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ENVIRONMENTAL ASSESSMENT

Coastal Vertebrate Exposure to Predicted Habitat Changes Due to Sea Level Rise

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Abstract Sea level rise (SLR) may degrade habitat for coastal vertebrates in the Southeastern United States, but it is unclear which groups or species will be most exposed to habitat changes. We assessed 28 coastal Georgia vertebrate species for their exposure to potential habitat changes due to SLR using output from the Sea Level Affecting Marshes Model and information on the species' fundamental niches. We assessed forecasted habitat change up to the year 2100 using three structural habitat metrics: total area, patch size, and habitat permanence. Almost all of the species ($n = 24$) experienced negative habitat changes due to SLR as measured by at least one of the metrics. Salt marsh and ocean beach habitats experienced the most change (out of 16 categorical land cover types) across the three metrics and species that used salt marsh extensively (rails and marsh sparrows) were ranked highest for exposure to habitat changes. Species that nested on ocean beaches (Diamondback Terrapins, shorebirds, and terns) were also ranked highly, but their use of other foraging habitats reduced their overall exposure. Future studies on potential effects of SLR on vertebrates in southeastern coastal ecosystems should focus on the relative importance of different habitat types to these species' foraging and nesting requirements. Our straightforward prioritization approach is applicable to other coastal systems and can provide insight to managers on which species to focus resources, what components of their habitats need to be protected, and which locations in the study area will provide habitat refuges in the face of SLR.

Keywords Coastal ecosystems · Endangered species · Habitat loss · Salt marsh · Sea level rise · Vulnerability

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Introduction

Coastal ecosystems have historically migrated inland in response to rising sea levels, but the current rate of environmental change may be too rapid for adaptation (Nicholls et al. 1999). Furthermore, the engineering of coastal ecosystems through the construction of sea walls and jetties, dredging, and beach nourishment will also prevent or hamper ecosystem migration, and coastal habitat will likely be lost (Nicholls et al. 1999; McGranahan et al. 2007). Habitat loss and fragmentation caused by sea level rise (SLR) in Southeastern U.S. coastal ecosystems could have dramatic effects on coastal vertebrate species (Craft et al. 2009; Woodrey et al. 2012). Species that are threatened or endangered due to other factors may be particularly vulnerable to habitat changes due to SLR, especially when populations are already declining or habitat is already limited or degraded (Van de Pol et al. 2010; Benscoter et al. 2013).

For state, federal, and non-governmental agencies tasked with allocating resources to species conservation and habitat management programs, broad-scale environmental changes that could affect multiple species of concern are a conundrum. Because climate change and sea level rise will affect some species more adversely than others, the prioritization of species with respect to their vulnerability is essential for effective conservation planning. To assess species' vulnerability to change, it can be useful to separately evaluate the three components of vulnerability: exposure to hazards, sensitivity to change, and adaptability or resilience to change (Turner et al. 2003; Dawson et al. 2011). SLR presents a hazard to which coastal species will be exposed to varying degrees depending on how they use coastal habitat (Brittain and Craft 2012; Woodrey et al. 2012). Threatened or endangered species tend to have high levels of sensitivity to change, and low levels of resilience (Benscoter et al. 2013), which increases the risk that exposure to additional hazards could cause local population declines or extinctions. Therefore, assessing the level of exposure to habitat changes from SLR for these species will provide an important first indication of their overall vulnerability.

The state of Georgia, USA, contains some of the most pristine remaining coastal habitat on the Atlantic seaboard, with 15 % of the remaining salt marsh on the Atlantic coast (USFWS 2007) and with over half of the state's barrier islands under some form of protection (federal, state, or private land trust). Despite this habitat protection, many vertebrate species in Georgia that use coastal habitats are already listed as species of concern by one or more regulatory or conservation agencies (Table 1). How populations of these species respond to changes in their habitats (relative resilience) will depend on the magnitude and extent of coastal habitat changes (relative exposure), how the species use coastal habitats, and each species' life history characteristics (relative sensitivity). We determined which species will experience the most exposure to habitat change from SLR, and quantified the ways in which that change will occur, as a first step toward estimating species' vulnerability to sea level rise. These predictions could be used to stimulate additional hypotheses about how species will respond to structural changes in their habitats (assessing resilience) and make recommendations for how to prioritize management of already threatened species.

In this study, we predicted the SLR exposure for 28 coastal Georgia vertebrate species using sea level rise model predictions and knowledge of species' life history characteristics and habitat preferences. To make our results broadly applicable to coastal changes throughout the Southeastern United States, we modeled changes to the species' fundamental niches using relationships gleaned from the literature. We used a broad definition of niche: the sum of all habitats that a species could use to satisfy foraging or nesting requirements (in the sense of the fundamental Grinnellian niche, Soberon 2007). We assumed that changes to habitats within the niche across three metrics (total area, patch size, and habitat permanence) would be broadly applicable to coastal habitat change across the southeast and that change across these metrics would have similar population level effects for each species. Total habitat area has long been recognized as a limiting factor on species presence and abundance in many ecosystems (MacArthur and Wilson 1967; Fahrig 1997); the negative relationship between species presence and habitat area loss is particularly well defined for coastal ecosystems because so much coastal habitat has already been converted for human use (Bertness et al. 2002; Shriver et al. 2004). Within the total habitat area, the size and configuration of habitat patches have also been shown to contribute to population density, with smaller, more isolated patches generally supporting relatively fewer individuals (Bender et al. 1998; Prugh et al. 2008). Habitat permanence refers to the concept that if total area and patch size remain the same over time, but habitat shifts in location, populations may still decline if they are dispersal limited (Hanski 1999; Benscoter et al. 2013). For example, the loss of a historic nesting site may mean lost reproductive opportunities for one or more breeding seasons (e.g., Burger 1982), and some species may be so philopatric that nest site shifts may reduce some individual's reproductive output to zero (e.g., Sheridan et al. 2010). Therefore, we assume that declines in any of these metrics indicate increased exposure to habitat changes from SLR for coastal populations.

