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Accounting for spatial patterns in deriving sea-level rise thresholds for salt marsh stability: More than just total areas?

Wei Wu

Division of Coastal Sciences, School of Ocean Science and Engineering, The University of Southern Mississippi, 703 East Beach Dr., Ocean Springs, MS 39564, USA

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ABSTRACT

Ecological threshold is an important concept to indicate the boundary of alternate states of ecosystems driven by environmental conditions and to facilitate evaluation of ecosystem resilience. Sea-level rise (SLR) thresholds for the stability of salt marshes, if studied in two dimensions, are generally derived based on total areas without systematic accounting for spatial patterns related to edges, shapes, and contagions of patches. As these spatial patterns are potentially important for functions and ecosystem services of salt marshes and they are likely to be impacted by SLR in a different way from the total areas, it is necessary to study SLR thresholds based on these spatial patterns to obtain a more comprehensive understanding of salt marsh resilience to SLR. This research compares the SLR thresholds based on these spatial patterns of salt marshes to those based on total areas alone across different spatial resolutions.

The spatial patterns of salt marshes were quantified by 26 commonly used landscape metrics, predicted from a mechanistic wetland change model. At spatial resolutions of 2–100 m, SLR thresholds were first derived using individual landscape metrics and then the first principal component that explained > 80% of total variance of these metrics showing threshold responses to SLR. In order to separate the effect of spatial configuration from composition, a neutral model which simulated the same amount of salt marsh change as the mechanistic model but at the random locations was applied. The SLR thresholds were derived based on the simulations from the neutral model and compared to those from the mechanistic model.

The results show that total area-based SLR thresholds do not comprehensively represent salt marshes' resilience to SLR. Particularly, I find 1) the derived SLR thresholds vary from 7.29 to 11.12 mm/yr for 2100 based on landscape metrics used, 2) the SLR threshold based on the first principal components (7.99 mm/yr) is smaller than that based on the total area only (8.40 mm/yr), 3) the SLR thresholds are scale dependent, and 4) the spatial configuration' effect on SLR thresholds is smaller for smaller salt marsh areas compared to larger salt marsh areas.

This study highlights the need to account for different spatial patterns of salt marshes and apply wetland maps with a spatial resolutions of 30 m or finer in deriving SLR thresholds, as using total areas alone or coarser-resolution maps may provide a biased interpretation that salt marshes are more resilient to SLR than they actually are.

1. Introduction

It is common for ecosystems to show nonlinear threshold responses to natural and anthropogenic drivers (Scheffer et al., 2001; Foley et al., 2015). In fact many ecosystems are subject to regime shift – abrupt change from one state to another after crossing a threshold or tipping point. An ecological threshold is a value or range of values of a driver or an ecosystem state variable beyond which a rapid and nonlinear change in ecosystem state, quality, property, or phenomena will occur (Groffman et al., 2006; Halpern et al., 2015, 2008). The rapid change is often irreversible leading to unwanted shifts in ecosystem state, altered ecosystem function, and degradation of ecosystem services (Hughes, 1994; Folke et al., 2004; Foley et al., 2015). In order to maintain ecosystem stability, it is important to understand the ecological thresholds and nonlinear response for better resource management (Foley et al., 2015). If crossing thresholds is not avoidable, then corresponding mitigation and adaption plans need to be in place to minimize the impacts associated with regime shift.

Coastal wetlands provide a variety of ecosystem services including high primary production, productive fisheries, habitats for many species, water quality improvement, blue carbon sequestration, flood control, storm protection, recreational opportunities, and cultural

E-mail address: wei.wu@usm.edu.

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values etc. (Costanza et al., 1997; Engle, 2011). However, coastal wetlands have been degraded or lost at an increasing rate, especially in the last few decades. One important driver that coastal wetlands show threshold response to is relative sea-level rise (RSLR), a combination of sea-level rise (SLR) and subsidence. Stability of coastal wetlands depends on whether accretion driven by sediment trapping from water columns and organic sediment contribution from root growth can keep up with RSLR, erosion driven by wave action, and decomposition of soil organic matters (Neubauer, 2008). Due to the feedbacks among inundation, sedimentation, and vegetation productivity, coastal wetlands may be able to keep up with low to moderate RSLR up to ~12 mm/yr (Jankowski et al., 2017). If RSLR exceeds a threshold, the feedbacks are interrupted and sedimentation rate is reduced to the point that the elevation cannot keep up with RSLR, leading to the permanent loss of coastal wetlands (Fagherazzi et al., 2006; Kirwan et al., 2010; Wang and Temmerman, 2013). Concerns arise if SLR continues to accelerate as predicted climate change will increase glacial and ice sheet melting and contribute to heat expansion (Fasullo et al., 2016). Therefore, it is important for resource managers to understand the SLR thresholds to anticipate the vulnerability of coastal wetlands.

SLR thresholds for stability of coastal wetlands are generally derived from one-dimensional metrics, either based on vertical accretion (Fagherazzi et al., 2006; Jankowski et al., 2017; Kirwan et al., 2010; Kirwan and Murray, 2007; Marani et al., 2007; Morris et al., 2016; Wang and Temmerman, 2013) or marsh length (Ratliff et al., 2015). However, two dimensional wetland distribution maps based on the vertical accretions under different SLR scenarios provide a more visual tool for resource managers to understand wetlands' resilience to SLR. When SLR thresholds are derived in two dimensions, total area is the most basic metric used (Wu et al., 2017). In fact, as total area is relatively easy to calculate, it has commonly been used to evaluate the conditions of coastal wetlands including the impact of sea-level rise on coastal wetlands (Alizad et al., 2018; Bourne, 2000; Coleman et al., 2008; Craft et al., 2009; Lin and Yu, 2018), and model values of coastal wetlands' services (Brander et al., 2012; Woodward and Wui, 2001). Spatial patterns other than total area in real-world landscapes, including the aspects of composition, shape, and arrangement, strongly influence ecological processes and are linked to ecological values of the landscapes (Uuemaa et al. 2013). Any changes in spatial patterns may interfere with critical ecological processes and therefore affect landscape integrity and ecosystem resilience or ecological thresholds. For example, patch shapes and connectivity are important in maintaining ecosystem functions. Fragmentation, involving not only reduced area, but also increased isolation and increased edge, degraded ecosystem functions, including biodiversity, carbon and nitrogen retention, productivity, and pollination (Haddad et al., 2015). Connectivity (Kukkala and Moilanen, 2017; Mitchell et al., 2013), or more broadly spatial composition and configuration (Lamy et al., 2016) are related to ecosystem services provided, such as hunting, fishing, carbon sequestration, and flood regulation etc. Therefore the relation between spatial patterns of salt marshes and SLR thresholds needs careful investigation.

Landscape metrics are a common and effective approach to quantify landscape patterns for categorical maps (Wu, 2000; Peng et al., 2010) although the metrics may suffer from problems of scale dependence and interpretability. They are frequently used in analyzing land use/land cover changes and serve as indicators for ecosystem functions (Uuemaa et al., 2009), but rarely applied to ecological thresholds. As many landscape metrics are not linearly related to total area, it is important to study how spatial metrics other than total area affect ecological thresholds. Wu et al. (2017) showed that the SLR threshold based on mean patch area was smaller than that based on total area at one retrograding wetland on the Mississippi Gulf Coast of the US.

As landscape metrics show dependence on spatial scales, ecological thresholds based on these landscape metrics are expected to show scale dependence. The response of landscape metrics to changing spatial scales fall into three categories: 1) predictable response with changing scale which can be quantified by using simple scaling equations, 2) less predictable staircase-like response, and 3) erratic response in response to changing scale (Wu et al., 2002). Similarly, the response of SLR thresholds to scale change likely falls into one of the three categories. The threshold is also temporal dependent as Wu et al. (2017) showed SLR thresholds differed when different years were targeted for maintaining stability of coastal wetlands.

Analysis of ecological thresholds is not straightforward due to nonlinear response of ecosystems to multiple environmental drivers that interact at diverse spatial and temporal scales (Groffman et al., 2006). A landscape model that accounts for these diverse environmental drivers and nonlinear dynamics is important in deriving SLR thresholds. Different types of models have been developed to predict the response of coastal wetlands to SLR and they range from statistical models to mechanistic models. Statistical models are generally simple to apply and require fewer data as inputs so they are appropriate at broad spatial scales, such as the entire northern Gulf of Mexico (Hardy and Wu, in review). In contrast, mechanistic models account for important ecological feedback, usually require more detailed data, and are appropriate to apply at narrower spatial scales.

This study aims to provide more accurate estimation of SLR thresholds by examining SLR thresholds based on a variety of spatial patterns of salt marshes at multiple spatial scales. Specific questions are

1) Is it necessary to account for spatial patterns other than total area in deriving SLR thresholds?
2) How do spatial resolutions of wetland maps affect derivation of SLR thresholds?
3) How does spatial configuration affect SLR thresholds derived?

It is not straightforward to identify the optimum landscape metrics that link to ecosystem processes due to the complex ecological processes and a large variety of metrics (Mander et al., 2005), and the current study on how landscape patterns impact SLR thresholds directly contribute to a better understanding of this key linkage in salt marsh ecosystems.

2. Methods

A mechanistic model was applied to predict salt marsh change at the Grand Bay National Estuarine Research Reserve (NERR), a retrograding delta in Mississippi, United States, for 2050 and 2100 under the scenarios of a variety of SLR rates ranging from 4 mm/year (current SLR rate) to 20 mm/year (an extremely high SLR rate) with an increment of 0.5 mm/year (Fig. 1). The RSLR is considered to be the same as the SLR as the subsidence rate is negligible in this study area based on the elevation change data and accretion data measured using the sediment elevation table and feldspar marker horizon technique at the Grand Bay NERR (personal communication with J. Pitchford). The model accounts for vegetation productivity, sedimentation, and hydrodynamics.

