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Rarity mediates species-specific responses of tropical reef fishes to protection

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Abstract

Marine protected areas (MPAs) are the most widely applied tool for marine biodiversity conservation, yet many gaps remain in our understanding of their species-specific effects, partly because the socio-environmental context and spatial autocorrelation may blur and bias perceived conservation outcomes. Based on a large data set of nearly 3000 marine fish surveys spanning all tropical regions of the world, we build spatially explicit models for 658 fish species to estimate species-specific responses to protection while controlling for the environmental, habitat and socio-economic contexts experienced across their geographic ranges. We show that the species responses are highly variable, with ~40% of fishes not benefitting from protection. When investigating how traits influence species' responses, we find that rare top-predators and small herbivores benefit the most from MPAs while mid-trophic level species benefit to a lesser extent, and rare large herbivores experience adverse effects, indicating potential trophic cascades.

KEYWORDS

community, marine-protected areas, spatial models, species-specific

INTRODUCTION

Over-exploiting marine resources is driving a strong decline in marine biodiversity (Sherman et al., 2023) and fish stocks (Juan-Jordá et al., 2022), undermining ecosystem functioning (Sherman et al., 2023) and Nature's Contributions to People (Eddy et al., 2021) like food security and cultural values (Seguin et al., 2022; Villéger et al., 2017). Yet, the increase of human population density near tropical reefs (Sing Wong et al., 2022) severely threatens fish species, depleting their abundance and increasing their likelihood of local extirpation or

even regional extinction (Cinner et al., 2018; MacNeil et al., 2020; Sherman et al., 2023).

Marine Protected Areas (MPAs), where certain or all human activities are prohibited, serve as a primary tool for mitigating the impact of overexploitation and various disturbances on fish populations (Grorud-Colvert et al., 2021; Marcos et al., 2021). Yet, these benefits generally depend on the level of protection (Grorud-Colvert et al., 2021), key MPA features such as age and size (Edgar et al., 2014), and a range of socio-economic and environmental factors (Cinner et al., 2018; Loiseau et al., 2021). Moreover, species interactions, species-habitat dependencies, transient

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responses and extreme events may blur expected patterns of increased fish occurrence, density and biomass within MPAs (Hopf & White, 2023; Kraufvelin et al., 2020; White et al., 2013). For instance, the cover of complex living corals can greatly affect the local abundance of many species, regardless of fishing restrictions (Russ et al., 2021), while extreme events can delay MPA benefits up to 10 years (Hopf & White, 2023). Conservation gains inside MPAs are also mediated by reef accessibility and nearby human density (Cinner et al., 2018).

Most studies on the effect of protection focus on individual MPAs and the community level, such as total fish density or biomass of commercial species (Cinner et al., 2018; Edgar et al., 2014; Giakoumi et al., 2017; Nowakowski et al., 2023). Species-specific responses to protection across MPAs and social-environmental contexts are less clear (Lefcheck et al., 2021; Yan & Bellwood, 2023). On the one hand, fishing can impact the entire food web and body-size spectra (Soler et al., 2018; Zgliczynski & Sandin, 2017) so most species should benefit from MPAs. On the other hand, according to the mesopredator release hypothesis (Crooks & Soulé, 1999), if large predator species are overfished in an area, medium-sized prey species may thrive. In that context, exploited reefs may host a different species composition, potentially including more species, compared to protected reefs (Boulanger et al., 2021; Loiseau et al., 2021). Yet, no general pattern has emerged in the proportion of species responding positively and negatively to protection.

Species-specific responses to protection are expected to vary according to the traits underlying vulnerability to fishing such as trophic position or body size (Abesamis et al., 2014). Moreover, in a global context where large-ranged species tend to increase in regional occupancy through time and small-ranged species tend to decrease (Xu et al., 2023), some recent studies report more protection benefits for rare than for common species (Barnes et al., 2022; Cooke et al., 2023). These findings have critical conservation implications but the mechanisms and ecological processes underlying such patterns remain unclear. The extent to which MPAs are more effective for populations of rare species is unknown and unquantified. Therefore, a crucial aspect in the design of effective conservation strategies lies in comprehending how rarity, and its relationship to other traits may affect species' responses to protection.

Large-scale analyses of species-specific MPA benefits remain challenging for a number of reasons. In particular, extreme variability between regions in the socio-economic and environmental context, that determines MPA effectiveness (Cinner et al., 2018; Hopf & White, 2023), may exceed variability among protected and unprotected areas within regions (MacNeil et al., 2020). This means that, for any given fish species, MPAs may provide an effective conservation solution in one location, but not in another. Thus, understanding

the global effectiveness of MPAs for sustaining or rebuilding populations of any given reef fish species across its entire geographic distribution requires explicit consideration of environmental, habitat and socio-economic context. Since some critical factors may be missed by local surveys but are spatially structured (food preferences, fishing gears) they should be included in comparative analyses of MPA benefits through spatial auto-covariates (Dalongeville et al., 2022) or spatial random effects (Paradinas et al., 2023).

Here, we evaluate whether individual reef fish species show generalizable responses to protection in several categories of MPAs across their geographic ranges. We applied spatial linear mixed models to test the effect of protection on the occurrence, abundance, and biomass of 650 fish species from a large empirical database containing nearly 3000 underwater surveys of tropical reefs around the world, encompassing 57 MPAs. To capture the 'pure' or marginal effect of protection in our models, we controlled for spatial autocorrelation and a large set of habitat, environmental and socioeconomic factors derived from global databases, high-resolution satellite imagery and deep learning algorithms. Our goal was to determine (1) the proportion of species that respond positively versus negatively to protection, (2) the correlations between species responses to different levels of protection and finally (3) how traits and rarity may influence species-specific responses to protection.

MATERIALS AND METHODS

Our methodological framework encompasses three main steps described in [Figure 1](#).