Methods

Species Niche Definition

We selected 28 vertebrate species for this study that have coastal populations in Georgia and were either listed as threatened or endangered by the GA Department of Natural Resources or the U.S. Fish and Wildlife Service or were identified as a species of conservation concern by either of two nationally recognized non-profit conservation organizations (Table 1). We did not evaluate all coastal, listed species, but chose species so that all of the coastal habitat types in Georgia would be represented within at least one species' niche. Our species list also skews toward birds

Table 1 Georgia coastal vertebrate species and their conservation status as measured by federal (U.S. Fish and Wildlife Service) and state governmental agencies (Georgia Department of Natural Resources), national bird conservation groups (WC: Waterbird Conservation of the Americas, SCP: U.S. Shorebird Conservation Plan), and a national conservation non-profit organization [NatureServe (NS), provided for completeness, but not used for species selection because most species had not been reviewed since 1996]

Group	Common name	Scientific name	Federal	State	WC/SCP	NS
Rails	Black Rail	*Laterallus jamaicensis*	T?	S2	1	G3
	King Rail	*Rallus elegans*		S4	2	G4
	Clapper Rail	*Rallus crepitans*			3	G5
	Yellow Rail	*Coturnicops noveboracensis*			2	G4
Shorebirds	Wilson's Plover	*Charadrius wilsonia*		S2	2	G5
	American Oystercatcher	*Haematopus palliatus*		S2	2	G5
	Piping Plover	*Charadrius melodus*	T	S1	1	G3
	Red Knot	*Calidris cantus*	T?	S3	1	G4
	Ruddy Turnstone	*Arenaria interpres*			2	G5
	Sanderling	*Calidris alba*			2	G5
	Whimbrel	*Numenius phaeopus*			2	G5
Marsh/wading birds	Least Bittern	*Ixobrychus exilis*			2	G5
	Wood Stork	*Mycteria americana*	E	S2	2	G4
	Little Blue Heron	*Egretta caerulea*		S4	2	G5
	Tricolored Heron	*Egretta tricolor*		S4	2	G5
	Snowy Egret	*Egretta thula*			2	G5
Terns	Gull-billed Tern	*Gelochilidon nilotica*		S1	2	G5
	Least Tern	*Sternula antillarum*		S3	2	G4
	Black Skimmer	*Rynchops niger*		S1	2	G5
Passerines	Seaside Sparrow	*Ammodramus maritimus*	T?	S3		G4
	Painted Bunting	*Passerina ciris*		S3		G5
	Saltmarsh Sparrow	*Ammodramus caudacutus*		S3		G4
Raptor	Swallow-tailed Kite	*Elanoides forficatus*		S2		G5
Reptiles	Diamondback Rattlesnake	*Crotalus adamanteus*	T?	S4		G4
	Diamondback Terrapin	*Malaclemys terrapin*		S3		G4
Amphibians	Gopher Frog	*Rana capito*		S3		G3
	Dwarf Siren	*Pseudobranchus striatus*		S3		G5
Mammal	Marsh Rabbit	*Sylvilagus palustris*				G5

Species that do not have a rank under a category were either not assessed or were not considered to be of concern by that agency. Federal abbreviations: E = endangered, T = threatened, T? = considered for listing as threatened. State abbreviations: S1 = critically imperiled, S2 = imperiled, S3 = vulnerable, S4 = apparently secure. WC/SCP abbreviations: 1 = highly imperiled, 2 = high concern, 3 = moderate concern. NS abbreviations (rounded global status): G3 = vulnerable, G4 = apparently secure, G5 = secure

because more information is available on these species' niches than other vertebrate groups. For each species, foraging and nesting (if applicable) niches were defined based on available information from the literature (Table 2). Foraging and nesting niches were separately defined because some species use substantially different habitats for these activities, and foraging and nesting adequately defined most of the used landcover categories for all species. Habitat types used for the fundamental niche were defined by the Sea Level Affecting Marshes Model (SLAMM) landcover categories (Fig. 1). We only included landcover categories in a niche if they were reported as commonly used by a species and not occasional or incidental uses. We make no assumptions about how much or of what quality habitat is required to sustain occupancy, survival, or reproductive success, but simply assume that the current habitat available is necessary for current population status. Online Appendix 1 lists habitat type definitions and literature used to define species' niches.

Sea Level Rise Model

The Sea Level Affecting Marshes Model Version 6.0 [SLAMM (Clough et al. 2010)] was run for the entire

Table 2 Habitat definitions for nesting and foraging activities for species on the Georgia coast that are potentially vulnerable to habitat changes from sea level rise

