

# Using habitat suitability models to predict changes in seagrass distribution caused by water management practices<sup>1</sup>

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**Abstract:** Habitat suitability (HS) models can help elucidate the relationship between organisms and their environment and simulate the potential impacts of human activities on species distributions. Here, we developed HS models for *Thalassia testudinum* and *Halodule wrightii*, two seagrasses found in Biscayne Bay (Florida, USA). These species are mostly found in nearshore habitats of the bay that are highly susceptible to changes in water quality because of their proximity to the city of Miami and activities and projects associated with the restoration of the Florida Everglades. The HS models parameterized with data collected at >900 sites highlighted salinity as a key factor determining habitat suitability for these seagrass species. *Thalassia's* suitable habitat was associated with higher, more stable salinity compared with that of *Halodule*, which was associated with lower salinity and shallower depths. Both species benefited under a simulated scenario of increased freshwater flow, but *Halodule's* suitable habitat increased by 71% compared with that of *Thalassia's*, which exhibited only an 18% increase. HS models such as those described here provide spatial modeling tools that can contribute science-based input into the management of coastal resources within an adaptive management framework.

**Résumé :** Les modèles d'adéquation de l'habitat (HS) peuvent aider à clarifier la relation entre les organismes et leur milieu et à simuler l'impact des activités humaines sur la répartition des espèces. Nous mettons au point ici des modèles HS pour *Thalassia testudinum* et *Halodule wrightii*, deux herbes marines habitant la baie de Biscayne (Floride, É.-U.). Ces espèces se retrouvent surtout dans les habitats près de la rive de la baie, qui sont très susceptibles aux changements de la qualité de l'eau à cause de la proximité de la ville de Miami et des activités et projets associés à la restauration des Everglades de Floride. Le modèle HS paramétrisé avec des données prélevées à >900 sites souligne la salinité comme le facteur principal qui détermine si les habitats sont convenables pour ces espèces d'herbes marines. L'habitat convenable pour *Thalassia* est associé à une salinité plus élevée et plus stable, alors que celui d'*Halodule* est associé à des salinités plus faibles et des profondeurs moins grandes. Les deux espèces sont avantagées par un scénario simulé de débit accru d'eau douce, mais l'habitat convenable à *Halodule* augmente de 71 %, mais celui de *Thalassia* de seulement 18 %. Les modèles HS, comme ceux que nous décrivons, représentent des outils de modélisation spatiale qui peuvent fournir une contribution de nature scientifique à la gestion des ressources côtières dans un cadre de gestion adaptative.

[Traduit par la Rédaction]

## Introduction

Seagrass communities worldwide provide key ecological, economic, and societal services, such as organic carbon production, nutrient cycling, sediment stabilization, enhanced biodiversity, trophic transfers to adjacent habitats, recreation and tourism opportunities, and essential habitat to both commercial and recreationally valuable fisheries species (Orth et al. 2006). Unfortunately, seagrass communities have not escaped the patterns of drastic declines that other coastal ecosystems like coral reefs and mangroves have experienced in

the recent past (Gardner et al. 2003; Duke et al. 2007), and patterns of major decline and shifts in community structure have been documented for seagrass communities worldwide (Waycott et al. 2009). Among the main causes of the decline in seagrass abundance and distribution are those directly related to coastal development and overexploitation, such as chemical pollution, eutrophication, sedimentation, physical impacts of boating and fishing activities, and modifications to the trophic structure (e.g., Duarte 2002; Waycott et al. 2009). Considering both the importance of these ecosystem engineers in terms of the key services they provide, as well

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as their recent precipitous decline, there is a pressing need to develop science-based management tools that will aid in the conservation of seagrass community resources.

Habitat suitability (HS) modeling and other mapping and spatial prediction techniques have become crucial tools in conservation ecology and resource management (Guisan and Zimmermann 2000; Hirzel et al. 2002; Elith et al. 2006). HS modeling is based on Hutchinson's (1957) concept of the ecological niche, defined as a hypervolume in the multidimensional space of environmental variables within which a species maintains a viable population (Hirzel et al. 2002). Because the HS modeling framework offers the potential to assess and understand species' niche requirements and distribution, these models are ideal tools for the study and prediction of the impacts of both human and natural disturbances and provide a predictive framework that can be used to address "what if?" scenarios at appropriate spatial scales (Gross and DeAngelis 2001; Guisan and Thuiller 2005; Hirzel et al. 2006). Such scenarios can prove extremely useful within an adaptive management framework to help visualize potential impacts of management actions in time to take mitigation actions.