Occurrence and abundance data

Overall, 2959 tropical reef transects on 1631 sites were surveyed between 2008 and 2019 by Reef Life Survey (RLS) divers following a standardized protocol of underwater visual census (UVC) along 50m transect lines; full details can be found in Edgar and Stuart-Smith (2014) and Edgar et al. (2020). All fish species observed within duplicate 5-m wide belts were recorded, and their abundance (i.e. density) and size distributions counted or estimated (therefore allowing biomass calculation) (Edgar et al., 2020). Multiple 50×10m belt transects were surveyed at each site (mean=1.67, SD ±0.6), each with different fine-scale habitat factors recorded using photo-quadrats. Reef sites were distributed among 53 ecoregions with a median number of 17.5 transects per ecoregion.

Starting with the list of all fish species recorded in these standardized surveys, we subset to those recorded on at least 30 transects (658 species) to have enough

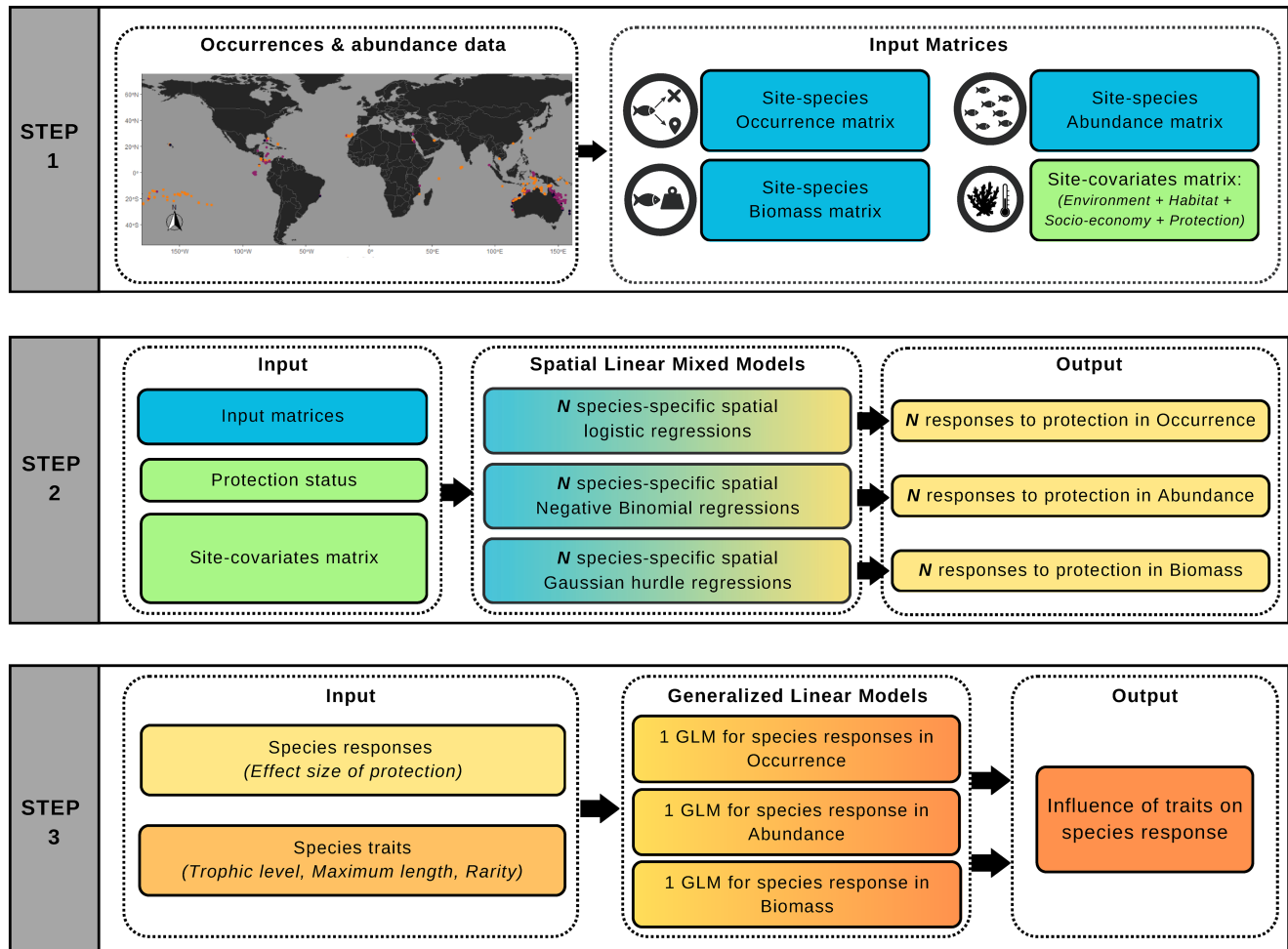


FIGURE 1 Workflow chart describing the three main steps of our analyses assessing responses to protection of 658 fish species, in terms of occurrence, abundance and biomass. We controlled for habitat, environmental and socioeconomic factors but also spatial autocorrelation. Species-specific responses were assessed separately for three levels of protection: high (old, and large effective no-take areas), medium (no-take areas that did not match age, size, or enforcement criteria) and low protection (all other types of restriction). Step 1: Creation of input data matrices from reef Life Survey; step 2: Modelling the effect of protection on each species occurrence, abundance and biomass; step 3: Testing the influence of traits on species responses using the model estimates from step 2. Colours on the map indicate if the site is protected (orange for protected sites, purple for fished sites).

observations for modelling (see GitHub repository in the Data availability section). In doing so, we excluded the rarest species from the analyses but reduced uncertainty of models' outputs (Thuiller et al., 2019). For species with a maximum abundance above 500 individuals, we removed the observations with the highest 1% of abundances, which represented either particular circumstances (e.g. extreme planktonic inputs), data errors or inaccuracies. For each species metric (occurrence, abundance and biomass), we computed a site-species matrix (Figure 1, Step 1).

Socio-environmental factors

To control for the context of transects and then be able to isolate the effect of protection, we gathered a total of 95 factors that encompass environmental, habitat and

socioeconomic aspects and computed a site-factor matrix (Figure 1, Step 1).