Group	Species	2	3	4	5	6	7	8	10	11	12	15	16	17	19	20	23
Rails	Black Rail				N,F	N,F										N,F	
	King Rail				N,F	N,F										N,F	
	Clapper Rail							N,F								N,F	
	Yellow Rail							F								F	
Shorebirds	Wilson's Plover								F	F	N,F						
	American Oystercatcher								F	F	N,F						
	Piping Plover								F	F	F						
	Red Knot								F	F	F						
	Ruddy Turnstone								F	F	F						
	Sanderling								F	F	F						
	Whimbrel							F	F	F	F						
Marsh/wading birds	Least Bittern				N,F	N,F						F				F	
	Wood Stork	N[a]	N,F	N,F	F	F		F				F		F		F	N,F
	Little Blue Heron	N[a]	N,F	N,F	F							F				F	N,F
	Tricolored Heron	N[a]	N	N	F			F				F				F	N,F
	Snowy Egret	N[a]	N	N	F			F				F				F	N,F
Terns	Gull-billed Tern				F	F	F	F	N,F	F	N,F						
	Least Tern								N		N	F	F	F	F[b]		
	Black Skimmer								N	F	N			F	F[b]		
Passerines	Seaside Sparrow							N,F								F	
	Painted Bunting	N,F					N,F										
	Saltmarsh Sparrow							F								F	
Raptor	Swallow-tailed Kite	F	N,F	N,F	F	F										F	
Reptiles	Diamondback Rattlesnake	N,F															
	Diamondback Terrapin	N[c]						F	N		N		F	F			
Amphibians	Gopher Frog	F[d]	N	N								N					
	Dwarf Siren		N,F	N,F								N,F					
Mammal	Marsh Rabbit	F[e]	F	F	N,F	N,F	N,F	F[e]									

Habitat categories drawn from Sea Level Affecting Marshes Model (SLAMM) habitat codes: 2 = undeveloped dry land, 3 = swamp, 4 = cypress swamp, 5 = inland fresh marsh, 6 = tidal fresh marsh, 7 = transition salt marsh, 8 = salt marsh, 10 = estuarine beach, 11 = tidal flat, 12 = ocean beach, 15 = inland open water, 16 = riverine tidal open water, 17 = estuarine open water, 19 = open ocean, 20 = brackish marsh, 23 = tidal swamp

N nesting niche, *F* foraging niche

[a] Only adjacent to water

[b] Near shore (within 50 m)

[c] Only adjacent to foraging habitat

[d] Near breeding habitat (within 100 m)

[e] Only adjacent to freshwater

Georgia coast (Bryan, Camden, Chatham, Glynn, Liberty, and McIntosh counties, from the coastline to approximately 50-km inland, which is the minimum range covered by any of the counties, Fig. 1). SLAMM incorporates information on current landcover distributions, historical sea level rise, soil accretion rates and patterns, salinity, and tidal amplitude to make predictions for future landcover changes (Craft et al. 2009, Clough et al. 2010). SLAMM is a GIS-based model with inputs and outputs stored as map grid data. Conversion from one landcover type to another at each annual time step is determined primarily by transitions in the elevation and salinity distribution of grid cells. Elevation is determined by the relative magnitudes of accretion and sea level rise rates. This version of SLAMM allowed for variable accretion rates for different landcover categories and incorporated data-based, detailed salinity models for Georgia estuaries. Inputs

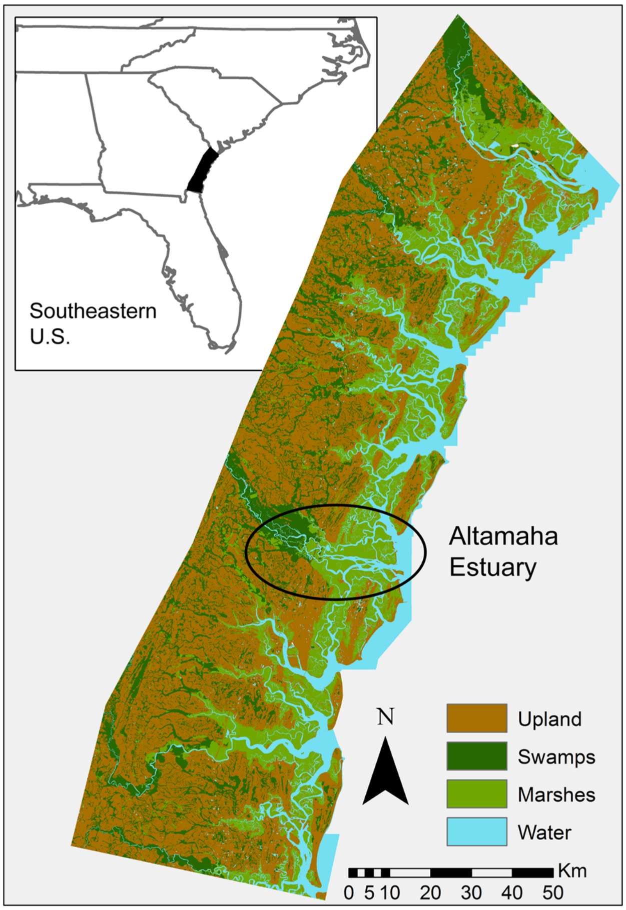

Fig. 1 The study area of entire length of the Georgia coast (approximately 50 km from shoreline) and its associated landcover types as defined and used in the Sea Level Affecting Marshes Model based on National Wetlands Inventory data. *Insert* shows the position of the study area (in *black*) within the Southeastern United States

to the model included current landcover data [2007 National Wetland Inventory data (USFWS 2007)], a digital elevation model [Light Detection And Ranging (LiDAR) derived elevation data for coastal Georgia, scaled to the 28-m resolution of landcover data], and National Oceanic and Atmospheric Administration tidal gage data (www.tidesandcurrents.noaa.gov). The model was used to predict landcover distributions assuming a 1-m rise in sea level from 2007 to 2100. We used SLAMM output raster maps of 20 landcover types at five time periods (2007, 2025, 2050, 2075, and 2100) to model species' exposure to SLR (C. Alexander, Skidaway Institute of Oceanography, unpublished data).

