Ecosystem Services 63 (2023) 101543

Contents lists available at ScienceDirect

Ecosystem Services

journal homepage: www.elsevier.com/locate/ecoser

Full Length Article

Seagrass ecosystem services show complex spatial patterns and associations

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ARTICLE INFO

Keywords:
Ecosystem services
Enhancement value
Marine foundation species
Natural capital
Seagrass
Spatial relationships
Spatial variation

ABSTRACT

Seagrass beds support rich biodiversity and provide a range of important ecosystem services, and thus widespread seagrass degradation and decline has prompted broader efforts to protect and restore these habitats. Limited resources for seagrass management and restoration could be better directed by leveraging information about the potential patterns of ecosystem service supply. However, compared to many terrestrial and marine ecosystems, the spatial patterns and relationships among different seagrass ecosystem services are still poorly understood. Focusing on the Florida Gulf Coast as a study system, we performed one of the first spatially explicit assessments of multiple ecosystem services provided by seagrass beds. We developed or modified existing spatial models for five ecosystem services: biodiversity enhancement, nursery habitat, blue carbon, recreation, and coastal protection, using a combination of empirical and model datasets. Using these spatial models, we identified key predictors and quantified the marginal effect of seagrasses on each service. Our models revealed that seagrasses significantly enhance the supply of multiple services, but that there was considerable spatial variation within and among these services, resulting in distinct hotspots where seagrasses are most valuable in providing different services. Contrary to the expectation that all seagrass services will be positively correlated with one another because they are strongly related to seagrass characteristics, we also found positive and negative associations among services, revealing the potential for both co-benefits and trade-offs associated with seagrass management decisions. Finally, we found that biodiversity was not a reliable proxy for most services, as is sometimes assumed, highlighting the need for direct assessments of seagrass services. Our findings emphasize the importance of considering distinct predictors of different ecosystem services when assessing potential delivery from seagrasses and other foundation species, especially when planning and prioritizing ecosystem conservation and restoration projects.

1. Introduction

Coastal and marine ecosystems that feature foundation species, such as seagrass beds, coral reefs, salt marshes, oyster reefs, and mangrove swamps, support rich biodiversity and provide important ecosystem services that contribute to human health, well-being, and livelihoods (Barbier et al., 2011). However, these habitats have faced widespread environmental degradation and disturbance, leading to compromised ecological integrity and a diminished capacity to provide ecosystem services (Brondizio et al., 2019). Recent international agreements have highlighted the urgency of preserving and restoring marine habitats that are essential for supporting biodiversity and ecosystem services (CBD, 2021; UNEA, 2019). Nevertheless, conservation planning and site selection for restoration aimed at promoting the delivery of multiple services remains a significant challenge without comprehensive ecosystem service assessments (Lester et al., 2020).

Seagrass beds provide many important ecosystem services, resulting in a multitude of ecological, socioeconomic, and cultural benefits (Mtwana Nordlund et al., 2016). They can provide habitat to a variety of species, including bivalves, crustaceans, fishes, and sea turtles (Mtwana Nordlund et al., 2016; Orth et al., 1984), thus enhancing the biodiversity of coastal waters (McHenry et al., 2021). Seagrass beds can also serve as a nursery areas for recreationally and commercially harvested species during their early life stages, thereby supporting fisheries and coastal livelihoods (Lefcheck et al., 2019; Unsworth et al., 2019a). Seagrasses can play a role in protecting coastal shorelines from erosion and storm damage by reducing wave energy and currents and by stabilizing sediments (Arkema et al., 2013; Hansen and Reidenbach, 2012). These habitats can also promote the accumulation and burial of organic material in marine sediments (Fourqurean et al., 2012; McHenry et al.,

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https://doi.org/10.1016/j.ecoser.2023.101543
Received 5 October 2022; Received in revised form 3 June 2023; Accepted 5 July 2023