Environmental factors

We collected a total of 36 environmental factors at the site scale expected to influence fish occurrence and abundance metrics (Asch et al., 2018), comprising minimum, maximum, and mean monthly values per year for chlorophyll-a concentration, net primary productivity, pH, sea surface salinity and sea surface temperature (Supplementary Material). We also included Degree Heating Weeks, an index of coral bleaching risk (Hughes et al., 2017) measured over both 1-year and 5-year periods, corresponding to the most recent available years (Table S1).

Habitat factors

We also collected 48 habitat factors (Table S1) assumed to influence fish species distribution and diversity (Mellin et al., 2009). First, we collected 38 variables at the site scale related to the high-resolution benthic and geomorphic reef types from the Allen Coral Atlas (2022). This public coral reef database, developed using satellite images from 2017 to 2018, underwent ground-truthing and analysis through artificial intelligence methods, as detailed by Li et al. (2020) and Kennedy et al. (2021). Site-scale benthic reef and geomorphic habitats were respectively classified into 6 and 11 classes. We computed two buffer areas around each reef survey site, 500 m and 10 km diameter each, to extract surface percentages for each benthic and geomorphic class. Since some buffers could contain non-geomorphic and/or non-benthic surfaces (land or deep-sea), sums did not add up to 100% of buffer surfaces. Then, we calculated the percent cover by the non-land and non-deep sea portions of the buffers as a measure of reef habitat extent. To control for habitat coverage, we included factors corresponding to the sums of benthic reef and geomorphic habitat surface, at each buffer size.

Second, RLS divers take 20 photoquadrats of the benthic habitat at the transect scale. These are later scored in the office by a scientist with experience in benthic habitats, to generate transect level percentage cover of various coral, macroalgal, other sessile invertebrate and substrate categories. We summarized these categories into nine broadly comparable factors: live hard corals, crustose coralline algae, algae, rubble, microalgae, rocks, sand, seagrass and other invertebrates. We imputed missing values (where habitat had not yet been scored from the RLS photoquadrats) using the *missForest* package (Stekhoven & Buehlmann, 2012), and verified through cross-validation with a mean Pearson correlation of 0.75 between imputed and true data. Finally, we added depth at the transect scale as a factor.

Socioeconomic factors

We included eight socioeconomic factors at the country scale to explain fish species occurrence, abundance and biomass: the conflict index, the human development index, the voice and accountability index, the control of corruption index, the natural resources index, the absence of violence and terrorism index, the number of environmental non-governmental organizations and the dependency on marine resources (Supplementary Material). We also computed the travel time between each transect and the nearest populated pixel, the total number of inhabitants within 500 km, and total human gravity, which is a measure that sums gravities of each populated pixel within 500 km (Cinner et al., 2018).

Protection levels

Since the age, size and enforcement of MPAs have been demonstrated to strongly influence their ecological effectiveness (Claudet et al., 2008; Edgar et al., 2014; Nowakowski et al., 2023), we took these features into account when classifying our MPAs. High protection refers to no-take areas with high or medium enforcement that are larger than 10 km² and have been established at least 10 years before the survey, a conservative approach given the home range of reef fish species (Krueck et al., 2018) and the impact of disturbance on the lag in MPA benefits (Hopf & White, 2023).

Medium protection refers to no-take areas with high or medium enforcement but that are either less than 10 km² or 10-years old. Low protection refers to no-take MPAs with low enforcement and all MPAs with restrictions on some fishing gears. Finally, unprotected areas refer to fishing grounds. Creating more subcategories (young and large medium, old and small low protection, etc.) would have drastically reduced the number of species occurrences per sub-category, preventing running and convergence of many species-specific models, so the easiest way to account for age and size was to classify old and large protected areas as highly protected.

Data analyses

For each species, we included all transects from ecoregions in which the species was recorded on at least five transects. This meant that any transects on which the species was not observed within these ecoregions were treated as 'absences' for that species. Absences in other ecoregions were not included in the models. An additional 44 species were removed because they had less than five occurrences in unprotected areas or did not occur at least five times in at least one of the protection levels.

Principal component analysis

Since our goal was to capture the effect of protection for each species after accounting for the socio-environmental contexts, we performed separate principal component analyses (PCA) on all factors except protection for each species. This allowed us to reduce the set of factors and feed the models with uncorrelated explanatory variables. Because of the possible disproportionate influence of an ecoregion with many more transects than others in the PCA, each transect was weighted as the inverse number of transects in its ecoregion, allowing for an equal influence of each ecoregion. For each species, the entire set of 95 factors was standardized and then reduced to the minimal number of dimensions (ranging from 3 to 14,

mean = 8.51, SD \pm 2.21) necessary to explain at least 70% of the variance across its subset of transects.

Generalized linear mixed models

We used generalized linear mixed models (GLMM) to estimate the effect of protection levels on species occurrence, abundance and biomass while controlling for PCA axes and spatial autocorrelation using a random spatial term (*spaMM* package [Rousset & Ferdy, 2014]). A random spatial term captures patterns that may not be explained by the other components of the model, and thus accounting for omitted spatially-structured factors in our data set (Paradinas et al., 2023).

For each species, we computed three spatial GLMMs (Figure 1, Step 2): a logistic regression to model occurrence probabilities, a negative binomial regression to model abundances including zeros, and a hurdle Gaussian model combining the output of the logistic regression to a Gaussian model on zero-truncated data to model log species biomass (Brown et al., 2021). To assess the quality of our models, we computed the area under the curve (AUC) for logistic regressions, and the R-squared (R^2) for negative binomial and Gaussian models. Residuals and model fits were visually checked with the *DHARMA* package (Hartig, 2018).