Exposure to SLR

Each species' foraging and nesting niche was quantified for each time period of the SLAMM outputs. Changes to habitats within the niche over time were evaluated by three metrics: total area, patch size, and habitat permanence. These metrics are commonly used in the analysis of raster-based landscapes [e.g., FRAGSTATS (McGarigal et al. 2012)]. We assessed these metrics for species' niches using the R packages "raster" (Hijmans 2013) and "sp" (Bivand et al. 2008). Total area was the change in the total number of identified habitat cells over time, which was normalized by dividing each time period's area by the 2007 area. Patch size was measured by finding adjacent cells of habitat (8-neighbor rule—horizontal, vertical, and diagonal neighbors counted as adjacent) and then finding the mean number of cells within patches for each time period (also normalized by dividing by the 2007 mean patch size). Because assessing habitat permanence requires looking at the change in the location of habitat between two time periods, we measured the acceleration of change in permanence in relation to a baseline permanence level. Habitat permanence was measured by finding the fraction of habitat cells that were also habitat in the previous time period. The decrease in permanence from 2007–2025 was set as a baseline with which all other permanence differences were divided to create the permanence estimate, which resulted in no permanence estimate for 2007 and a permanence estimate of one for 2025.

To create a quantitative habitat change score for each metric, a linear model of the change through time was created and the slope of the line indicated the severity of the change [at year 2007 (year 2025 for permanence), all models had fixed intercepts at one so that slopes would be directly comparable among species]. Scores were then normalized across all species for nesting and foraging niches by subtracting the mean nesting or foraging score (across all species and metrics) and dividing by the standard deviation of the nesting or foraging scores. Within each metric and niche type combination, these normalized scores were then ranked across species, with greater losses (more negative slopes) assigned higher ranks. Ranks were then averaged across the three metrics within both foraging and nesting niches which allowed us to directly compare the species in each niche. The final rank was the higher of either the nesting or foraging ranks.

Niche Definition Validation

To determine whether the defined niches were adequately describing the actual distributions of the species, we used locations collected through routine surveys and censuses provided by the Georgia Department of Natural Resource's Natural Heritage Program (GNHP, Georgia Department of Natural Resources 2013) for a subset of the species to validate our definition of the species' niches for the 2007 data (Online Appendix 1). Although GNHP locations were available for many of the species in our list, we did not verify niches for species that were likely to have a high proportion of locations outside of their fundamental niche (e.g., fly-over observations of terns and wading birds). We also only included a species if it had ≥25 locations. Using those criteria, we matched locations for Diamondback Terrapin, Diamondback Rattlesnake, wading bird colonies (including Wood Stork, Little Blue Heron, Tricolored Heron, and Snowy Egret), Painted Bunting, and Wilson's Plover with the species' combined foraging and nesting niches (only nesting niche for wading bird colonies). The locations were first buffered by 30 meters (approximate raster cell size) to account for both GPS error in the points and landcover classification error in the raster datasets. The fraction of buffered locations that fell within the defined niche gave an estimate of the accuracy of the fundamental niche definition.

Results

All of the species had a negative score for at least one of the habitat change metrics, except for four species of non-nesting shorebirds that had all positive scores, and 68 % of the species had negative scores for at least half (three or more out of six) of the metrics (Table 3). The common habitat feature among the top four species (Seaside Sparrow, Saltmarsh Sparrow, Clapper Rail, and Yellow Rail) with the highest limiting exposure ranks for habitat change

Table 3 Exposure scores (non-normalized) for nesting and foraging niches across three metrics of change: area reduction, patch size reduction, and permanence

Group	Species	Nesting scores				Foraging scores			
		Area	Patch	Perm.	Rank	Area	Patch	Perm.	Rank
Rails	Black Rail	0.044	−0.005	−0.016	16.3	0.044	−0.005	−0.016	**16**
	King Rail	0.044	−0.005	−0.016	16.3	0.044	−0.005	−0.016	**16**
	Clapper Rail	−0.006	−0.187	−0.033	8	−0.006	−0.187	−0.033	**3.7**
	Yellow Rail					−0.006	−0.187	−0.033	**3.7**
Shorebirds	Wilson's Plover	−0.186	−0.275	0.297	**7.3**	0.329	0.043	0.006	22
	American Oystercatcher	−0.186	−0.275	0.297	**7.3**	0.329	0.043	0.006	22
	Piping Plover					0.329	0.043	0.006	**22**
	Red Knot					0.329	0.043	0.006	**22**
	Ruddy Turnstone					0.329	0.043	0.006	**22**
	Sanderling					0.329	0.043	0.006	**22**
	Whimbrel					0.005	−0.154	−0.010	**12.3**
Marsh/wading birds	Least Bittern	0.025	−0.059	−0.015	**13.3**	0.029	0.029	−0.015	16.7
	Wood Stork	−0.011	−0.051	−0.025	10	−0.006	−0.061	−0.018	**9**
	Little Blue Heron	−0.011	−0.051	−0.025	**10**	0.002	−0.009	−0.017	13
	Tricolored Heron	−0.011	−0.051	−0.025	10	0.003	−0.090	−0.025	**9**
	Snowy Egret	−0.011	−0.051	−0.025	10	0.003	−0.090	−0.025	**9**
Terns	Gull-billed Tern	−0.109	−0.176	0.012	**8**	0.008	−0.088	−0.007	15.7
	Least Tern	−0.109	−0.176	0.012	**8**	0.029	0.029	0.004	19.7
	Black Skimmer	−0.109	−0.176	0.012	**8**	0.589	0.174	0.058	28
Passerines	Seaside Sparrow	−0.030	−0.157	−0.049	5.3	−0.006	−0.187	−0.033	**3.7**
	Painted Bunting	−0.015	−0.054	−0.007	12.7	−0.015	−0.054	−0.007	**12.3**
	Saltmarsh Sparrow					−0.006	−0.187	−0.033	**3.7**
Raptor	Swallow-tailed Kite	−0.027	−0.040	−0.012	12.7	−0.009	−0.111	−0.008	**9.7**
Reptiles	Diamondback Rattlesnake	−0.014	−0.067	−0.008	12	−0.014	−0.067	−0.008	**11**
	Diamondback Terrapin	−0.063	−0.140	−0.161	**5**	−0.001	−0.192	−0.021	6.7
Amphibians	Gopher Frog	−0.027	−0.037	−0.012	13.3	−0.015	−0.036	−0.008	**12**
	Dwarf Siren	−0.027	−0.037	−0.012	13.3	−0.027	−0.037	−0.012	**9.7**
Mammal	Marsh Rabbit	0.019	−0.043	−0.036	12.3	−0.015	−0.057	−0.010	**10**