To address Question 1 on whether landscape patterns other than total area should be considered in deriving SLR thresholds, 26 commonly used landscape metrics (McGarigal et al., 2012) that indicate different spatial patterns of salt marshes simulated from the mechanistic model were calculated. Then the SLR thresholds based on these landscape metrics were derived. Furthermore, a principal component analysis (PCA) on all landscape metrics that showed threshold responses to SLR was conducted. PCA was chosen to reduce the dimension of the correlated landscape metrics and effectively integrate different aspects of spatial patterns represented by the variety of landscape metrics. Then, the SLR threshold was derived based on the first principal component which explained > 80% of total variance of these landscape metrics.

To examine how SLR thresholds based on different landscape metrics respond to different spatial scales (Question 2), the cells of the original wetland predictions at a spatial resolution of 2 m were

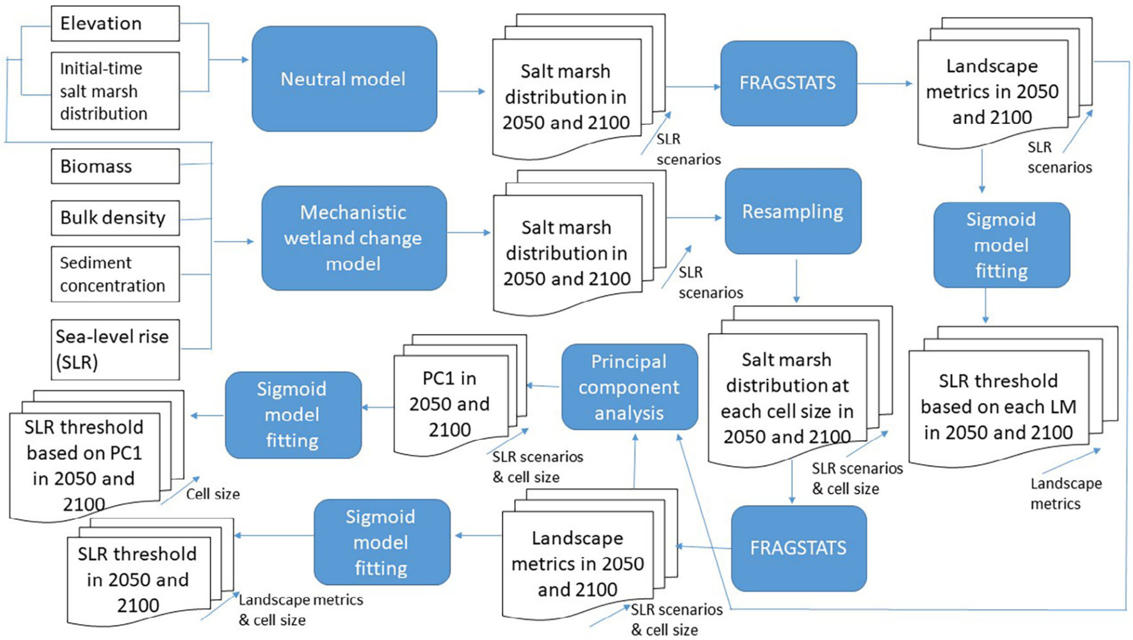

Fig. 1. Flow chart of analyses conducted in this study, including model simulations to predict salt marsh distributions in 2050 and 2100, calulations of landscape metrics of salt marshes, resampling to change cell size of salt marsh distributions, first principal component analysis to combine landscape metrics, and sigmoid model fitting on landscape metrics or the first principal component (PC1) versus SLR to derive SLR thresholds.

aggregated to generate maps of coarser resolutions of 10–100 m with an increment of 10 m, and then the SLR thresholds were derived at different spatial resolutions following the methods addressing Question 1.

Finally, in order to separate the effect of spatial configuration (patch shapes and spatial arrangements) from spatial composition (Question 3), a neutral model was applied to simulate the same amount of wetland change as the mechanistic model but at the random locations, then the SLR thresholds were derived, and the thresholds from both types of models were compared.

2.1. Study area

The Grand Bay NERR (30.37°N, 88.43°W, see Fig. 2 in Wu et al. (2017)) is located in southeastern Mississippi, United States, with an area of about 3000 ha of extensive salt marshes dominated (> 90%) by *Juncus roemerianus* and a small area of *Spartina alterniflora* at the fringe of marshes. The Grand Bay delta started to form in the late Holocene at the mouth of the Escatawpa River but it stopped growing when the Escatawpa river changed its course westward toward the Pascagoula River (Otvos, 2007). Adjacent to the salt marshes is a shallow estuarine area of about 2800 ha and a mean water depth of 0.6–0.9 m influenced by diurnal astronomical tides with an annual mean range of about 0.6 m and a maximum range during the summer months of 0.6–0.9 m. The climate is subtropical with hot and humid summers and mild winter conditions (Peterson et al., 2007).

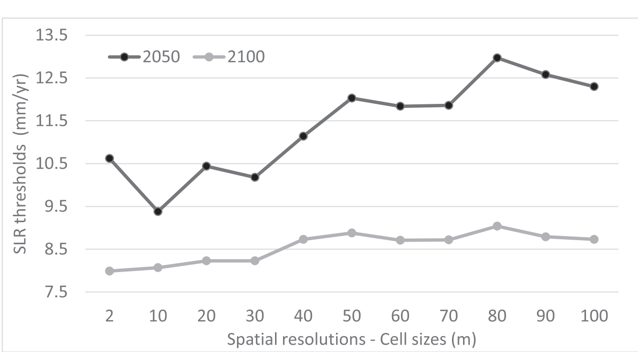

Fig. 2. The sea-level-rise (SLR) thresholds based on the first principal components at different spatial resolutions (cell sizes) from 2 m to 100 m for 2050 and 2100. The SLR thresholds at the cell sizes of coarser than 30 m are larger than those at the cell size of 30 m and finer, showing coarser resolutions may lead to the misconception that salt marshes are more resilient to SLR than they actually are.

2.2. Mechanistic model to simulate coastal wetland change under SLR

The mechanistic model (Wu et al., 2017), adapted from the Marsh Equilibrium Model (MEM) (Morris et al., 2002) and a simplified hydrodynamic model (Dean and Dalrymple, 1991; Fagherazzi and Furbish, 2001; Friedrichs and Aubrey, 1996; Kirwan and Murray, 2008), simulates elevation change of salt marshes at the annual step driven by SLR, accretion, and erosion. The accretion is contributed by organic matters from root growth and mineral sediments in water columns settling on marsh platforms with or without aboveground biomass' trapping. The erosion is assumed to be driven by depth-limited waves. When elevation of salt marsh platform is below mean low water level, the model converts salt marshes to open water.

This model was applied to predict wetland change by 2050 and 2100 under a variety of SLR rates ranging from 4 to 20 mm/year with an increment of 0.5 mm/year. These SLR scenarios are based on global SLR scenarios without considering local subsidence variability. The initial wetland map is based on the 1988 national wetland inventory (NWI) data (Shirley and Battaglia, 2006), classified to salt marshes, estuarine open water, and other land types. More details on the model and its application at the Grand Bay NERR can be found in Wu et al. (2017).

2.3. Landscape metrics

To represent the spatial pattern of salt marshes, 26 commonly used landscape metrics at the class level that do not require extra inputs other than wetland maps were calculated using Fragstats (McGarigal et al., 2012). All the available landscape metrics were selected initially as it was not clear which ones should be omitted due to limited knowledge and lack of guidance on relation between landscape metrics

Table 1
First principal component related metrics at multiple spatial resolutions in 2050: The variances explained, the sea-level rise (SLR) thresholds (unit: mm/yr), the lower and upper boundaries of sea-level rise rate for areas of maximum rate of change (unit: mm/yr), and the landscape metrics with the largest three absolute values of correlation with the first principal component (there may be more than three landscape metrics due to tie correlations). The numbers in the parentheses indicate the categories each landscape metric falls into: 1 - area/density/edge metrics, 2 - shape metrics, and 3 - aggregation/contagion/ interspersion metrics.

Spatial resolution	Variance explained (%)	SLR threshold	Low range for maximum change rate zone	High range for maximum change rate zone	Landscape metrics with the largest correlations with PC1		
					Largest correlation	Second largest correlation	Third largest correlation
2 m	86.81	10.62	7.00	14.50	LPI (1)	CA (1)	DIVISION
10 m	83.15	9.38	6.50	13.00	DIVISION (3)	PAFRAC (2)	CA (1)
20 m	86.36	10.44	6.00	15.00	CA (1)	DIVISION (3)	LPI (1)
30 m	84.92	10.18	6.00	15.00	SHAPE_MN (2)	DIVISION (3) CA (1)	LPI (1)
40 m	86.12	11.14	7.50	15.00	CONTIG_MN (2)	PARA_MN (2)	GYRATE_MN (1)
50 m	90.08	12.03	7.50	16.50	CA (1) LPI (1) SHAPE_MN (2)	GYRATE_MN (1)	AI (3)
60 m	87.38	11.84	7.50	16.50	CA (1)	PARA_MN (2)	GYRATE_MN (1)
70 m	89.77	11.86	7.50	16.00	SHAPE_MN (2)	CA (1)	CONTIG_MN (2)
80 m	87.53	12.97	8.00	18.00	SHAPE_MN (2)	CONTIG_MN (2)	PAFRAC (2)
90 m	90.95	12.58	8.00	18.00	SHAPE_MN (2)	CONTIG_MN (2)	CA (1)
100 m	88.68	12.30	7.00	17.50	SHAPE_MN (2)	CA (1)	GYRATE_MN (1)

Table 2
First principal component related metrics at multiple spatial resolutions in 2100: The variances explained, the sea-level rise (SLR) thresholds (unit: mm/yr), the lower and upper boundaries of sea-level rise rate for areas of maximum rate of change (unit: mm/yr), and the landscape metrics with the largest three absolute values of correlation with the first principal component (there may be more than three landscape metrics due to tie correlations). The numbers in the parentheses indicate the categories each landscape metric falls into: 1 - area/density/edge metrics, 2 - shape metrics, and 3 - aggregation/contagion/ interspersion metrics.