In this study, we develop a HS model for seagrasses within Biscayne Bay, Florida. Biscayne Bay is a shallow, subtropical lagoon adjacent to the city of Miami that is heavily influenced by upstream water management practices associated with the managed hydrology of the Florida Everglades watershed (Browder et al. 2005). HS models are used here to evaluate the impacts of increased freshwater flows (and associated decreases in salinity) into Biscayne Bay on the distribution of two seagrass species with distinct salinity tolerances. A central goal of the Comprehensive Everglades Restoration Plan (US Army Corps of Engineers and South Florida Water Management District 2010, [http://www.evergladesplan.org/about/about\\_cerp\\_brief.aspx](http://www.evergladesplan.org/about/about_cerp_brief.aspx)) is to restore the natural flow of fresh water into coastal lagoons that have undergone drastic declines in the abundance of benthic and mobile organisms and communities partly blamed on the modified hydrology (Browder et al. 2005). To reduce hypersalinity and return to a more natural mode of freshwater delivery (e.g., replacing canal drainage with sheetflow and groundwater delivery), additional fresh water within the watershed will be diverted into critical nearshore areas of Biscayne and Florida bays (Davis and Ogden 1994) with unknown ecological consequences. Here, we use HS models parameterized with extensive field data to test the hypothesis that the increased flow of fresh water into littoral habitats of Biscayne Bay will increase the spatial distribution of the low-salinity-tolerant seagrass species *Halodule wrightii* and will decrease the dominance of *Thalassia testudinum*, a species commonly associated with higher salinity values (Lirman and Cropper 2003; Lirman et al. 2008; Lirman and Serafy 2009).

The statistical approach used here to generate suitability maps for two dominant seagrass species (*T. testudinum* and *H. wrightii*) is the ecological niche factor analysis (ENFA) (Hirzel et al. 2002). The ENFA algorithm compares the distribution of "presence" observations in the multidimensional space created by environmental variables with the environmental variance across the study area to calculate a HS index (Hirzel et al. 2002; Rood et al. 2010). While ENFA is used

here specifically to evaluate potential changes in seagrass distribution under a "decreased salinity" scenario prompted by changes to the regional Everglades hydrology, this approach has wide applicability to other organisms and habitats. In fact, ENFA has been utilized effectively in the past to generate HS maps for terrestrial flora and fauna, as well as marine species as different as whales and corals (e.g., Hirzel and Arlettaz 2003; Bryan and Metaxas 2007; MacLeod et al. 2008).