Negative scores mean greater exposure and result in higher (closer to 1) ranks. Scores were normalized and then ranked, with average ranks shown for both nesting and foraging niches. Bold and underlined ranks are the higher of the two ranks for each species, which indicates the limiting niche under sea level rise

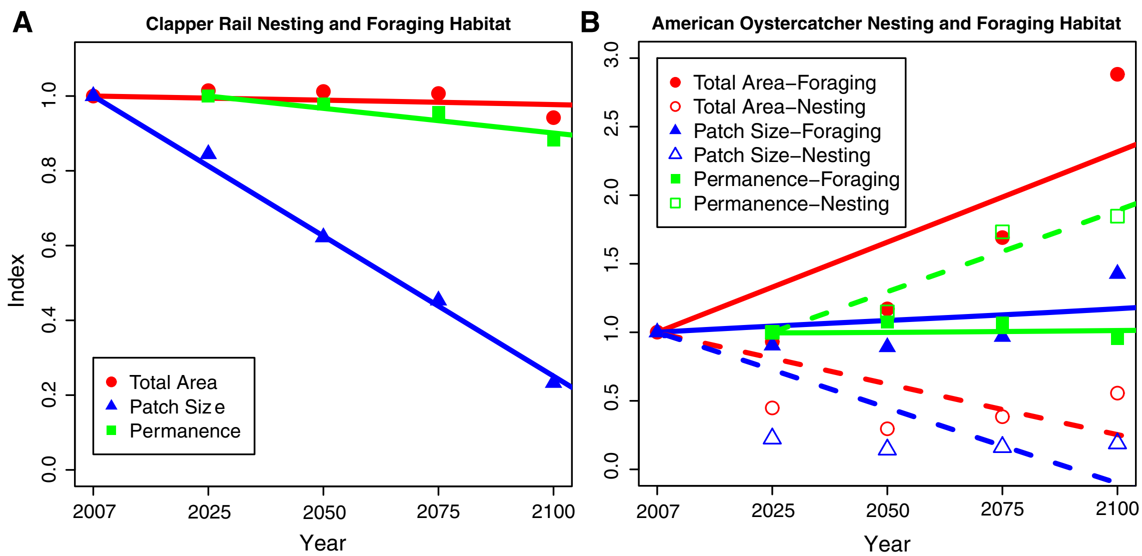

Fig. 2 Exposure to habitat change for Clapper Rail (**a**) and American Oystercatcher (**b**) from 2007–2100. Points are assessments of the metrics at each time period and the *slope of the lines* represent the slope of the best fit line to quantify the exposure score. More *negative slopes* indicate more exposure to habitat changes from sea level rise. In **b**, foraging habitat is *closed points/solid lines*, and nesting habitat is *open points/dashed lines*

from SLR was their use of salt marshes. The mean limiting rank for all species that used salt marshes was 7.0 ± 0.9 SE whereas the mean limiting rank for species that did not use salt marshes was 13.4 ± 1.3 SE. Most of the habitat change exposure from using salt marshes came from the reduction in patch size (Table 3), whereas exposure to salt marsh habitat area loss and permanence reduction were minimal (Fig. 2a). Those species that can use upland habitats (e.g., Diamondback Rattlesnake, Marsh Rabbit, Gopher Frog) were generally ranked lower because upland habitats were relatively stable given the large amount of area in the GA coastal region that will not be directly affected by sea level rise. Species that used primarily freshwater habitats (Black and King Rails, wading birds, and both amphibians) were also ranked lower because the rate of loss or alteration of these habitats was not as high as for saltwater habitats.

Species that nest exclusively on beaches (shorebirds, terns, and terrapins) had very high exposure to nesting niche changes as beach habitat was reduced in area, and became more fragmented (patch size reduction). Shorebirds and terns had very low ranks for foraging niche exposure, though, because their foraging habitat improved substantially for at least one of the metrics, especially the total area metric (Table 3; Fig. 2b). As salt marsh declined in area and was fragmented by sea level rise, tidal flats increased in area, which is a common foraging ground among these species. Diamondback Terrapins ranked highly in both nesting and foraging categories because they nest on beaches and forage in salt marshes.

Niche definitions validated relatively well with greater than 50 % of the buffered locations for most tested species falling within the defined fundamental niche. Diamondback Terrapin had the highest correct classification rate (96 %), followed by Painted Bunting (93 %), Diamondback Rattlesnake (64 %), Wilson's Plover (53 %), and wading bird colonies (47 %). Species that had niches that more often overlapped with known locations were those that had more broadly defined niches.