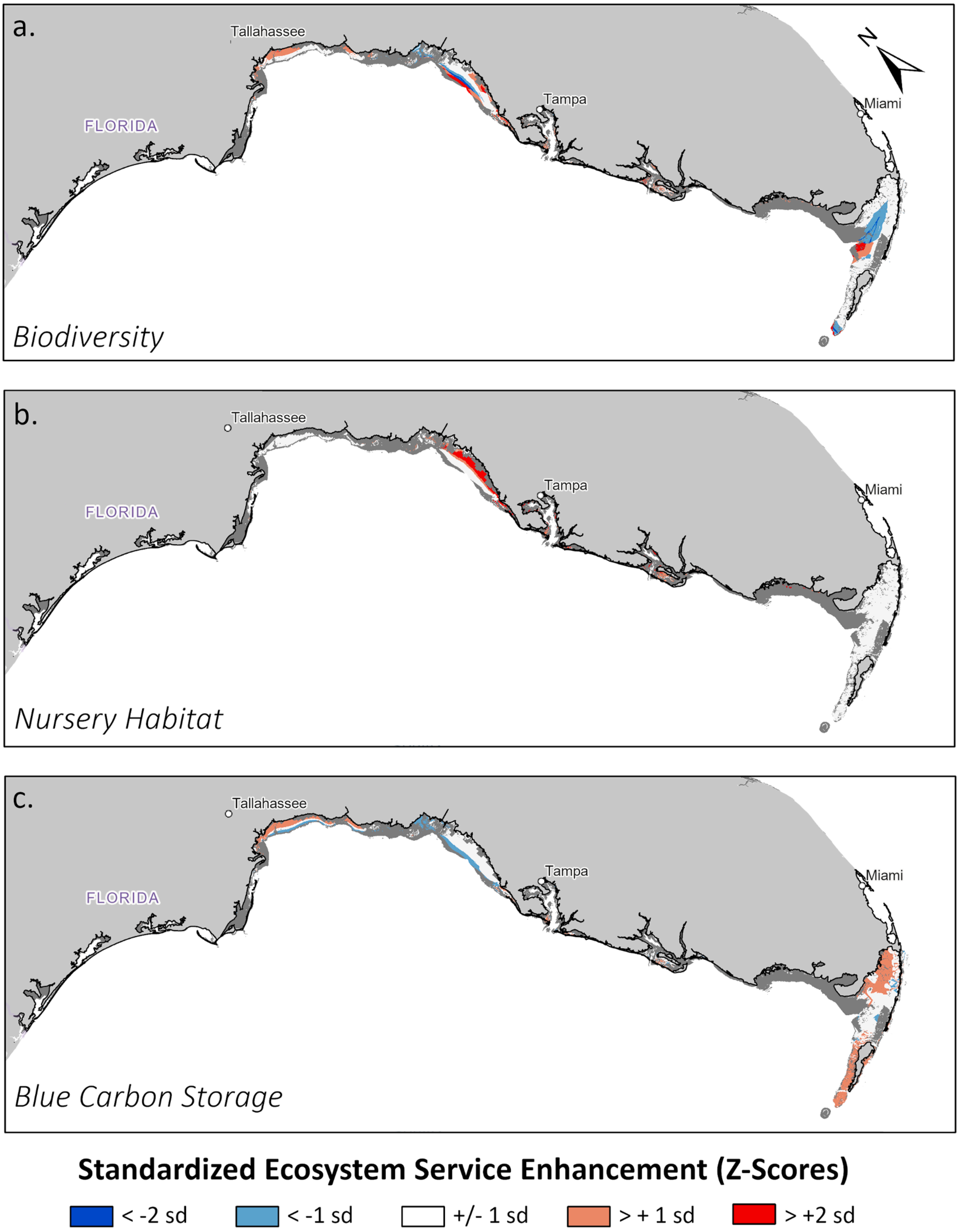

Fig. 1. Spatial variation in the standardized ecosystem service enhancement values of seagrasses, quantified as the additional ecosystem service supply resulting from seagrass presence per hectare compared to the prediction for that location if it was unvegetated. Values show how pixels fall relative to the mean enhancement level for the region in units of standard deviation (i.e., Z-scores). Gray areas denote unvegetated areas within the 4 m depth contour—the depth range within which seagrass can be reliably assessed from aerial surveys.

2023), establishing substantial "blue carbon" stocks with the potential to contribute to climate change mitigation. Lastly, seagrasses can support coastal recreation by positively influencing water quality, biodiversity, and fisheries habitat (Mtwana Nordlund et al., 2016; Unsworth et al., 2019a).

Despite growing recognition of the diverse ecosystem services provided by seagrass beds, potential patterns of service supply are still poorly understood. The capacity of an ecosystem to provide services (i.e., ecosystem service supply; Burkhard et al. 2012) is expected to vary depending on the environmental conditions and ecological processes controlling ecosystem structure and functioning (Barbier et al., 2011; Koch et al., 2009; Mattone et al., 2022; Townsend et al., 2018). For

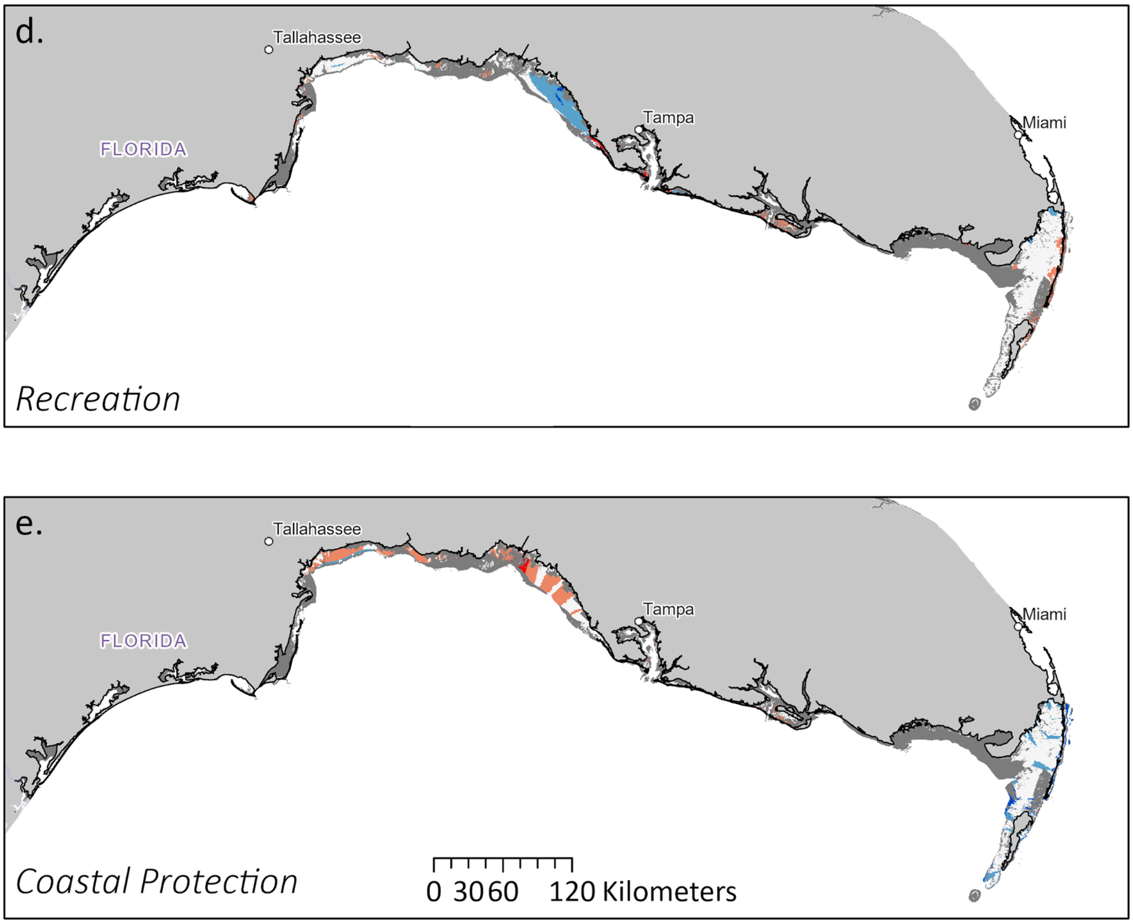

Fig. 1. (*continued*).

instance, oceanographic conditions and the presence of other foundation species, such as oyster reefs and mangroves, have been found to impact the biodiversity-support and nursery habitat functions of seagrasses via their effects on settlement, growth, and survival rates across a seascape (McHenry et al., 2021; Olson et al., 2019). Additionally, the resulting benefits and value of these services to society may depend on a variety of socio-economic factors. As examples, the importance of coastal protection services is expected to differ depending on the population density and vulnerability of coastal communities (Arkema et al., 2013), while recreation services are likely linked to accessibility and the perceived quality of coastal environments (McLachlan et al., 2013). Even services that do not show significant geographic variation in their value to people (e.g., blue carbon storage) can still vary based on characteristics of seagrasses vegetation (Mazarrasa et al., 2018; McHenry et al., 2023). However, the lack of comprehensive sampling and robust predictive models for seagrass systems has hindered our ability to accurately describe potential patterns of ecosystem service supply and value.

Understanding patterns of co-variation among ecosystem services is vital for effective seagrass management and ensuring the provision of multiple benefits. Often it is logically assumed that the services provided by a single habitat type will be positively correlated with one another because they are all strongly driven by characteristics of the foundation species (i.e., seagrass cover and density) (Koch et al., 2009; Liquete et al., 2016; Mazarrasa et al., 2018; McCloskey and Unsworth, 2015; Twomey et al., 2020; Wawo, 2017). Similarly, the biodiversity associated with marine foundation species is often regarded as a reliable proxy of the supply of other services, given the positive associations previously observed between diversity and ecosystem function (Balvanera et al., 2014; Benayas et al., 2009; Duarte, 2000). However, these assumptions may frequently prove false due to the diverse factors influencing spatial patterns of service supply and value (Stephens et al., 2015). The degree to which different services are correlated has important implications for management action. Positive associations among ecosystem services could lead to synergistic outcomes from management and restoration actions (i.e., co-benefits), while negative associations may result in benefits trade-offs (Bennett et al., 2009; Cord et al., 2017). Therefore, comprehensive assessments of seagrass ecosystem services are imperative to inform decision-making and to effectively balance trade-offs in seagrass conservation and restoration project.

