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Funding information

Gulf Research Program of the National Academies of Sciences, Engineering and Medicine, Grant/Award Number: 2000009025

Editor: Alana Grech

Abstract

Aim: Seagrass beds are declining globally and are increasingly vulnerable to sea level rise (SLR), which could have consequences for the rich biodiversity they support. Spatial variation in the role of seagrass beds in enhancing biodiversity is poorly resolved, limiting our ability to set priorities for conservation and restoration. We aimed to model the biodiversity enhancement value of seagrass beds.

Location: Florida Gulf Coast, USA.

Methods: We used generalized additive mixed models (GAMMs) to describe the distribution, total cover and species composition of seagrass beds and to estimate their effects on spatial patterns of faunal species richness under three scenarios. Specifically, we: (a) quantified the biodiversity enhancement value of current seagrass beds, (b) inferred the biodiversity value of potential restoration areas and (c) projected potential changes in the distribution and biodiversity enhancement value of seagrass beds due to SLR using low (+0.50 m) and high (+1.0 m) SLR forecasts for 2100.

Results: Current seagrass beds supported 43%–64% more species than unvegetated habitats, even when accounting for spatial variability in predicted faunal richness due to other environmental, seascape, temporal and geographic factors. Seagrass restoration in potential habitats would also increase biodiversity in the near-term (i.e., 43%–45% above unvegetated levels). However, model projections indicate that SLR could result in significant losses of current seagrass beds and potential restoration areas, causing contracted distributions and lower seagrass cover. Overall, these changes could result in significant reductions in the enhancement value provided by seagrasses. Although, there could also be many suitable locations for seagrasses by 2100, with some having either comparable or potentially increased enhancement value.

Main conclusions: Our findings highlight the importance of considering spatial variation in biodiversity benefits when planning for seagrass conservation and restoration and when managing the impacts of SLR.

KEYWORDS

biodiversity, biogenic habitat, conservation, enhancement value, habitat restoration, management, sea level rise, seagrass, species distribution models

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1 | INTRODUCTION

Biogenic habitats such as seagrass beds, kelp forests, coral reefs and mangrove swamps are known to play an important role in enhancing marine biodiversity (Bruno & Bertness, 2001). These habitats also face many anthropogenic stressors (e.g., pollution, sedimentation and climate change) and are threatened worldwide, with implications for associated species and the ecosystem services provided by these diverse systems. This includes seagrass beds, which are formed by marine plants in shallow coastal waters, create essential habitat for a variety of fauna (e.g., crustaceans, bivalves, and fishes; Orth et al., 1984), and provide a range of ecosystem services including nursery habitat for fished species and opportunities for nature-based tourism and recreation (Nordlund et al., 2016). Despite their importance, many seagrass ecosystems are in decline because of intensifying impacts from boating activity, coastal development and land use changes (Waycott et al., 2009). Climate change-driven sea level rise (SLR) is also expected to shift suitable habitats for seagrass species in the coming decades (Saunders et al., 2013; Valle et al., 2014), with some locations becoming too deep to support seagrass growth and others becoming potential areas of colonization. Predicting the consequences of these impacts on the faunal species that depend on seagrass beds requires a better understanding of the spatial variability and interacting drivers of seagrass-associated biodiversity.

Such predictions are crucial to help management safeguard seagrass-associated biodiversity in the face of mounting environmental change. Seagrass conservation and well-planned restoration strategies have shown great promise (van Katwijk et al., 2016), prompting calls for their widespread use, such as within the Post-2020 Global Biodiversity Framework (CBD, 2020). However, to maximize biodiversity benefits these strategies need spatially explicit information for identifying where seagrass beds currently persist, where conservation could have the largest effects on faunal biodiversity now, and where seagrass could be restored and support biodiversity, now and under future climate scenarios. Yet, for many regions, the spatial distribution and community structure (e.g., total seagrass cover and species composition) of seagrass beds are poorly resolved at scales relevant to management and restoration decisions (McKenzie et al., 2020; Unsworth et al., 2019). Additionally, estimating spatial variation in the number of additional species supported by the presence of seagrass beds (hereafter called biodiversity enhancement value) remains a significant challenge because of the complexity of coastal ecosystems and the limited spatial and temporal coverage of most ecological studies (Hughes et al., 2009; Loh et al., 2019).

The biodiversity enhancement value of seagrass beds is likely determined by a variety of factors. For example, the presence, abundance and species composition of seagrasses are linked to faunal richness and abundance patterns (McCloskey & Unsworth, 2015; Ray et al., 2014), but seagrass communities can vary considerably along environmental gradients of depth, nutrients, light availability, temperature and salinity (Duarte et al., 2007; Jayathilake &

Costello, 2018; Uhrin & Turner, 2018). The spatial distribution and abundance of seagrass-associated fauna may also vary in response to environmental conditions (e.g., ocean temperature, phytoplankton production, pH and dissolved oxygen) that can fluctuate across space and over diel, seasonal, annual and inter-annual time-scales, especially for more mobile fauna like marine fishes (Faletti et al., 2019; Garwood et al., 2013; Unsworth et al., 2007). Additionally, seascape features like habitat connectivity and proximity to anthropogenic stressors can affect seagrass patterns and associated fauna at landscape scales (Bittner et al., 2020; Gilby et al., 2018). However, the relative influence of these potentially interacting factors on faunal biodiversity patterns has not been previously explored.

Species distribution models (SDMs) provide a promising opportunity for assessing the biodiversity enhancement value of seagrass beds. SDMs have been used in a variety of contexts for exploring species-environmental relationships and for inferring species distribution, abundance and richness patterns across unsampled areas and under different climate scenarios (Elith & Leathwick, 2009; Ferrier & Guisan, 2006; Guisan & Thuiller, 2005). They have been used to describe the historic distribution of seagrass beds (Bittner et al., 2020), to identify places where seagrasses could survive if restored (Adams et al., 2016) and to project how climatically suitable habitats for seagrass beds might shift with the onset of climate change (Valle et al., 2014). Here, we expand on this body of work by developing a suite of SDMs to predict the biodiversity enhancement value of seagrass beds (Figure S1.1). We use these models to quantify spatial variation in biodiversity enhancement value under different management and sea level scenarios, considering the interactive effects of seagrass bed characteristics, environmental conditions and seascape features on faunal biodiversity. We parameterize and apply our models to the Florida Gulf Coast (FGC)—a region known for its expansive tropical seagrass beds and rich associated fauna. We use our models to describe current patterns and explore how seagrass distributions and their contributions to biodiversity could be affected by conservation and restoration and by expected SLR. Although we focus on the FGC, this work informs a broader understanding of the biogeography of seagrass ecosystems and provides a modelling framework for assessing potential changes in their biodiversity enhancement value with climate change.