## Materials and methods

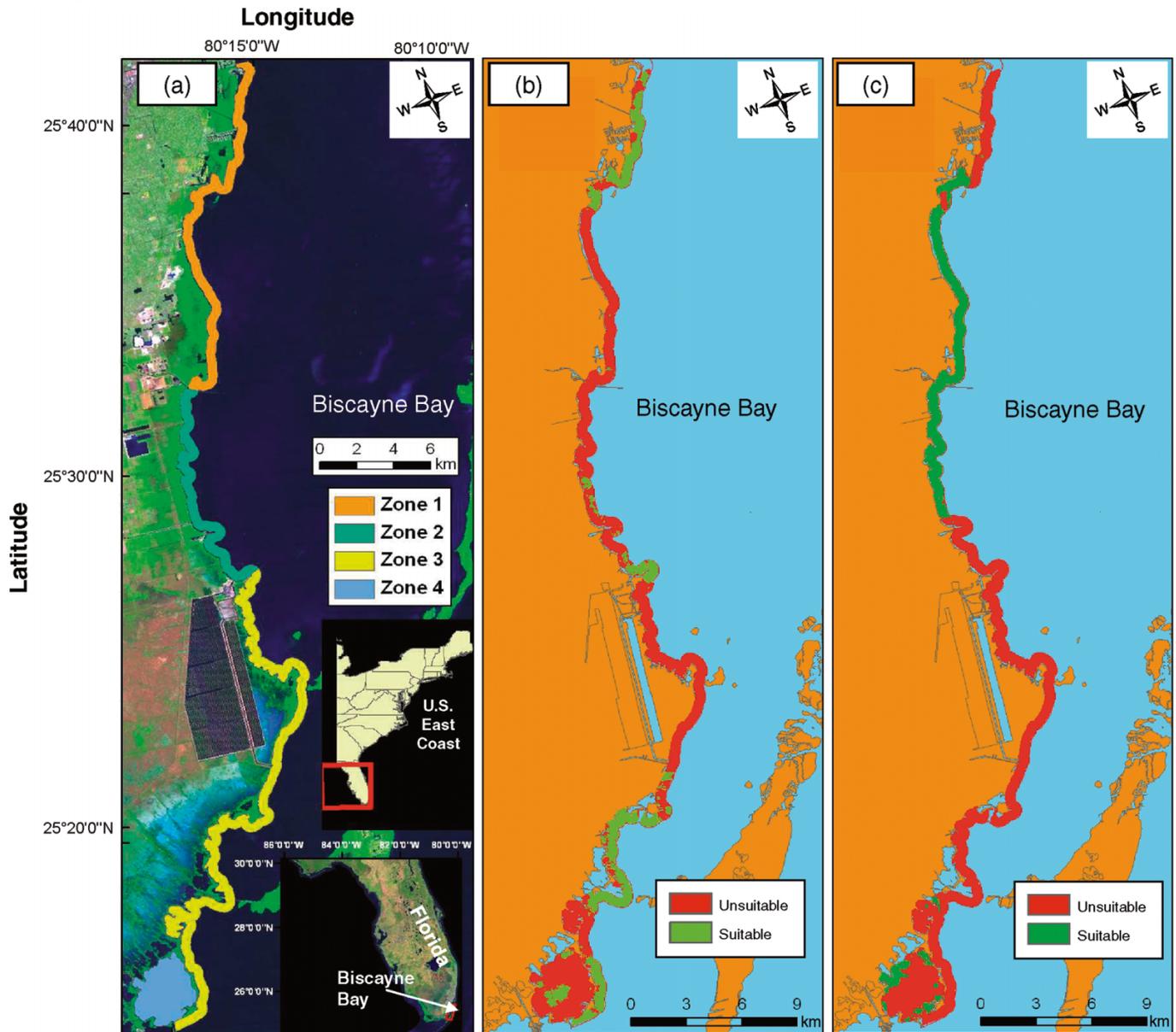
### Study site

The study area for this project is western Biscayne Bay, Florida (Fig. 1a), a shallow subtropical lagoon adjacent to the city of Miami and downstream of the Florida Everglades. The hydrology of the Everglades has been severely modified over the last 100 years by the construction of a massive water management system that has altered the quantity, quality, and delivery method of fresh water into the coastal bays (Davis and Ogden 1994; Browder and Ogden 1999). Historical patterns of sheetflow have been replaced by canals as the main method of delivery of fresh water into littoral habitats. Presently, areas with pulsed canal discharges experience drastic fluctuations in salinity over short periods, especially in the wet season (July–September) when water is flushed into coastal bays for flood protection. This study concentrated on benthic habitats <500 m from shore where the effects of freshwater pulses are concentrated. Based on previously documented hydrodynamic and salinity patterns, the study region was divided into four distinct zones or basins: Zone 1, Matheson Hammock to North of Black Point; Zone 2, south of Black Point to Turkey; Zone 3, Turkey Point to Barnes Sound; and Zone 4, Manatee Bay (Lirman et al. 2008) (Fig. 1a).

### Data collection

All environmental and biological data were collected as part of a monitoring program designed to evaluate patterns of seagrass abundance and distribution in relationship to freshwater inflow into Biscayne Bay (Lirman et al. 2008). Survey sites are selected using a stratified random sampling design with salinity zone and distance to shore buffers (<100, 100–200, 200–300, 300–400, 400–500 m) as strata (Lirman et al. 2008; Lirman and Serafy 2009). The data used for this study were collected in the wet seasons of 2008–2010. While seasonal changes in submerged aquatic vegetation abundance and distribution have been documented, only data from the wet season were considered because both the abundance for both target seagrass species and freshwater flows are highest during the wet season. As the environmental and biological data collected during the wet season showed limited interannual variation (Lirman and Serafy 2010), data collected in 2008, 2009, and 2010 were combined in this study. At each site, digital images of the bottom are collected to document the abundance, diversity, and distribution of seagrasses, as well as water-quality data (Lirman et al. 2008). In this study, only data for *T. testudinum* and *H. wrightii*, the two dominant seagrass species in the study region were used. Environmental data collected at each site included light reaching the seagrass canopy ( $\mu\text{E}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ ; 1 einstein = 1 mol of photons), depth (m), temperature ( $^{\circ}\text{C}$ ),

