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Mapping Habitat Quality and Threats for Eastern Black Rails (*Laterallus jamaicensis jamaicensis*)

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Abstract.—Documenting the spatial distribution of high-quality habitat patches, the distributions of threats and protected areas, and the vulnerability of habitat patches to changes in environmental conditions is vital for conservation of rare species. Range-wide species distribution models were developed for Black Rails (*Laterallus jamaicensis*) to predict the distribution of high-quality habitat patches for breeding Eastern Black Rails (*L. j. jamaicensis*). Overlay analyses were conducted to quantify the distribution of habitat relative to human development and existing protected areas, as well as the vulnerability of the best habitat to future sea level rise. The amount of high-quality habitat varied among states (0.4-7.6% of area) and was relatively rare throughout the subspecies' range (3.3% of area). Human development was common but the amount varied spatially among states (2.2-15.3% of area). Higher-quality breeding habitat was more common on federal lands (9.4% of area) and protected areas (6.4% of area), yet 33-42% of the highest-quality habitat patches were vulnerable to sea level rise of 0.61-1.83 m. Our results imply that even though many of the highest-quality habitat patches may be less likely sites for development they are often vulnerable to rising seas, and thus maintenance of existing high-quality habitat patches may be difficult without management that takes into account the likelihood of future inundation. *Received 13 August 2020, accepted 15 July 2021.*

Key words.—habitat model, habitat suitability, spatially-explicit model, species distribution model, wetland birds

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Habitat loss and degradation is a common result of human modification of natural landscapes that contributes to population decline and extinction risk for many plants and animals (Norris 2008; Sodhi *et al.* 2009; Potts *et al.* 2010; Martinuzzi *et al.* 2015). Documenting the spatial distribution of high-quality habitat, as well as the distributions of anthropogenic threats and existing protected areas, is therefore vital for efforts to conserve rare species over large regions (Scott *et al.* 1993, 2002). Effective habitat conservation over time also requires an understanding of the vulnerability of high-quality habitat patches to temporal changes in the environment, especially given recent large-scale changes in environmental conditions that affect many species (Franklin 2010; Harrity *et al.* 2020). Yet, a basic understanding of the distribution and vulnerability of high-quality habitat is lacking for many rare species. These knowledge gaps hinder the implementation of conservation and monitoring efforts strategically across large landscapes to aid recovery of rare but widely distributed species. Describing the distribution of high-quality habitat and its vulnerability to future change thus provides important information needed to plan cost-effective conservation over large scales to facilitate species persistence.

Many secretive marsh birds are species of conservation concern that have been negatively affected by large-scale degradation of wetlands (Eddleman *et al.* 1988; Conway and Droege 2006; Conway and Gibbs 2011; Stevens and Conway 2020a). Black Rails (*Laterallus jamaicensis*) are among the rarest secretive marsh birds in North America (Eddleman *et al.* 1994; Conway and Sulzman 2007; Steidl *et al.* 2013), and their breeding range has declined considerably in recent decades (> 70%; Stevens and Conway 2020b; Stevens and Conway 2020c). A recent range-wide assessment of the distribution of breeding Black Rails reported that occupancy was negatively impacted by human development and modification of wetland hydrology across multiple spatial scales (Stevens and Conway 2020a). However, the Black Rail has a large geographic distribution and both habitat relationships and anthropogenic threats likely vary among regions. The Eastern subspecies of Black Rail (*L. j. jamaicensis*) persists in a heavily fragmented and human altered landscape (Watts 2016) and was recently listed as threatened under the U.S. Endangered Species Act (U.S. Department of Interior 2020). Consequently, a broad-scale spatial assessment of habitat quality and threats focused explicitly on the eastern subspecies is warranted and will contribute to habitat conservation and monitoring efforts for this subspecies.

We used species distribution models recently developed using data collected over the range of the Black Rail within the contiguous USA (hereafter referred to as range-wide; Stevens and Conway 2020a; Stevens and Conway 2020b) to predict habitat suitability for breeding Black Rails throughout coastal areas of the eastern USA. Specifically, the objectives of this study were: (1) describe the amount and location of high-quality Black Rail breeding habitat in the eastern USA; (2) map the distribution of anthropogenic threats related to human development that likely constrain the breeding distribution of Eastern Black Rails; (3) overlay the distribution of high-quality breeding habitat (in #1 above) with the protected status of the landscape to better understand vulnerability of habitat patches to future development; and (4) describe the vulnerability of high-quality habitat to plausible scenarios of future sea-level rise. Collectively, these results will inform both the existing status and conservation potential of breeding habitat for Eastern Black Rails.