2 | METHODS

2.1 | Overview

For our modelling framework, we compiled datasets from monitoring, remote-sensing and modelled sources (see Appendix S1 in Supporting Information; Figure S1.1, Table S1.1). To estimate the biodiversity enhancement value of seagrass beds, we first modelled seagrass bed characteristics because spatially continuous data were not available. Existing seagrass datasets provide only point observations with many gaps in sampling throughout the region. We developed SDMs describing the spatial distribution, total cover and

species composition of seagrass beds at unsampled locations. Next, we developed a second set of SDMs to explore how seagrass bed characteristics, together with environmental conditions and seascape features, shape patterns of faunal biodiversity. We quantified spatial patterns of enhancement value from seagrass beds under different modelled scenarios—within confirmed seagrass beds and in areas where seagrass beds could survive if recovered. Finally, we explored how model predictions would change based on two SLR projections, identifying climate-resilient locations for seagrass conservation and restoration.

2.2 | Study area

Our study area spans the Florida Gulf Coast (FGC) including all subtidal areas within the 4-m depth contour. The FGC has seagrass beds known to support a variety of ecologically and economically important fish, crustaceans and shellfish species and these species have been monitored in the region, providing long-term datasets needed for model development. According to aerial survey maps from the Florida Fish and Wildlife Conservation Commission (FWCC; Figure S1.2), this region contains 7,800 km² of seagrass beds comprised by turtle grass (*Thalassia testudinum*), manatee grass (*Syringodium filiforme*), shoal grass (*Halodule wrightii*) and other species. The region also has significant variation in seagrass abundance (i.e., total seagrass cover) and species composition, environmental conditions and seascape structure, allowing us to resolve the importance of each of these attributes.

2.3 | Datasets

We used datasets from the Florida FWCC Fisheries Independent Monitoring (FIM) programme to model the distribution and community structure of seagrass beds and patterns of associated faunal biodiversity (FWCC, 2017). The FIM programme quantifies the monthly abundance for marine fishes and invertebrates from all habitats within nearshore areas, major bays and estuaries in Florida. FIM uses a stratified random sampling design to distribute effort across different hydrological zones, habitat types (such as seagrass beds), shoreline types and depth strata. Monthly sampling is conducted at randomly selected sites within each zone. The FIM survey uses multiple sampling gears to survey a wide range of species and depths, including a seine net survey (21.3-m net length; 3.2-mm mesh size; <1.8-m water depth) and an otter trawl survey (6.1-m aperture width; 38-mm mesh size; 3-mm mesh liner; 1.8–4-m water depth). At each sampling location, FIM also collects information on seagrass community structure (e.g., total seagrass cover, occurrence of dominant seagrass species), environmental conditions (e.g., bottom type, depth) and seascape features (e.g., presence of oyster reefs and mangroves within 100 m). For model development, we acquired all seine and otter trawl survey data available for our study area between 1997 and 2017. We used data from both vegetated

and unvegetated habitats (Figure S1.3) to capture the range of conditions influencing seagrass communities and faunal biodiversity in seagrass and non-seagrass areas.

We used spatial data layers (Table S1.1) to describe spatial variation in potential predictors across the study area and to extrapolate model predictions to unsampled locations. We used global remote sensing and data-assimilating model products assembled by BioOracle to characterize the long-term annual sea surface temperature, salinity, nitrates, primary productivity of phytoplankton in the water column, dissolved oxygen, pH and current velocity of coastal waters (Tyberghein et al., 2012). We used sediment property layers describing the distribution of four grain sizes (i.e., mud, sand, gravel and rocks) from US Geological Survey's usSEABED products. We used a depth layer from the National Oceanic and Atmospheric Administration's Coastal Relief Model. We calculated the long-term annual minimum light availability at the seabed using Beer-Lambert's law and the spatial layers for depth, the average photosynthetically active radiation (PAR) at the surface and the minimum light attenuation coefficient of the water column (Kd490) from BioOracle (Assis et al., 2018), where:

$$\text{Light availability} = \text{PAR} \times e^{(-Kd490 \times \text{Depth})} \quad (1)$$

We calculated the nearest distances to shore and to a river mouth as proxies for the influence of land-based anthropogenic stressors (e.g., nutrient pollution, sedimentation and freshwater input) using ArcGIS Version 10.7. Lastly, we used aerial survey maps of adjacent mangrove and oyster reefs from the Florida FWCC's Geodata Library to calculate proximity to these seascape features. All spatial layers were re-sampled to match the cell size of the finest resolution data layer (i.e., 93 m by 93 m) using the nearest neighbour method ("raster" R library). All analyses were conducted using R version 4.0.4 (R Core Team, 2021) and RStudio version 1.2.1335 (RStudio, 2020).

2.4 | Seagrass and faunal biodiversity models

We used generalized additive mixed models (GAMMs; "mgcv" R package), because they are increasingly used to describe, and forecast changes in species distribution, abundance and diversity patterns (Abrahms et al., 2019; Wood, 2012). Like generalized additive models, GAMMs perform well in comparison to other approaches and make no a priori assumption about the shape of the relationship between species responses and potential covariates. They also allow for the incorporation of random effects and spatially weighted covariance structures, which can be used to account for residual spatial auto-correlation associated with spatially clustered and/or repeated sampling designs (Zuur et al., 2009).

For the seagrass models, we modelled four response variables—total seagrass cover and the probability of occurrence for three dominant seagrass species (i.e., turtle grass, manatee grass and shoal grass)—because each of these variables could influence faunal biodiversity and is monitored by the FIM programme. To model total

seagrass cover, we used a Tweedie error distribution with a log link function because of its highly flexible form and ability to accommodate zero inflated abundance datasets (Schmidt & Garbutt, 1985; Tanaka et al., 2019); altering the Tweedie power parameter using a data adaptive procedure allows for the analysis of Gaussian, Poisson and over dispersed counts. For modelling the distribution of dominant seagrass species, we used a binomial error distribution with a log link function. We related each seagrass response variable to potential predictors that are known to influence seagrasses in Florida and other regions, including environmental and seascape variables (see Table S1.1 for variable descriptions and data sources). Temporal variables were included as fixed effects to account for seasonal and inter-annual trends (month and year) as well as random effects to account for repeated within-year sampling at some stations (Table S1.1). We also accounted for geographic variation in the responses using a Gaussian process smoother of the latitude and longitude of each observation (Wood, 2003). We applied thin-plate splines to each model predictor and allowed for possible interactive effects between environmental, seascape, geographic and temporal variables using tensor product smoothers. To reduce the potential for spatially auto-correlated errors, we thinned the model input datasets by systematically removing observations closer than 93 metres apart ($N = 10,931$ survey records retained), using the “spThin” R package (Aiello-Lammens et al., 2015). We tested for spatial autocorrelation of the residuals using variograms and a Mantel test. We then applied a spatially weighted covariance structure when necessary to control for residual spatial autocorrelation in the errors (Table S1.2). We identified important predictors of total seagrass cover and the probability of seagrass species by performing model selection based on the Akaike's Information Criterion (AIC) using a full subset information theoretic approach implemented with the “FSSGam” R package (Fisher et al., 2018).