**Fig. 1.** (a) Study area with the delineated zones. Study site zonification was based on the hydrodynamics and salinity regimes of Biscayne Bay. Habitat suitability maps are shown for (b) *Thalassia testudinum* and (c) *Halodule wrightii*. Unsuitable areas appear in red and suitable areas in green.



and salinity (ppt) at the bottom, all key factors known to influence seagrass abundance and distribution (Fonseca and Bell 1998; Fourqurean et al. 2003; Lirman and Cropper 2003; Zimmerman and Dekker 2007). All geographic information system (GIS) layers (geo-coded biological and physical data) were converted into raster format as required by BioMapper (i.e., a kit of GIS and statistical tools, developed by Hirzel et al. 2008, designed to build HS models and maps for animals or plants). Data on percent cover of *T. testudinum* and *H. wrightii* for each site were converted into presence-absence data (i.e., Boolean presence map) using a threshold of  $\geq 50\%$  for *T. testudinum* and  $\geq 40\%$  for *H. wrightii*. The threshold values were selected based on observations of the frequency distribution of high-percent cover values for both species. The high threshold selected provides the most con-

servative estimate of HS and highlights, spatially, “hot-spots” with ideal conditions for each species under the scenarios simulated. After this reclassification, the shapefile points were transformed into a raster file with 25 m cell size using ArcGIS 9.3 (ESRI, Redlands, California). An ordinary kriging interpolation procedure was used to create continuous surfaces for the environmental variables (average root-mean square standardized = 1.12). The Spatial Analyst extension in ArcMap (ESRI) was used for this procedure, with 10 neighborhood points and a window search of 500 m used as interpolation parameters.

#### Ecological niche factor analysis (ENFA)

ENFA analyses were performed using BioMapper software (Hirzel et al. 2008). The purpose of using ENFA was to iden-

tify the niche of *T. testudinum* and *H. wrightii* and interactions of environmental variables defining the spatial distribution of the targeted seagrass species within the study area. Similar to principal component analysis, ENFA summarizes predictor variables into a subset of uncorrelated factors with ecological relevance. In ENFA, the first or “marginality” factor describes the mean of the species distribution in relation to the mean of the environmental conditions in the study area (Hirzel et al. 2002). Marginality coefficients range from  $-1$  to  $1$ ; the higher its absolute value, the further the species departs from the mean available habitat with respect to a corresponding variable. All the subsequent factors, referred to as “specialization factors”, indicate how restricted the species’ niche is in relation to environmental conditions (Hirzel et al. 2002). Specialization coefficients range from  $-1$  to  $1$ , and the higher the absolute value, the more restricted is the range of the focal species with respect to the corresponding variable. By combining the marginality and specialization of individual predictor variables, ENFA computes global marginality and specialization coefficients (Hirzel et al. 2002). Moreover, a tolerance coefficient ( $T$ ), ranging from  $0$  to  $1$ , can be calculated as the inverse of the specialization coefficient. A species with a tolerance coefficient close to  $0$  can be considered as a “specialist”, commonly found in a very narrow range of conditions (Reutter et al. 2003).

### Habitat suitability maps

HS maps were constructed based on the marginality and specialization factors calculated. The number of factors included for the HS maps is determined by a comparison of eigenvalues with the MacArthur’s broken-stick distribution (Jackson 1993; Hirzel et al. 2002). After the factor maps were created, a HS score was calculated by comparing the factor values within each map cell with the median of the species distribution on the selected environmental factor (Hirzel et al. 2002). An overall HS index for each cell is created by combining the cells’ HS value for each factor using a weighted mean. The overall HS index ranges from  $1$  to  $100$ , where higher values indicate more suitable habitat. It is important to note here that HS maps were constructed for each species independently and that these models do not include a “competition” factor.