Spatial resolution	Variance explained (%)	SLR threshold (mm/yr)	Lower boundary for maximum change rate zone	Upper boundary for maximum change rate zone	Landscape metrics with the largest correlations with PC1		
					Largest correlation	Second largest correlation	Third largest correlation
2 m	91.44	7.99	7.00	9.00	DIVISION (3)	CA (1)	PAFRAC (2)
10 m	92.24	8.07	7.00	9.50	CA (1) DIVISION (3)	PAFRAC (2)	LPI (1)
20 m	89.76	8.23	7.00	9.50	CA (1)	DIVISION (3)	PAFRAC (2) LPI (1)
30 m	94.3	8.23	7.00	9.50	SHAPE_MN (2)	CONTIG_MN (2)	CA
40 m	93.64	8.73	7.00	10.50	CONTIG_MN (2)	SHAPE_MN (2)	GYRATE_MN (1)
50 m	91.09	8.88	7.00	10.50	SHAPE_MN (2)	CONTIG_MN (2)	AI (3)
60 m	93.02	8.71	7.00	10.50	CONTIG_MN (2)	SHAPE_MN (2)	CA (1)DIVISION (3)
70 m	91.23	8.72	7.50	10.00	SHAPE_MN (2)	PLAD (3)	CA (1)
80 m	89.33	9.04	7.00	11.00	CONTIG_MN (2)	PARA_MN (2)	AI (3)
90 m	95	8.79	7.50	10.00	SHAPE_MN (2)	AI (3)	PARA_MN (2)
100 m	92.15	8.73	7.50	10.00	SHAPE_MN (2)	CONTIG_MN (2)	CA (1)

and SLR thresholds. The landscape metrics fall into three categories: 1) area/density/edge metrics, 2) shape metrics, and 3) aggregation/contagion/ interspersion metrics. The first category includes total area (CA), percentage of coastal wetlands (PLAND), number of patches (NP), patch density (PD), total edge (TE), edge density (ED), landscape shape index (LSI), normalized landscape shape index (NLSI), largest patch index (LPI), mean patch area (AREA_MN), and mean radius of gyration (GYRATE_MN). The second category includes perimeter-area fractal dimension (PAFRAC), mean perimeter-area ratio (PARA_MN), mean shape index (SHAPE_MN), mean fractal index (FRAC_MN), mean related circumscribing circle (CIRCLE_MN), and mean contiguity index (CONTIG_MN). The third category includes percentage of like adjacencies (PLADJ), clumsiness index (CLUMPY), aggregation index (AI), interspersion and juxtaposition index (IJI), landscape division index (DIVISION), splitting index (SPLIT), effective mesh size (MESH), patch cohesion index (COHESION), and mean Euclidean nearest neighbor distance (ENN_MN). The description of these metrics are available in Fragstats documents (https://www.umass.edu/landeco/research/fragstats/documents/fragstats.help.4.2.pdf, last accessed on January 26, 2019).

Then the landscape metrics which showed typical threshold responses to SLR and can be described as following a sigmoid curve were selected. The landscape metrics which did not show an asymptotic value or monotonic response (e.g., quadratic function) were removed. If the correlation between two landscape metrics was larger than 0.999, the thresholds based on them were very similar, so only one landscape metric was kept. Similar numbers of metrics remained in each category of the landscape metrics when the selection was made. The rest of the landscape metrics may still be correlated but the ecological thresholds based on them were different so they remained in the following analyses.

2.4. Threshold derivation

The mechanistic model predicted salt marsh distributions under 33 different SLR rates for 2050 and 2100, and from these, the SLR rate thresholds for stability of salt marshes were derived. Beyond the SLR thresholds, salt marshes would transit to a less desirable state with much smaller and fragmented salt marsh landscape due to loss of salt marshes to open water.

To identify the ecological thresholds based on the landscape metrics, a sigmoidal regression approach (Osland et al., 2013) was applied

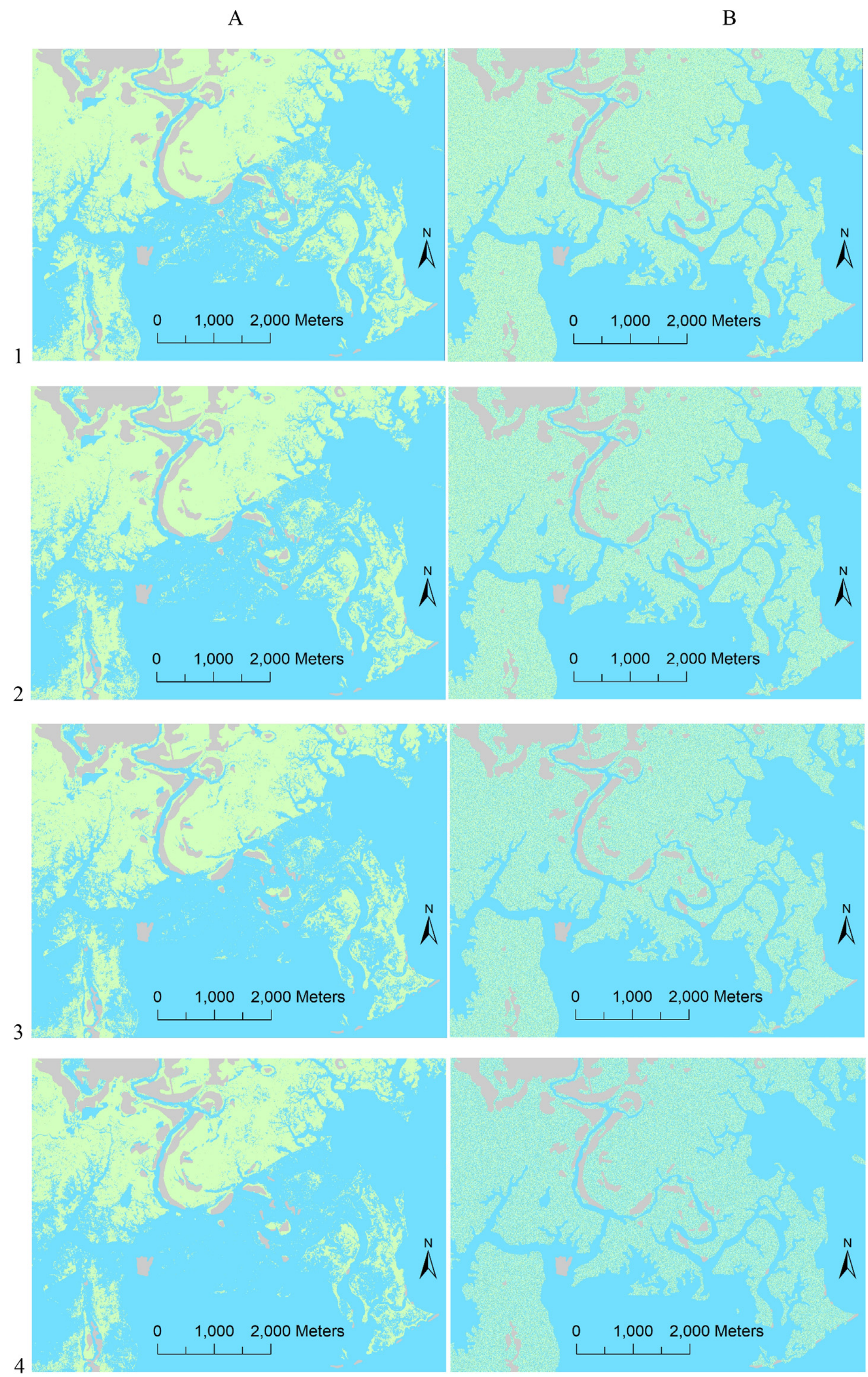

Fig. 3. Salt marsh distributions predicted from the mechanistic model (A: left column) and the neutral model (B: right column) in 2050 at the spatial resolution of 2 m under the sea-level rise rate of 10.0 (1), 10.5 (2), 11.0 (3), 11.5 (4), and 12.0 mm/yr. Total area-based SLR thresholds are 11.88 mm/yr for 2050 from both models.

to model the relation between a particular landscape metric and SLR rate, and then, the inflection point on the fitted sigmoid curve was determined as the threshold. The analysis was done using the 4-parameter function package "drc" available in R (https://cran.r-project.org/web/packages/drc/drc.pdf, last accessed on January 26, 2019). Additionally, the SLR threshold based on the first principal component which explained a majority of variance of these landscape metrics was also derived. Principal component analysis was conducted using the R package "FactoMineR" (https://cran.r-project.org/web/packages/FactoMineR/FactoMineR.pdf, last accessed on January 26, 2019).

Finally, the area of maximum rate of change for salt marshes' spatial patterns, represented by the first principal component of the landscape metrics, was identified, and the lower and upper boundaries of SLR rates for the area were determined using the "features" package in R (https://cran.r-project.org/web/packages/features/features.pdf, last accessed on February 7, 2019). The area of maximum rate of change lies between the local maxima and minima peaks of the second derivative of the sigmoidal model (Osland et al., 2014).