To model faunal biodiversity, we quantified the functional relationship between the observed species richness (i.e., the number of fish and invertebrate species per sampling event) and potential seagrass, environmental, seascape, temporal and geographic predictors using GAMMs (Table S1.1). We modelled faunal species richness directly (as opposed to deriving estimates from stacked SDMs of individual faunal species) because this approach has been shown to perform well at describing current patterns of biodiversity (Biber et al., 2020) and can offer more reliable projections of biodiversity change than stacked SDMs (Harris et al., 2018). We developed separate models for shallow waters (i.e., 1–2 m) based on seine surveys ($N = 6,897$ records) and deep waters (i.e., 2–4 m) based on otter trawl surveys ($N = 2,896$ records) to account for potential differences in sampling efficiency between gear types. Our model development methods were the same as those used for the seagrass models described above, except we used GAMMs with a negative binomial error distribution with a log link function (see Appendix S1 for more details).

For seagrass and faunal biodiversity models, performance and predictive skill was assessed using several metrics, including adjusted R-squared ($\text{adj-}R^2$) and root mean squared error (RMSE) values for

the total seagrass cover and faunal biodiversity models. We used the area under the curve (AUC) to assess the seagrass species models and calculated the accuracy rate of the total seagrass cover model to discriminate between seagrass presence and absence. The final models' predictive capabilities were evaluated using a Monte Carlo cross-validation procedure that randomly splits the full dataset 50 times into 75% training and 25% testing data, and then refits each model to quantify the relationship between observed and predicted values in the testing datasets. We also evaluated each final model's transferability across space by performing spatial block cross validation (“CVBlock” R package), where we randomly removed data from different 1 km by 1 km spatial blocks and tested each model's predictive skill using data from the removed spatial blocks (Valavi et al., 2019). From the cross-validation procedures, we calculated the average performance and predictive skill of each model using the previously described metrics (i.e., $\text{adj-}R^2$, RMSE, AUC and/or accuracy rate). All models maintained their explanatory and predictive performance during cross-validation (Table S1.3).

2.5 | Model uncertainty

We quantified the pointwise prediction error of the total seagrass cover and faunal biodiversity models using the average RMSE between observed and predicted values from the Monte-Carlo cross-validation procedure, as described above. We then calculated the pointwise prediction error of the current enhancement value estimates by propagating the RMSEs of the faunal biodiversity models between the modelled and counterfactual prediction scenarios (Table S1.4). We quantified the overall uncertainty of the mean estimates for total cover, faunal biodiversity, current biodiversity enhancement value and enhancement value with restoration by propagating the RMSE through the calculation of the average values (see Appendix S1 for more detail).

2.6 | Mapped predictions

We generated mapped predictions of total seagrass cover and species composition across the study area using the final seagrass models and spatial layers of important model predictors. We averaged monthly predicted seagrass values per 93 m-by-93 m pixel across the summer growing season (June–September) and the years 2016–2020 to obtain maps representing the time-averaged predictions of seagrass cover and the probability of occurrence for the three seagrass species given current environmental conditions. We considered the total predicted distribution of seagrass beds to be the spatial extent of all locations with a predicted total seagrass cover of >5%. We also generated map predictions of faunal biodiversity using the final models and spatial layers for important model predictors, including the seagrass model predictions just described. Predictions represent the time-averaged summer faunal biodiversity, matching the temporal resolution of the seagrass predictions.

2.7 | SLR projections

We used a global SLR scenario from the latest Intergovernmental Panel on Climate Change report (i.e., RCP 8.5) predicting a rise of between approximately 0.61 and 1.1 m above current sea level by 2100 (Oppenheimer et al., 2019). Given that local SLR in Florida has generally followed global mean SLR over the last couple of decades, a global scenario was considered appropriate (Geselbracht et al., 2015). We used a low end (+0.5 m) and high end (+1.0 m) projection and applied both to our study region by modifying current layers for variables that would be most directly impacted by SLR. Specifically, for each scenario we adjusted depths based on SLR, identified a new shoreline based on adjusted depths and calculated the future nearest distance to shore and river input for each pixel. Lastly, we derived future minimum annual light availability layers for each location using the future depth and Equation 1.

2.8 | Scenarios

We created three primary scenarios to estimate the biodiversity enhancement value of seagrass beds, that is, the number of additional species supported by the presence of seagrass per sampling event. For each scenario, we compared model predictions of faunal biodiversity assuming seagrass beds are present at the level predicted by our seagrass models to those representing various counterfactual conditions. The first scenario estimates **current enhancement value** and thus was geographically constrained to the extent of confirmed seagrass beds (i.e., areas that have been previously surveyed and found to have seagrass beds by Florida FWCC aerial surveys between 1985 and 2019; <https://geodata.myfwc.com/datasets/seagrass-habitat-in-florida/>). We compared current conditions to counterfactual conditions where all confirmed seagrass beds are lost from the study area (i.e., all spatial data layers for important seagrass predictors are set to zero prior to generating faunal biodiversity predictions). We calculated the current enhancement value as the spatially explicit difference in predicted faunal biodiversity between the current and counterfactual conditions.

The second scenario estimates **enhancement value with restoration**, that is, the number of species added per sampling event by the successful restoration of seagrass beds, and was constrained to areas where seagrass beds are absent from FWCC maps but could potentially survive if restored according to seagrass model predictions (i.e., locations with predicted total seagrass cover >5% outside of confirmed seagrass beds). The counterfactual conditions presumed that these areas are restored to the level of seagrass cover predicted by our models. We calculated the enhancement value with restoration as the difference in predicted faunal biodiversity between the counterfactual restoration conditions and the continued absence of seagrass beds.

The third scenario estimates **enhancement value with SLR** of confirmed seagrass beds and potential restoration areas and was