This paper assessed spatial patterns and associations among five ecosystem services provided by seagrass beds along the entire Gulf coast of Florida. We used a suite of spatial models to evaluate the capacity of seagrasses to enhance delivery of faunal biodiversity, nursery habitat for fished species, blue carbon storage, coastal protection, and recreation. In this context, we defined ecosystem service enhancement as the additional ecosystem service supply resulting from the persistence of seagrass beds, relative to the services provided if these beds were unvegetated habitats. While modeling the supply of ecosystem services helps to understand the current state of service provisioning in seagrasses, determining the potential enhancement of services by seagrass beds sheds light on the potential outcomes of management and restoration decisions. Our models were informed by and validated using data about how both natural and human factors vary along the study region. We used these models to i) identify key predictors and ii) quantify spatial variation in the enhancement effect of seagrasses for each service. We also iii) explored relationships among different services to understand the potential co-benefits and trade-offs of seagrass management.

Table 1
Performance and predictive skill of regression-based ecosystem service models.

Ecosystem Services Models		**Full Model Performance**	**Model Predictive Skill**
Continuous Response		Adj-R^2	Adj-R^2
Biodiversity	Faunal Biodiversity of Shallow Waters (# of species per seine survey)	0.33	0.33 ± 3.1E-04
	Faunal Biodiversity of Deep Waters (# of species per otter trawl survey)	0.34	0.33 ± 4.8E-04
Blue Carbon Storage	Standing Stock of Blue Carbon (Megagram of Organic Carbon per hectare)	0.43	0.37 ± 4.0E-03
Recreation	Visitation Rate (Photo-Use-Days per square kilometer)	0.67	0.57 ± 6.7E-04
Binomial Response		AUC	AUC
Nursery Habitat	Pink Shrimp (Probability of occurrence)	0.88	0.87 ± 4.3E-03
	Gray Snapper (Probability of occurrence)	0.93	0.93 ± 3.0E-03
	Lane Snapper (Probability of occurrence)	0.89	0.88 ± 3.5E-03
	Sheepshead (Probability of occurrence)	0.95	0.95 ± 3.3E-03
	Spotted Seatrout (Probability of occurrence)	0.93	0.87 ± 2.4E-03
	White Grunt (Probability of occurrence)	0.89	0.92 ± 7.0E-03
Qualitative Index			
Coastal Protection	Exposure Ranking of Shorelines Adjacent to Seagrass Beds	NA	NA

Notes: Performance was assessed by the Adjusted R^2 (Adj-R^2) and Area Under the Curve (AUC) values for continuous and binomial response variables, respectively. Predictive skill was also assessed using similar metrics (± standard error) following a Monte Carlo cross-validation procedure.

2. Materials and methods

2.1. Study area

Our study spans the Florida Gulf Coast (FGC) from Perdido Key to Key West, FL. We focus on water depths from zero to four meters (Fig. 1)—the depth range within which seagrasses can be reliably assessed from aerial surveys. According to aerial surveys and ground truthing conducted by Florida Fish and Wildlife Conservation Commission (FWCC), this region contains approximately 680,000 ha of seagrass beds comprised primarily of turtle grass (*Thalassia testudinum*), manatee grass (*Syringodium filiforme*), and shoal grass (*Halodule wrightii*). These seagrass beds exhibit variation in continuity, cover, and species composition (McHenry et al., 2021). The region is influenced by large-scale oceanographic gradients (e.g., ocean temperature, salinity, and current speeds) driven by the Gulf of Mexico's Loop Current, which brings warm Caribbean waters north through the central Gulf, approaching Florida from the west and running south along the coast and eventually east through the Florida Strait (Gopalakrishnan et al., 2013; McKinney et al., 2021). These gradients are further modified by heterogeneous inputs of freshwater, nutrients, and sediments which enter from multiple river outlets (McKinney et al., 2021). Various other marine foundation species, including mangrove swamps, salt marshes, oyster reefs, and coral reefs, also common in the region.

Seagrasses are highly connected to coastal communities in Florida. Approximately 76% of Florida residents live in coastal counties (United States Census Bureau, 2023). Half a million Floridians working in ocean-based industries, contributing $25 billion per year to gross domestic product (Kildow et al., 2016). Fisheries are important economic and cultural drivers in Florida, producing commercial seafood, creating local employment and income, and attracting millions of anglers to Florida's shores each year (Florida Fish and Wildlife Conservation Commission, 2023; Kildow et al., 2016; Lorenzen et al., 2017). Florida's seagrass beds also attract multiple forms of recreation and tourism, including scalloping, boating, manatee- and turtle-watching, and other water-related activities (Granneman et al., 2021).

2.2. Ecosystem service models

We used models to quantify spatial variation in the supply of five ecosystem services from seagrass beds, including biodiversity enhancement, nursery habitat, blue carbon storage, recreation, and coastal protection services. We used or modified previously published models for biodiversity enhancement, blue carbon, and coastal protection services (Arkema et al., 2013; McHenry et al., 2021; McHenry et al., 2023), but parameterized new models for recreation and nursery habitat, using published or publicly available empirical and spatial datasets specific to the FGC, including data for both vegetated and unvegetated areas (FWCC FIM, 2017; Wood et al., 2013). A variety of predictor variables were considered during model selection—a full list of potential predictor variables, including descriptions and data sources, can be found in the Supporting Information (Table S1). For all models except coastal protection, model selection was conducted based on Akaike's Information Criterion (i.e., $\Delta \leq -2$ AIC). Model selection allowed for the influence of individual and interactive effects of potential seagrass, environmental, and seascape predictors. Model performance and predictive skill were evaluated using a Monte Carlo cross-validation procedure (McHenry et al., 2021; McHenry et al., 2023). In addition to maintaining their predictive skill during cross validation, these models performed well in explaining contemporary patterns of each service (Table 1). For the coastal protection model, we used an existing model with a single fixed structure and thus did not conduct the same model selection and validation steps. We mapped each ecosystem service at the 1-hectare scale for all pixels containing confirmed seagrass beds according to aerial maps from the Florida FWCC (FWCC, 2022). Using model outputs for each service, we quantified the **ecosystem service enhancement value of seagrass beds** as the additional ecosystem service supply resulting from the presence of seagrass beds in that pixel compared to the prediction if that pixel was unvegetated. All model outputs were processed and analyzed in RStudio version 1.4 (RStudio Core Team, 2020) and visualized using ArcGIS Pro version 2.9.3 (ESRI, 2022).