PCA dimensions selection

To ensure that model coefficients are unbiased and the effect of protection is independent from other factors, we calculated a Variance Inflation Factor (VIF) on each set of dependent variables to evaluate collinearity (Zuur et al., 2010). We included PCA axes in their order of relative importance and iteratively excluded those displaying a VIF greater than 5 from each model until no axis exceeded this threshold (Zuur et al., 2010). We checked that when the first axis was removed (40 species), the second axis would be kept in the analysis, and vice-versa, to capture most of the social-environmental context. If protection was the variable displaying the highest VIF, the corresponding species was removed from the analysis (15 species removed).

Species-specific responses to protection

To assess species-specific responses, we used the ratio between the estimated occurrence probability (or abundance, or biomass) inside and outside MPAs as an effect size measure. Estimated biomass was the product of the zero-truncated Gaussian estimate back-transformed to the normal scale and the associated occurrence probability from the logistic regression. This effect size was computed separately for each species, for each of the

three levels of protection in comparison to unprotected areas: a value of 2 for abundance means that the species is twice as abundant inside than outside protected areas, while a value of 0.5 means that the species is half as abundant inside than outside while controlling for the social-environmental context and space. A value of 1 would imply that protection has no effect on that species. When visualizing distributions, since a ratio's distribution is highly asymmetric and right-skewed, we used their log-transformed values to obtain a symmetric distribution in which positive and negative values respectively imply positive and negative protection effects.

Relationships with species traits

In order to test whether species considered more vulnerable to human pressures showed greater positive responses to protection, we considered three key traits to explain MPA effect sizes (Figure 1, Step 3). Since prey and predator species may respond differently to protection (Bond et al., 2019), and since larger species are more likely to be caught by fisheries (Allendorf & Hard, 2009; Graham et al., 2005) we included maximum body length and trophic level in our models. Since a given species can be targeted (consumed, sold) or not depending on the region (gears, diet preferences) we prefer to use continuous proxies of vulnerability to fishing instead of a categorical commercial classification. We also included rarity in the analyses since rare and common species may respond differently to protection (Barnes et al., 2022; Cooke et al., 2023). In order to understand the interplay between all three variables, we included the interactions between traits in our models.

Rarity was defined as deciles of species' number of occurrences to detect variation at a finer scale than if we used a binary variable (1 corresponds to the 10% rarest species, 10 to the most frequent). There was no circularity in using occurrence data to compute rarity for these models since the response variable was a ratio between two estimates (i.e. rarer species do not necessarily have a lower ratio).

To test for a potential species dependence to shared evolutionary history, we first performed a phylogenetic generalized least squares analysis (pGLS) based on the phylogeny published by Rabosky et al. (2018) to estimate Pagel's lambda through maximum likelihood. We then used Gamma Generalized Linear Models (GLMs) to test the effect of traits on effect sizes, and represented the outputs on the natural scale for easier interpretation. We finally performed a stepwise model selection with the *stepAIC* function (*MASS* package [Venables & Ripley, 2002]), to select the most parsimonious model with a subselection of traits. Partial plots of model outputs were drawn with the *visreg* function (*visreg* package, [Breheny & Burchett, 2017]), and interaction plots were generated by graphing quantitative

variables at the 10th, 50th and 90th percentiles. All reported R^2 values are Nagelkerke's pseudo R-squared values (Nagelkerke, 1991). To test if the observed R^2 values can be obtained at random or not, and consequently to assess the extent to which species traits explain the variation in protection effect sizes, we simulated 999 datasets with randomized effect size values while conserving trait combinations in order to avoid creating new functional entities. We then compared the observed R^2 values to those expected at random, that is by calculating the number of simulated R^2 values greater or equal to the observed R^2 value and then by dividing this number by 1000 (number of randomizations + 1).

RESULTS

Models' accuracy

We ran a total of 1974 GLMMs on 658 species. Some of the species-specific effect sizes could not be estimated when the number of observations was too low in a given protection level. Logistic regressions (occurrence) yielded effect sizes for 536, 503 and 355 species for low, medium and high protection levels, respectively, with AUC values ranging from 0.65 to 0.99 (mean = 0.93, SD \pm 0.07). Negative binomial regressions (abundance) yielded effect sizes for 412, 365 and 243 species for low, medium and high protection levels, respectively, with pseudo- R^2 values ranging from 0.01 to 0.99 (mean = 0.55, SD \pm 0.25). Hurdle Gaussian models (biomass) yielded effect sizes for 467, 334 and 313 species for low, medium and high protection levels, respectively, with pseudo- R^2 values ranging from 0.01 to 0.99 (mean = 0.46, SD \pm 0.24) (Figure S1). We used a Kolmogorov–Smirnov test (KS test) to compare the observed and expected distribution of residuals and a combined adjusted quantile test to test the homogeneity of residuals (Hartig, 2018). The distributions of p -values associated with these model diagnostics can be found in Figure S2. Residual plots for the 10 models displaying the lowest p -values on these tests can be found in Figure S3. Since these tests are sensitive and may provide low p -values given the large number of observations, even with a visual inspection confirming a reliable fit, we did not remove any model based on this statistical criterion.

Distributions of species responses

We found that 55%, 61% and 65% of species-specific log-transformed effect sizes (hereafter 'effect sizes') on occurrence were positive for low, medium and high protection, respectively, after controlling for the social-environmental context and space. For the remaining species, this probability of occurrence decreases with protection. This pattern of increasing proportion of

positive species effect size with increasing protection level was also detected for abundance with 56%, 60% and 69% of species effect sizes being positive for low, medium and high protection, respectively. It was also detected in terms of biomass with 54%, 58% and 63% of species effect sizes being positive for low, medium and high protection, respectively.

The distributions of species effect sizes were quasi-Gaussians with a median effect size of protection on occurrence increasing from 0.06, 0.11 to 0.15 for low, medium and high protection, respectively (Figure 2). The median effect size of protection on species abundance increased from 0.11, 0.16, to 0.30, for low, medium and high protection, respectively (Figure 2). The median effect size of protection on species biomass increased from 0.09, 0.13, to 0.19 for low, medium and high protection, respectively (Figure 2). Back-transforming these medians to the natural scale shows that half the species displayed an increase of at least 16% in occurrence, 35% in abundance and 22% in biomass under high protection compared to a fished area under a similar social-environmental context.