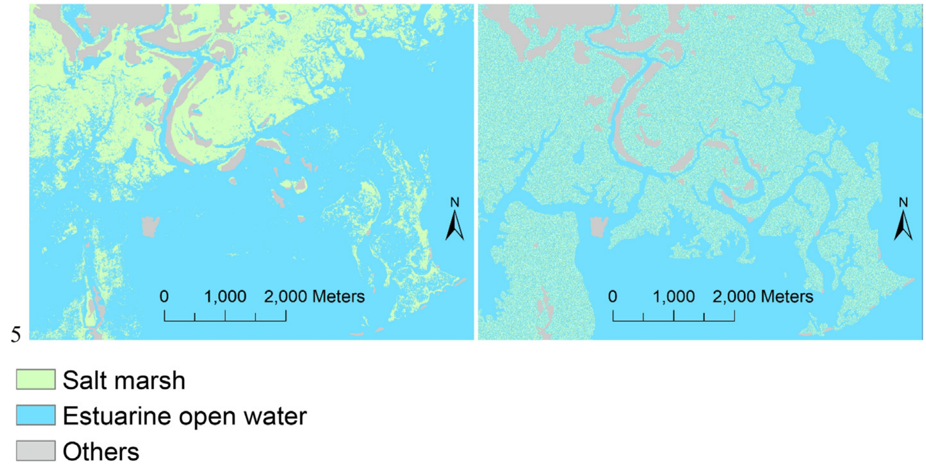

Fig. 3. (*continued*)

2.5. Spatial scale's impact on SLR derivation

My model simulations were based on the spatial inputs with a fine spatial resolution of 2 m; therefore, the predicted salt marsh distributions had the same fine spatial resolution. In order to investigate how spatial resolution affected threshold derivations, the cells of the predicted salt marsh maps were aggregated to 10–100 m with an increment of 10 m using the majority rule. Then Step 3 and 4 noted above were repeated to obtain the SLR thresholds based on the landscape metrics and first principal components at different spatial resolutions. Due to the less predictable behavior of landscape metrics' response to different spatial extents, how the change of spatial extent affected SLR thresholds was not examined.

2.6. Neutral model

To separate the effects of spatial configuration from spatial composition of salt marshes on SLR thresholds, a neutral model called the random constraint match model (RCM) (Hagen-Zanker and Lajoie, 2008; Wu et al., 2015) was applied to simulate salt marsh change. The RCM simulated the same amount of changes of salt marshes as the mechanistic model but it chose random locations for the changes instead of basing the changes on underlying ecological processes as in the mechanistic model. Therefore, the spatial configurations of the predicted salt marsh distributions from the two types of models differed while their spatial compositions stayed the same.

3. Results

The results show that total area-based SLR thresholds do not comprehensively represent salt marshes' resilience to SLR. Particularly, I find 1) the derived SLR thresholds vary by spatial patterns considered and landscape metrics used, 2) they are scale-dependent and the change across spatial resolutions for each individual landscape metric-based threshold is different, 3) the derived SLR thresholds based on the first principal components are smaller than those based on the total areas only for both 2050 and 2100 when spatial resolutions are finer than 30 m, 4) the derived SLR thresholds based on the first principal components show scale dependence and they increase with cell size for both 2050 and 2100 in general, and 5) the spatial arrangements' effect on SLR thresholds is smaller under the smaller marsh areas compared to under the larger marsh areas.

3.1. SLR thresholds based on a variety of landscape metrics at different spatial resolutions

The SLR threshold of ~8 mm/yr based on the total area in 2100 at each spatial resolution is comparable to the threshold derived for the similar estuaries (e.g., microtide and similar suspended sediment concentrations) (Kirwan et al., 2010), slightly larger than SLR threshold of ~7 mm/yr based on the model derived from the first principle (Morris et al., 2016).

The SLR threshold based on each individual landscape metric for 2100 is smaller than for 2050 (Tables S1 and S2), showing the target year for stability of salt marshes needs to be explicitly considered when it comes to SLR thresholds as wetland change is a dynamic process that requires a larger stress level to collapse in the nearer future compared to the more distant future.

The SLR thresholds vary by landscape metrics used, larger or smaller than total area-based thresholds, indicating SLR thresholds based on total areas represent only a partial aspect of resilience of salt marshes to SLR and other spatial patterns quantified by different landscape metrics need to be considered.

The landscape metrics that show threshold responses to SLR following sigmoid curves differ at different spatial resolutions; some consistently show this type of threshold response to SLR across all the resolutions. I particularly examined the 13 landscape metrics which remained in at least seven spatial scales out the eleven (2, 10, 20, …, 100 m) investigated. For 2050 salt marsh predictions, the majority of landscape metrics generate larger values of SLR thresholds as the spatial resolutions become coarser, including AREA_MN, GYRATE_MN, SHAPE_MN, PARA_MN, CONTIG_MN, FRAC_MN, and CIRCLE_MN (Table S1). Four landscape metrics generate the SLR thresholds that do not vary much with the spatial resolutions, include CA, CLUMPY, COHESION, and AI. The thresholds based on CA remain similar across all the spatial resolutions, while the thresholds based on CLUMPY, COHESION, and AI fluctuate but are maintained around a certain value across all the resolutions. In addition, two landscape metrics, LPI and DIVISION, lead to smaller SLR thresholds as the spatial resolutions become coarser. The change across scales are similar for 2100 (Table 2). The exception is that COHESION shows a declining trend with coarser resolution for 2100. For the spatial resolutions finer than 30 m, SLR thresholds based on the shape metrics are unanimously smaller than the total-area based thresholds.

Though the SLR thresholds based on the landscape division index at the spatial resolutions between 2 and 30 m differ slightly, the values of the index at the SLR thresholds for any given resolution at 30 m and finer in 2050 and 2100 are all 0.974 (Tables S1 and S2), indicating that larger index values than 0.974 would lead to rapid salt marsh collapse. In addition, the values of salt marsh area at the SLR thresholds are around 1020–1030 ha for any wetland maps of 50 m and finer, indicating that any areas smaller than that could lead to rapid salt marsh collapse.

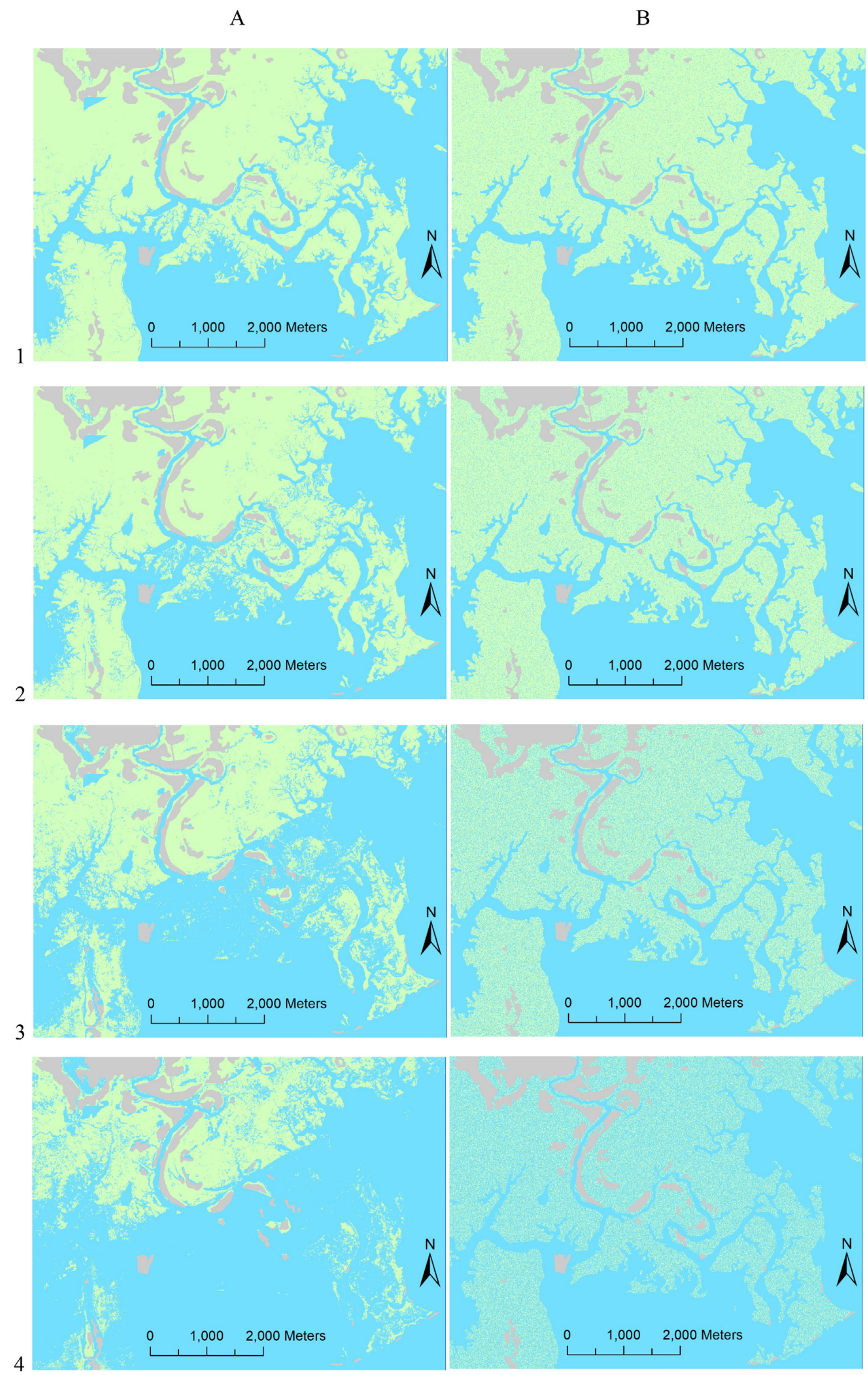

Fig. 4. Salt marsh distributions predicted from the mechanistic model (A: left column) and the neutral model (B: right column) in 2100 at the spatial resolution of 2 m under the sea-level rise rate of 7.0 (1), 7.5 (2), 8.0 (3), 8.5 (4), and 9.0 mm/yr. Total area-based SLR thresholds are 8.40 mm/yr for 2100 from both models.