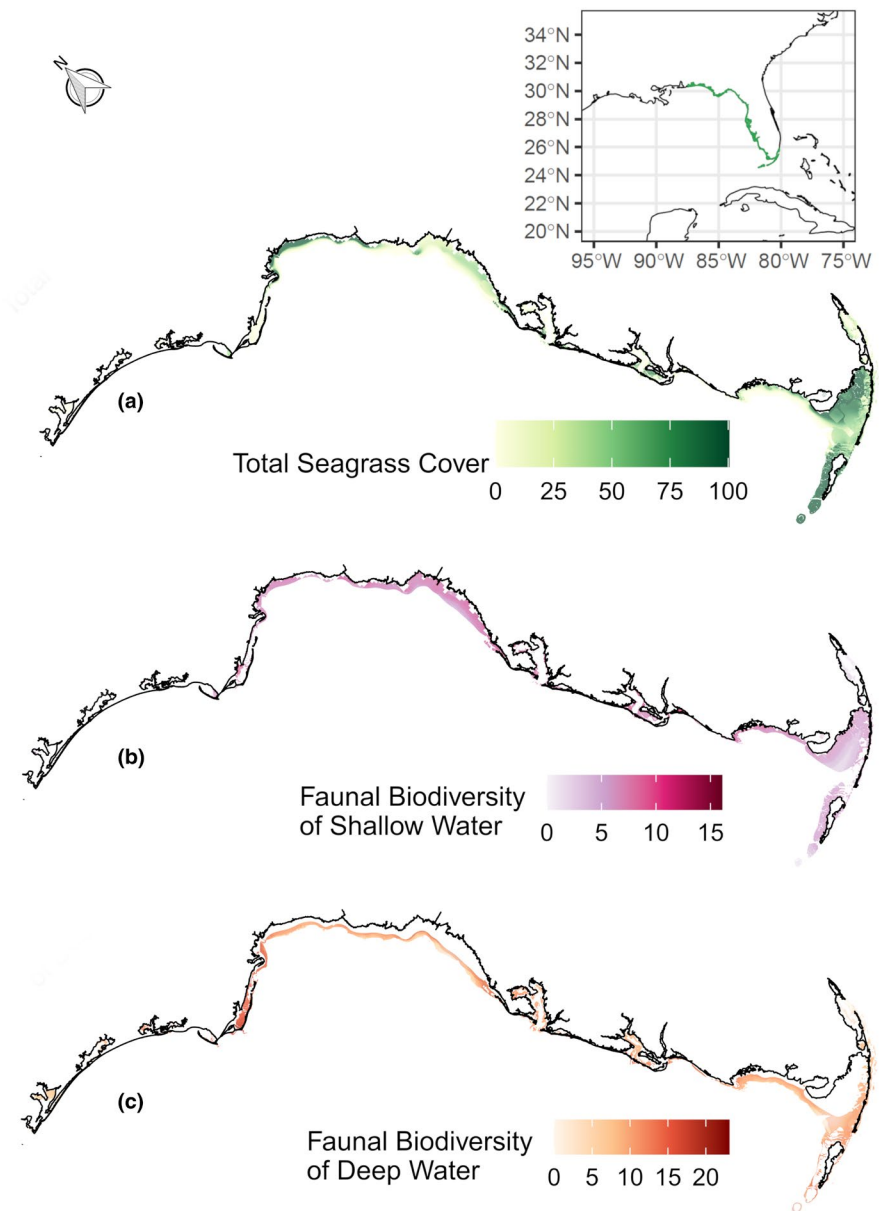
constrained to the total predicted distribution of seagrass beds at the current sea level, plus those areas that could become suitable for seagrass beds at 2100 according to model projections (i.e., locations with a projected total seagrass cover >5%) given the low end (+0.5 m) and high end (+1.0 m) SLR projection. We focus on SLR (and not on other expected impacts of climate change, such as temperature, pH or dissolved oxygen) because those other factors were not significant predictors in our total seagrass cover or biodiversity models. We quantified the biodiversity enhancement value of these future projected seagrass beds by comparing faunal biodiversity predictions assuming biodiversity is present at the levels predicted by our models, to the those that presumed seagrasses are totally lost from the study area by 2100. We calculated the future enhancement value as the spatially explicit difference in faunal biodiversity between the two predictions. Using the “SDMToolbox” R package, we considered potential changes in the predicted extent and geographic distribution of features, including confirmed seagrass beds, potential restoration areas and high enhancement value areas (VanDerWal et al., 2014). Due to high uncertainty associated with projecting the spread of seagrass beds into newly submerged habitats, we focused solely on changes occurring within fully submerged areas at the current sea level.

3 | RESULTS

3.1 | Current seagrass beds

Seagrass beds had a predicted distribution of 9,195 km² along the FGC under current environmental conditions (Figure 1a; Table 1). 6,540 km² (71%) of that distribution corresponded to confirmed seagrass beds that have been mapped using aerial surveys (Figure S1.2); the remaining areas are not confirmed to have seagrasses but are predicted to be able to support them, that is, they are potential restoration areas (Table 1). Total seagrass cover varied considerably across the study area with the most expansive high cover areas constrained closer to shore and concentrated in the Big Bend and Florida Bay regions (Figure 1a; Figure 2a; Table 1). Our model indicates total seagrass cover is generally highest in shoal waters (i.e., <1 m) and in areas without rocks, farther away from rivers and where the annual nitrate range was low (adjusted-R² = 0.34; Figure S1.4; Table S1.5). Seagrass species composition also varied across the study area (Figure S1.5) with all three dominant species having strong associations with water depth but different depth distributions and relationships to other factors (Table S1.5). Turtle grass had the greatest probability of occurrence at intermediate depths (0.5–1.5 m), in areas farther away from river inputs, and with moderate annual ocean temperatures (Figure S1.6; AUC = 0.91). In comparison, manatee grass had the greatest probability of occurrence in slightly deeper waters (1–2 m) and in areas closer to shore (Figure S1.7; AUC = 0.91). Lastly, shoal grass had the greatest probability of occurrence in shoal waters, in areas nearest to river inputs and with high light availability at the seabed (Figure S1.8; AUC = 0.82).

FIGURE 1 The predicted (a) distribution and total cover of seagrass beds (%), (b) faunal biodiversity in shallow waters (# of species per seine survey) and (c) faunal biodiversity in deep waters (# of species per otter trawl survey) under current conditions in the Florida Gulf Coast (FGC). Model predictions of faunal biodiversity are constrained to the sampling depth ranges of the original seine and otter trawl surveys (0–2 m and 2–4 m, respectively) to avoid inappropriate model extrapolation. Inset map shows the location of the FGC (green) relative to the Gulf of Mexico and the northern Caribbean



3.2 | Current faunal biodiversity patterns

Predicted faunal biodiversity varied across the study area in both shallow (0–2 m) and deeper waters (2–4 m; Figure 1b,c). The average predicted faunal biodiversity of deep waters was considerably higher than shallow waters (i.e., 11 ± 0.004 species per otter trawl versus 7 ± 0.003 species per seine), likely due to the greater sampling efficiency of otter trawl surveys (Figure 2b; Table 1). Nevertheless, biodiversity estimates from the two models were highly correlated, indicating general agreement about current hotspots for faunal biodiversity ($r = 0.88$). Faunal biodiversity patterns were explained by a similar combination of seagrass, environmental and seascape factors, but with differing relationships between the two models (Figure S1.9–Figure S1.10; Table S1.6; adjusted $R^2 = 0.33$ – 0.34). For instance, faunal biodiversity was positively related to total seagrass cover in shallow waters (Figure S1.9) and increased by the presence of seagrass beds (regardless of the total cover) in deep waters (Figure S1.10). Faunal biodiversity also generally

increased in the presence of mud and decreased with distance from shore in shallow waters in both models. However, there was a significant interaction between distance to shore and seagrass presence in the deep water model indicating that seagrass beds have a stronger enhancement effect the further they are from shore (Figure S1.10). A significant interaction between total seagrass cover and annual maximum phytoplankton production in the shallow water model also indicated a stronger enhancement effect of seagrass cover in areas with higher phytoplankton production (Figure S1.9).

