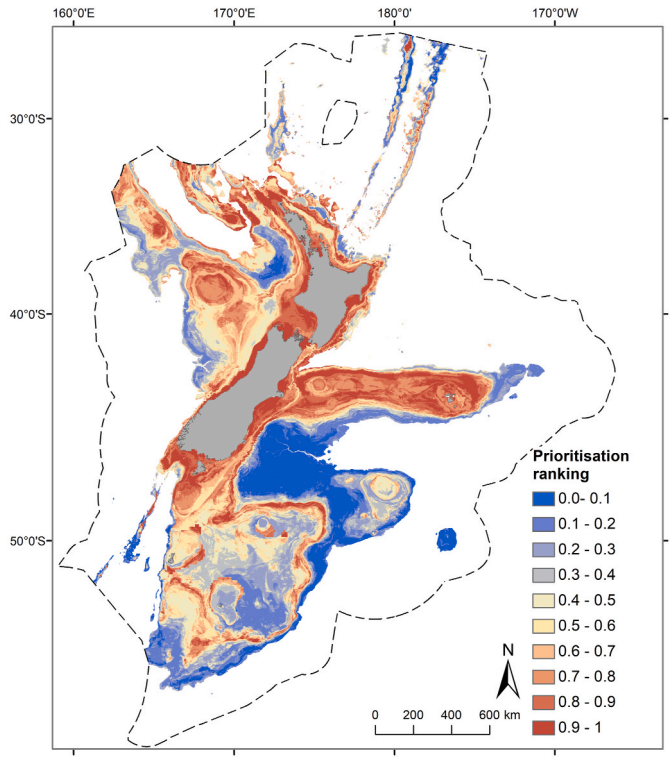

Fig. 4. Conservation priority for 1 km grid cells in New Zealand's marine area to the outer limits of the ECS to depths of 2000 m, based on a *Zonation* a ranking analysis using equally weighted species composition and turnover layers at a 30-group GF classification and a richness layer with a weight of 50. Prioritisation ranking values ranging from 0 to 1 where low values indicate low conservation priority and high values indicate high conservation priority.

these goals might in turn influence the selection of layers to use for ranking (Rowden et al., 2019). Equally, conservation planning analysis may aim to quantify the minimum area needed in order to protect a specific proportion of all species (e.g., Moilanen (2007); Sutcliffe et al. (2015)). Ultimately, decisions on which performance measures are used remain policy or stakeholder driven choices, even if implementation considerations are also important.

Despite some of these uncertainties in being able to parameterise the conservation ranking analysis in the absence of good information on individual species' distributions, some generalities emerge. We recommend the selection of a moderate number of classification groups, that balances out the complexity of the system under consideration with the ease of communication (e.g., in our case between 20 and 100 groups would be manageable – here 30 groups were sufficient). In addition, while we started our analyses using information describing spatial variation in species composition alone, addition of layers describing both species turnover and species richness significantly improved ranking performance, emphasising the value in using complementary measures of biodiversity distribution (as in more theoretical examples, e.g., Arponen et al. (2008)). We suggest equally weighting these different measures of biodiversity as a starting point, e.g., each of the 30 layers of species composition and turnover weighted as 1 and the species richness layer weighted as 30 (so that on aggregate each group of layers has a weighting of 30). However, we have only explored these results using demersal fish in New Zealand – results may differ if using different taxa groups (e.g., benthic invertebrates, macroalgae, etc) or at different locations (with different patterns or strengths of environmental structuring). Where conservation objectives include broader suites of taxa, consideration is also required of how best to include distribution data for other taxonomic groups that are important contributors to marine biodiversity, including benthic invertebrates, pelagic species, and macroalgae. GF analysis provides options for merging several estimates of turnover (e.g., Ellis et al. (2012); Pitcher et al. (2012)) to facilitate this next step. However, further exploration into optimal group number and weighting may be required when expanding this methodology to new taxonomic groups.

The methodology presented here addresses a key challenge in designing marine reserve networks, which is the availability of sufficient data to ensure representativeness of patterns of biodiversity and community assemblages within an MPA network. A suite of ecological criteria are typically used in designing MPA networks (e.g., Clark et al., 2014; Dunstan et al., 2016), with representation being one of many criteria typically also including protection for threatened taxa, areas important for life history stages, rarity and uniqueness. While this classification is based on demersal fish, other classifications have been developed to inform representation of other aspects of the oceans with limited sampling (pelagic environments: Kavanaugh et al., 2016; mesopelagic zone: Sutton et al., 2017; deep sea: Watling et al., 2013). A number of spatial planning approaches have used habitat maps and/or classifications in addition to other ecological criteria to inform placement of MPAs within a network (e.g., Evans et al., 2015; Everson, 2017; Virtanen et al., 2018). Classification approaches can also inform global priorities and targets for marine conservation by providing robust scientific representations of poorly sampled environments to inform more qualitative aspects of Aichi target 11 (Rees et al., 2018). These classifications can be used to provide broad scale information in stakeholder planning processes, that include objectives of marine biodiversity protection (Davies et al., 2018) as well as mitigating impacts of seafloor disturbance and other stressors (Cryer et al., 2016; Penney and Guinotte, 2013).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ocecoaman.2021.105855.

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