2.3. Biodiversity enhancement

We estimated **biodiversity enhancement** value as the number of additional faunal species supported by the presence of seagrasses using the spatial models presented and described by McHenry et al. (2021). In this paper, Generalized Additive Mixed Models (GAMMs) were used to examine the statistical relationship between faunal species richness and potential predictors representing local conditions that could influence species habitat use, growth, and survival (Table S1). The response variable was the observed faunal richness—or the number of adult fish and invertebrate species per sampling event—(hereafter called faunal biodiversity) at a site, determined by two depth-stratified surveys conducted between 1997 and 2017 by the Florida Fish and Wildlife Conservation Commission's Fisheries Independent Monitoring (FWCC FIM) program (FWCC FIM, 2017). Separate models were parameterized for shallow waters (0–2 m), surveyed by seine nets, and deeper waters (2–4 m), surveyed by otter trawls (FWCC FIM, 2017). The model selection process considered the potential effects of: seagrass characteristics (e.g., total seagrass cover and species composition), environmental conditions (e.g., ocean temperature, phytoplankton productivity and sediment properties), and seascape factors (e.g., the adjacency of shore and other marine foundation species) (Table S1). The final models presented by McHenry et al. (2021) accounted for the effects of seagrass presence and total seagrass cover, phytoplankton productivity, distance from shore, silt content, seasonality, and geographic position (Fig. S1; Fig. S2). We calculated biodiversity enhancement by comparing mapped predictions of faunal biodiversity assuming seagrasses are present at current levels to counterfactual predictions that assume the absence of seagrasses. Because the survey types have different sampling efficiencies, we rescaled the enhancement values as a fraction of the maximum biodiversity enhancement of each depth zone and combined them into a single map of biodiversity enhancement value in units of number of species per sampling event per hectare of seagrass (Δ spp.) rescaled between 0 and 1.

2.4. Nursery habitat

We developed new models to estimate **nursery habitat enhancement** value as the additional probability of occurrence of juveniles of associated species resulting from the presence of seagrasses. Since nursery habitat value is likely to be species-specific, we focused on six representative species that are known to occupy seagrass beds as juveniles and be commercially or recreationally fished in the Gulf of Mexico, including mangrove snapper (*Lutjanus griseus*), lane snapper (*Lutjanus synagris*), white grunt (*Haemulon plumierii*), spotted seatrout (*Cynocsion nebulosus*), sheepshead (*Archosargus probatocephalus*), and pink shrimp (*Farfantepenaeus durorarum*) (Acosta et al., 2007; Fodrie et al., 2020; Kupschus, 2003; Luo et al., 2009; Murphey and Fonseca, 1995). For each species, we used presence-absence records for juvenile life stages from the FWCC FIM datasets described above in "Biodiversity Enhancement" (FWCC FIM, 2017). We developed a generalized additive model (GAM) with binomial error distribution for each species using the mgcv library in RStudio (Wood, 2012), relating the presence of juveniles to variables representing local conditions that could influence rates of juvenile settlement, growth, and survival. During model selection, we considered potential predictors including: seagrass characteristics such as seagrass presence-absence, seagrass total cover, and presence of specific seagrass species (e.g., shoal grass); environmental variables such as water depth, sediment composition, ocean temperatures, salinity, current velocity, pH, dissolved oxygen, and phytoplankton productivity; and seascape factors such as the adjacency to shore, river outlets, and other nursery habitats like mangroves and oyster reefs (Table S1). The final models for juvenile fish and invertebrate occurrence were species-specific. For example, the final model for pink shrimp accounted for ocean temperature and the presence of shoal grasses, whereas the final model for gray snapper accounted for ocean temperature, the proximity of river inputs, and total seagrass cover (Fig. S3). For each nursery species, we generated mapped predictions for the probability of juvenile occurrence using the final models (Fig. S3) and spatial layers for significant model predictors. Using model outputs, we generated a composite nursery habitat map, representing the summed probability of encountering juveniles of one or more of the six focal species in each location. We calculated the nursery habitat enhancement value of seagrasses by comparing the composite nursery habitat map assuming seagrasses are present at their current levels to a counterfactual map in which seagrasses are absent, in units of the probability of occurrence per sampling event per hectare of seagrass (Δ nursery probability ha^{-1}).

2.5. Blue carbon storage

We estimated **blue carbon enhancement** value as the additional amount of organic carbon stored in marine sediments resulting from the presence of seagrass beds using an existing model presented and described by McHenry et al. (2023). The authors used a GAM with a Gaussian error distribution to quantify the relationship between sedimentary organic carbon stocks and potential predictors representing local conditions that could affect the production and/or deposition of organic material to the seabed. The response variable was the standing stock of sedimentary organic carbon, determined from sediment cores collected and analyzed from vegetated and unvegetated sites (McHenry et al., 2023). The model selection process considered the potential effects of seagrass characteristics (e.g., total seagrass cover and species composition), environmental conditions (e.g., ocean temperature and sediment properties), and seascape factors (e.g., the adjacency of shore, rivers, and other marine foundation species like oysters and mangroves as allochthonous carbon sources) (Table S1). The final model accounted for the effects of total seagrass cover, proximity of oyster reefs, and distance from river outlets on organic sedimentary carbon stocks (Fig. S4). We used the final model to generate mapped predictions of the potential carbon standing stocks associated with seagrass beds across our study area (McHenry et al., 2023). We then calculated blue carbon enhancement by comparing mapped predictions of blue carbon standing stocks assuming seagrasses are present at current levels to counterfactual predictions assuming the absence of seagrasses, in units of megagrams of organic carbon per hectare (Δ Mg C_{org} ha^{-1}).

2.6. Recreation

We developed a new model to estimate **recreation enhancement** value, as the additional visitation resulting from the presence of seagrass beds. We used the Natural Capital Project's Integrated Valuation of Ecosystem Services and Trade-offs (InVEST) Toolbox to acquire datasets describing historic coastal visitation rates along the FGC. The InVEST Recreation database provides an open-source application programming