3.3 | Biodiversity enhancement value

3.3.1 | Current enhancement value

Confirmed seagrass beds had approximately 43% and 64% more species compared to the counterfactual conditions for shallow and

TABLE 1 Metrics of projected seagrass ecosystem change in the Florida Gulf Coast, including current estimates and predicted deltas (i.e., future minus current) for the year 2100 under RCP 8.5 low end (+0.5 m) and high end (+1.0 m) sea level rise scenarios

Metrics	Metric definition	Current sea level	Delta values at +0.5 m sea level	Delta values at +1.0 m sea level
Seagrass bed area (km ²)	The total extent of predicted seagrass beds based on the final model of seagrass cover	9,195	-1,176	-2,293
Total seagrass cover (%)	The average prediction from the final seagrass cover model, indicating the percentage of the ground surface covered by seagrasses	41 ± 0.03	-11	-19
Confirmed seagrass area (km ²)	The total extent of predicted beds that can be confirmed by FWCC aerial survey data	6,540	-471	-1,094
Potential restoration areas (km ²)	The extent of predicted beds falling outside of FWCC maps	2,655	-705	-1,198
Northern extent of seagrass beds (km)	The lower 5% quartile latitudinal position of predicted seagrass pixels	3,320	0	-1
Central Distribution of Seagrass Beds (km)	The "centre of gravity" or the abundance weighted centre of predicted seagrass pixels	2,904	-16	-41
Southern Extent of Seagrass Beds (km)	The upper 95% quartile latitudinal position of predicted seagrass pixels	2,729	-2	-3
Seagrass beds position relative to shore (km)	The distance between the current shoreline and the predicted central distribution of seagrass beds	2	-1	-2
Faunal biodiversity in shallow waters (# per seine survey)	The average prediction from the final shallow water faunal biodiversity model (0–2 m)	7 ± 0.003	0	-1
Faunal biodiversity in deep waters (# per otter trawl survey)	The average prediction from the final deep water faunal biodiversity model (2–4 m)	11 ± 0.004	-1	-2
Current enhancement value				
Shallow waters	The average estimated contribution of current seagrass beds to faunal biodiversity	3 ± 0.007	-1	-1
Deep waters		7 ± 0.012	-3	-3
Enhancement value of restoration				
Shallow waters	The average estimated contribution of potential restoration areas to faunal biodiversity	3 ± 0.014	-2	-2
Deep waters		5 ± 0.015	-3	-4

Note: The overall uncertainty on the mean estimates from model predictions are provided following the "±" sign.

deep waters, respectively. On average, shallow seagrass beds supported an additional 3 (±0.007) species per seine and deep seagrass beds supported an additional 7 (±0.012) species per otter trawl when controlling for important environmental, seascape, temporal and geographic variables (Figure 2c; Table 1). Nearly 80% of seagrass beds had at least some enhancement value (i.e., adding ≥1 species) and 30% had high enhancement value (i.e., above average). Seagrass beds offering high biodiversity enhancement value were generally more common in shallow waters (Figure 3a), particularly in the Big Bend and central regions of Florida where peak annual phytoplankton production and total seagrass cover are highest (Figure S1.11a). By comparison, deep water seagrass beds with high enhancement value were rare (Figure 3a), with the highest enhancement value seagrass beds concentrated mainly off the Spring Coast and Florida Keys where they can persist further from shore and have a more

outsized effect on faunal biodiversity (Figure S1.11a). High enhancement seagrass beds, occupying 1,272 km² of shallow water and 625 km² of deep water seagrass beds, could be high priorities for near-term conservation (Figure 3a).

3.3.2 | Enhancement value of restoration

Seagrass restoration within all current unconfirmed seagrass beds could lead to an average return of 3 (±0.014) species per seine and 5 (±0.015) species per otter trawl for shallow and deep waters, respectively (Figure 2c; Table 1). Approximately 95% of potential areas could add at least some value and 25% would offer above average value. Potential restoration areas with high enhancement value were again more widespread in shallow waters (Figure 3b) and were