Relationships between species responses

Within each level of protection, species-specific effect sizes displayed an average Pearson's correlation of 0.67 (\pm 0.16 SD) between occurrence and abundance, 0.74 (\pm 0.16 SD) between occurrence and biomass and 0.51 (\pm 0.08 SD) between abundance and biomass. On the other hand, within each species response type (occurrence, abundance and biomass), effect sizes displayed an average Pearson's correlation of 0.54 (\pm 0.22 SD) between high and medium protection, 0.55 (\pm 0.37 SD) between high and low protection and 0.72 (\pm 0.13 SD) between medium and low protection.

Species traits underpinning responses to protection

Since there was a very low phylogenetic signal (Pagel's λ = 0.02), we only presented results of Gamma GLMs (model residuals in Figure S4). After a stepwise selection, some traits and interactions were removed from each model. Effect sizes of high protection on species occurrences were mainly driven by fish trophic level and length (R^2 = 0.19, randomization p -value = 0.007), and modulated by a strong interaction between both variables (p < 0.001), showing a threefold increase in occurrence probability inside MPAs for small-bodied herbivores, a nearly twofold increase inside MPAs for small-bodied top-predators, medium herbivores and large-bodied top-predators, compared to outside. In contrast, mid-trophic level species displayed lower benefit (~50%), and large bodied herbivores showed no response to protection

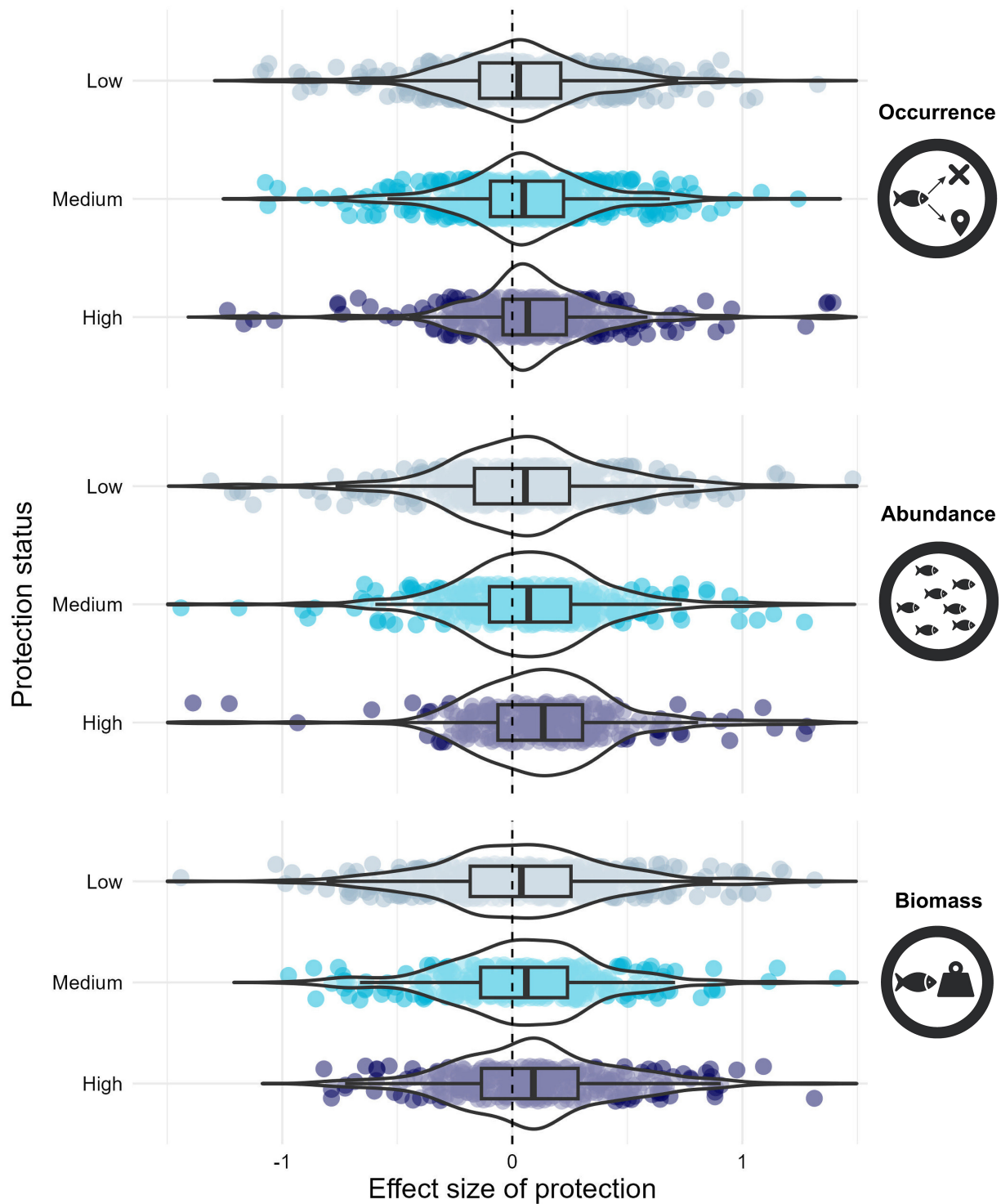


FIGURE 2 Boxplots and associated distributions of log-transformed effect sizes of low, medium and high protection on fish probability of occurrence, abundance and biomass. Each dot represents a single species, and positive values correspond to an increase inside MPAs compared to similar fished areas, while negative values correspond to a decrease. We used log-transformed data in this plot since the asymmetric distribution of a ratio on the natural scale would not facilitate the visualization of differences.

(Figure 3). Our models did not provide better R^2 values than those expected at random when considering the effect of medium protection (observed $R^2=0.04$, randomization test: $p=0.21$), and low protection on occurrence (observed $R^2=0.20$, randomization test: $p=0.19$).