3.2. SLR thresholds based on the first principal components

The first principal component, which is combinations of the landscape metrics, explains more than 80% of their total variance, and therefore comprehensively represents landscape patterns and salt marsh conditions at each spatial resolution. Based on the correlations of each individual landscape metric and the first principal components (Tables S3 and S4), area, shape and aggregation related landscape metrics all play important roles in determining SLR thresholds. The total area of salt marshes is among the top three landscape metrics that relate to the first principal components across the majority of the spatial scales, though it may not have the largest correlation. The landscape division index is among the top three landscape metrics that correlate to the first principal components at the spatial resolutions of 30 m and finer, and it is also the only landscape metric in the aggregation/contagion/interspersion metrics category that leads to smaller SLR thresholds than the total area-based thresholds across all the spatial resolutions. For the resolutions coarser than 30 m, mean shape index

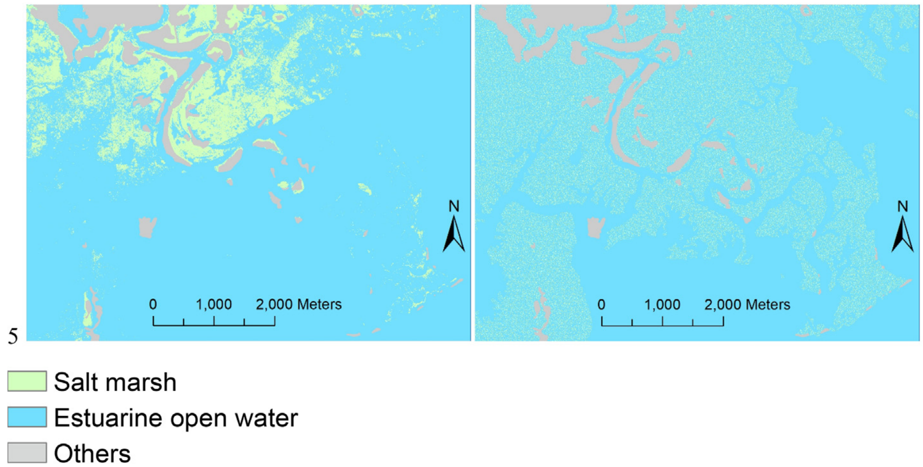

Fig. 4. (*continued*)

Table 3
Sea level rise (SLR) thresholds (unit: mm/yr) for individual landscape metric and first principal component based on the simulations from the mechanistic and neutral models for 2050 and 2100 at the spatial resolution of 2 m, lower and upper boundaries of sea-level rise rate for areas of maximum rate of change (unit: mm/yr), and the values of the landscape division index at the SLR thresholds. The numbers in the parentheses of Column 1 indicate the categories each landscape metric falls into: 1 - area/density/edge metrics, 2 - shape metrics, and 3 - aggregation/contagion/ interspersion metrics. NA = A particular landscape metric not selected in the final analysis for the SLR thresholds at any given spatial resolution.

Landscape metrics	Mechanistic model – 2050	Neutral model – 2050	Mechanistic model – 2100	Neutral model – 2100
CA (1)	11.88	11.88	8.40	8.40
LPI (1)	12.15	11.43	NA	8.09
PAFRAC (2)	8.72	NA	7.58	NA
CLUMPY (3)	13.27	10.79	NA	8.10
COHESION (3)	16.49	14.10	11.12	9.15
DIVISION (3)	10.36	10.47	7.96	7.95
AI (3)	13.67	NA	9.22	NA
AREA_MN (1)	7.79	NA	7.29	NA
GYRATE_MN (1)	8.14	8.49	7.39	7.47
SHAPE_MN (2)	NA	9.17	NA	7.69
PARA_MN (2)	NA	NA	NA	NA
CONTIG_MN (2)	NA	8.34	NA	7.44
FRAC_MN (2)	NA	NA	NA	7.80
CIRCLE_MN (2)	NA	NA	NA	8.37
ENN_MN (3)	NA	8.02	NA	NA
IJI	NA	8.93	NA	NA
PC1	10.62	9.59	7.99	7.98
Lower boundary	7.0	7.5	7.0	7.0
Upper boundary	14.5	12.0	9.0	9.0
DIVISION at the DIVISION-based SLR threshold	0.9736	0.9748	0.9739	0.9745

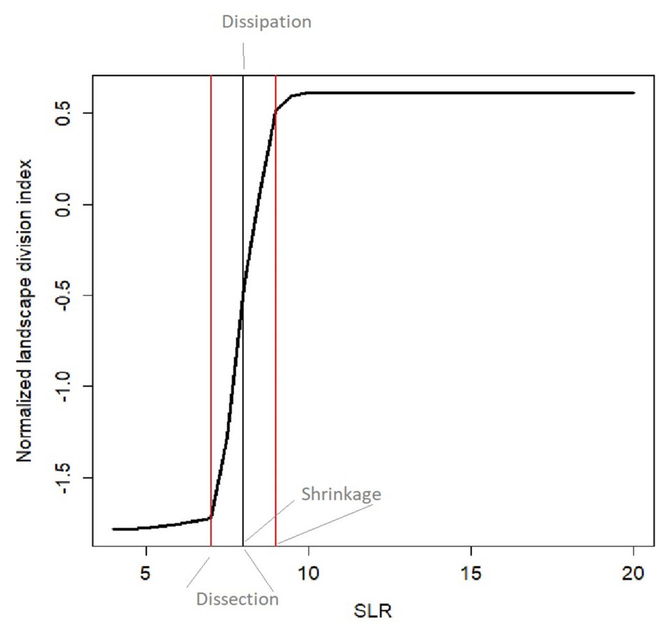

Fig. 5. The relation beween normalized landscape division index and sea-level rise (SLR) rate for 2100 at the spatial resolution of 2 m. The SLR thresholds (black) and upper and lower boundaries (red) of SLR rate for the area of maximum rate of change are indicated by the vertical lines. The corresponding stages of fragmentation including dissection, dissipation, and shringage are shown.

(indicating shape complexity) shows high correlation with the first principal components. At the finest spatial resolution (cell size of 2 m), larger total area and smaller landscape division index of salt marshes produce larger scores of the first principal components for both 2050 and 2100. Therefore, the larger scores of the first principal components represent better conditions of salt marshes in general.

The derived SLR thresholds based on the first principal components (Fig. 2), are smaller than those based on the total areas alone at the spatial resolutions of 30 m and finer for both 2050 and 2100. In general, the SLR thresholds increase with cell sizes, and the increase is particularly pronounced beyond 30 m (Fig. 2). As larger SLR thresholds mean higher resilience of salt marshes to SLR, marsh distribution maps coarser than 30 m could lead to the misconception that salt marshes are more resilient to SLR than they actually are. On the other hand, the areas of maximum rate of change are similar across the spatial resolutions for a particular year (Tables 1 and 2), and the lower boundaries of the areas are similar for 2050 (6.0–7.0 mm/yr) and 2100 (7.0 mm/yr) for the maps finer than 30 m, and the upper boundaries of the areas are larger for 2050 than for 2100 (Figs. 3A and 4A).

3.3. The effect of spatial arrangements on SLR thresholds

At the original resolution of 2 m, the SLR threshold based on the first principal component from the neutral model is smaller than that from the mechanistic model based on the 2050 simulations, whereas the thresholds for 2100 are similar from both models (Table 3). As the total areas of salt marshes from both types of models are the same, the difference of SLR thresholds is mainly the effect of spatial configuration. Here it is mainly the effect of spatial arrangements as no shape-related metrics are maintained in deriving SLR thresholds from both types of

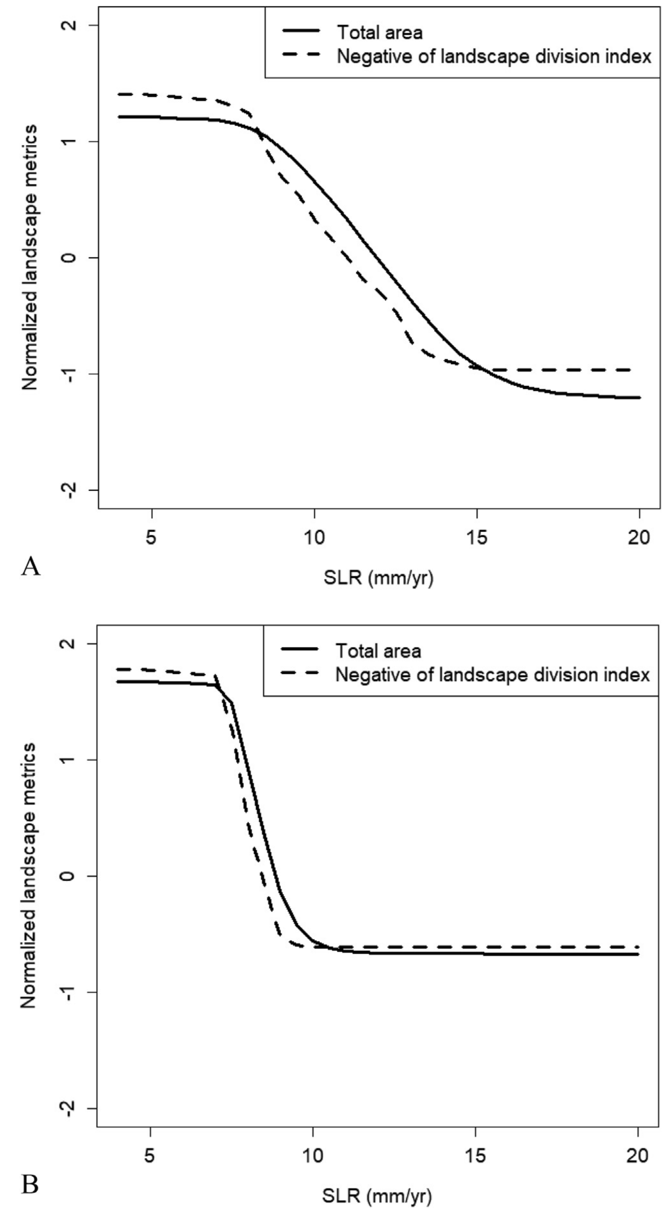

Fig. 6. Negative of landscape division index and total area (normalized to the similar ranges) vs. sea-level-rise (SLR) rate for 2050 (A) and 2100 (B) simulated from the mechanistic model at the spatial resolution of 2 m.

models for both years. Due to the nature of the neutral model, its simulated landscape is more fragmented than the landscape derived from the mechanistic model. This is shown in smaller SLR thresholds for CLUMPY and COHESION based on the neutral model simulations compared to the mechanistic model simulations. The spatial arrangements due to ecosystem processes play a more important role in affecting SLR thresholds as the wetland areas are larger (2050 vs. 2100; Figs. 3B and 4B). Ecosystem processes tend to increase patch connection through different mechanisms, such as root expansion and bio-hydro-geomorphological feedback that facilitate the maintenance of salt marshes, serving to improve the resilience of salt marshes. They may not effectively do so when the total area of salt marshes becomes smaller, especially considering that salt marsh landscape is naturally fragmented due to the environment's geomorphology and hydrodynamics, inferred from the similar SLR thresholds for 2100 from both types of models. In addition, both neutral and mechanistic models show that DIVISION larger than 0.974 would lead to rapid salt marsh collapse (Table 3).