METHODS

We used a range-wide species distribution model for Black Rails (Stevens and Conway 2020b; Stevens and Conway 2020c) to describe spatial heterogeneity in breeding habitat quality for Eastern Black Rails. Our analyses used the spatially-explicit Black Rail distribution model developed by Stevens and Conway (2020c), which was a raster representation of a predictive multi-scale occupancy model that was built using spatially-extensive field survey data (2,885 call-broadcast surveys conducted from 2000-2012; Stevens and Conway 2020b). All details of statistical and spatial model development are described in Stevens and Conway (2020a; 2020b; 2020c), and the resulting model predicts Black Rail occupancy probability during the breeding season (as an indicator of breeding season habitat quality) at a 30-m pixel resolution over the extent of the Black Rail breeding range within the contiguous USA (i.e., the breeding range as defined by the U.S. Geological Survey (USGS) Gap Analysis Project (GAP) (USGS-GAP 2011)). For the purposes of this paper, we limited our spatial analysis of habitat to the segment of the GAP breeding range located along the Atlantic and Gulf Coasts of the U.S. (i.e., excluding interior populations of Eastern Black Rails located in non-coastal states; Fig. 1), and hereafter refer to this region as the coastal range of the Eastern Black Rail. Within this coastal range, all occupancy predictions were limited to individual spatial pixels located within 500 m of existing emergent wetlands in order to accommodate potential location errors in the accuracy of existing wetland layers (i.e., excluding areas without emergent wetlands based on National Wetland Inventory data (NWI); classification described by Cowardin *et al.* 1979). Our analyses provided predictions of habitat quality at a fine spatial resolution over a large extent for the Eastern Black Rail, where habitat quality at each pixel was a function of habitat and disturbance covariates demonstrated to influence occupancy of Black Rails across their breeding range within the contiguous USA (i.e., amount of scrub-shrub wetland, low-intensity human development, and artificially-flooded wetland habitats measured over their optimal spatial extents; Stevens and Conway 2020b). We conducted all analyses within ArcMap 10.5.1 (ESRI, Redlands, California, USA), or using the raster package (Hijmans and van Etten 2012) within program R version 4.0.1 (R Core Team 2020).

We characterized the distribution of high-quality habitat patches and the anthropogenic threats to habitat across the Eastern Black Rail breeding range along the Atlantic and Gulf Coasts (Fig. 1), and on a state-by-state basis within this region. To describe the distribution of habitat quality, we assessed the empirical distribution of predicted habitat quality (occupancy probability) among all pixels (i.e., across the study area; Fig. 1), including summary statistics (mean, median, and SD calculated across the study area) and the proportion of area within each state covered by high-quality habitat based on 3 metrics: proportion of pixels > median value, proportion of pixels > 75th percentile of values, and proportion of pixels > 1-SD above the mean value (hereafter referred to as highest-quality habitat). We visualized the highest-quality habitat patches in each area to identify habitat hotspots by mapping the individual pixels whose occupancy probability was > 1-SD above the mean value of all pixels across the Eastern Black Rail's coastal range.

We assessed the distribution of anthropogenic threats related to human development throughout the Eastern Black Rail's coastal range by using the most recently developed National Landcover Database (2016 NLCD; Jin *et al.* 2019; Homer *et al.* 2020). We used the 2016 NLCD database to characterize all pixels within

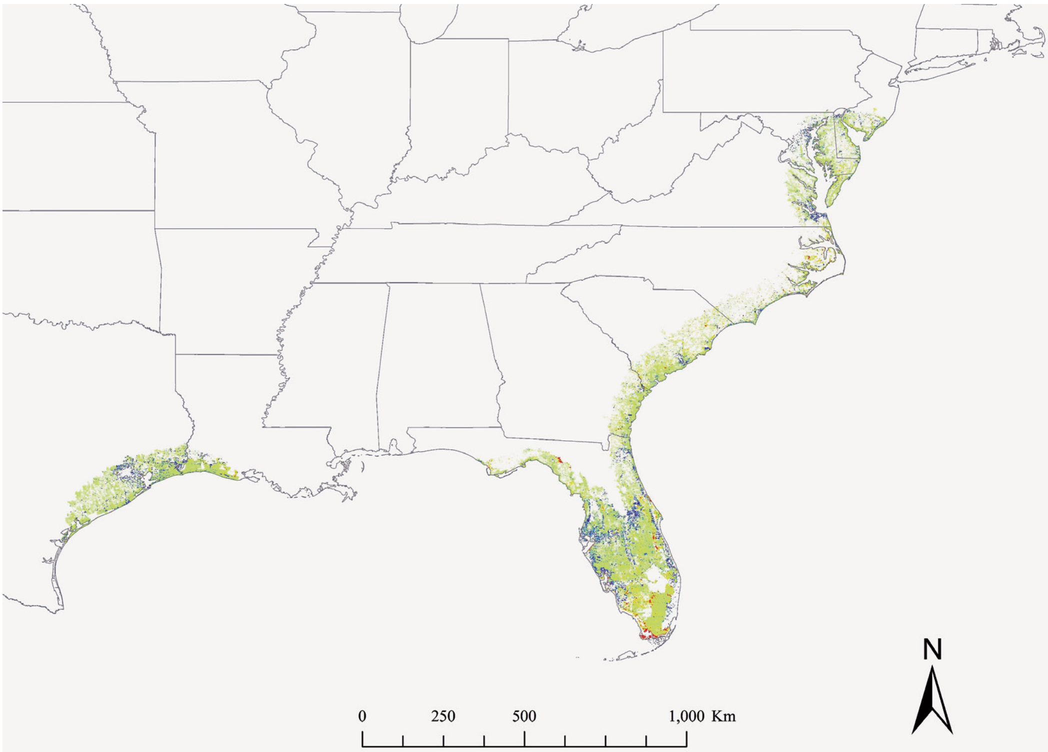

Figure 1. Map of predicted habitat quality for breeding Eastern Black Rails (*Laterallus jamaicensis jamaicensis*) in coastal portions of the United States. Cooler colors represent poorer habitat quality and warmer colors represent better habitat quality (i.e., greater probability of occupancy).