Discussion

Almost all of the species that we evaluated will be exposed to some habitat changes from SLR, but we identified species that relied heavily on salt marshes (some rails, marsh sparrows, and Diamondback Terrapins) as being among the most exposed to future habitat changes on the Georgia coast. Salt marshes are a globally important ecosystem that is threatened by a multitude of anthropogenic actions, but one of the primary threats is SLR because these marshes only exist at particular points in the tidal range (Adam 2002; Craft et al. 2009). The salt marshes in Georgia represent an important stronghold of this ecosystem: Georgia contains about 15 % of the remaining salt and brackish marsh habitat on the Atlantic coast of the United States but has only about 5 % of the total coastline length (USFWS 2007). Species that live in salt marshes are often specialists (Greenberg and Maldonado 2006), and specialization may be a primary reason that these species are vulnerable, as they may not be able to shift to other kinds of habitat as salt marsh habitat is lost and reconfigured. Therefore, these species may have low resiliency in addition to being exposed to high amounts of habitat change.

The loss and reconfiguration of salt marsh habitat with SLR are consistent with previous findings for the Georgia coast (Craft et al. 2009), but it is somewhat surprising that salt marsh habitats still appear to be so affected by SLR given that Version 6 of SLAMM predicts more conservative losses for salt marsh habitat. This newest version better accounts for variable sediment accretion across landcover types (allowing salt marshes to keep up with SLR more effectively), which leads to a reduction in the overall predicted loss of salt marsh. The prediction from the previous model version was up to 45 % loss of saltmarsh with 82 cm of SLR over 100 years (Craft et al. 2009), whereas the newest version only predicts up to 6 % loss with 1 m of SLR over 100 years. Despite this more positive outlook for areal loss, salt marsh species are still predicted to be among the most exposed to habitat changes, primarily because patches of salt marsh habitat will become much more fragmented (as measured by a reduction in patch size). This finding, that moderate areal loss could be accompanied by structural changes that degrade the quality of remaining habitat, highlights the importance of examining the mechanisms by which habitat change will occur so that specific management recommendations can be made. Salt marsh bird species are known to be sensitive to changes in habitat patch size, with lower species occupancy rates in smaller patches (Benoit and Askins 2002; Shriver et al. 2004). Because SLR will primarily impact salt marsh by reducing patch size, the integrity of large existing patches of salt marsh will be an important consideration in any management goal regarding conservation of salt marsh birds.

Species that relied on beach habitats were also exposed to large habitat changes. For the considered species, beaches are primarily used as nesting habitat, and the species that nest only on ocean beaches (Diamondback Terrapins, shorebirds, and terns) will have high exposure to nesting habitat changes through areal loss and fragmentation (i.e., patch size reduction). Beach habitats were relatively persistent in space compared to other habitat types. Beach habitat loss and fragmentation will happen primarily by reduction in beach width, which has been shown to affect shorebirds' habitat site selection, with wider beaches attracting more nesting and foraging activity (Gaines and Ryan 1988; Dugan et al. 2008). Wider beaches also reduce nest predation risk for beach-nesting turtles (Wetterer et al. 2007). Beach width, then, is an important consideration in any management aimed at protecting high quality nesting habitat for these species.

Two beach-nesting species in our study, Wilson's Plover and American Oystercatcher, already have low nesting success on Georgia beaches from other anthropogenic stressors like development and the rise in mesopredators such as raccoons (Bergstrom 1988; McGowan et al. 2005; Sabine et al. 2006), and the added threat of SLR may send populations of these species into steep declines. However, unlike species that primarily use salt marsh habitat, these beach-nesting species use other habitats (in addition to ocean beaches) as foraging grounds. Some of these other habitats, such as tidal flats, will likely increase in area due to sea level rise, especially as salt marsh becomes more fragmented, thus potentially making foraging activities easier for these species. There is evidence that nesting habitat, and not foraging habitat, is limiting some American Oystercatcher populations (Nol 1989, Davis et al. 2001), but it is not as well understood which habitats are limiting for Wilson's Plover and Diamondback Terrapin populations. However, given the large predicted changes to beach habitats, it is clear that nesting success for beach-nesting species will diminish as sea level rises, increasing likelihood of local extirpations. Conservation directed at improving nesting success for all beach-nesting species could use existing species-specific management plans, such as the successful American Oystercatcher recovery plan (Brown et al. 2008), as blueprints for broader efforts that encompass more species.

Through our exposure scoring scheme, we emphasized physical changes to habitat (area and patch size reduction, spatial shifting of habitat), but changes to the biological components of habitats could reduce the overall quality of remaining habitat even further (Didham et al. 2007). Increasing edge density could provide avenues of invasion for non-native species and predators (Paton 1994; Holway 2005). Changes in tidal flooding regimes could affect the availability of aquatic prey species (Galbraith et al. 2002). Some of our metrics will affect some species more than others, for instance, changes to permanence may matter more to migratory birds than species that do not leave their habitats, especially those with the same nesting and foraging habitat. It is also possible that some of the species that we have studied will exhibit positive responses to negative trends in our metrics. For example, a species may thrive in fragmented habitat because of increased access to mates, prey, etc. Investigations of how other variables could affect the quality of remaining habitat are some of the next steps for determining relative sensitivity to SLR. These studies should focus on mechanisms whereby habitat changes affect demographic rates of populations (Lampila et al. 2005). For example, studies on how reduction in patch size affects populations should investigate variable survival, reproductive rates, or body condition indices to uncover mechanisms behind possible population declines associated with fragmentation. It will also be important to identify the limiting habitat types within a species niche (e.g., a species may be able to use brackish and salt marsh, but salt marshes are population sources and brackish marshes are population sinks), and which part of the species life cycle is limiting to population growth (e.g., if a species is limited by nesting habitat, losses of foraging habitat due to SLR will not affect the population as adversely as losses to nesting habitat would).