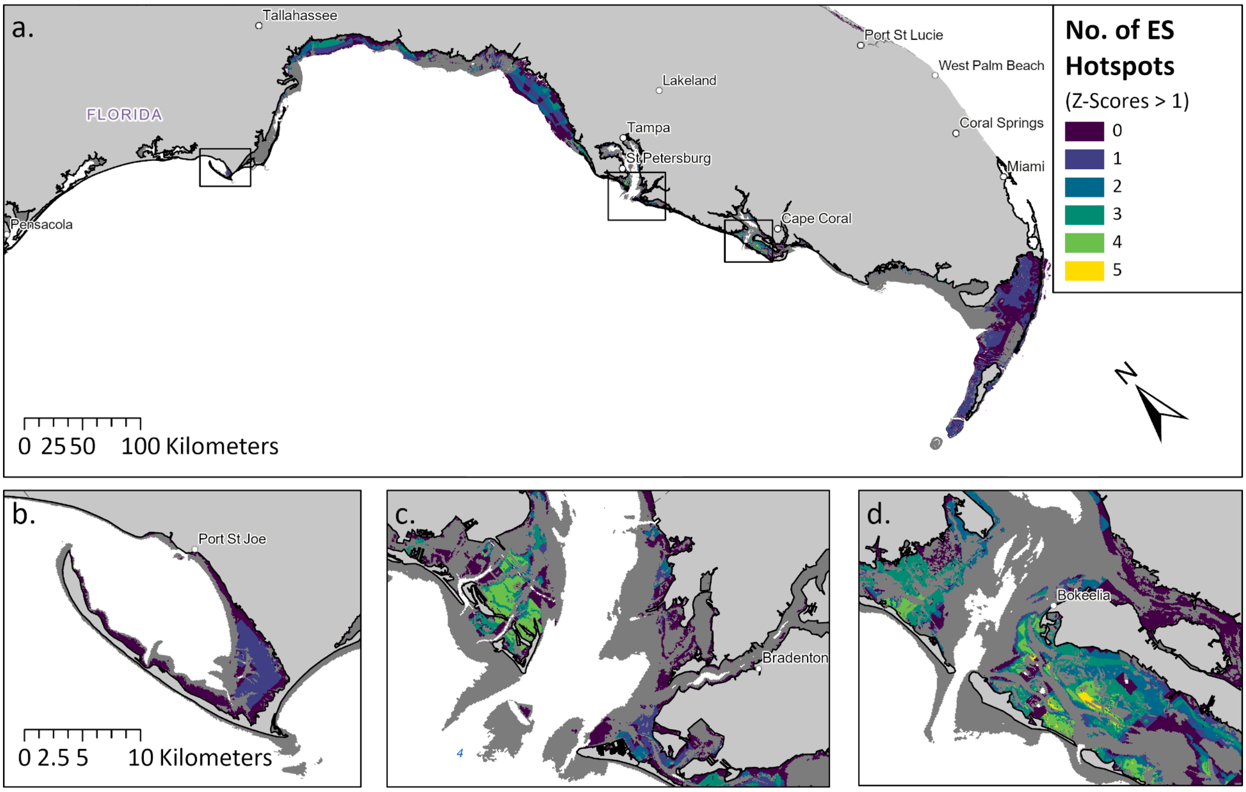

Fig. 2. Spatial distribution and overlap of ecosystem service hotspots (i.e., Z-Score $\geq$1) for seagrasses on the Florida Gulf Coast (a), with inset maps for Saint Joseph Bay (b), Tampa Bay (c), and Charlotte Harbour (d). Gray areas denote unvegetated areas within the 4 m depth contour—the depth range within which seagrass can be reliably assessed from aerial surveys.

interface to estimate coastal visitation rates, using the average number of photographs uploaded per year for a given map pixel to the social media website, Flickr, as a proxy (called "photo-user-days"; PUD) (Sharp et al., 2014; Wood et al., 2013). We downloaded the annual PUD of each 1 km^2 pixel across our study area, averaged across months between 2007 and 2017. We used a GAM trained in RStudio using the mgcv library (Wood, 2012) to quantify the relationship between the log-transformed annual visitation rate and potential predictors influencing the accessibility, importance, and quality of seagrasses for recreation. During model selection, we considered the effects of: seagrass characteristics, such as seagrass presence-absence, seagrass total cover, presence of specific seagrass species, and the configuration of seagrass beds; environmental conditions, such as water depth and ocean temperatures; seascape factors such as the adjacency of shore, rivers, and marine foundation species (i.e., coral reefs, oyster reefs, mangroves, and salt marshes); and socioeconomic factors, such as the adjacency of boat ramps, marinas, roads, beaches and locally managed recreation areas (e.g., Florida's Aquatic Preserve system) (Wood et al., 2013; Table S1). Our final model accounted for the effects of nearby roads (#/km^2), coastal populations (#/km^2), marinas (presence-absence), boat ramps (presence-absence), as well as the interactive effects of seagrass cover and the proximity of beaches (Fig. S5). We generated model predictions of the average annual visitation rates associated with contemporary seagrass beds, using the final GAM model and spatial layers for each significant predictors in R. We calculated the recreation enhancement value of seagrasses in each map pixel, by comparing predictions of coastal visitation assuming seagrasses are present at current levels to counterfactual predictions that assume the absence of seagrasses, in units of log-scale annual photo-user-days per square kilometer of seagrass (Δ PUD km^{-2}).

2.7. Coastal protection

We estimated **coastal protection enhancement** value as the relative value derived from coastal protection services provided by seagrasses (i.e., wave attenuation and erosion reduction) by modifying an existing model developed and described by Arkema et al (2013). We used the Natural Capital Project's InVEST Coastal Vulnerability model, which creates a qualitative index of the relative exposure of the shoreline to erosion and storm inundation, using spatial datasets on the surge potential, wind speeds, and wave power of coastal areas, the degree of coastal relief, and the distribution of other coastal habitats (e.g., coral reefs and mangroves) (Table S1) (Arkema et al., 2013; Silver et al., 2019). We used the coastal exposure index to characterize where additional wave attenuation and erosion reduction services provided by seagrasses are most valuable, assigning the index to raster pixels based on the coastline they protect and multiplying the index by 1 for sections of the coastline where seagrass is present and by 0 for sections without seagrass. We then discounted the protection provided by seagrasses found below 3 m depth (to 60% of the value of shallower seagrasses) to account for the diminished effect of seagrasses on wave attenuation with water depth, as previously estimated through synthesis of empirical data (Twomey et al., 2020). The resulting map describes variation in coastal protection enhancement by seagrasses according to a qualitative ranking of coastal exposure on a scale of 0 to 5, where higher values equate to a greater degree of coastal protection provided by seagrass.

2.8. Spatial patterns and co-variation of ecosystem service enhancement

We mapped the enhancement of seagrass beds on each service using model outputs. We standardized the ecosystem service enhancement maps relative to the mean of each service in units of standard deviation (i.e., Z-scores) in order to visualize potential hotspots and cold spots of service supply and to allow for easier comparisons across services. We considered hotspots to be locations where standardized enhancement values were $\geq$1 and we considered cold spots to be locations where standardized enhancement values were ≤ -1. Additionally, we explored

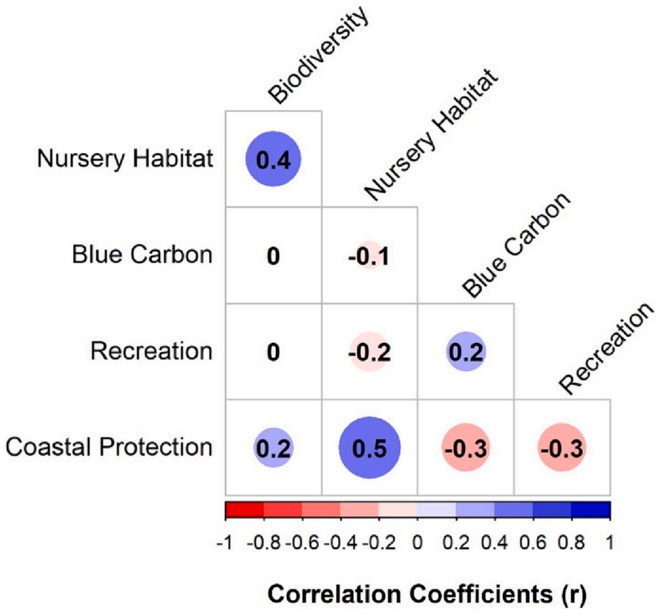

Fig. 3. Correlation coefficients among five ecosystem services from seagrass beds in the Florida Gulf Coast. Services are quantified by the standardized enhancement effect of seagrasses relative to levels predicted if the location were unvegetated. Colors and sizes of the circles represent the direction and magnitude of the correlation between services.

potential associations between the supply of different ecosystem services by calculating correlation coefficients among the standardized enhancement values. We considered strongly associated services to have correlation coefficients that are: ≥ 0.25 and ≤ -0.25. Lastly, we compared the main predictors of seagrass ecosystem service enhancement to identify possible underlying factors influencing the spatial patterns and relationships among services.