the study region as either developed (i.e., classified as any of the four NLCD development categories) or not developed. We also used the 2016 NLCD Landcover Change Index database to identify pixels that changed from not-developed to developed (or vice versa) during the 2001 - 2016 period, and visually mapped developed areas relative to the highest-quality breeding habitat for Black Rails. These two datasets provided the most recent assessment of human development over the entire USA, and they also provide a description of which areas have been modified during the 21st century. In addition to visual assessment of anthropogenic development, we also calculated the proportional coverage of these metrics throughout the Eastern Black Rail's coastal range to characterize the magnitude of human development across the region.

To compare the distribution of breeding habitat in areas that are currently protected relative to the entire coastal range, we calculated the summary metrics described above for pixels residing in areas that are unlikely to be developed. First, we calculated habitat quality for pixels residing in lands that are federally owned and controlled by the following agencies: U.S. Department of the Interior: Bureau of Land Management, Bureau of Reclamation, National Park Service, and U.S. Fish and Wildlife Service; the U.S. Department of Agriculture, Forest Service; and U.S. Department of Defense (USA_Federal_Lands_Append dataset, updated 6-5-2020, published by ESRI, Redlands, California). Because federal ownership alone does not include many state-, local-, and privately-owned lands that are unlikely to be developed (e.g., state and local parks, private lands enrolled in conservation easements), we also described habitat quality for pixels residing within areas considered to be protected by the U.S. Department of the Interior, Geological Survey Protected Areas database (PAD 2.0; USGS-GAP 2018). Specifically, we categorized lands as protected if the Protected Areas database labelled them as federal lands, state and local parks, conservation areas, and nature preserves (so-called "fee" and "designated" lands), marine protected areas, or private lands enrolled in conservation easement programs. This facilitated assessment of habitat quality for Eastern Black Rails relative to multiple definitions of protected status.

Lastly, we used the National Oceanic and Atmospheric Association (NOAA) sea-level rise projection models (NOAA 2020) to describe the vulnerability of existing habitat patches to plausible future changes in sea level. Specifically, we mapped the 0.61 m, 1.22 m, and 1.83 m sea-level rise projections onto the distributions of the highest-quality habitat patches to describe the vulnerability of these sites to several plausible scenarios of sea level rise. These sea-level rise projections are spatial but not temporal in scale. Specifically, they forecast which spatial locations would be affected by sea level rise of different magnitudes (e.g., 0.61 m, 1.22 m, 1.83 m) without predicting when a given magnitude is likely to occur.

RESULTS

High-quality breeding habitat for Eastern Black Rails was relatively rare across the subspecies' coastal range (Table 1, Figs. 1-2; online Appendix Figs. A1-A3). Approximately 3% of the pixels (1 pixel = 900 m^2 = 0.09 ha) had predicted occupancy probabilities greater than 1-SD larger than the mean of all pixels across the study area (Table 1), and the model predicted that the largest proportion of highest-quality breeding habitat (> 1-SD larger than mean for entire study area) was located in North Carolina, South Carolina, and Florida, USA. Development was common within the Eastern Black Rail's coastal range, where approximately 11% of the area was categorized as developed, but only 2% changed development status since 2001 (Table 2). Both the amount of development and recency of development varied spatially among states (Table 2; online Appendix Figs. A4-A28). Throughout the Eastern Black Rail's coastal range, higher-quality breeding habitat was more common on federal lands and protected areas (Table 1). For example, the highest-quality breeding habitat represented approximately 9% and 6% of federal lands and protected areas (as opposed to 3% of the entire area). However, current hotspots of the highest-quality breeding habitat in most states were vulnerable to potential rises in sea level (i.e., area covered by rising seas; online Appendix Figs. A4-A8), and this result was consistent regardless of the magnitude of change (online Appendix Figs. A4-A28). For example, approximately 33 - 42% of the highest quality habitat across the study area was in locations covered by the sea level rise projections (proportional coverage: 0.61 m = 0.330, 1.22 m = 0.394, 1.83 m = 0.418).

New Jersey

Average probability of Eastern Black Rail breeding season occupancy for New Jersey (0.240) was similar to that for the entire coastal range (0.242), although New Jersey had a higher proportion of habitat that was better than the median (0.378) and better than the 75th percentile (0.328) of habitat quality (Table 1). The highest-quality habitat was rare in New Jersey (proportionally, 50% less common compared to the study area). The proportion of Eastern Black Rail breeding habitat located on federal lands and protected areas that was better than the median or better than the 75th percentile was similar to or less than the proportion located at all pixels within the state (i.e., similar or worse than for all of New Jersey) and was similar to comparable sites across the Eastern Black Rail's entire coastal range (i.e., similar to all federal lands and protected areas; Table 1). The proportion of highest-quality breeding habitat for Eastern Black Rails on federal lands and protected areas was larger than for all pixels within New Jersey, but was substantially less than comparable sites across the coastal range. The proportion of pixels categorized as developed was similar to the Eastern Black Rail's entire coastal range, as was the recency of development (Table 2). Current hotspots of the highest-quality habitat in New Jersey appear to be located away from developed sites, but these hotspots are vulnerable to potential changes in sea level (online Appendix Fig. A4).