4. Discussion

The most important finding of my research here shows that we will likely overestimate the salt marshes' resilience to SLR if we base the SLR thresholds on total areas alone, therefore landscape patterns other than total areas should be considered in studying SLR thresholds for salt marshes' stability.

4.1. Spatial patterns and landscape metrics

Spatial patterns are mainly classified into five components: 1) number of patch types, 2) proportion of each patch type, 3) spatial arrangements of patches, 4) patch shape, and 5) contrast between neighboring patches (Li and Reynolds, 1994; Peng et al., 2010). Generally, the first three are more important than the latter two in determining landscape patterns. This is consistent with my research results that the total area and landscape division index, which represent proportion of patch type and spatial arrangements of patches, respectively, are consistently selected among the top three landscape metrics that correlate to the first principal components when spatial resolutions are 30 m and finer for both 2050 and 2100 landscapes. The number of patch types is the same for all the landscapes.

The research results show that the SLR thresholds vary with the landscape metrics they are base on, but which landscape metric should be used for SLR thresholds is not straightforward. In fact, the optimal metrics for individual studies will be unique, depending on both biological processes and statistically robust metrics that are appropriate for study objectives, so no single landscape metric is superior than the others all the time (Wang et al., 2014). Furthermore, the landscape metrics are generally highly correlated (Peng et al., 2010). For example, the high correlation between spatial composition and configuration makes it difficult to separate habitat amount from habitat configuration that drives variation in a changing landscape. The high correlation likely leads to the conclusion that habitat fragmentation has negligible effect on biodiversity after habitat amount is accounted for (Fahrig, 2003). This is controversial to many other studies that show the negative or mixed effects of patch isolation, edge effects, and other factors (Bailey et al., 2010; Didham, 2010). To resolve this and set a general guideline on how to apply the large variety of landscape metrics in relating to ecological processes, the multivariate analysis which takes advantage of correlated variables should be considered. The principal component analysis applied in this study offers an effective and convenient approach to comprehensively account for different spatial patterns simultaneously and is transferrable to other studies on links between spatial patterns and ecological processes.

4.2. Modeling techniques to link landscape metrics to ecological thresholds

Despite some research that illustrates that the ecological relevance of many landscape metrics is unproven, questionable, and inconsistent (Corry and Nassauer, 2005; Kupfer, 2012; Tischendorf, 2001), the landscape metrics will continue to be used as simple and intuitive tools for assessing and monitoring changes in landscape patterns and underlying processes (Chen et al., 2008; Kupfer, 2012). They have been used in the research of biodiversity and habitat analysis (Tscharntke et al., 2012), water quality, hydrological processes (Yuan et al., 2015), urban road network, aesthetics of landscape and its management, planning and monitoring (Schröder, 2006; Uuemaa et al., 2009). In different landscape patterns, total area of habitats and fragmentation or connectivity of landscapes are particular of interests as habitat loss and fragmentation are among the main causes for changes in biodiversity and distribution of organisms, degradation of ecosystem functions such as decreasing biomass and altering nutrient cycles (Taylor et al., 1993; Andrén and Andren, 1994; Baillie et al., 2004; Wu, 2013; Haddad et al., 2015; Niebuhr et al., 2015; Hu et al., 2016; Wilson et al., 2016; Nichol et al., 2017; Desmet, 2018). In order to improve the use of landscape patterns to illuminate ecological processes, mechanistic models like what was applied here are key (Kareiva and Wennergren, 1995) to enhancing our understanding because these models contain key processes that drive landscape change. Therefore, the landscape patterns are directly the result of the underlying processes. This provides the foundation that landscape patterns can be used to infer relevant ecological processes such as wetlands' threshold response to SLR. Furthermore, the neutral models applied are clearly an important tool to distinguish the effect of spatial configuration due to ecosystem processes from spatial composition.

4.3. Spatial scales

Scale dependence of landscape metrics has been a focus in landscape ecology and scale is comprised of both cell size and spatial extent. In general, high-resolution landscape maps are preferred as they reveal detailed spatial patterns. However, the high-resolution maps may not be available or necessary, and there exists tradeoff between spatial resolution and computation time. Therefore, the selection of an appropriate scale depends on availability of data and ecological questions. The choice directly affects the results of ecological studies (Mayer and Cameron, 2003; Purtauf et al., 2005). Current coastal wetland maps are mainly derived from aerial photographs and satellite images and the most commonly used medium-resolution and free images are Landsat images, so the wetland maps derived from those have a spatial resolution of 30 m and finer, for example, both national land cover dataset and NOAA-coastal change analysis program data have a spatial resolution of 30 m. They are suitable for landscape pattern analysis and can serve as appropriate base maps to derive SLR thresholds. This study takes a step further to study how the landscape metrics at different cell sizes affect the derivation of SLR thresholds, beyond the impact of scales on landscape metrics themselves (Wu et al., 2002).

Total area-based SLR thresholds do not comprehensively represent salt marshes' resilience to SLR. Nevertheless, the SLR thresholds based on total areas of salt marshes are not sensitive to spatial resolutions, making total area a useful metric to apply for fine to medium resolutions.

4.4. Ecological thresholds

Ecological threshold is a useful concept to help understand ecological functions, and the threshold responses represent important and common ecosystem processes. Therefore it is important to apply a mechanistic model in the real-world and derive the SLR thresholds based on a variety of landscape patterns more than total areas alone from the model predictions to understand salt marshes' resilience to SLR comprehensively and accurately, as done in this study. Furthermore, how ecological processes relate to spatial patterns remains among the key questions in landscape ecology but the linkage is largely unfulfilled (Li and Wu, 2004; Wu, 2013; Wu and Hobbs, 2002). The derivation of the SLR thresholds based on different landscape metrics offers improved understanding of the fundamental questions of how landscape process and patterns are correlated (Jaeger, 2000), as the threshold values and the areas of maximum rate of change can relate to different phases of ecological processes. For example, the threshold and the area of maximum rate of change of the landscape division index in this study can represent different stages of the fragmentation processes, which include perforation, incision, dissection, dissipation, shrinkage, and attrition based on geometric characterization (Forman, 1995; Jaeger, 2000). Within the area of maximum rate of change for the division index, the range between the lower boundary and threshold represents the stage of dissection. The threshold value represents the largest increasing rate of the division index, corresponding to the stage of dissipation, and the range between the threshold value and the upper boundary of the area of the maximum rate of change represents the shrinkage phase (Fig. 5).

The thresholds of the landscape division index are closest to the thresholds based on the first principal components at the spatial resolutions of 30 m and finer (Tables 1 and 2, S1 and S2). Compared to the total areas, the negatives of the landscape division index values show a steeper decline with increasing SLR (Fig. 6). After SLR exceeds the thresholds, it will take some time before the salt marshes are locked into a less desirable new state (Wu et al., 2017). This lagging effect offers a window of opportunity for the salt marshes to return to previously more desirable conditions (Hughes et al., 2013). However, the steeper slope of the landscape division index makes the window of opportunity narrower and ecosystems less likely to recover. This also highlights that both landscape configuration and landscape composition need to be accounted for when it comes to deriving SLR thresholds for salt marsh stability.

From the derivation of the areas of the maximum rate of change and threshold values, any SLR rate larger than 7 mm/yr would pose a potential threat to the salt marshes in the Grand Bay NERR. The 7 mm/yr falls into the very likely range of SLR predictions in 2100 in the RCP 3 climate change scenario (Horton et al., 2014). Therefore, SLR will likely cause salt marshes in the Grand Bay NERR to disappear quickly even under the most conservative climate change scenario.

5. Conclusion

This study highlights the need to account for spatial patterns in addition to total area in analyzing salt marshes' resilience to SLR, as the derived SLR thresholds vary by spatial patterns considered. The research recommends a multivariate analysis on the landscape metrics to reduce dimensionality and account for spatial patterns comprehensively in deriving SLR thresholds. At the finest spatial resolution, the SLR threshold based on total area for 2100 is 8.40 mm/yr, larger than the threshold based on the first principal component (7.99 mm/yr). The sea-level rise thresholds based on other landscape metrics range from 7.39 to 11.12 mm/yr. This study also recommends the application of spatial resolution of wetland maps be 30 m or finer in deriving SLR thresholds as maps with coarser resolutions may provide biased predictions that salt marshes are more resilient to SLR than they actually are. Furthermore, the spatial arrangements' effect on SLR thresholds is smaller under the smaller marsh areas compared to under the larger marsh areas.

The study provides methods that allow for more accurate and comprehensive estimation of SLR thresholds and directly contributes to the enhanced understanding of the key question of linking ecological processes to spatial patterns.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.04.008.

References

Alizad, K., Hagen, S.C., Medeiros, S.C., Bilskie, M.V., Morris, J.T., Balthis, L., Buckel, C.A., 2018. Dynamic responses and implications to coastal wetlands and the surrounding regions under sea level rise. PLoS One 13, e0205176.

Andrén, H., Andren, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71, 355. https://doi.org/10.2307/3545823.

Bailey, D., Schmidt-Entling, M.H., Eberhart, P., Herrmann, J.D., Hofer, G., Kormann, U., Herzog, F., 2010. Effects of habitat amount and isolation on biodiversity in fragmented traditional orchards. J. Appl. Ecol. 47, 1003–1013. https://doi.org/10.1111/j.1365-2664.2010.01858.x.