3. Results

3.1. *Ecosystem service enhancement value*

Seagrass beds have the potential to significantly increase the supply of all ecosystem services relative to predictions for unvegetated conditions (Table 1; $p < 0.001$, Wilcoxon Two-Sided Rank Sum Tests). According to our models, seagrasses increased the faunal biodiversity of coastal waters on average by fifty percent of the maximum enhancement value. Seagrasses increased the combined probability of encountering any of the six juvenile nursery species in a sample by 3%; although nursery enhancement varied by species (Table S3; $p < 0.001$, Wilcoxon Two-Sided Rank Sum Tests), with spotted seatrout showing the strongest enhancement effect. Seagrass beds also increased blue carbon stocks by 2.5 megagrams of C_{org} per hectare, increased the annual average coastal visitation rate by 1.0 log-scaled photo-users per day per year, and were associated with a coastal protection enhancement value of 3 out of 5.

There was considerable variation in the level of ecosystem service enhancement provided by seagrasses, with the coefficient of variation (CV) differing across services. The spread of the standardized ecosystem

Table 2
Primary predictors of ecosystem service enhancement by seagrass beds.

Ecosystem Service Models	Biodiversity Enhancement		Nursery Habitat						Blue Carbon	Recreation	Coastal Protection
Main Predictors	Faunal Biodiversity of Shallow Waters	Faunal Biodiversity of Deep Waters	Pink Shrimp	Gray Snapper	Lane Snapper	Sheepshead	Spotted Seatrout	White Grunt	Standing Stocks of Blue Carbon	Visitation Rate	Coastal Exposure Index
Seagrass Variables											
Seagrass Cover (7)	X			X	X	X	X	X	*		
Seagrass: Presence – Absence (3)		X								X	*
Shoal grass: Presence – Absence (1)			X								
Environmental Variables											
Phytoplankton Productivity (2)	X							X			
Mud: Presence (2)	*	*									
Sea Surface Temperature (3)			*	*	*						
Dissolved Oxygen (4)			*	*	*		*				
Bathymetry and Topography (3)					X		X				*
Physical Exposure (1)											*
Seascape Variables											
Distance to Shore (6)	*	X	X			X	*	*			
Distance to River Outlets (3)				X					*		*
Adjacent Foundation Species (2)									*		*
Socioeconomic Variables											
Adjacent Access Points, Management Areas, and Coastal Population (1)										X	

Notes: "*" indicates variable inclusion in the final model; "X" shows an interaction term between seagrass and other factors modifying the enhancement effect of seagrasses. Frequency of inclusion of each variable is shown parenthetically.

service enhancement values was greatest for nursery habitat (CV = 187.0) and recreation (CV = 123.5), followed by biodiversity (CV = 77.1), blue carbon (CV = 53.1), and coastal protection (CV = 19.3).

3.2. Spatial patterns and co-variation of ecosystem service enhancement

Spatial patterns of ecosystem service enhancement by seagrasses varied by service (Fig. 1), with minimal overlap among the hotspots (i.e., Z-Score ≥ 1) or cold spots (i.e., Z-Score ≤ -1) of different services. While nursery habitat enhancement was greatest in nearshore waters off the central west coast of Florida (Fig. 1b), biodiversity enhancement values peaked in further offshore of the central west coast and Florida Keys (Fig. 1a). Blue carbon enhancement was highest in nearshore waters off the South Florida and Big Bend regions (Fig. 1c). Recreation enhancement was the most spatially concentrated out of the five services, occurring off Tampa Bay, Key Largo, and Key West (Fig. 1d). Finally, coastal protection enhancement gradually increased latitudinally, with the greatest values along the central west coast and Big Bend (Fig. 1e). As a result, seagrasses that supported hotspots for multiple ecosystem services were rare (Fig. 2). Forty five percent of seagrass beds (309,141 ha) represented hotspots for at least one ecosystem service (e.g., Saint Joseph Bay, Fig. 2b), but seagrasses supporting two or more service hotspots covered just 13% of beds (90,886 ha). Only 5% (32,826 ha) of seagrasses supported more than three services, less than 1% (3,052 ha) supported four or more services, and seagrasses representing hotspots for all five services covered just 83 ha of the study area and were concentrated in small patches along the central Florida Coast, such as within Tampa Bay (Fig. 2c) and Charlotte Harbor (Fig. 2d).

Correlation coefficients revealed positive and negative associations in the supply of different ecosystem services from seagrass beds (Fig. 3). Biodiversity enhancement was positively correlated with total nursery habitat enhancement (r = 0.36) but was uncorrelated with other services. Coastal protection enhancement was also positively correlated with total nursery habitat enhancement (r = 0.48) but was negatively correlated with blue carbon and recreation enhancement (r = −0.27 and r = −0.29, respectively). Lastly, nursery habitat enhancement for individual species showed unique associations with other ecosystem services. For instance, pink shrimp had a negative correlation with recreation and blue carbon enhancement (r = −0.50 and r = −0.30, respectively; Table S4). By contrast, nursery habitat for sheepshead was positively correlated with recreation enhancement (r = 0.34).

3.3. Predictors of ecosystem service enhancement by seagrasses

Including multiple ecological, environmental, seascape, and socioeconomic predictors improved the overall performance and predictive skill of the ecosystem services models (Table 1; Table S5). The most important determinants of service enhancement depended on the ecosystem service (Table 2). The enhancement of biodiversity, nursery habitat, blue carbon, and recreation services was primarily influenced by total seagrass cover. Except for blue carbon, the influence of seagrass beds on service supply was additionally shaped by nonlinear interactions with other factors, such as water depth, proximity to rivers, and phytoplankton productivity in the water column (Fig. S4). For instance, biodiversity enhancement values increased with the total cover of seagrasses and the phytoplankton productivity of the water-column as well as with the distance of seagrass beds from shore (Fig. S1; Fig. S2). Nursery habitat enhancement also varied according to seagrass characteristics, in addition to showing species-specific zonation patterns relative to water depth, adjacent rivers, and distance to shore (Fig. S3). Recreation enhancement increased with the total cover of seagrasses, especially for seagrass beds that are further away from beaches (Fig. S5). Finally, coastal protection enhancement by seagrasses decreased with depth and increased with the degree of physical exposure of adjacent shorelines related to surge potential, coastal relief, wave exposure, wind exposure, and the decreasing prevalence of other coastal habitats (Fig. S6). These distinct predictors for each service led to the lack of strong spatial correlations among services.