Delaware

Average probability of Eastern Black Rail breeding season occupancy across Delaware (0.236) was similar to that for the entire coastal range (0.242), as was the proportion of habitat that was better than the median (0.301; Table 1). However, the proportion of breeding habitat that was better than the 75th percentile (0.209) and the highest-quality habitat (0.005) were rare in Delaware, and were less common as compared to the entire coastal range. The proportion of Eastern Black Rail breeding habitat located on federal lands and protected areas that was better than the median or better than the 75th percentile

Table 1. Summary statistics of predicted breeding season occupancy probability for Eastern Black Rails (*Laterallus jamaicensis jamaicensis*). Statistics include the mean, median, and standard deviation (SD) of all pixel values (1 pixel = 900 m^2 = 0.09 ha), the proportion of pixels whose values were greater than the range-wide median (> 50%) or 75th percentile (> 75%), and the proportion of pixel values >1-SD larger than the range-wide mean occupancy probability (> 1-SD). Each metric was calculated over the species' entire coastal range and for each state (all sites), as well as within federally owned land and protected areas within those spatial extents. State-specific metrics that are higher (+) or lower (-) than the range-wide values are indicated via superscript.

Spatial extent	Mean	Median	SD	> 50%	> 75%	> 1-SD
Species entire coastal range						
All sites	0.242	0.254	0.058	0.301	0.250	0.033
Federal lands	0.263	0.254	0.051	0.398	0.357	0.094
Protected areas	0.260	0.254	0.041	0.357	0.309	0.064
New Jersey						
All sites	0.240$^{(-)}$	0.254	0.052$^{(-)}$	0.378$^{(+)}$	0.328$^{(+)}$	0.016$^{(-)}$
Federal lands	0.252$^{(-)}$	0.254	0.030$^{(-)}$	0.298$^{(-)}$	0.265$^{(-)}$	0.018$^{(-)}$
Protected areas	0.254$^{(-)}$	0.254	0.029$^{(-)}$	0.372$^{(+)}$	0.328$^{(+)}$	0.023$^{(-)}$
Delaware						
All sites	0.236$^{(-)}$	0.254	0.054$^{(-)}$	0.301	0.209$^{(-)}$	0.005$^{(-)}$
Federal lands	0.249$^{(-)}$	0.254	0.050$^{(-)}$	0.299$^{(-)}$	0.244$^{(-)}$	0.042$^{(-)}$
Protected areas	0.248$^{(-)}$	0.254	0.038$^{(-)}$	0.341$^{(-)}$	0.242$^{(-)}$	0.010$^{(-)}$
Maryland						
All sites	0.237$^{(-)}$	0.254	0.053$^{(-)}$	0.177$^{(-)}$	0.136$^{(-)}$	0.009$^{(-)}$
Federal lands	0.244$^{(-)}$	0.254	0.042$^{(-)}$	0.183$^{(-)}$	0.142$^{(-)}$	0.009$^{(-)}$
Protected areas	0.249$^{(-)}$	0.254	0.034$^{(-)}$	0.183$^{(-)}$	0.145$^{(-)}$	0.014$^{(-)}$
Virginia						
All sites	0.237$^{(-)}$	0.254	0.057$^{(-)}$	0.359$^{(+)}$	0.262$^{(+)}$	0.010$^{(-)}$
Federal lands	0.223$^{(-)}$	0.254	0.071$^{(+)}$	0.352$^{(-)}$	0.284$^{(-)}$	0.012$^{(-)}$
Protected areas	0.251$^{(-)}$	0.254	0.032$^{(-)}$	0.279$^{(-)}$	0.203$^{(-)}$	0.011$^{(-)}$
North Carolina						
All sites	0.252$^{(+)}$	0.254	0.055$^{(-)}$	0.470$^{(+)}$	0.419$^{(+)}$	0.076$^{(+)}$
Federal lands	0.262$^{(-)}$	0.255	0.055$^{(+)}$	0.552$^{(+)}$	0.514$^{(+)}$	0.132$^{(+)}$
Protected areas	0.262$^{(+)}$	0.255	0.047$^{(+)}$	0.520$^{(+)}$	0.467$^{(+)}$	0.104$^{(+)}$
South Carolina						
All sites	0.250$^{(+)}$	0.254	0.045$^{(-)}$	0.488$^{(+)}$	0.419$^{(+)}$	0.035$^{(+)}$
Federal lands	0.252$^{(-)}$	0.254	0.051	0.497$^{(+)}$	0.443$^{(+)}$	0.059$^{(-)}$
Protected areas	0.254$^{(-)}$	0.254	0.044$^{(+)}$	0.449$^{(+)}$	0.393$^{(+)}$	0.042$^{(-)}$
Georgia						
All sites	0.251$^{(+)}$	0.254	0.039$^{(-)}$	0.321$^{(+)}$	0.269$^{(+)}$	0.021$^{(-)}$
Federal lands	0.254$^{(-)}$	0.254	0.029$^{(-)}$	0.267$^{(-)}$	0.237$^{(-)}$	0.023$^{(-)}$
Protected areas	0.254$^{(-)}$	0.254	0.036$^{(-)}$	0.328$^{(-)}$	0.274$^{(-)}$	0.025$^{(-)}$
Florida						
All sites	0.241$^{(-)}$	0.254	0.064$^{(+)}$	0.302$^{(+)}$	0.271$^{(+)}$	0.046$^{(+)}$
Federal lands	0.273$^{(+)}$	0.254	0.053$^{(+)}$	0.477$^{(+)}$	0.444$^{(+)}$	0.135$^{(+)}$
Protected areas	0.265$^{(+)}$	0.254	0.042$^{(+)}$	0.399$^{(+)}$	0.367$^{(+)}$	0.088$^{(+)}$
Louisiana						
All sites	0.246$^{(+)}$	0.254	0.048$^{(-)}$	0.189$^{(-)}$	0.174$^{(-)}$	0.021$^{(-)}$
Federal lands	0.247$^{(-)}$	0.254	0.042$^{(-)}$	0.063$^{(-)}$	0.057$^{(-)}$	0.001$^{(-)}$
Protected areas	0.244$^{(-)}$	0.254	0.049$^{(+)}$	0.069$^{(-)}$	0.062$^{(-)}$	0.004$^{(-)}$
Texas						
All sites	0.234$^{(-)}$	0.254	0.059$^{(+)}$	0.184$^{(-)}$	0.143$^{(-)}$	0.004$^{(-)}$
Federal lands	0.248$^{(-)}$	0.254	0.032$^{(-)}$	0.121$^{(-)}$	0.097$^{(-)}$	0.003$^{(-)}$
Protected areas	0.246$^{(-)}$	0.254	0.040$^{(-)}$	0.172$^{(-)}$	0.142$^{(-)}$	0.011$^{(-)}$