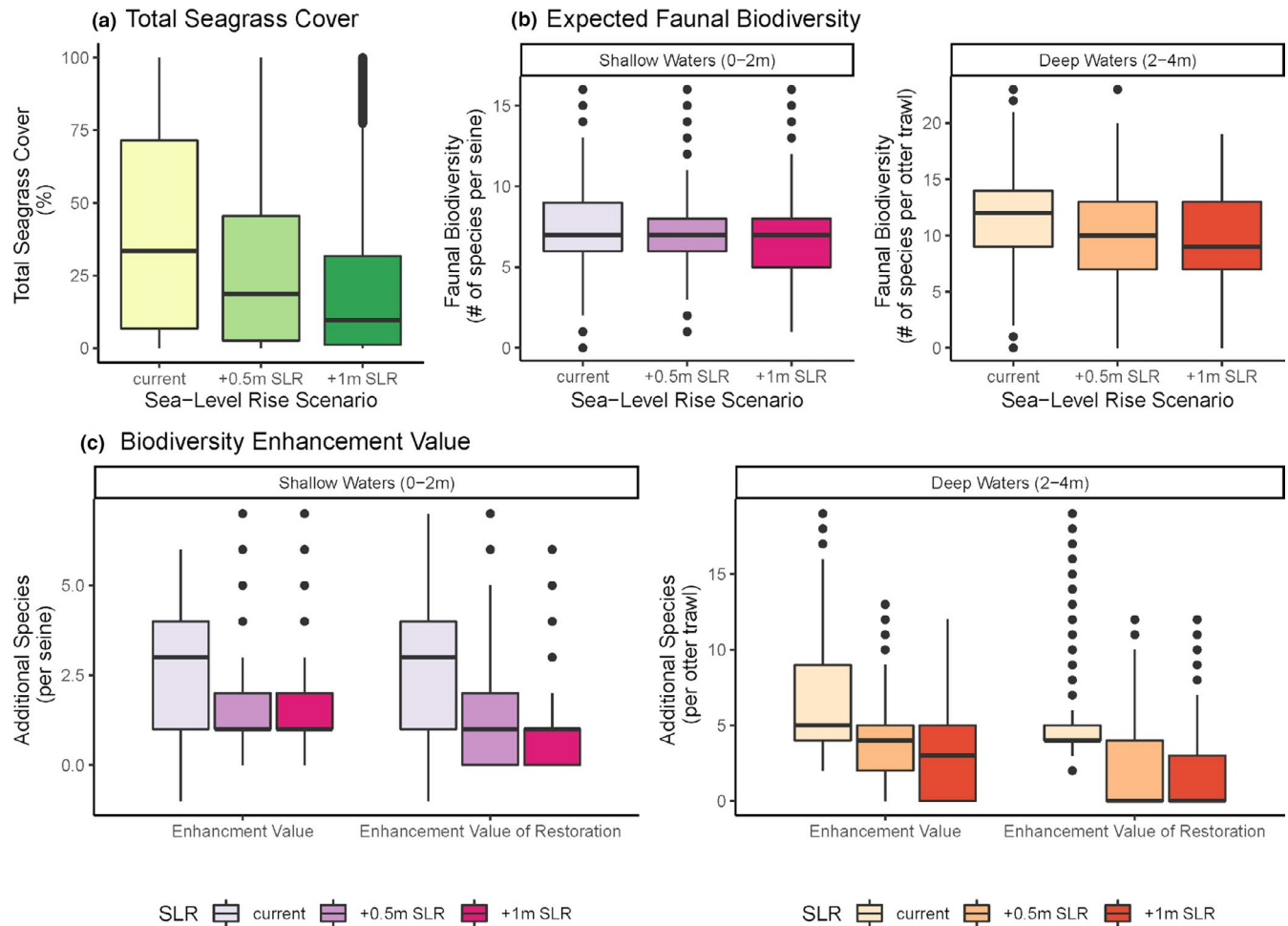


FIGURE 2 Predicted spatial variation in the (a) total seagrass cover and (b) faunal biodiversity and (c) biodiversity enhancement value by gear type/depth at the current sea level and at low (+0.5 m) and high (+1.0) sea level rise (SLR) scenarios. Boxplots of enhancement value compare predicted values for map pixels within confirmed seagrass beds and potential restoration areas at the current sea level to model projections for the same spatial extents

primarily located off South Florida where there is the most expansive area of unconfirmed seagrass beds (Figure S1.2; Figure S1.11b). These areas, occupying 469 km² of shallow water and 189 km² of deep water restoration areas, could be high priorities for seagrass restoration in the near term (Figure 3b).

3.3.3 | Enhancement value with SLR

We projected substantial losses of both current seagrass beds and potential restoration areas with SLR. For every metre of SLR, we predict the central distribution of seagrasses would shift southward by approximately 40 km and contract shoreward by 2 km while seagrass area shrinks by 2,000 km² and total cover declines by 20% (Figure 2a; Table 1). Of the area lost, approximately half (471–1,094 km²) was projected to occur within confirmed areas of seagrass, with the remaining losses occurring within potential restoration areas (705–1,198 km²; Table 1). Overall, these changes could substantially reduce the faunal biodiversity of coastal waters and the enhancement value of current seagrass beds by 1 species per seine (–33%) in shallow waters and

by 3 species per otter trawl (–43%) in deep waters per metre of SLR (Figure 2b,c; Table 1), particularly for the high-end SLR scenario where declining cover and seagrass loss was most pronounced (Figure S1.12; Figure S1.13). We also found there could be substantial reductions in the enhancement value of potential restoration areas, which were projected to lose an even higher percentage of enhancement value in deep waters and in the high-end scenario. The average enhancement value of potential restoration areas could decline by 2 species per seine (–66%) in shallow waters and 4 species per otter trawl (–80%) in deep waters per metre of SLR (Figure 2c; Table 1). Despite these projected losses, most seagrass beds (90%) and potential restoration areas (81%) remaining suitable by 2100 could continue to provide some enhancement value, with roughly 40% of those areas yielding similar or even higher biodiversity benefits (Figure 4).

4 | DISCUSSION

Our study provides the first spatially explicit assessment of the biodiversity enhancement value of seagrass beds. We use our modelling

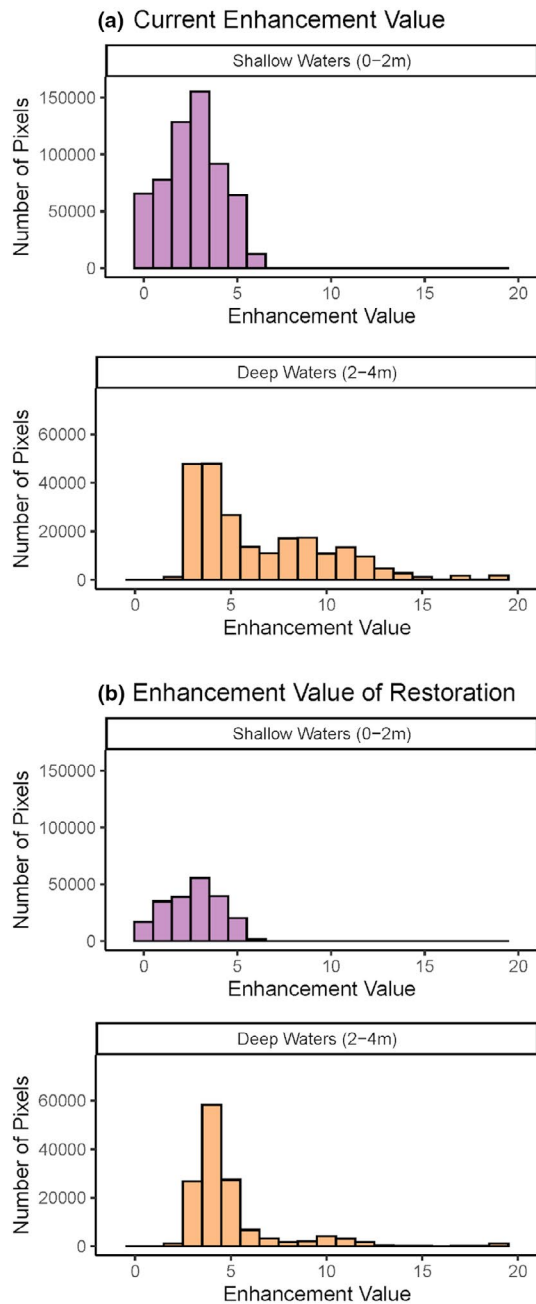


FIGURE 3 Frequency of map pixels representing (a) current enhancement value from confirmed seagrass beds and (b) enhancement value from potential restoration areas at the current sea level by gear type/depth along the Florida Gulf Coast. Enhancement value estimates are reported in terms of the additional number of species per sampling event supported because of the presence of seagrass in shallow waters (0–2 m; purple) and deep waters (2–4 m; orange)

framework to explore how biodiversity enhancement value varies across space and how patterns could be impacted by continued seagrass loss, habitat restoration and SLR. Previous studies have mainly focused on predicting the current distribution (Jayatilake & Costello, 2018), restoration potential (Adams et al., 2016; Bittner et al., 2020) and climate vulnerability of seagrass beds (Valle et al., 2014) without considering the implications for associated

fauna because of uncertainty about the interacting drivers and spatial patterns of seagrass-associated biodiversity. We find that current seagrass supports 43%–64% more species than comparable unvegetated areas because of positive effects of seagrass bed presence and total cover on faunal richness. There is also extensive potential for near-term gains in biodiversity enhancement value with seagrass restoration (i.e., 43%–45% more species) (Table 1). However, the enhancement value of these areas is unlikely to be spatially uniform due to the interacting influence of shore proximity and phytoplankton productivity on faunal biodiversity. Biodiversity benefits of seagrasses could also be undermined by SLR, as depth was one of the most important predictors of seagrass presence and cover (Figure 2). Despite projecting overall losses in biodiversity benefits, we find that most remaining seagrasses could continue to offer enhanced biodiversity if properly conserved or restored, with many locations potentially conferring similar or even increased value by 2100 (Figure 4). Our findings emphasize the need to consider spatial variation in biodiversity benefits when planning for seagrass conservation and restoration and when managing the impacts of SLR.