Effect sizes of high protection on abundances were driven by species maximum body length, trophic level and rarity (observed $R^2=0.296$, randomization test: $p=0.01$). We found moderate evidence of interaction between all three variables ($p<0.05$), indicating that

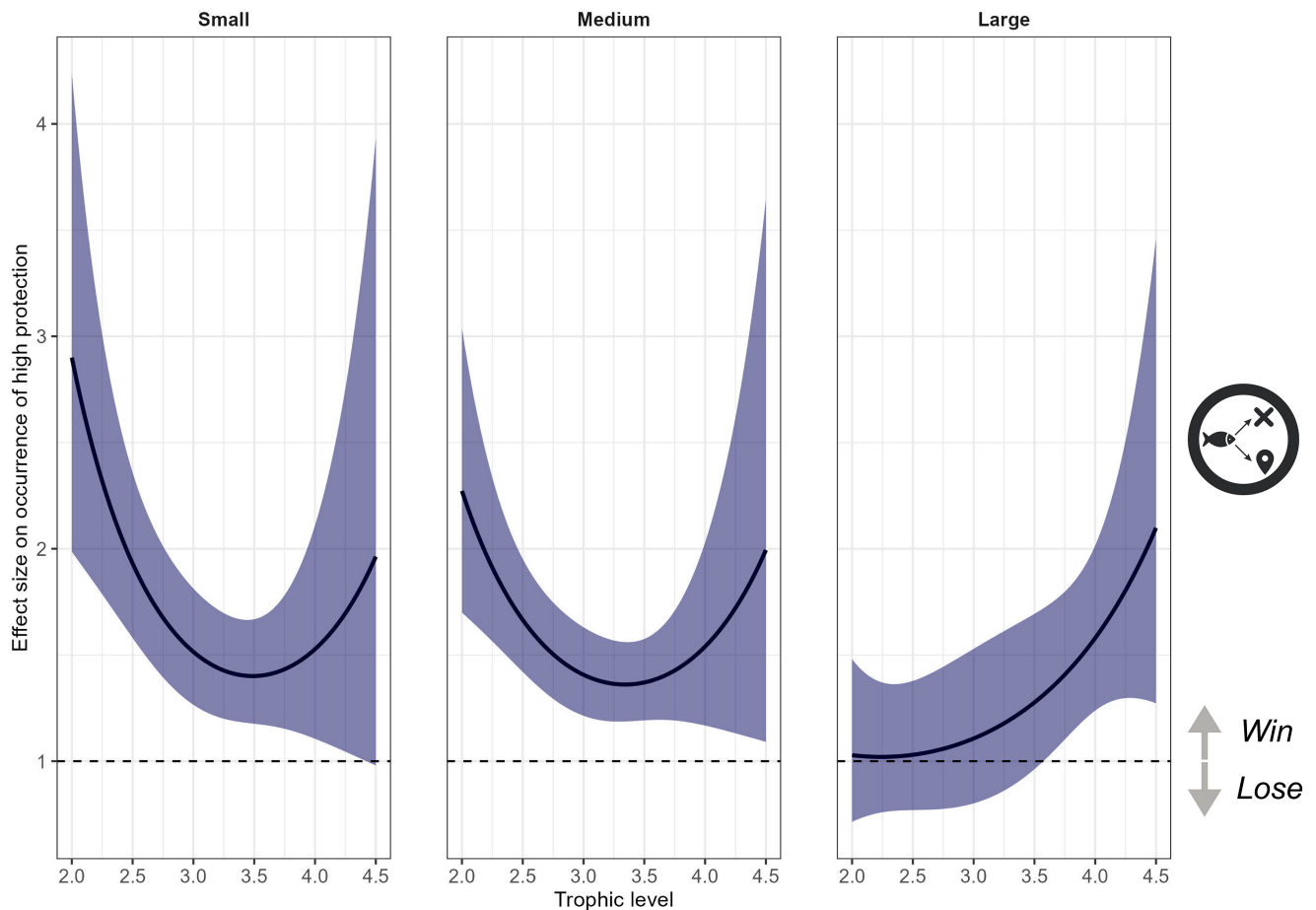


FIGURE 3 Models' graphical representation of the interaction between species maximum body length and trophic level in the response to high protection in terms of occurrence probability. Small, medium and large species correspond to species at the 10th, 50th and 90th percentile for maximum body length. Effect sizes are plotted on the natural scale in order to facilitate interpretation of the model outputs: a value of 2 represents a twofold increase inside protected areas compared to outside while controlling for social-environmental factors and space.

very frequent species displayed the weakest responses to protection, while rare small- and medium-bodied herbivores displayed the largest increases (up to 10-fold and fivefold, respectively; [Figure 4](#) and [Figure S5](#) for confidence intervals). Weak effect of traits was observed on species abundances in medium protection levels (observed $R^2=0.08$, randomization test: $p=0.07$) while no significant effect of traits was detected for the low level of protection (observed $R^2=0.07$, randomization test: $p=0.41$).

Effect sizes of high protection on fish biomass were driven by species rarity, length and trophic level (observed $R^2=0.29$, randomization test: $p=0.01$) with moderate interaction between the three variables ($p<0.05$). We found nearly no increase in biomass inside MPAs for very frequent species, whatever their size or trophic level. Rare small-bodied herbivores and rare large-bodied top-predators displayed the strongest responses with a nearly 15-fold increase in biomass. Small-bodied top-predators displayed a sixfold increase, while medium-bodied herbivores and top-predators displayed a sevenfold increase inside MPAs. Although they displayed a twofold increase,

mid-trophic level species always displayed lower responses at small and medium body lengths. We found a 40% decrease in biomass under high protection for rare large-bodied herbivores. Common species displayed intermediate values between rare and very frequent species ([Figures 4](#) and [S6](#) for confidence intervals).