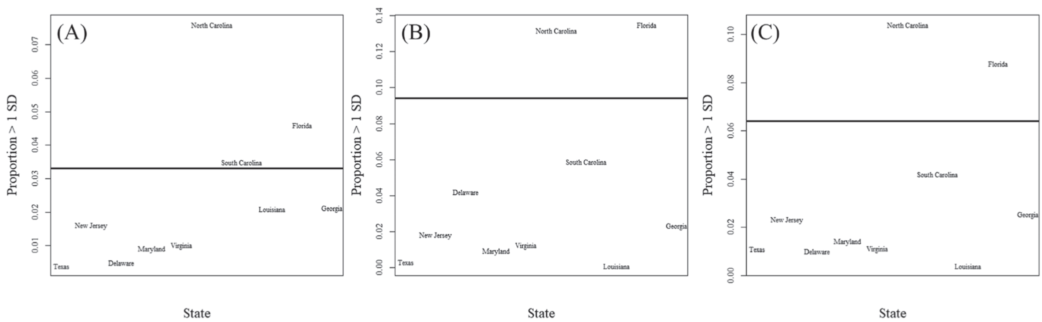

Figure 2. The proportion of 30-m pixel values in each state that were > 1 standard deviation higher than the range-wide mean occupancy probability for Eastern Black Rails (*Laterallus jamaicensis jamaicensis*), as compared to the same metric calculated range-wide (solid lines). Each metric was calculated over the entire coastal range of Eastern Black Rails and for each state (A), as well as within federally owned land (B) and protected areas (C) within those spatial extents.

was similar to or larger than the proportion at all pixels within the state but smaller as compared to the entire coastal range (i.e., worse than for all federal lands and protected areas; Table 1). The proportion of highest-quality Eastern Black Rail breeding habitat on federal lands and protected areas was larger than for all sites within state, but was substantially less as compared to the entire coastal range. The proportion of pixels categorized as developed (0.153) was greater than for the entire coastal range, as was the recency of development (Table 2). Current hotspots of the highest-quality habitat for Eastern Black Rails in Delaware appear to be located away from developed sites, but these hotspots are vulnerable to changes in sea level (online Appendix Fig. A4).

MARYLAND

Average probability of Eastern Black Rail breeding season occupancy across Maryland (0.237) was similar to that of the entire coastal range (0.242), but the proportion of habitat patches that were better than the median (0.177), better than the 75th percentile (0.133), or the highest-quality habitat (0.009) were less common in Maryland as compared to the entire coastal range. The proportion of Eastern Black Rail breeding habitat located on federal lands and protected areas that was better than the median, better than the 75th percentile, or the highest-quality habitat was similar to or slightly larger than the proportion at all pixels within the state, but was considerably smaller as compared to the coastal range (i.e., worse

Table 2. Proportion of 30-m pixels that are currently developed (2016 National Landcover database; Jin *et al.* 2019; Homer *et al.* 2020; Proportion developed) and proportion that changed from not-developed to developed (or vice versa) during 2001-2016 (2016 landcover change index data; Proportion changed), calculated for the species' entire coastal range and for each state. State-specific metrics that are higher (+) or lower (-) than the range-wide values are indicated by superscript.