SLR models can also be improved with respect to both spatial and landcover class resolution. Poorer niche validation rates (for Wilson's Plover and wading bird colonies) were likely due to the low resolution (28-m cell size) of the SLAMM datasets that may miss small habitat features or misclassify edge habitats. Using aerial imagery to visually verify the locations for Wilson's Plover and wading bird colonies that were not predicted by the SLAMM niches showed that a majority of these locations were indeed on edges between habitats (e.g., edges between beaches and upland habitat for Wilson's Plover) or were on small habitat features (e.g., wading bird colonies in small groves of trees in the middle of open water). If species rely heavily on these fine-scale habitat features, the model may not adequately represent changes to the fundamental niche of the species. We have assigned very broad definitions of species niches and this may overestimate the amount of habitat available to some species. For example, we assigned the niche of Black Rails as brackish and tidal freshwater marshes, but only a small subset of these marshes with high elevations and certain species of grasses are usable habitat for Black Rails. Similarly, we assigned Gopher Frog nesting habitat to be all freshwater swamps, but breeding sites are typically ephemeral aquatic sites within forested wetlands (Greenberg 2001). This kind of detail on landcover type is not available for a model like SLAMM because it is not known how every unique community will respond to SLR (e.g., no information on accretion, and erosion rates for high marsh). Obviously, more detailed data will make for more detailed predictions, but there is general consistency in the predictions between this version of SLAMM and previous versions. Salt marsh still experiences the most loss relative to other landcover types, even if that loss is lower in magnitude (Craft et al. 2009), indicating that the patterns we focus on here will be maintained even with more detailed models.

Although we have a long way to go to adequately assess species vulnerability to SLR, we present a deductive, broad-scale model that provides a first step toward prioritizing species on which to focus conservation resources. The model results indicated that species using salt marsh and beach habitats are most exposed to habitat changes brought about by SLR; thus, maintenance of these habitats may be an important consideration in conservation plans for these species. These results and management implications likely apply to similar coastal systems such as the northern Atlantic coast of Florida, and coastal South Carolina, where SLR will have similar effects on coastal habitats because of the common geological features and processes within this portion of the Georgia Bight (Hayes 1994). Additionally, the model can show specific salt marsh and beach locations where species may have strongholds in the future and could be potential preservation targets for managers. In order for salt marshes to persist, they must be able to migrate further inland. Man-made obstructions, such as sea walls and bulkheads, can be absolute barriers. In other areas, where inland migration is possible, it can simply take long periods of time for conversions to occur between forests and marshes (Brinson et al. 1995). A gradual conversion from brackish and tidal influenced fresh marshes to salt marshes will be the easiest mode of salt marsh migration (Brinson et al. 1995), and locations with extensive area to allow this movement will likely have high conservation value. On the Georgia coast, the largest such location is the Altamaha estuary where the full suite of tidal marsh communities are contiguous (Fig. 1). Here, the estuary has experienced little (recent) development that would impede marsh migration, and a large proportion of the estuary is owned by state and federal governments, as well as The Nature Conservancy. Beach habitats will be best preserved in areas with high rates of sedimentation from both estuarine and oceanic sources. Beaches will also be maintained in developed areas, which may attract nesting activities despite these being locations where nests are particularly vulnerable, possibly leading to the creation of an ecological trap (Sabine et al. 2006; Peters and Otis 2006). The interaction between pressures from SLR and coastal development will likely play a large role in the future of these species, as many of the habitats with the most SLR exposure are also those that are most threatened by development. As we struggle with how to allocate resources to coastal communities (both human and natural), tools that help managers to prioritize those species and communities most vulnerable to SLR will be invaluable.

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References

Adam P (2002) Saltmarshes in a time of change. Environ Conserv 29:39–61

Bender DJ, Contreras TA, Fahrig L (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. Ecology 79:517–533

Benoit LK, Askins RA (2002) Relationship between habitat area and the distribution of tidal marsh birds. Wilson Bull 114:314–323

Benscoter AM, Reece JS, Noss RF, Brandt LA, Mazzotti FJ, Romañach SS, Watling JI (2013) Threatened and endangered subspecies with vulnerable ecological traits also have high susceptibility to sea level rise and habitat fragmentation. PLoS ONE 8:e70647

Bergstrom PW (1988) Breeding biology of Wilson's Plovers. Wilson Bull 100:25–35

Bertness MD, Ewanchuk PJ, Silliman BR (2002) Anthropogenic modification of New England salt marsh landscapes. Proc Natl Acad Sci 99:1395–1398

Bivand RS, Pebesma EJ, Gomez-Rubio V (2008) Applied spatial data analysis with R. Springer, New York. http://www.asdar-book.org/

Brinson MM, Christian RR, Blum LK (1995) Multiple states in the sea-level induced transition from terrestrial forest to estuary. Estuaries 18:648–659

Brittain RA, Craft CB (2012) Effects of sea-level rise and anthropogenic development on priority bird species habitats in coastal Georgia, USA. Environ Manag 49:473–482

Brown S, Simons T, Schulte S, Sanders F, Winn B, Truitt B, Wilke A, Johnston S, Melvin S, the American Oystercatcher Working Group (2008) A business plan for conservation of the American Oystercatcher: a ten year plan to secure a keystone coastal species. Submitted to the National Fish and Wildlife Foundation, Manomet MA. https://www.manomet.org/sites/default/files/publications_and_tools/NFWF_AMOY_BusinessPlan.pdf

Burger J (1982) The role of reproductive success in colony-site selection and abandonment in Black Skimmers (*Rynchops niger*). Auk 99:109–115