### Validation and HS maps reclassification

BioMapper uses a  $k$ -fold cross-validation and adaptation of the continuous Boyce index to evaluate the predictive power of the HS maps created (Boyce et al. 2002). The seagrass presence data were partitioned evenly into two to three partitions, where data were assigned randomly to each partition. One partition is used to validate the HS model created by the left-out partitions. This process was repeated according to the total number of partitions (e.g.,  $k$  partitions). Then, each HS score was divided in four bins. The number of validation points that fell into each bin was counted and combined with the total area covered by each bin in the study to provide a predicted-to-expected ( $P/E$ ) frequency of presence for each bin. If the HS map is completely random, a  $P/E = 1$  is expected for all bins. Thus, if the model is adequate, low bins with low HS should have a  $P/E < 1$ , while bins with high HS should have a  $P/E > 1$ , with a monotonic increase between these values (Hirzel et al. 2008). The Boyce

index, computed using a Spearman’s rank correlation between the  $P/E$  and the HS bins, can be used to measure the model predictive power of the model. Finally, the Boyce curve (e.g.,  $P/E$  vs. HS values) for each validation procedure was used to reclassify the HS map scores (HS ranges  $0$ – $100$ ) into suitable and unsuitable classes. A  $P/E = 1$  was assigned as the cutoff to classify the HS index into suitable or unsuitable habitat. HS values with  $P/E < 1$  were classified as unsuitable (i.e.,  $P/E < 1$ , the model predicts fewer present than expected by chance), and HS values with  $P/E > 1$  were classified as suitable. The marginal class was assigned to HS values depending on the shape of the curve of the model and the proximity of HS values within a bin to  $P/E = 1$ .

### Model extrapolation and salinity scenarios

The BioMapper and ENFA frameworks provide the opportunity to simulate and test environmental scenarios and their predicted impacts on species distributions. In this case, the HS models created were used to test the potential impacts of increased freshwater inflow into nearshore Biscayne Bay on the dominant seagrass species in this area. One scenario of increased freshwater flow was chosen based on the goals of the Everglades Restoration Project to restore the salinity in the nearshore habitats to mesohaline conditions (i.e.,  $5$  to  $20$  ppt) (Davis and Ogden 1994; US Army Corps of Engineers and South Florida Water Management District 2010). To parameterize and generate the HS under an increased freshwater scenario, the baseline ENFA model was run as described except for salinity patterns, which were changed to simulate higher freshwater inputs. The tool used to simulate the salinity values for this scenario was the Biscayne Bay Salinity and Hydrodynamic Model (Wang et al. 2003). The minimum salinity values from the 1996–2005 wet seasons (the time period simulated by the model) were calculated using the hydrodynamic and salinity model. The simulated salinity values were extracted for each of the seagrass survey points used to develop the original ENFA and were interpolated to create a continuous salinity surface (i.e., salinity raster map). ArcGIS 9.3 was used to estimate the area covered by the suitable and unsuitable areas modeled by the original and extrapolated HS models. The area was estimated within each zone and compared to assess percent change of suitable area between the “baseline” and “increased freshwater – decreased salinity” scenarios.

## Results

### Ecological niche description

The overall marginality for *H. wrightii* was  $1$ , showing that the conditions at the sites where *H. wrightii* was present deviated from the average conditions in the whole study area. The marginality factor explained over  $40\%$  of the variance and the presence of *H. wrightii* was strongly associated with below-average salinity values and shallower depths (Table 1). The overall marginality for *T. testudinum* was  $0.4$ , showing that the optimum niche conditions for *T. testudinum* were similar to the average conditions in the study area. The tolerance coefficient  $T$  was  $0.75$ , indicating a wider niche for *T. testudinum* than for *H. wrightii* ( $T = 0.65$ ). The marginality and first specialization factors explained approximately  $60\%$  of the variance for *T. testudinum*. In contrast with

**Table 1.** Scores of the ecological niche factor analysis (ENFA) for *Thalassia testudinum* and *Halodule wrightii*.

Environmental variable	<i>Thalassia testudinum</i>			<i>Halodule wrightii</i>		
	Marginality	Specialization 1	Specialization 2	Marginality	Specialization 1	Specialization 2
Light	<b>-0.945</b>	-0.137	0.148	0.104	<b>-0.553</b>	-0.025
Depth	0.179	0.311	-0.25	<b>-0.524</b>	<b>0.623</b>	-0.135
Salinity	0.041	<b>0.546</b>	<b>0.772</b>	<b>-0.823</b>	-0.37	0.305
Temperature	-0.271	<b>0.766</b>	-0.565	0.194	0.411	<b>0.942</b>
Explained specialization	0.227	0.368	0.31	0.438	0.345	0.178
Cumulative explained specialization	0.227	0.595	0.905	0.438	0.783	0.961

**Note:** The marginality scores indicate the average distance between the ecological conditions at which these species were present and the average environmental conditions within the study area. Specialization scores indicate the proportion of environmental conditions present in the study area that were found to be occupied by these two seagrass species. Bold numbers show the environmental variables with the highest factor loading.