Extent	Proportion developed	Proportion changed
Species' entire coastal range	0.109	0.016
New Jersey	0.113$^{(+)}$	0.010$^{(-)}$
Delaware	0.153$^{(+)}$	0.028$^{(+)}$
Maryland	0.113$^{(+)}$	0.008$^{(-)}$
Virginia	0.123$^{(+)}$	0.010$^{(-)}$
North Carolina	0.079$^{(-)}$	0.008$^{(-)}$
South Carolina	0.082$^{(-)}$	0.010$^{(-)}$
Georgia	0.063$^{(-)}$	0.009$^{(-)}$
Florida	0.123$^{(+)}$	0.017$^{(+)}$
Louisiana	0.022$^{(-)}$	0.003$^{(-)}$
Texas	0.126$^{(+)}$	0.029$^{(+)}$

than for all federal lands and protected areas; Table 1). The proportion of the state categorized as developed (0.113) was comparable to the proportion for the entire coastal range, but the proportion of recently development areas (0.008) was smaller (Table 2). Current hotspots of the highest-quality habitat in Maryland appear to be located east of Chesapeake Bay and away from developed areas, and most of these hotspots appear invulnerable to plausible changes in sea level (online Appendix Fig. A5).

Virginia

Average probability of Eastern Black Rail breeding season occupancy across Virginia (0.237) was similar to the entire coastal range (0.242; Table 1). The proportion of habitat patches that were better than the median (0.359) and better than the 75th percentile (0.262) were larger than for all sites within the coastal range, yet the highest-quality habitat was less common (0.010). The proportion of Eastern Black Rail breeding habitat located on federal lands and protected areas in Virginia that was better than the median or better than the 75th percentile was typically similar or smaller than the amount located at all pixels within the state and was proportionally lower as compared to the subspecies' coastal range (i.e., worse than for all federal lands and protected areas; Table 1). The proportion of highest-quality Eastern Black Rail breeding habitat on federal lands and protected areas in Virginia was slightly larger as compared to all pixels within the state, but was also smaller as compared to the entire coastal range. The proportion of the state categorized as developed (0.123) was similar to the entire coastal range, as was the recency of development (Table 2). Current hotspots of the highest-quality habitat in Virginia appear to be located away from developed sites, but these hotspots are vulnerable to potential changes in sea level (online Appendix Fig. A5).

North Carolina

Average probability of Eastern Black Rail breeding season occupancy across North Carolina (0.252) was similar to the entire coastal range (0.242; Table 1). However, the proportion of habitat patches that were better than the median (0.470), the proportion better than the 75th percentile (0.419), and the highest-quality habitat (0.076) in North Carolina were much more common than for the entire coastal range. The proportion of Eastern Black Rail breeding habitat located on federal lands and protected areas in North Carolina that was better than the median, better than the 75th percentile, or considered the highest-quality habitat was also larger than the proportion located at all pixels within the state and larger as compared to the subspecies' coastal range (i.e., better than for all federal lands and protected areas; Table 1). The proportion of the state categorized as developed (0.079) and the proportion of recently developed areas (0.008) were smaller as compared to all sites (Table 2). Current hotspots of the highest-quality habitat in North Carolina appear to be located away from developed sites, but many of these hotspots are vulnerable to changes in sea level (online Appendix Fig. A6).

South Carolina

Average probability of Eastern Black Rail breeding season occupancy across South Carolina (0.250) was similar to the entire coastal range (0.242; Table 1). However, the proportion of habitat patches that were better than the median (0.488) and the proportion better than the 75th percentile (0.419) in South Carolina were more common as compared to the entire coastal range. The highest-quality habitat (0.035) in South Carolina was proportionally similar to the coastal range (0.033). The proportion of Eastern Black Rail breeding habitat located on federal lands and protected areas in South Carolina that was better than the median and better than the 75th percentile were similar to or slightly smaller than the proportion at all pixels within the state, but larger as compared to the subspecies' entire coastal range (i.e., better than for all federal lands and protected areas; Table 1). The highest-quality Eastern Black Rail breeding habitat was more common on federal lands and protected areas in South Carolina as compared to all pixels within the state, but was less common as compared to sites across the coastal range. The proportion of the state categorized as developed (0.063) and the proportion of recently developed areas (0.009) were smaller than for all sites (Table 2). Current hotspots of the highest-quality habitat in South Carolina appear widely distributed but away from developed sites, and many of these hotspots are vulnerable to changes in sea level (online Appendix Fig. A6).