Clough JS, Park RA, Fuller R (2010) SLAMM 6 Beta Technical Documentation: Release 6.0.1 Beta, pp 1–51. Warren Pinnacle Consulting, Inc., Warren, Vermont

Craft C, Clough J, Ehman J, Joye 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

Davis MB, Simons TR, Groom MJ, Weaver JL, Cordes JR (2001) The breeding status of the American Oystercatcher on the east coast of North America and breeding success in North Carolina. Waterbirds 24:195–202

Dawson TP, Jackson ST, House JI, Prentice IC, Mace GM (2011) Beyond predictions: biodiversity conservation in a changing climate. Science 332:53–58

Didham RK, Tylianakis JM, Gemmell NJ, Rand TA, Ewers RM (2007) Interactive effects of habitat modification and species invasion on native species decline. Trends Ecol Evol 22:489–496

Dugan JE, Hubbard DM, Rodil IF, Revell DL, Schroeter S (2008) Ecological effects of coastal armoring on sandy beaches. Mar Ecol 29:160–170

Fahrig L (1997) Relative effects of habitat loss and fragmentation on population extinction. J Wildl Manag 61:603–610

Gaines EP, Ryan MR (1988) Piping plover habitat use and reproductive success in North Dakota. J Wildl Manag 52:266–273

Galbraith H, Jones R, Park R, Clough J, Herrod-Julius S, Harrington B, Page G (2002) Global climate change and sea level rise: potential losses of intertidal habitat for shorebirds. Waterbirds 25:173–183

Georgia Department of Natural Resources. 2013. Nongame conservation section biotics database. Wildlife Resources Division, Social Circle, GA. http://www.georgiawildlife.com. Accessed 9, 2012

Greenberg CH (2001) Spatio-temporal dynamics of pond use and recruitment in Florida gopher frogs (*Rana capito aesopus*). J Herpetol 35:74–85

Greenberg R, Maldonado JE (2006) Diversity and endemism in tidal-marsh vertebrates. Stud Avian Biol 32:32–53

Hanski I (1999) Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87:209–219

Hayes MO (1994) The Georgia bight barrier system. In: Davis RA Jr (ed) Geology of holocene barrier island systems. Springer, New York, pp 233–304

Hijmans RJ (2013). Raster: Geographic data analysis and modeling. R package version 2.1–49. http://CRAN.R-project.org/package=raster

Holway DA (2005) Edge effects of an invasive species across a natural ecological boundary. Biol Conserv 121:561–567

Lampila P, Monkkonen M, Desrochers A (2005) Demographic responses by birds to forest fragmentation. Conserv Biol 19:1537–1546

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton, NJ

McGarigal K, Cushman SA, Ene E (2012) FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. http://www.umass.edu/landeco/research/fragstats/fragstats.html

McGowan CP, Simons TR, Golder W, Cordes J (2005) A comparison of American Oystercatcher reproductive success on barrier beach and river island habitats in coastal North Carolina. Waterbirds 28:150–155

McGranahan G, Balk D, Anderson B (2007) The rising tide: assessing the risks of climate change and human settlements in low elevation coastal zones. Environ Urban 19:17–37

Nicholls RJ, Hoozemans FMJ, Marchand M (1999) Increasing flood risk and wetland losses due to global sea-level rise: regional and global analyses. Glob Environ Change 9:69–87

Nol E (1989) Food supply and reproductive performance of the American Oystercatcher in Virginia. Condor 91:429–435

Paton PW (1994) The effect of edge on avian nest success: how strong is the evidence? Conserv Biol 8:17–26

Peters KA, Otis DL (2006) Shorebird roost-site selection at two temporal scales: is human disturbance a factor? J Appl Ecol 44:196–209

Prugh LR, Hodges KE, Sinclair AR, Brashares JS (2008) Effect of habitat area and isolation on fragmented animal populations. Proc Natl Acad Sci USA 105:20770–20775

Sabine JB, Schweitzer SH, Meyers JM (2006) Nest fate and productivity of American Oystercatchers, Cumberland Island National Seashore, Georgia. Waterbirds 29:308–314

Sheridan CM, Spotila JR, Bien WF, Avery HW (2010) Sex-biased dispersal and natal philopatry in the diamondback terrapin, *Malaclemys terrapin*. Mol Ecol 19:5497–5510

Shriver WG, Hodgman TP, Gibbs JP, Vickery PD (2004) Landscape context influences salt marsh bird diversity and area requirements in New England. Biol Conserv 119:545–553

Soberon J (2007) Grinnellian and Eltonian niches and geographic distributions of species. Ecol Lett 10:1115–1123

Turner BL, Kasperson RE, Matson PA, McCarthy JJ, Corell RW, Christensen L, Eckley N, Kasperson JX, Luers A, Martello ML (2003) A framework for vulnerability analysis in sustainability science. Proc Natl Acad Sci USA 100:8074–8079

US Fish and Wildlife Service (USFWS) (2007) National Wetlands Inventory website. U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC. http://www.fws.gov/wetlands/

Van de Pol M, Ens BJ, Heg D, Brouwer L, Krol J, Maier M, Exo KM, Oosterbeek K, Lok T, Eising CM, Koffijberg K (2010) Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? J Appl Ecol 47:720–730

Wetterer JK, Wood LD, Johnson C, Krahe H, Fitchett S (2007) Predaceous ants, beach replenishment, and nest placement by sea turtles. Environ Entomol 36:1084–1091

Woodrey MS, Rush SA, Cherry JA, Nuse BL, Cooper RJ, Lehmicke AJJ (2012) Understanding the potential impacts of global climate change on marsh birds in the Gulf of Mexico region. Wetlands 32:35–49