A similar, but more nuanced pattern was found for the effect of medium protection level on biomass (observed $R^2=0.20$, randomization test: $p=0.009$). We found a moderate interaction among the three variables ($p<0.05$). Again, there was no effect of protection on very frequent species, and the highest responses to protection were displayed by rare small-bodied herbivores and rare top-predators with nearly tenfold increases, while rare medium-bodied herbivores and rare top-predators displayed sevenfold increases. Mid-trophic level species of all sizes displayed no response to protection whether they were common or rare, and rare large species displayed intermediate responses with a two- to threefold increase ([Figure S7](#)). The model testing the effect of low protection on biomass did not provide better R^2 values than those expected at random (observed $R^2=0.14$, randomization test: $p=0.21$).

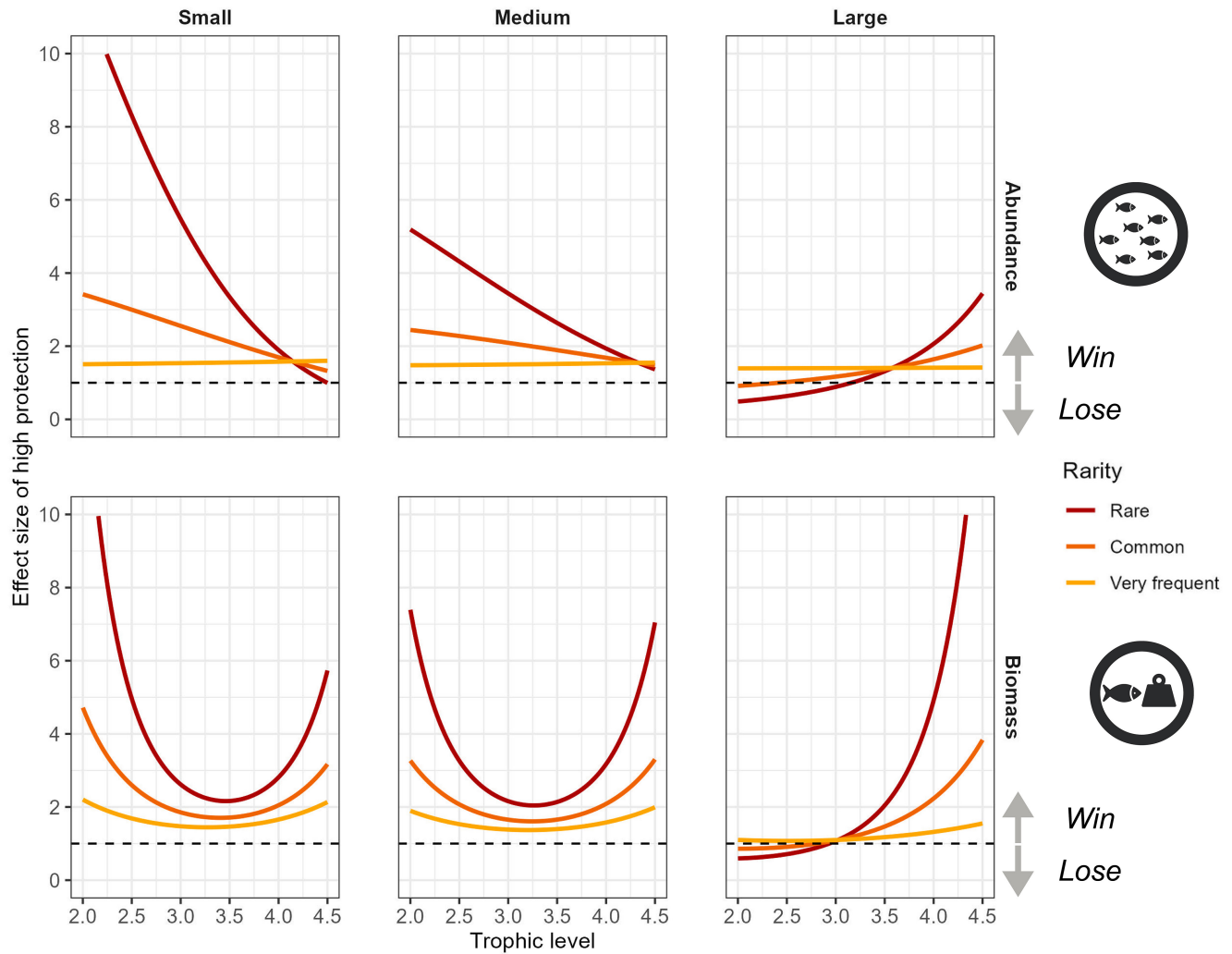


FIGURE 4 Model's graphical representation of the three-way interaction between species rarity, trophic level and maximum body length in the effect size of high protection on fish abundance and biomass. Small, medium and large species correspond to species at the 10th, 50th and 90th percentile for maximum body length, and rare, common and very frequent species correspond to the same percentiles in terms of occurrences with yellow, orange and red colours corresponding to very frequent, common and rare species, respectively. Effect sizes are plotted on the natural scale in order to facilitate interpretation of the model outputs: a value of 2 represents a twofold increase inside protected areas compared to outside while controlling for social-environmental factors and space.

DISCUSSION

Protected areas are widely recognized as prominent tools for safeguarding biodiversity against anthropogenic impacts, but most studies addressing this topic are conducted at the community scale (Cinner et al., 2022) or on particular functional groups (e.g. Donovan et al., 2023) and taxa (Smallhorn-West et al., 2020). By investigating species-specific responses of tropical reef fishes to protection in terms of occurrence, abundance and biomass, at a global scale, and controlling for a wide range of socio-environmental factors and space, we reveal that although many species appear to be benefiting from the current global MPA networks, more than a third of the fish species studied are negatively related to protection. We highlight that species responses to protection are generally stronger inside highly protected

MPAs (i.e. old, large, well-enforced no-take reserves) than in MPAs under medium or low protection, which is consistent with previous analyses carried out at the community level (Edgar et al., 2014; Giakoumi et al., 2017; Nowakowski et al., 2023). We also show that species responses vary across ecological traits that are linked to fisheries vulnerability, that is, fish trophic level and maximum body length. More intriguing, we reveal that rarity mediates species responses through interactions within these traits.