Georgia

Average probability of Eastern Black Rail breeding season occupancy probability across Georgia (0.251) was similar to the entire coastal range (0.242), as were the proportion of habitat that was better than the median (0.321), better than the 75th percentile (0.269), and the proportion of the highest-quality habitat (0.021). The proportion of Eastern Black Rail breeding habitat located on federal lands and protected areas in Georgia that was better than the median or better than the 75th percentile were similar to or less than the proportion at all pixels within the state and smaller as compared to sites across the entire coastal range (i.e., worse than for all federal lands and protected areas; Table 1). The amount of highest-quality Eastern Black Rail breeding habitat on federal lands and protected areas was slightly larger than for all pixels within the state, but was substantially less compared to the coastal range. The proportion of the state categorized as developed (0.063) was less than the coastal range (0.109), as was the proportion recently developed (0.009; Table 2). Current hotspots of the highest-quality habitat in Georgia appear widely distributed but away from developed sites, and most of these hotspots are vulnerable to changes in sea level (online Appendix Fig. A7).

Florida

Average probability of Eastern Black Rail breeding season occupancy across Florida (0.241) was similar to the entire coastal range (0.242), as were the proportion of habitat patches better than the median (0.302), the proportion better than the 75th percentile (0.271), and the highest-quality habitat (0.046). The proportion of Eastern Black Rail breeding habitat located on federal lands and protected areas in Florida that was better than the median, better than the 75th percentile, or considered the best habitat was larger than the proportion at all pixels within the state and larger as compared to the entire coastal range (i.e., better than for all federal lands and protected areas; Table 1). The proportion of the state categorized as developed (0.123) was larger as compared to all sites (0.109), but the proportion of recently developed areas (0.017) was similar to all sites across the coastal range (0.016; Table 2). Current hotspots of the highest-quality habitat in Florida are widely distributed and located away from developed sites, any many of these hotspots, particularly in south Florida, are vulnerable to changes in sea level (online Appendix Fig. A7).

Louisiana

Average probability of Eastern Black Rail breeding season occupancy across Louisiana (0.246) was similar to the entire coastal range (0.242), but the proportion of habitat patches that were better than the median (0.189), better than the 75th percentile (0.174), or the highest-quality habitat (0.021) were less common as compared to the entire coastal range. The proportion of Eastern Black Rail breeding habitat located on federal lands and protected areas in Louisiana that was better than the median, better than the 75th percentile, or the highest-quality habitat was also smaller than the amount at all pixels within the state, and was considerably smaller as compared to the entire coastal range (i.e., worse than for all federal lands and protected areas; Table 1). Consequently, Louisiana had the smallest proportion of federal and protected lands categorized as quality habitat according to any of the habitat-quality thresholds used. The proportion of the state categorized as developed

(0.002) was also small as compared to the coastal range (0.109), as was the proportion of recently developed areas (0.003; Table 2). Hotspots of the highest-quality habitat were located away from developed sites but are highly vulnerable to changes in sea level (online Appendix Fig. A8).

Texas

Average probability of Eastern Black Rail breeding season occupancy across Texas (0.234) was consistent with the entire coastal range (0.242), but the proportion of habitat patches that were better than the median (0.184), better than the 75th percentile (0.143), or the highest-quality habitat (0.004) were less common as compared to the entire study area. The proportion of Eastern Black Rail breeding habitat located on federal lands and protected areas that was better than the median or better than the 75th percentile was similar to or smaller than the proportion at all pixels within the state, and smaller as compared to the coastal range (i.e., worse than for all federal lands and protected areas; Table 1). The proportion of highest-quality Black Rail breeding habitat located on federal lands and protected areas in Texas was similar to or larger than all pixels within the state, but was considerably smaller as compared to the entire coastal range (i.e., worse than for all federal lands and protected areas). The proportion of the state categorized as developed (0.126) was the second largest among all states, and the proportion recently developed (0.029; Table 2) was the largest among all states. Few hotspots of the highest-quality habitat were located in Texas, and nearly all of them were vulnerable to development, changes in sea level, or both (online Appendix Fig. A8).

DISCUSSION

We provide a broad-scale assessment of breeding season habitat that predicts the spatial distribution of quality habitat patches and threats for Eastern Black Rails throughout the subspecies' coastal range. Existing threats from human development varied among states, as did the recency of changes in human development. The highest-quality habitat patches were rare and unevenly distributed within and among states, and habitat quality was often better in locations that were federally owned or under some type of protected status. Despite the predicted benefits of existing protected areas for Eastern Black Rails, the highest-quality habitat patches in most states were frequently covered by overlays projecting sea level rise. Thus, even habitat patches that are unlikely to be fully developed are vulnerable to modest rises in sea level. This implies that maintenance of existing high-quality patches of Eastern Black Rail breeding habitat in coastal states over long-time scales may be difficult without active management and restoration that takes rising seas and future inundation into account.

Habitat loss and fragmentation, human disturbance, and sea level rise are all established threats to Eastern Black Rail persistence (Watts 2016; U. S. Fish and Wildlife Service 2019). Our results corroborate these threats and help put them into a spatial context. The patchy and relatively rare distribution of the best habitat also leaves Eastern Black Rails especially vulnerable to stochastic events (e.g., extreme weather), which are another threat to the subspecies (U. S. Fish and Wildlife Service 2019). Moreover, synergistic effects of multiple threats are likely to reduce Eastern Black Rail persistence simultaneously (U. S. Fish and Wildlife Service 2019), and we demonstrate that many patches predicted to have the best habitat either already are or are likely to be affected in the future by both human development and changes to sea level. The wetland-upland ecotone that Black Rails use for nesting and foraging will likely be further constricted by these synergistic effects. As sea level rise pushes the ecotones inland and to higher elevations, useable areas will likely be restricted and pinched by anthropogenic habitat loss and past conversion of wetlands to other land uses, such as agriculture or development (Watts 2016).