Expanding on previous work (Bittner et al., 2020), our models provide the first large-scale synoptic maps of seagrass bed distribution, total cover and species composition for the Florida Gulf Coast (FGC). Our seagrass models show the importance of depth, water clarity and water quality for determining seagrass bed distribution, abundance and species composition, which is consistent with previous observations from the tropical Atlantic and other regions (Hale et al., 2004; Iverson & Bittaker, 1986). Depth and factors influencing light availability (e.g., nitrate levels or irradiance at the seabed) were common predictors across four seagrass response variables. Proximity to shore and river input were also frequently selected, suggesting that freshwater input and nutrient pollution from land based sources also play a key role in shaping seagrass communities. Ocean temperature was not a significant predictor of seagrass cover and was only significant in the model of turtle grass occurrence.

Our faunal biodiversity models confirm the enhancement effect of seagrass beds (Orth et al., 1984) while providing a more nuanced accounting of the factors influencing seagrass associated fauna, including seagrass cover, phytoplankton production, proximity to shore, sediment properties, seasonality and geographic position. Novel interactions uncovered by our models also reveal the potential for substantial spatial variability in the level of biodiversity enhancement provided by seagrasses in this region. In shallow waters, the positive, nonlinear interaction between total seagrass cover and phytoplankton productivity likely reflects their converging effects on food webs (Edgar, 1990; Gagné et al., 2020). In deep waters, the significant interaction between seagrass presence and shore proximity is likely related to the diminished effect of river inputs, the greater water-column volume available for fish and the food subsidies and habitat structure provided by seagrasses (Heck & Wetstone, 1977). These interactive drivers have not previously been quantified and are likely key to understanding and anticipating changes in the biodiversity support from these systems.

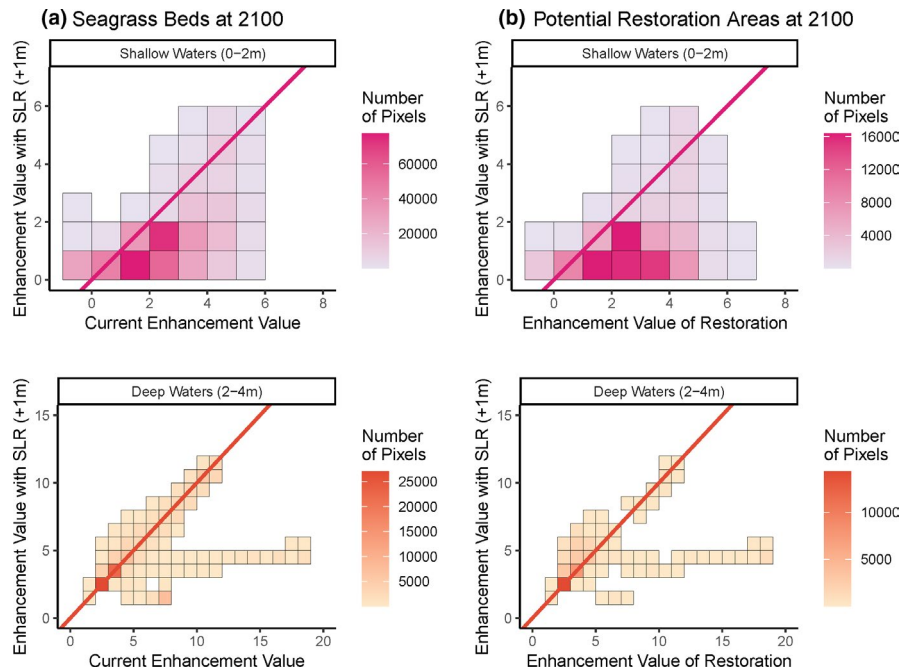


FIGURE 4 Comparison of the (a) current enhancement value of seagrass beds and (b) enhancement value of potential restoration areas between the current sea level and the high end SLR scenario (i.e., +1 m above current) for all areas still suitable for seagrass at 2100. Axes represent the relative enhancement value, or the additional number of species per sampling event supported by the presence of seagrass, in that scenario. Each cell represents the frequency of map pixels with confirmed seagrass beds and restoration areas that are deemed suitable at 2100 and exhibit a specific change in enhancement value for shallow waters (0–2 m; pink) and deep waters (2–4 m) along the Florida Gulf Coast. Cells falling along the 1:1 line are projected to have a similar enhancement value with SLR. Cells falling above the 1:1 line are projected to have higher biodiversity enhancement value by year 2100, meanwhile those falling below the 1:1 line could have lower biodiversity enhancement value

Combining our seagrass and faunal biodiversity model predictions, we gain important insights about the biodiversity benefits of seagrass beds. We quantify the number of species threatened by continued seagrass loss and identify where those losses could be most extreme, in addition to quantifying the biodiversity benefits from seagrass restoration and identifying where restoration could have the greatest impact. The biodiversity benefits from seagrasses are more widespread in shallow waters, especially in northern regions where there is a convergence of high cover seagrass beds and peak phytoplankton productivity. Deep water seagrass beds also offer the potential for substantial biodiversity benefits, but that value is largely constrained to southern regions where depth, water quality and water clarity conditions allow seagrasses to persist further from the shore. While the enhancement values may seem modest, they represent large percentages of the total predicted faunal biodiversity for seagrass beds in this region. Additionally, many of these species are ecologically, economically and recreationally important, including pink shrimp (*Farfantepenaeus duorarum*), blue crab (*Callinectes sapidus*), black seabass (*Centropristis striata*) and bay scallops (*Argopecten irradians*), which all associate with seagrasses more frequently than with unvegetated habitats (Figure S1.14). Some of these species are also species of concern (e.g., snapper and grouper species, Hughes et al., 2009). Lastly, our estimates likely represent a lower bound of potential biodiversity enhancement because we do not consider all

taxonomic groups linked to seagrass system, such as turtles, elasmobranchs and infauna (Hughes et al., 2009).