**Table 2.** Descriptive statistics for salinity (ppt), temperature (C°), light (microeinsteins·s<sup>-1</sup>·m<sup>-2</sup>; 1 µE = 1µmol of photons), and depth (m) values within the cells classified as unsuitable and suitable for *Thalassia testudinum* and *Halodule wrightii*.

		<i>Thalassia testudinum</i>		<i>Halodule wrightii</i>	
		Unsuitable	Suitable	Unsuitable	Suitable
Salinity (ppt)	Mean (SD)	27.27 (7.06)	29.77 (3.81)	31.69 (3.89)	22.69 (5.17)
	Median	26.96	30.10	31.4	23.5
	Variance	49.90	14.49	15.1	26.69
	Min.–max.	3.9–42.0	0–38.1	19.0–42.0	3.9–33.6
	ANOVA <i>F</i>	32.66		830.00	
	Significance	<i>p</i> < 0.001		<i>p</i> < 0.001	
Temperature (C°)	Mean (SD)	32.10 (2.03)	30.76 (2.10)	31.16 (2.24)	32.54 (1.63)
	Median	32.20	30.88	31.4	32.4
	Variance	4.12	4.42	5.03	2.66
	Min.–max.	22.2–39.80	22.80–35.70	22.2–38.0	28.0–39.8
	ANOVA <i>F</i>	64.35		93.07	
	Significance	<i>p</i> < 0.001		<i>p</i> < 0.001	
Light (µE·s <sup>-1</sup> ·m <sup>-2</sup> )	Mean (SD)	628.85 (521.12)	425.07 (412.82)	512.50 (462.37)	623.42 (531.28)
	Median	520.09	271.62	359.65	476.32
	Variance	2.72×10 <sup>5</sup>	1.70×10 <sup>5</sup>	2.14×10 <sup>5</sup>	2.82×10 <sup>5</sup>
	Min.–max.	5.6–1990.6	2.0–1941.3	3.8–1745.8	2.0–1996.2
	ANOVA <i>F</i>	32.66		8.35	
	Significance	<i>p</i> < 0.001		<i>p</i> < 0.05	
Depth (m)	Mean (SD)	1.05 (0.54)	1.46	1.29 ( )	0.78 ( )
	Median	0.93	1.40	1.2	0.8
	Variance	0.30	0.34	0.34	0.1
	Min.–max.	0.3 – 2.9	0.3–3.5	0.3–3.5	0.3–1.9
	ANOVA <i>F</i>	211.20		215.40	
	Significance	<i>p</i> < 0.001		<i>p</i> < 0.001	

**Note:** Differences in environmental variables between unsuitable and suitable areas were tested using a one-way analysis of variance (ANOVA).

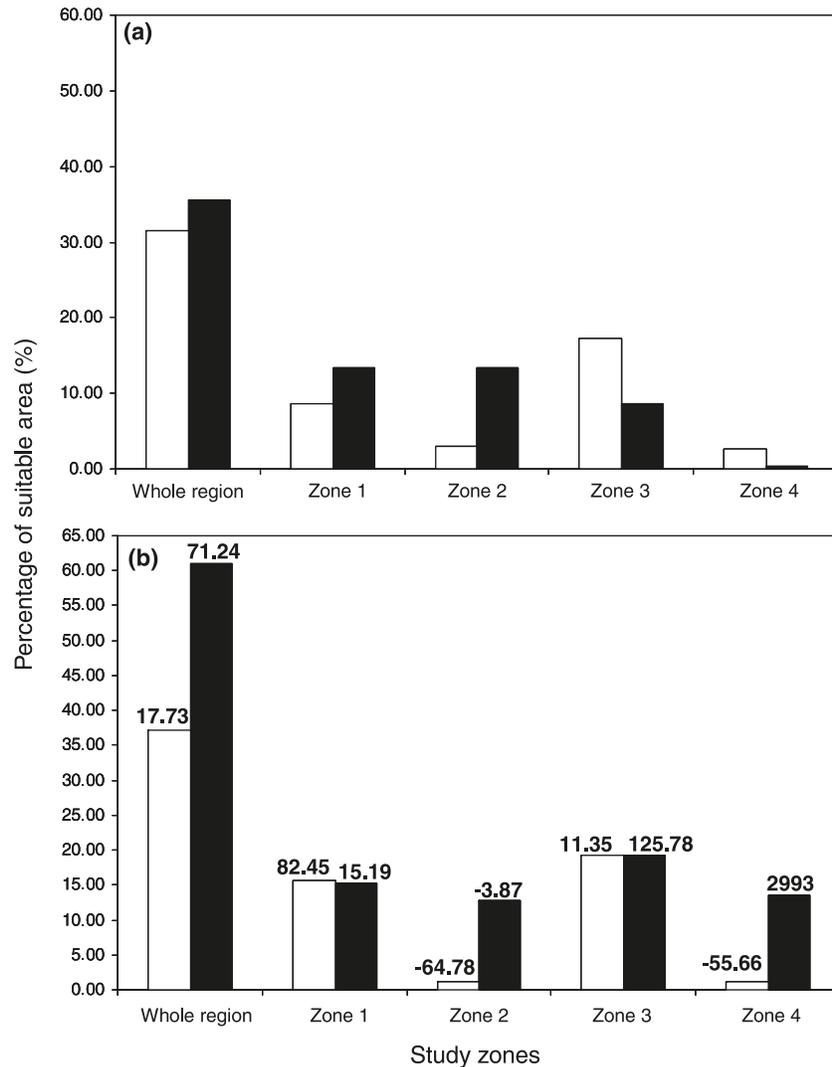
*H. wrightii*, the presence of *T. testudinum* was strongly associated with below-average light and above-average temperature and salinity (Table 1).