4. Discussion

Despite growing research and policy attention to coastal marine ecosystem services, the spatial patterns and associations across multiple benefits are largely unknown for seagrasses (Mtwana Nordlund et al., 2016). Using a suite of spatial models, we assessed the capacity of seagrasses to support five key ecosystem services along the Florida Gulf Coast (FGC). As expected, we found notable spatial variation in the enhancement effect of seagrass beds on biodiversity, nursery habitat, blue carbon storage, recreation, and coastal protection services (Fig. 1). However, due to the differences among the primary predictors of service supply, we found different spatial patterns and even distinct hotspots for where seagrasses were most valuable in providing different services (Fig. 2). Forty-five percent of seagrass beds represented hotspots for at least one ecosystem service, but less than 13% of seagrasses supported hotspots for two or more services. While previously undocumented for seagrass systems, these findings align with previous studies from mangroves and other habitats showing the potential for complex spatial interactions among coastal and marine ecosystem services (Alemu et al., 2021; Bennett et al., 2009).

Spatial variation in seagrass ecosystem services resulted from a complex interplay of ecological, environmental, and socio-economic processes (Table 2), consistent with previous research (Arkema et al., 2017; Gagné et al., 2020; Koch et al., 2009; Mazarrasa et al., 2018; Nagelkerken, 2009). Seagrass cover emerged as a common predictor, but its effect was often modified by other factors resulting in distinct patterns of service enhancement. For instance, hotspots of biodiversity enhancement value were associated with higher seagrass cover and phytoplankton productivity (McHenry et al., 2021), emphasizing the importance of habitat structure and food subsidies to fish and invertebrate species (Edgar, 1990; Gagné et al., 2020; McCloskey and Unsworth, 2015). For nursery habitat, juvenile fishes and invertebrates showed species-specific zonation patterns with respect to water depth, adjacent rivers, and distance to shore. For example, lane snapper and spotted seatrout showed preferences for high cover seagrass beds in deeper waters and farther from shore, potentially reflecting connectivity within and between foraging and adult habitats (Borland et al., 2022; Nagelkerken et al., 2015); whereas white grunt and sheepshead tended to associate with high cover seagrasses in shallow and nearshore areas, presumably where there is lower predation pressure due to wave action and turbidity (Nagelkerken, 2009). Blue carbon storage linearly increased with the overall cover of seagrass vegetation, but background levels of sedimentary organic carbon were driven partially by the proximity of riverine inputs and oyster reefs as allochthonous carbon sources (McHenry et al., 2023). Recreation enhancement increased with seagrass cover when further from beaches, but decreased with cover when closer to beaches, potentially reflecting differences in the recreational activities taking place across the seascape (i.e., boat vs. shore-based fishing). Finally, coastal protection enhancement patterns reflected the increasing surge potential and decreasing prevalence of tropical foundation species (i.e., mangroves and coral reefs) at higher latitudes (Table S6) (Koch et al., 2009). Our findings highlight the context dependent nature of ecosystem service supply from seagrass beds.

Contrary to the logical assumption that all seagrass ecosystem services would be positively correlated because they are strongly driven by seagrass characteristics, we found few strong positive associations among services (Fig. 3). However, the positive associations we found highlight the potential for co-benefits from proposed seagrass management and restoration projects. Seagrasses providing greater nursery habitat enhancement tended to support higher biodiversity, which was expected given the potential for shared predictors affecting relative habitat quality and rates of dispersal, settlement, and survival among faunal species (Liquete et al., 2016). Seagrass beds with greater nursery enhancement also provided greater coastal protection enhancement, particularly off the west central coast of Florida. While not previously demonstrated, this association could result from converging ecological and hydrodynamic factors. For instance, seagrasses could play a more important nursery habitat role with the increasing absence of other marine foundation species (e.g., mangroves and coral reefs) at higher latitudes (Heck Jr et al., 2003; McDevitt-Irwin et al., 2016), an absence which also increases the need for additional coastal protection services in our model. Additionally, the same increased physical exposure (Fig. S6) that creates a greater need for additional coastal protection services could potentially facilitate dispersal of larvae to nearshore areas (Brown et al., 2016; Pineda et al., 2007), benefiting the nursery habitat role of seagrasses. Future research is necessary to understand the nature of the link between these two critical seagrass ecosystem services.

Aside from nursery habitat, we found that biodiversity enhancement by seagrasses was not strongly correlated with any of the other seagrass services (Fig. 3). This finding suggests that biodiversity may not always be a reliable proxy for other seagrass services. Of course, it is possible that additional positive associations could emerge from assessments accounting for a broader variety of ecosystem services more directly affected by faunal biodiversity (e.g., eco-tourism). Additionally, we measured biodiversity enhancement as the effect of seagrasses on faunal species richness; it is possible other metrics, such as functional diversity, could provide more informative indicators of ecosystem service supply. Although counter to some expectations (Balvanera et al., 2014; Benayas et al., 2009; Duarte, 2000), the poor correspondence between biodiversity enhancement and others seagrass services is not entirely surprising given that numerous studies have found neutral or even negative relationships across a variety of terrestrial, aquatic, and marine settings (Chan et al., 2006; Manhães et al., 2016; Turner et al., 2007). These findings contribute to a growing body of work demonstrating a more nuanced relationship between biodiversity and ecosystem functioning.

The negative associations that we found suggest potential conflicts when prioritizing areas to maximize multiple ecosystem services. Although not previously documented, the negative association between coastal protection and blue carbon could reflect increased resuspension or reduced deposition of organic carbon in areas with higher wave, tidal, and storm surge exposure (and thus higher coastal protection enhancement) (Fonseca and Bell, 1998; Mazarrasa et al., 2018). These locations experiencing more water motion may have less capacity to accumulate carbon (Fig. S6). The negative relationship may also result from covariance with other marine foundation species (e.g., oyster reefs), which are positively associated with seagrass carbon (Table 2) (McHenry et al., 2023) and also provide coastal protection, reducing the need of the additional coastal protection provided by seagrasses (Chen et al., 2017; Fodrie et al., 2017). The negative association between coastal protection and recreation enhancement could reflect a human preference for waters with less hazardous boating conditions with lower wave exposure and/or coastlines with charismatic foundation species, e.g., mangroves (McLachlan et al., 2013).