With projected SLR, we predict distributional shifts shoreward and substantial overall seagrass losses, especially in deeper waters where the decline in irradiance is likely to be most pronounced. Additionally, our models indicate there could be a general southward contraction in seagrass distribution, likely due to the higher water clarity of coastal waters at southern latitudes (Figure S1.15) and a narrowing region with sufficient irradiance to support seagrass beds in more northern waters. Our study expands on previous research on seagrasses and SLR (Davis et al., 2016; Valle et al., 2014), projecting negative consequences of these changes for associated fauna. Nevertheless, we find that some locations could provide similar or higher enhancement value—especially in southern regions where optimal conditions for seagrasses seem to be maintained—offering opportunities to colonize newly submerged areas and safeguard biodiversity as sea levels change.

Our analysis provides estimates of the enhancement value of seagrass beds and potential restoration areas based on time-averaged predictions for seagrass and associated faunal richness. However, several factors could influence whether estimated enhancement values are realized. For one, we do not account for the effects of harmful algal blooms, boating activity or fishing pressure due to insufficient publicly available data. These factors could undermine realized biodiversity enhancement either through impacts to seagrass

beds or marine faunal populations (Lapointe et al., 2015; Sagerman et al., 2020). We also do not account for herbivory, which could affect seagrass communities positively or negatively depending on the context (Scott et al., 2018) and may have a growing influence with the tropicalization of herbivore populations (Heck et al., 2015). Lastly, ocean temperature and other environmental factors likely to change with climate change (e.g., pH and dissolved oxygen) were not significant predictors of total seagrass cover or faunal biodiversity. Thus, we did not incorporate ocean warming or acidification in the predictions we developed to examine the impact of SLR. However, it is likely these factors would play a more important role over a larger geographic scale or in other regions. They could also become more important drivers within our study region as climate changes intensify (Strydom et al., 2020), exceeding levels observed within our datasets. Furthermore, ocean temperature was a significant predictor of turtle grass occurrence, suggesting that even moderate ocean warming could have an indirect impact if shifts in seagrass species composition result in changes in total seagrass cover. Future work could explore how these changing factors influence seagrass biodiversity enhancement value using our approach.

Our study provides the first regional assessment of the vulnerability of seagrass ecosystems and their associated biodiversity to SLR. While our framework provides a useful starting point for proactive seagrass conservation and restoration, we likely underestimate the suitable distribution for seagrass beds at 2100 because our study focuses solely on the subtidal zone at the current sea level. Some newly submerged locations could become seagrass beds—either through natural or facilitated colonization. The extent of seagrass establishment in future submerged areas will depend on many factors not included in this study, such as the suitability of newly submerged substrates for seagrass growth as well as physical and oceanographic conditions of these areas (e.g., light availability, nitrate levels, phytoplankton productivity, storm frequency). There may also be significant barriers, such as remnants of terrestrial ecosystems and man-made infrastructure, that would make seagrass establishment too difficult and costly (Saunders et al., 2013). Nevertheless, our approach could be extended to help identify the most suitable and feasible places to establish these novel seagrass ecosystems, as appropriate spatial datasets become available.

There are important limitations associated with our model predictions. For instance, comparisons of enhancement value estimates between shallow and deep waters are complicated by the differing sampling efficiencies and depth ranges of the two FIM gear types used for faunal biodiversity model development. We cannot determine whether higher faunal biodiversity and enhancement value estimates in deep waters relate to the higher efficiency of otter trawls or a greater volume of water-column available for fish species at depth. Previous work provides evidence for increasing faunal abundance, biomass and body mass with depth and for differing species assemblages between shallow and deeper seagrass beds (Hayes et al., 2020; Jones et al., 2021). Nevertheless, direct comparison of our model outputs from the two depth zones should be avoided without more standardized sampling methods. We also used

composite aerial survey data from FWCC to distinguish between previously confirmed seagrass beds and potential restoration areas, but these maps could be incomplete or out of date in some locations due to the costs, logistics and delayed processing time associated with aerial mapping surveys. As such, some locations we identify as confirmed seagrass beds may represent potential restoration areas (and vice-versa). More precise estimates could be obtained as new aerial survey or satellite data are collected and analysed. Lastly, the overall uncertainty in our estimates of regional averages of total cover, faunal biodiversity and enhancement value is quite small (Table 1). However, our models carry considerable uncertainty in making individual point estimates (Table S1.4), likely due to local factors not accounted for in our models (e.g., unmeasured ecological drivers and varied histories of human impact from land use change and coastal development). Thus, our model estimates are more useful and appropriate for time-averaged geographic comparisons than for real-time predictions at specific sites.

5 | CONCLUSIONS

Our study provides new understanding of the biodiversity enhancement value of seagrass habitats, with implications for spatial management of these systems in the face of mounting environmental change. Our approach provides insights into the spatial drivers and variability of biodiversity enhancement benefits of seagrasses and how this enhancement value is likely to be impacted by SLR. The mapped predictions can inform spatial planning for conservation and restoration, allowing for seagrass percent cover, seagrass diversity and/or faunal diversity to be prioritized when selecting protected areas or restoration sites (Figure 3; Lester et al., 2020). In the long term, our model projections of future seagrass distribution and enhancement value can also help managers gauge how proposed conservation and restoration sites might fare with the onset of SLR and to identify places that may be most resilient to climate change. Our study is most applicable to tropical seagrass systems. However, our approach is broadly relevant to seagrasses and other biodiversity enhancing systems (e.g., oyster reefs and mangrove swamps) around the world. Future work could adopt our modelling framework to explore the biodiversity enhancement benefits and vulnerability of these systems to climate change and other global stressors.

ACKNOWLEDGEMENTS

This research was funded by the Gulf Research Program of the National Academy of Sciences, Engineering and Medicine under award number 2000009025. We thank the Florida Fish and Wildlife Conservation Commission's Fisheries Independent Monitoring program for providing us with seagrass and fauna monitoring datasets. We also thank the members of the Rasster lab at Florida State University (FSU), including both graduate students and undergraduate trainees, who provided valuable feedback on this work. We thank Dr Daniel Okamoto from the FSU Department of Biological Science for early conversations about model development. Lastly,

we thank Heather Welch from the National Oceanic Atmospheric Administration National Marine Fisheries Service for sharing code and advice related to the development of the Rshiny application.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13379>.

DATA AVAILABILITY STATEMENT

The authors confirm that the data supporting the models and the findings of this study are publicly available. Weblinks to underlying datasets can be found in the references section and supplementary information. The final models, outputs and R code used for modelling and subsequent scenario analysis are available in a Github repository (<https://github.com/jenmchenry1/Modeling-the-Biodiversity-Enhancement-Value-of-Seagrass-Beds>). Model outputs can also be viewed via an RShiny App (http://jennifermchenry.shinyapps.io/seagrass_bev/).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: McHenry, J., Rassweiler, A., Hernan, G., Uejio, C. K., Pau, S., Dubel, A. K., & Lester, S. E. (2021). Modelling the biodiversity enhancement value of seagrass beds. *Diversity and Distributions*, 27, 2036–2049. <https://doi.org/10.1111/ddi.13379>