### Habitat suitability

The Boyce Index for the *H. wrightii* and *T. testudinum* HS models were  $0.78 \pm 0.03$  and  $0.87 \pm 0.09$ , respectively, demonstrating very good predictive power. When suitable and unsuitable areas for the two seagrass species were compared, significant differences in the mean values of the environmental variables were documented (analysis of variance (AN-

OVA), *p* < 0.05 for all comparisons; Table 2). The suitable area for *T. testudinum* concentrated mostly in areas with higher salinity and depth, while suitable habitat for *H. wrightii* concentrated in shallower areas with lower salinity. The total suitable habitat within the study region was similar for *H. wrightii* and *T. testudinum* (Fig. 2a). However, a large proportion of the suitable habitat for *H. wrightii* was concentrated in Zones 1 and 2, the northern portion of the study site, whereas suitable habitat for *T. testudinum* showed a more even distribution among all zones, reaching a maximum in Zone 3 (Figs. 1b, 1c; Fig. 2a).

**Fig. 2.** Percentage of suitable area for *Thalassia testudinum* (solid bars) and *Halodule wrightii* (open bars) within the study region: (a) baseline conditions, (b) decreased salinity scenario. The numbers on top of the bars on panel (b) represent the percent change between the baseline and the decreased salinity scenario.



### Decreased salinity scenario

When the baseline HS maps were compared with HS maps simulated under an increased freshwater inflow scenario, suitable area for both *H. wrightii* and *T. testudinum* increased. However, the percent change in the area of *H. wrightii* suitable habitat (71.24% increase in suitable habitat in the low-salinity scenario compared with the baseline) was greater than the percent change for *T. testudinum* (17.73% increase). The large increase in the suitable habitat for *H. wrightii* was driven by large increases in HS in Zones 3 (125.78% increase) and 4 (2993% increase). Most of the change in HS for *T. testudinum* concentrated in Zone 1 (82.45% increase) (Fig. 2b).

### Discussion

HS models based on ENFA were successfully developed for the two dominant seagrass species in Biscayne Bay, Florida. These tools provided both insights into the physical drivers that influence the distribution of these species as well as

a framework to evaluate how niche breadth and HS might change in restoration scenarios of increased fresh water and reduced salinity. The two species exhibited different niche requirements; *T. testudinum* can be classified as a generalist and *H. wrightii* as a specialist. This niche pattern is consistent with the commonly accepted paradigm of seagrass community succession and resource competition where *T. testudinum* is recognized as a competitive-dominant able to monopolize space under low-nutrient conditions when temperature and salinity exhibit restricted variability (Zieman 1976, 1982; Lirman and Cropper 2003). *Halodule wrightii* is frequently categorized as an early successional pioneer species able to occupy spaces recently disturbed or fluctuating environments (Montague and Ley 1993; Lirman and Cropper 2003).