Baillie, J.E.M., Hilton-Taylor, C., Suart, S.N., 2004. 2004 IUCN Red List of Threatened Species. A Global Species Assessment.file:///C:/Wu/Literature2018_2/Taylor_Connectivity is a vital element of landscape structure.pdf. IUCN, Gland, Switzerland and Cambridge, UK.

Bourne, J., 2000. Louisiana's vanishing wetlands: going, going. Science (80-.) 289, 1860–1863.

Brander, L.M., Wagtendonk, A.J., Hussain, S.S., McVittie, A., Verburg, P.H., de Groot, R.S., van der Ploeg, S., 2012. Ecosystem service values for mangroves in Southeast Asia: a meta-analysis and value transfer application. Ecosyst. Serv. 1, 62–69. https://doi.org/10.1016/j.ecoser.2012.06.003.

Chen, L., Liu, Y., Lü, Y., Feng, X., Fu, B., 2008. Pattern analysis in landscape ecology: progress, challenges and outlook. Acta Ecol. Sin. 28, 5521–5531. https://doi.org/10.1016/S1872-2032(09)60011-1.

Coleman, J.M., Huh, O.K., Braud, D., 2008. Wetland loss in world deltas. J. Coast. Res. 24, 1–14. https://doi.org/10.2112/05-0607.1.

Corry, R.C., Nassauer, J.I., 2005. Limitations of using landscape pattern indices to evaluate the ecological consequences of alternative plans and designs. Landscape Urban Plann. 72, 265–280. https://doi.org/10.1016/j.landurbplan.2004.04.003.

Costanza, R., Arge, R., De Groot, R., Farberk, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Suttonkk, P., van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253–260. https://doi.org/10.1038/387253a0.

Craft, C., Clough, J., Ehman, J., Jove, S., Park, R., Pennings, S., Guo, H., Machmuller, M., 2009. Forecasting the effects of accelerated sea-level rise on tidal marsh ecosystem services. Front. Ecol. Environ. 7, 73–78. https://doi.org/10.1890/070219.

Dean, R.G., Dalrymple, R.A., 1991. Water wave mechanics for engineers and scientists. Advanced Series on Ocean Engineering Vol. 2. World Scientific Publishing Company, New Jersey.

Desmet, P.G., 2018. Using landscape fragmentation thresholds to determine ecological process targets in systematic conservation plans. Biol. Conserv. 221, 257–260. https://doi.org/10.1016/j.biocon.2018.03.025.

Didham, R.K., 2010. The ecological consequences of habitat fragmentation. Encycl. Life Sci. 61, 1–11. https://doi.org/10.1017/CBO9781107415324.004.

Engle, V.D., 2011. Estimating the provision of ecosystem services by Gulf of Mexico coastal wetlands. Wetlands. https://doi.org/10.1007/s13157-010-0132-9.

Fagherazzi, S., Carniello, L., D'Alpaos, L., Defina, A., 2006. Critical bifurcation of shallow microtidal landforms in tidal flats and salt marshes. Proc. Natl. Acad. Sci. 103, 8337–8341. https://doi.org/10.1073/pnas.0508379103.

Fagherazzi, S., Furbish, D.J., 2001. On the shape and widening of salt marsh creeks. J. Geophys. Res. Ocean. 106, 991–1003. https://doi.org/10.1029/1999JC000115.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515.

Fasullo, J.T., Nerem, R.S., Hamlington, B., Church, J.A., Stocker, T.F., Nerem, R.S., Chambers, D., Choe, C., Mitchum, G.T., Boening, C., Willis, J.K., Landerer, F.W., Nerem, R.S., Fasullo, J., Fasullo, J.T., Boening, C., Landerer, F.W., Nerem, R.S., Hanna, E., Shepherd, A., Haigh, I.D., Moser, S.C., Trenberth, K.E., Fasullo, J.T., Cazenave, A., Watson, C.S., Mitchum, G.T., Douglas, B.C., Douglas, B.C., Church, J.A., White, N.J., Church, J.A., White, N.J., Jevrejeva, S., Moore, J.C., Grinsted, A., Woodworth, P.L., Ray, R., Douglas, B., Hay, C.H., Morrow, E., Kopp, R.E., Mitrovica, J.X., Minnis, P., McCormick, M.P., Thomason, L.W., Trepte, C.R., Church, J.A., White, N.J., Arblaster, J.M., Gleckler, P.J., Gregory, J.M., Lowe, J.A., Tett, S.F.B., Slangen, A., Slangen, A.B.A., Fasullo, J.T., Lawrence, D.M., Swenson, S.C., Tapley, B.D., Trenberth, K.E., Dai, A., Abraham, J.P., Nerem, R.S., Chambers, D.P., Leuliette, E.W., Mitchum, G.T., Giese, B.S., Kay, J.E., Lamarque, J.F., Lamarque, J.F., Lawrence, D.M., Church, J.A., 2016. Is the detection of accelerated sea level rise imminent? Sci. Rep. 6, 31245. https://doi.org/10.1038/srep31245.

Foley, M.M., Martone, R.G., Fox, M.D., Kappel, C.V., Mease, L.A., Erickson, A.L., Halpern, B.S., Selkoe, K.A., Taylor, P., Scarborough, C., 2015. Using ecological thresholds to inform resource management: current options and future possibilities. Front. Mar. Sci. 2, 1–12. https://doi.org/10.3389/fmars.2015.00095.

Folke, C., Carpenter, S.R., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C.S., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annu. Rev. Ecol. Evol. Syst. 35, 557–581. https://doi.org/10.2307/annurev.ecolsys.35.021103.30000021.

Forman, R.T.T., 1995. Land Mosaics. The Ecology of Landscapes and Regions. Cambridge University Press, Cambridge.

Friedrichs, C.T., Aubrey, D.G., 1996. Uniform bottom shear stress and equilibrium hypsometry of intertidal flats. Mix. Estuaries Coast. Seas 50, 405–429. https://doi.org/10.1029/CE050p0405.

Groffman, P.M., Baron, J.S., Blett, T., Gold, A.J., Goodman, I., Gunderson, L.H., Levinson, B.M., Palmer, M.A., Paerl, H.W., Peterson, G.D., Poff, N.L., Rejeski, D.W., Reynolds, J.F., Turner, M.G., Weathers, K.C., Wiens, J., 2006. Ecological thresholds: The key to successful environmental management or an important concept with no practical application? Ecosystems. https://doi.org/10.1007/s10021-003-0142-z.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Appl. Ecol. 1–9. https://doi.org/10.1126/sciadv.1500052.

Hagen-Zanker, A., Lajoie, G., 2008. Neutral models of landscape change as benchmarks in the assessment of model performance. Landscape Urban Plann. 86, 284–296. https://doi.org/10.1016/j.landurbplan.2008.04.002.

Halpern, B.S., Frazier, M., Potapenko, J., Casey, K.S., Koenig, K., Longo, C., Lowndes, J.S., Rockwood, R.C., Selig, E.R., Selkoe, K.A., Walbridge, S., 2015. Spatial and temporal changes in cumulative human impacts on the world's ocean. Nat. Commun. 6, 1–7. https://doi.org/10.1038/ncomms8615.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R., Watson, R., 2008. Global map impact marine. Science (80-.) 319, 948–952. https://doi.org/10.1126/science.1149345.

Hardy, T., Wu, W., in review. Modeling spatial variability of the resilience of coastal wetlands to sea level rise in the northern Gulf of Mexico using Bayesian multi-level models. J. Geophys. Res.

Horton, B.P., Rahmstorf, S., Engelhart, S.E., Kemp, A.C., 2014. Expert assessment of sea-level rise by AD 2100 and AD 2300. Quat. Sci. Rev. 84, 1–6. https://doi.org/10.1016/j.quascirev.2013.11.002.

Hu, G., Feeley, K.J., Yu, M., 2016. Habitat fragmentation drives plant community assembly processes across life stages. PLoS One 11, 8–10. https://doi.org/10.1371/journal.pone.0159572.

Hughes, T.P., 1994. Catastophes, phase shifts and large-scale degradation of a Caribbean coral reef. Science 265, 1547–1551. https://doi.org/10.1126/science.265.5178.1547.

Hughes, T.P., Linares, C., Dakos, V., van de Leemput, I.A., van Nes, E.H., 2013. Living dangerously on borrowed time during slow, unrecognized regime shifts. Trends Ecol. Evol. 28, 149–155. https://doi.org/10.1016/j.tree.2012.08.022.

Jaeger, J.A.G., 2000. Landscape division, splitting index, and effective mesh size: New measures of landscape fragmentation. Landscape Ecol. 15, 115–130. https://doi.org/10.1023/A:1008129329289.

Jankowski, K.L., Törnqvist, T.E., Fernandes, A.M., 2017. Vulnerability of Louisiana's coastal wetlands to present-day rates of relative sea-level rise. Nat. Commun. in revision 14792. https://doi.org/10.1038/ncomms14792.

Kareiva, P., Wennergren, U., 1995. Connecting landscape patterns to ecosystem and population processes. Nature 373, 299–302. https://doi.org/10.1038/373299a0.

Kirwan, M.L., Guntenspergen, G.R., D'Alpaos, A., Morris, J.T., Mudd, S.M., Temmerman, S., 2010. Limits on the adaptability of coastal marshes to rising sea level. Geophys. Res. Lett. 37, L23401. https://doi.org/10.1029/2010GL045489.

Kirwan, M.L., Murray, A.B., 2008. Ecological and morphological response of brackish tidal marshland to the next century of sea level rise: Westham Island, British Columbia. Global Planet. Change 60, 471–486. https://doi.org/10.1016/j.gloplacha.2007.05.005.

Kirwan, M.L., Murray, A.B., 2007. A coupled geomorphic and ecological model of tidal marsh evolution. Proc. Natl. Acad. Sci. U.S.A. 104, 6118–6122. https://doi.org/10.1073/pnas.0700958104.

Kukkala, A.S., Moilanen, A., 2017. Ecosystem services and connectivity in spatial conservation prioritization. Landscape Ecol. 32, 5–14. https://doi.org/10.1007/s10980-016-0446-y.