High-quality habitat patches for Eastern Black Rails are vulnerable to the combined effects of sea level rise and human development, and this result is not surprising given the importance of coastal areas to the subspecies. A large majority of existing presence records come from coastal areas, especially records from recent decades, which clearly demonstrates the importance of coastal wetlands to maintenance of breeding populations (Watts 2016). Our model corroborates occurrence records that point to coastal areas in North Carolina, South Carolina, and Florida as strongholds for Eastern Black Rail conservation, but may underpredict the quality of habitat for other important regions (e.g., coastal areas of Texas). Our model also corroborates the notion that Eastern Black Rail breeding habitat in some areas (e.g., Louisiana) may be peripheral and less important overall to the subspecies (Watts 2016). Nonetheless, Eastern Black Rails in Florida and Texas appear highly vulnerable to both human development and sea level rise; both states had more development than the average across the range and Texas also had more recent changes (i.e., post 2000) in development. Thus, while the species status assessment for Eastern Black Rails suggested conversion of habitat to urban development may have slowed (U. S. Fish and Wildlife Service 2019), our results suggest this slowing pattern may not hold in some coastal areas that historically provided high-quality habitat for the subspecies.

Our models predict the spatial distribution of high-quality habitat for Eastern Black Rails across coastal states of the Eastern USA, yet unknown variables and stochastic factors undoubtedly affect the distribution of rails within and among these areas because not all suitable habitat is typically occupied (Watts 2016). Some regions (e.g., the northern Atlantic Coast, Chesapeake Bay) appear to have suitable habitat patches that are relatively common and widely dispersed, but have nonetheless undergone apparent population collapses in recent decades (Watts 2016; U. S. Fish and Wildlife Service 2019). Thus, predicted habitat hot spots in these areas may have already experienced severe reductions in breeding populations, and either support reduced populations or no longer support viable populations of Eastern Black Rails. It is unclear why disconnects between population dynamics and existing habitat conditions exist, but these discrepancies may be related to changes in hydrology that are not captured by our models (i.e., important components of habitat missing from the models). Given the narrow range of water depths that determine available habitat for Black Rails and their limited ability to tolerate short-term fluctuations in water levels during the breeding season (Eddleman *et al.* 1994), hydrologic change in coastal areas as a result of ongoing sea level rise (e.g., increased frequency and duration of coastal flooding) is hypothesized to make otherwise suitable habitat unavailable (Watts 2016). However, Eastern Black Rails are also particularly vulnerable to stochastic events given the small size and spatially isolated nature of their populations, and consequently local extinctions could occur in the absence of hydrologic change.

These analyses described the spatial distribution of high-quality habitat patches and threats affecting Eastern Black Rails, but should be viewed as a starting point for characterizing habitat suitability over broad extents that can be improved with additional data and modeling. Our spatial models leveraged information from surveys conducted across the Black Rail range within the United States to predict habitat quality for the data-limited Eastern Black Rail subspecies. As such, the analyses used survey data for both the California and Eastern Black Rail subspecies to develop data-driven predictions (Stevens and Conway 2020a, 2020b) and, in doing so, effectively ignored spatial heterogeneity in habitat use patterns (i.e., different optimal habitat dependent on local or regional context), as well as any differences in habitat use between the subspecies. Thus, regional variation in habitat relationships are not accounted for with the existing models. It is also likely that key habitat relationships may differ between subspecies, and that additional covariates (e.g., availability of high marsh) and recent wetland changes (e.g., coastal flooding) not captured by the range-wide model are affecting breeding season occupancy for Eastern Black Rails. These discrepancies may have contributed to mischaracterization of the quality of habitat in some areas (e.g., Texas), or suggested that quality habitat exists in areas that have already been extirpated due to changes in environmental conditions not captured by the models. Moreover, the field surveys used to develop range-wide habitat models for Black Rails by Stevens and Conway (2020a) did not sample potential habitat equally among states (or in proportion to its availability). For example, we had minimal survey data available from some states (e.g., North Carolina, Georgia, Louisiana) or had sampling locations that only covered a small area of potential habitat (e.g., New Jersey, Maryland, South Carolina, Texas). Spatial heterogeneity in the amount of survey data among regions, paired with spatial heterogeneity in habitat relationships, could result in better predictive accuracy in locations that received more field sampling and thus contributed more information to estimation of model parameters. Additional analyses to develop predictive habitat models specific to the Eastern Black Rail are currently underway (B. Stevens, unpubl. data), and our spatial analyses could be easily replicated to aid conservation decision making at a smaller, regional scale with refined models developed to identify important local habitat patches. Nonetheless, this work places habitat quality and several important threats in a spatial context at a combination of fine spatial resolution and broad extent that were not previously possible, and thus provides important context for ongoing efforts to monitor and conserve Eastern Black Rail populations.

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