Our first result, that is, more than one third of fish species have lower occurrence probability, abundance or biomass inside than outside MPAs, unveils how the surplus of total fish abundance or biomass inside MPAs compared to outside is actually driven by the sum of individual positive responses, hiding the negative individual responses that mitigate conservation

benefits at the community scale. Besides, species' responses are not so trivially correlated between occurrence, abundance, and biomass, meaning that species may experience different benefits from MPAs. For instance, the leopard coral grouper (*Plectropomus leopardus*) displays a fourfold increase in biomass but only a 23% increase in occurrence probability inside highly protected MPAs compared to fished areas. The lowest mean correlation between effect sizes is between abundance and biomass. Therefore, some species benefit more from MPAs in terms of increased number of individuals rather than increased growth to larger sizes, and vice-versa. Some medium-sized species of the *Melichthys* genus (Balistidae), for instance, display higher responses to low than to higher levels of protection, probably because low protection cannot restore large populations of top predators such as sharks or groupers which may deplete prey populations (Newsome et al., 2017).

Second, although we found a positive response to protection for a majority of species, the response varied depending on interactions between trophic level and maximum body length. Indeed, the predominant positive response in fish occurrence seems driven by top-predators and herbivores. It confirms that large predators, intrinsically vulnerable to fishing (Abesamis et al., 2014) and thus most threatened in fished areas, show high benefits from MPAs (Cinner et al., 2018). Yet the U-shaped curves show that responses to protection are not linear across trophic levels with herbivores and top-predators benefiting more than mid-trophic level species at small and medium body lengths, suggesting that the presence of large predators in MPAs exerts a top-down control on mesopredators, that in turn release their control over smaller herbivores which exhibit the highest benefits (Graham et al., 2017). Indeed, small- and medium-bodied species have shorter generation times than large ones, allowing them to rapidly recover when fishing is restricted in a given area, while large herbivores cannot benefit from protection owing to the likely top-down control from higher trophic levels.

Third, despite the exclusion of the rarest species (less than 30 occurrences) due to the inherent difficulty to fit distribution models with too few observations (Thuiller et al., 2019), we reveal that rarity mediates the relationship between ecological traits and the response to protection in terms of abundance and biomass with very frequent and common species exhibiting lower effect size than comparatively rare herbivores and top-predators. Since the pattern is stronger in abundance and biomass compared to occurrence, we may hypothesize that MPAs provide a form of mitigation to Allee effects (Allee & Bowen, 1932; Gascoigne & Lipcius, 2004). Indeed, under a certain threshold of local population abundance, a decrease can occur in population growth rate due to the difficulty of individuals to meet and mate. By providing

a refugia for rare top-predators (Cinner et al., 2018), MPAs may create breeding hotspots where populations may remain above their Allee threshold (Aalto et al., 2019; Berec et al., 2007). Another refugia effect of highly protected areas on rare top predators is to allow the survival of some large-bodied individuals, which disproportionately contribute to the quantity of offspring and population persistence (Barneche et al., 2018; Marshall et al., 2021). The lower effect size of protection experienced by common predators could be explained by an increasing local competition, reducing the chances that any given species may thrive across many different MPAs.

Although we provide insights on the link between rarity and ecological traits to explain the response to protection over a large set of fish species across their entire ranges, our models explain only a third of the observed variation in the response to protection, at most. Including more traits may have increased the explanatory power of our models but to the detriment of the interpretability of our results. Another explanation for this limited explained variation is the underlying species-specific idiosyncrasy related to species interactions (e.g. co-occurrence patterns), that were not taken into account in our study. Nevertheless, we show that the R^2 values we obtain are not random, and we report consistent results among occurrence, abundance and biomass models, among different levels of protection, and also similar to effects reported for other taxa such as birds (Barnes et al., 2022; Martins et al., 2023). We suggest that rarity and potential Allee effects cannot be ignored in the design and implementation of MPAs (White et al., 2021) since the persistence of rare predators, which contribute disproportionately to the IUCN Red List of extinction risk (Dulvy et al., 2014; Harnik et al., 2012), critically depend on them.

One of our results was particularly interesting and unanticipated: approximately one-third of species seem to experience adverse effects following the establishment of MPAs. First, human activities disrupt the trophic structure of communities (Graham et al., 2017). The reversion towards a more 'natural' trophic structure resulting from the establishment of MPAs can trigger a shift in biomass distribution, leading to a reduction in the abundance and biomass of some species (Seguin et al., 2022). Secondly, the distribution of some species may largely encompass regions in which the majority of MPAs were declared of 'least resistance' to fishers, that is, where local habitats and fish populations were naturally poor (i.e. 'residual reserves'; [Devillers et al., 2015]). In light of these findings, it is suggested that in a world dominated by altered seascapes (Halpern et al., 2015) and human-dominated coastal areas (Williams et al., 2022), promoting highly protected marine areas and complementing them with less restrictive areas or other effective area-based conservation measures (OECM) could be a compromise between positive ecological outcomes for most species

while being more inclusive with locals and delivering contributions to people. This approach could maximize the number of species benefiting from some protection and would favour source-sink dynamics within MPA networks, and between MPAs and fished areas to maintain high regional or γ -diversity (Loiseau et al., 2021).

AUTHOR CONTRIBUTIONS

LS, DM, SM, FL and NL designed the study; CH, GE, MM, RSS and LV provided data for analyses; LS and NL performed the analyses; LS wrote the first draft of the manuscript and all the authors contributed substantially to the revisions.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data are available on Figshare at this DOI: <https://doi.org/10.6084/m9.figshare.24298570.v1>. Code is available on GitHub in this repository: https://github.com/Loic-sanchez/protection_fx_rarity. The data used in this paper come from a public database called Reef Life Survey.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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