Kupfer, J.A., 2012. Landscape ecology and biogeography: rethinking landscape metrics in a post-FRAGSTATS landscape. Prog. Phys. Geogr. 36, 400–420. https://doi.org/10.1177/0309133312439594.

Lamy, T., Liss, K.N., Gonzalez, A., Bennett, E.M., 2016. Landscape structure affects the provision of multiple ecosystem services. Environ. Res. Lett. 11, 124017. https://doi.org/10.1088/1748-9326/11/12/124017.

Li, H., Reynolds, J.F., 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps'. Ecology 75, 2446–2455.

Li, H., Wu, J., 2004. Use and misuse of landscape Índices. Landscape Ecol. 19, 389–399. https://doi.org/10.1023/B:LAND.0000030441.15628.d6.

Lin, Q., Yu, S., 2018. Losses of natural coastal wetlands by land conversion and ecological degradation in the urbanizing Chinese coast. Sci. Rep. 8, 1–10. https://doi.org/10.1038/s41598-018-33406-x.

Mander, U., Uller, F., Wrbka, T., 2005. Functional and structural landscape indicators: upscaling and downscaling problems. Ecol. Indic. 5, 267–272. https://doi.org/10.1016/j.ecolind.2005.04.001.

Marani, M., D'Alpaos, A., Lanzoni, S., Carniello, L., Rinaldo, A., 2007. Biologically-controlled multiple equilibria of tidal landforms and the fate of the Venice lagoon. Geophys. Res. Lett. 34, 1–5. https://doi.org/10.1029/2007GL030178.

Mayer, A.L., Cameron, G.N., 2003. Consideration of grain and extent in landscape studies of terrestrial vertebrate ecology. Landscape Urban Plann. 65, 201–217. https://doi.org/10.1016/S0169-2046(03)00057-4.

McGarigal, K., Cushman, S.A., Ene, E., 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. University of Massachusetts, Amherst, Massachusetts, USA.

Mitchell, M.G.E., Bennett, E.M., Gonzalez, A., 2013. Linking landscape connectivity and ecosystem services provision: current knowledge and research gaps. Ecosystems 16, 894–908.

Morris, J.T., Barber, D.C., Callaway, J.C., Chambers, R., Hagen, S.C., Hopkinson, C.S., Johnson, B.J., Megonigal, P., Neubauer, S.C., Troxler, T., Wigand, C., 2016. Contributions of organic and inorganic matter to sediment volume and accretion in tidal wetlands at steady state. Earth's Future 4, 110–121. https://doi.org/10.1002/2015EF000334.

Morris, J.T., Nietch, C.T., Kjerfve, B., Sundareshwar, P.V., Cahoon, D.R., 2002. Responses of coastal wetlands to rising sea level. Ecology 83, 2869–2877. https://doi.org/10.1890/0012-9658(2002) 083[2869:ROCWTR]2.0.CO;2.

Neubauer, S.C., 2008. Contributions of mineral and organic components to tidal freshwater marsh accretion. Estuarine Coast. Shelf Sci. 78, 78–88.

Nichol, J.E., Abbas, S., Fischer, G.A., 2017. Spatial patterns of degraded tropical forest and biodiversity restoration over 70-years of succession. Global Ecol. Conserv. 11, 134–145. https://doi.org/10.1016/j.gecco.2017.05.005.

Niebuhr, B.B.S., Wosniack, M.E., Santos, M.C., Raposo, E.P., Viswanathan, G.M., Da Luz, M.G.E., Pie, M.R., 2015. Survival in patchy landscapes: the interplay between dispersal, habitat loss and fragmentation. Sci. Rep. 5, 1–10. https://doi.org/10.1038/srep11898.

Osland, M.J., Enwright, N., Day, R.H., Doyle, T.W., 2013. Winter climate change and coastal wetland foundation species: Salt marshes vs. mangrove forests in the southeastern United States. Global Change Biol. 19, 1482–1494. https://doi.org/10.1111/gcb.12126.

Osland, M.J., Enwright, N., Stagg, C.L., 2014. Freshwater availability and coastal wetland foundation species: ecological transitions along a rainfall gradient. Ecology 95, 2778–2788. https://doi.org/10.1890/13-1269.1.

Otvos, E.G., 2007. Geological framework and revolutionary history. In: Grand Bay National Estuarine Research Reserve: An Ecological Characterization. Moss Point, Mississippi, pp. 22–46.

Peng, J., Wang, Y., Zhang, Y., Wu, J., Li, W., Li, Y., 2010. Evaluating the effectiveness of landscape metrics in quantifying spatial patterns. Ecol. Indic. 10, 217–223. https://doi.org/10.1016/j.ecolind.2009.04.017.

Peterson, M.S., Waggy, G.L., Woodrey, M.S., 2007. Grand Bay National Estuarine Research Reserve: An Ecological Characterization. Grand Bay National Estuarine Research Reserve, Moss Point, Mississippi.

Purtauf, T., Thies, C., Ekschmitt, K., Wolters, V., Dauber, J., 2005. Scaling properties of multivariate landscape structure. Ecol. Indic. 5, 295–304. https://doi.org/10.1016/j.ecolind.2005.03.016.

Ratliff, K.M., Braswell, A.E., Marani, M., 2015. Spatial response of coastal marshes to increased atmospheric CO2. Proc. Natl. Acad. Sci. 112, 15580–15584. https://doi.org/10.1073/pnas.1516286112.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413, 591–596. https://doi.org/10.1038/35098000.

Schröder, B., 2006. Pattern, process, and function in landscape ecology and catchment hydrology? How can quantitative landscape ecology support predictions in ungauged basins? Hydrol. Earth Syst. Sci. Discuss. 10, 967–979.

Shirley, L.J., Battaglia, L.L., 2006. Assessing vegetation change in coastal landscapes of the northern Gulf of Mexico. Wetlands 26, 1057–1070. https://doi.org/10.1672/0277-5212(2006) 26[1057:AVCICL]2.0.CO;2.

Taylor, P.D., Fahrig, L., Henein, K., Merriam, G., 1993. connectivity is a vital element of landscape structure. Oikos 68, 571. https://doi.org/10.2307/3544927.

Tischendorf, L., 2001. Can landscape indices predict ecological processes consistently? Landscape Ecol. 16, 235–254. https://doi.org/10.1023/A:1011112719782.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fr, J., Holt, R.D., Klein, A.M., Kleijn, D., Kremen, C., Doug, A., Laurance, W., Lindenmayer, D., Scherber, C., 2012. Landscape moderation of biodiversity patterns and processes – eight hypotheses. Biol. Rev. 87, 661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x.

Uuemaa, E., Antrop, M., Marja, R., Roosaare, J., Mander, Ü., 2009. Landscape metrics and indices: an overview of their use in landscape research imprint/terms of use. Living rev. Landscape Res. 3, 1–28. https://doi.org/10.12942/lrlr-2009-1.

Uuemaa, E., Mander, Ü., Marja, R., 2013. Trends in the use of landscape spatial metrics as landscape indicators: a review. Ecol. Indic. 28, 100–106. https://doi.org/10.1016/j.ecolind.2012.07.018.

Wang, C., Temmerman, S., 2013. Does biogeomorphic feedback lead to abrupt shifts between alternative landscape states? An empirical study on intertidal flats and marshes. J. Geophys. Res. 118, 229–240. https://doi.org/10.1029/2012JF002474.

Wang, X., Blanchet, F.G., Koper, N., 2014. Measuring habitat fragmentation: An evaluation of landscape pattern metrics. Methods Ecol. Evol. 5, 634–646. https://doi.org/10.1111/2041-210X.12198.

Wilson, M.C., Chen, X.Y., Corlett, R.T., Didham, R.K., Ding, P., Holt, R.D., Holyoak, M., Hu, G., Hughes, A.C., Jiang, L., Laurance, W.F., Liu, J., Pimm, S.L., Robinson, S.K., Russo, S.E., Si, X., Wilcove, D.S., Wu, J., Yu, M., 2016. Habitat fragmentation and biodiversity conservation: key findings and future challenges. Landscape Ecol. 31, 219–227. https://doi.org/10.1007/s10980-015-0312-3.

Woodward, R.T., Wui, Y.S., 2001. The economic value of wetland services: a meta-analysis. Ecol. Econ. 37, 257–270. https://doi.org/10.1016/S0921-8009(00)00276-7.

Wu, J., 2013. Key concepts and research topics in landscape ecology revisited: 30 years after the Allerton Park workshop. Landscape Ecol. 28, 1–11. https://doi.org/10.1007/s10980-012-9836-y.

Wu, J., 2000. Landscape Ecology: Patterns, Process. High Education Press, Beijing, Scale and Hierarchy.

Wu, J., Hobbs, R., 2002. Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. Landscape Ecol. 17, 355–365. https://doi.org/10.1023/A:1020561630963.

Wu, J., Shen, W., Sun, W., Tueller, P.T., 2002. Empirical patterns of the effects of changing scale on landscape metrics. Landscape Ecol. 17, 761–782. https://doi.org/10.1023/A:1022995922992.

Wu, W., Biber, P., Bethel, M., 2017. Thresholds of sea-level rise rate and sea-level rise acceleration rate in a vulnerable coastal wetland. Ecol. Evol. 7, 10890–10903. https://doi.org/10.1002/ece3.3550.

Wu, W., Yeager, K.M., Peterson, M.S., Fulford, R.S., 2015. Neutral models as a way to evaluate the Sea Level Affecting Marshes Model (SLAMM). Ecol. Modell. 303, 55–69. https://doi.org/10.1016/j.ecolmodel.2015.02.008.

Yuan, J., Cohen, M.J., Kaplan, D.A., Acharya, S., Larsen, L.G., Nungesser, M.K., 2015. Linking metrics of landscape pattern to hydrological process in a lotic wetland. Landscape Ecol. 30, 1893–1912. https://doi.org/10.1007/s10980-015-0219-z.