Our study contributes to a growing body of research showing complex spatial patterns and relationships among ecosystem services (Bennett et al., 2009), including several recent examples from the marine realm involving single and multi-ecosystem assessments (Alemu et al., 2021; Arkema et al., 2015; Buonocore et al., 2020; Gilby et al., 2020). We provide one of the first spatially explicit assessments of multiple ecosystem services provided by seagrass beds. Compared to terrestrial research, quantifying co-variation among multiple benefits from marine ecosystems has been a significant challenge due to the paucity of comprehensive sampling and predictive models for different services (Dewsbury et al., 2016; Townsend et al., 2018). Consequently, habitats such as seagrasses have often been over overlooked compared to more charismatic habitats, including coral reefs and mangroves, in the ecosystem service science literature (Unsworth et al., 2019b). Our study helps to bridge these data gaps, providing insights into the multi-service potential of this important systems.

Although the models used here are based on the best available datasets, there are certain limitations to this study. For example, our biodiversity enhancement model relies on faunal richness datasets for marine fish and invertebrate species, not considering other important groups linked to seagrass systems, such as turtles, elasmobranchs, and infauna (Sievers et al., 2019). As another example, we assessed nursery habitat as the probability of encountering juveniles of recreationally and commercially fished species. However, juvenile presence does not capture any contribution of seagrasses to growth rates, or other factors that affect how much those juveniles will contribute to fished stocks (Liquete et al., 2016). Blue carbon storage was estimated as the additional organic carbon buried in the marine sediments below seagrasses. However, these estimates are based on sampling efforts from the northern FGC (McHenry et al., 2023). Thus, our estimates of blue carbon enhancement may have higher uncertainty outside of the original sampling domain. For the recreation estimates, we used social media photos as an indicator of relative coastal recreation rates, recognizing that some activities may be better captured by Flicker datasets than others (i.e, shore- vs- boat-based activities) (Tenkanen et al., 2017; Wood et al., 2020).

Evaluating the contribution of seagrasses to coastal protection is particularly challenging given the limitations of existing models and empirical datasets. Our coastal protection model provides a qualitative ranking of the relative coastal exposure and protection received by the shorelines adjacent to seagrass beds, accounting for the potential diminishing effect of seagrasses on wave attenuation with water depth (Twomey et al., 2020). We expect that the coastal protection services provided by seagrasses could also be modified by other characteristics of seagrass beds (e.g., canopy height), although reliable spatial datasets are currently lacking for this region. Even though this approach provides a useful indication for where coastal protection services from seagrasses are most valuable, the model cannot currently provide estimates of the magnitude of erosion reduction and storm inundation avoidance resulting from seagrass persistence in these areas. We are also unable to validate model predictions against field datasets from Florida (Table 1), although the potential for more comprehensive data to be collected in the future does not invalidate the results we obtained from existing data. Indeed, several studies have found a reliable correspondence between areas with high exposure according to the InVEST model and empirical data on impacts from coastal hazards in the Gulf of Mexico and other systems (Arkema et al., 2013; Silver et al., 2019). Expanded empirical datasets on the relative canopy height, wave attenuation, and erosion reduction potential of seagrasses collected across a range of local contexts could help to better calibrate and validate model predictions about expected flooding and storm damage avoidance in this region.

Finally, we focused on measuring the supply of each service. Ultimately, an ecosystem service framework seeks to capture the value of ecosystem benefits to people, and thus should account for social preferences and values (Tallis et al., 2012), which themselves could vary along the coast. Thus, it is likely that even greater spatial variation, and possibly differing spatial relationships, could result when accounting for the nuanced ways that humans use and value seagrass benefits. For example, we considered the ecological, environmental, and seascape predictors of nursery habitat, but the potential value of seagrasses to commercial and recreational fisheries likely depends on the distribution and preferences of fishers. Similarly, the value of recreation services from seagrasses likely depends on the distribution and preferences of coastal residents. Lastly, although we do not evaluate the human need for coastal protection services here, the value to human populations likely varies depending on the characteristics of coastal communities and infrastructure, including their relative population density, socioeconomic vulnerabilities, and property values (Arkema et al., 2017; Arkema et al., 2013). While imperfect, our models provide useful indicators of ecosystem service supply, which can be modified as new datasets are collected to quantify spatial variation in the human valuation and demand for seagrass ecosystem services.

Our models are most applicable to seagrasses in the tropical Atlantic, but the approach could be applied to seagrasses and other marine foundation species (e.g., mangroves and oysters) wherever there are adequate spatial datasets on the distribution and total cover of those species. This approach could also be adapted to support more integrative multi-ecosystem assessments, in systems where there are compatible monitoring datasets for ecosystem service indicators. Additional research would be necessary to develop integrated service models to account for possible synergies or antagonistic interactions among different foundation species. However, this approach could be useful for exploring the relative ecosystem enhancement value of different coexisting foundation species as well as for investigating patterns of multifunctionality, functional redundancy, and diversity at ecosystem scales.

5. Conclusions

Our findings illustrate the importance of considering the distinct ecological, environmental, and social predictors of ecosystem service supply from seagrass beds, with implications for planning and prioritizing seagrass conservation and restoration projects (Lester et al., 2020). We found considerable spatial variation within and among seagrass services, including distinct service hotpots and complex relationships. We also found that biodiversity enhancement value was not a reliable proxy for all other services, as is sometimes assumed, highlighting the need for direct assessments and potentially other measures of biodiversity (e.g., functional diversity). Our model outputs can help to address a range of applied questions related to seagrass management. For example, the maps allow for various ecosystem services to be prioritized when selecting protected areas or restoration sites, using spatial optimization programs like Marxan and PrioritizR (Lester et al., 2020). Additionally, the resulting ecosystem services maps can help managers to gauge the likely co-benefits and trade-offs associated with different management options by identifying the efficiency frontiers for different combinations of services (Lester et al., 2013). However, the magnitudes of these effects may depend on stakeholder demand and preferences for different seagrass services (Cavender-Bares et al., 2015); opportunities to balance trade-offs could also become constrained as seagrasses decline and are lost due to sea-level rise and other human-driven environmental changes (McHenry et al., 2021). Therefore, future work could examine potential trade-offs in achieving different ecosystem service outcomes from conserving and restoring seagrasses, given different human preferences and climate scenario projections. As society better recognizes the diverse benefits provided by nature, conservation and management can leverage such models to maximize benefits and preserve ecosystem services for future generations.

Declaration of Competing Interest

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

Data availability

Citations and weblinks for raw datasets supporting each model are provided in the supplementary information. The R code and analyses supporting our findings are publicly available on Github (https://github.com/jennmchenry1/Seagrass-ecosystem-services-show-complex-spatial-patterns-and-associations). Model outputs can also be directly downloaded from the GRIIDC data repository (https://data.gulfresearchinitiative.org/data/H3.x875.000:0003). Finally, all mapped model predictions can be viewed and interacively explored via R Shiny App (https://jennifermchenry.shinyapps.io/Seagrass_ES_Explorer/).

Acknowledgements

We acknowledge funding from the Gulf Research Program of the National Academy of Sciences, Engineering and Medicine (Award Number: 2000009025). We thank Rasster Lab members at FSU for their valuable feedback.

Appendix A. Supplementary Information

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoser.2023.101543.

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