Salinity, associated with both marginality and specialization metrics, is particularly relevant for the ecology of seagrass species in Biscayne and Florida bays (Lirman and Cropper 2003; Browder et al. 2005; Herbert and Fourqurean 2009). Seagrass species have different responses to salinity,

and as salinity patterns change naturally or because of management decisions, ecological niches of some species may shrink, while those of other species may expand. For example, lower productivity and higher mortality of *T. testudinum* has been associated with low-salinity and high-salinity fluctuations (Lirman and Cropper 2003; Herbert and Fourqurean 2009). This pattern was reflected here by the larger broader specialization of *T. testudinum* around high-salinity areas. The suitable areas for *T. testudinum* were most prominent in central and south Biscayne Bay, where salinities are higher and more stable. In contrast, *H. wrightii* suitability was associated with lower salinity values, in agreement with Lirman and Cropper (2003), who suggested that *H. wrightii* growth rates are higher than those of *T. testudinum* only in areas where mean salinity values are drastically lowered and highly variable. In Biscayne Bay, suitable habitats for *H. wrightii* were concentrated in areas where salinities are lower and water clarity is diminished because of high freshwater discharge (Browder et al. 2005; Lirman et al. 2008).

When the restoration scenario (reduced salinity) was simulated, both species had an overall positive response to increases in freshwater deliveries. However, the magnitude and spatial distribution of this response was different for *H. wrightii* and *T. testudinum*. For the whole region, the amount of suitable habitat increased 71% for *H. wrightii* compared with only 18% for *T. testudinum*. Based on the spatial distribution of these changes, it appears that *H. wrightii* benefits greatly by the reduction in salinity on areas like Zone 4 where it is presently virtually excluded by the high mean salinity and lack of freshwater inflow. In contrast, decreased salinity in the same area reduced the niche value for *T. testudinum*. The biggest gain in habitat availability for *T. testudinum* under a decreased salinity scenario is in Zone 1, where episodic hypersalinity (>37 ppt) may play a role in limiting the distribution of *T. testudinum* presently. Based on the results of the HS simulation, it can be concluded that one of the key goals of the Everglades restoration, which plans to increase the abundance of *H. wrightii* and reduce the dominance of *T. testudinum*, would be achieved by increasing the flow of fresh water (and decreasing salinity) into western Biscayne Bay. While further simulations need to be conducted and other scenarios need to be developed, this early indication highlights the value of HS models such as the one described here to provide science-based input into the management of coastal resources.

In theory, ENFA values generated with a large number of environmental variables should characterize a species' ecological niche as described by Hutchinson (1957) as a hypervolume in the multidimensional space of ecological variables within which a species can maintain a viable population (Hirzel et al. 2002). However, the ENFA and HS models developed here based on a subset (i.e., light, temperature, salinity, depth) of all potential environmental factors influencing seagrass distribution could reflect, instead, the realized niche of these species (Ricklefs 2001). In this study, depth combined with salinity in most models to drive the habitat specialization patterns of both species in agreement with prior research on the effects of these factors on seagrass distribution (Vicente and Riviera 1982; Duarte 1991; Lirman and Cropper 2003). Nevertheless, further studies that include additional biotic (competition, predation, etc.) and abiotic (nutrients,

hydrodynamics, etc.) factors known to be good spatial predictors of submerged aquatic vegetation distribution (e.g., Fourqurean et al. 2003; Grech and Coles 2010; Collado-Vides et al. 2011) are clearly needed to fully elucidate these species' full ecological niche. In addition, it is important to note that HS models are unable to account for or predict species distribution under rapidly changing environmental conditions (Grech and Coles 2010). Therefore, the HS model presented here should be updated with time-series data to account for environmental variability and (or) combined with more flexible approaches such as presence-absence and probabilistic models (e.g., generalized additive model, Bayesian belief network) and fine mapping techniques to completely capture the strength and spatiotemporal dynamics of the seagrass-environment relationship.

The HS models developed here based on the ENFA framework are good tools to assess and compare the niche of seagrass species in Biscayne Bay. In addition, these models provided excellent spatial tools to predict the effects of one of the main components of the Everglades restoration plan (i.e., increasing the flow of fresh water into the coastal lagoons of South Florida) on the niche breadth and habitat suitability for *T. testudinum* and *H. wrightii*. Taking into consideration the value of these resources to the ecology and economy of Biscayne Bay, it is crucial that these and future spatial modeling efforts be incorporated into an adaptive management framework that will provide information to managers in a timely manner so that actions can be taken to reverse undesired or unexpected consequences of water management decisions.

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