3-2017

Poor transferability of a distribution model for a widespread coastal marsh bird in the southeastern United States

Nicolette S. Roach
Clemson University

Elizabeth A. Hunter
University of Georgia

Nathan P. Nibbelink
University of Georgia

Kyle Barrett
Clemson University

Poor transferability of a distribution model for a widespread coastal marsh bird in the southeastern United States

NICOLETTE S. ROACH,[1,3,†] ELIZABETH A. HUNTER,[2,4] NATHAN P. NIBBELINK,[2] AND KYLE BARRETT[1]

[1]*Department of Forestry and Environmental Conservation, Clemson University, 261 Lehotsky Hall, Clemson, South Carolina 29634 USA*
[2]*Warnell School of Forestry and Natural Resources, University of Georgia, 180 E Green Street, Athens, Georgia 30602 USA*

Abstract. Species distribution models have been applied across a wide range of spatial scales to generate information for conservation planning. Understanding how well models transfer through space and time is important to promote effective species–habitat conservation. Here, we assess model transferability in coastal tidal marshes of the southeastern United States using count data of a widespread marsh bird: the Clapper Rail (*Rallus crepitans*). We developed species–habitat models at a state level in both South Carolina and Georgia, and then assessed how well top models from each state predicted abundance in the other state. Internally (locally) validated models performed well with reasonable fit (SC: $R^2 = 0.35$, GA: $R^2 = 0.14$), and high significance ($P = 0.0005$); however, both models performed poorly when predicting abundance from the other state ($R^2 = 0.03$ and 0.003). To assess the consequences of this lack of transferability, we applied the South Carolina- and Georgia-derived parameter estimates to habitat features in South Carolina and identified the top 25% of tidal marsh habitat that each model predicted within the state. There was minimal overlap between model habitat quality predictions (<5%). Our results address the predictive power and uncertainties that arise from using habitat associations and climate models to predict species distributions or abundance in locations without training data. We discuss potential reasons model transferability was not successful and address the need for better regional datasets and the importance of intraspecific variability in response to environmental gradients.

[3] Present address: Department of Wildlife and Fisheries Sciences, Texas A&M University, 210 Nagle Hall, College Station, Texas 77843 USA.
[4] Present address: University of Nevada – Reno, 1664 N Virginia St., Mail Stop 0186, Reno, Nevada 89557 USA.
† **E-mail:** nroach@tamu.edu

INTRODUCTION

Knowledge of species–habitat relationships can shape management decisions (Pearce and Lindenmayer 1998, Raxworthy et al. 2003, Engler et al. 2004, Guisan and Thuiller 2005, Guisan et al. 2013) and support conservation planning (Ferrier 2002, Araújo et al. 2004). As landscapes become altered due to land-use and climate change, there is a growing need to understand species–habitat relationships across large regions and model uncertainty associated with those relationships (Elith and Leathwick 2009). Statistical assessment of how well species–habitat models derived in one region (or time) will transfer to a different region (or time) is preferable to the assumption that transferred models will perform well. Failure to assess transferability of habitat models may lead to over- or under-predicting habitat and poor conservation planning (Wenger and Olden 2012).

There are a number of explanations for why models of species–habitat associations may fail to transfer well across a geographic region. Limitations to modeling approaches and lack of knowledge about how species respond to environmental changes can make projections of species distributions challenging (Guisan and Zimmermann 2000, Dormann 2007, Vallecillo et al. 2009). For instance, species distribution models assume species are at equilibrium with their environments and that relevant environmental gradients have been adequately sampled (Fielding and Haworth 1995, Guisan and Zimmermann 2000, Whittingham et al. 2003, Norgues-Bravo 2009); however, many issues such as species invasions, disturbance, and climate change represent cases where species records are unrepresentative of equilibrium conditions (Elith and Leathwick 2009). Additionally, models may assume immediate species response to climate change (Araújo et al. 2005) but in reality dispersal limitations and alterations to networks of biotic interactions may prevent rapid evolutionary adaptations (Loehle and LeBlanc 1996, Pearson and Dawson 2003). Many current species occurrence datasets suffer problems from spatial autocorrelation, which may reduce the estimated heterogeneity among the environmental gradients or populations sampled and can generate problems in the calibration and validation of species–habitat models (Araújo et al. 2005). Previous studies found that when important ecological predictors are not included in the modeling process, transferability may be compromised (Fielding and Haworth 1995, Graf et al. 2006, Randin et al. 2006, Varela et al. 2009). In order to achieve greater transferability, predictor variables should be ecologically relevant to the target species and homogenous across predicted areas (Mac Nally 2000, Peterson and Nakazawa 2008, Rödder and Lötters 2010).

The ecology of species or populations can provide insight into model transfer efficiency. For instance, transferability of distribution models for widespread plant species was influenced more by dispersal capability and other ecological factors than it was by model algorithms (Dobrowski et al. 2011). Difficulties in transferability can arise when there are differences in species demographics and productivity between regions (Gray et al. 2009), or when there are various levels of spatial heterogeneity among ecological relationships (Fielding and Haworth 1995). Mismatches between model predictions and actual species distributions may arise from localized adaptations to habitats in one region that were not modeled in another. Obtaining localized data may be necessary to enact effective conservation measures for a specific area.

Species distribution models that transfer well across space or time would be particularly valuable to conservation planning and coastal management in marsh ecosystems where there are large-scale regional planning efforts in place. Coastal marsh ecosystems are relatively homogenous in vegetation structure and climate, and face similar threats (i.e., sea-level rise, coastal development, salt water intrusion). In the United States, these systems are distributed across a wide latitudinal gradient and it remains unevaluated how well models constructed in one place will predict species habitat use in other regions. The southeastern United States supports ~15,000 km^2 of intact tidal marsh habitat, nearly 15 times that of the northeast and the pacific coasts combined (Greenberg et al. 2006). The impending threat of sea-level rise suggests a need to critically evaluate species distribution model transferability in coastal systems in order to help enact effective coastal wildlife management plans.

Marsh bird populations in North America have declined from habitat loss and fragmentation; as a result of sea-level rise, these species are of special concern in many coastal states (Eddleman et al. 1988, Conway and Sulzman 2007). We selected the Clapper Rail (*Rallus crepitans*) as a representative species for evaluating model transferability in coastal systems because they are relatively abundant along the Atlantic Coast, where they spend their entire life cycle in salt marshes, yet selective in nesting habitat choice (Rush et al. 2010). Clapper Rails occupy high trophic levels and their life history and vulnerability to threats from sea-level rise make them an indicator of marsh ecosystem function (Rush et al. 2009). Our main objective was to assess what environmental variables influenced Clapper Rail abundance in a portion of the southeastern United States (South Carolina and Georgia) and determine how well models would transfer across a region (between these two states). By collecting data from both South Carolina and Georgia, we expected reasonable
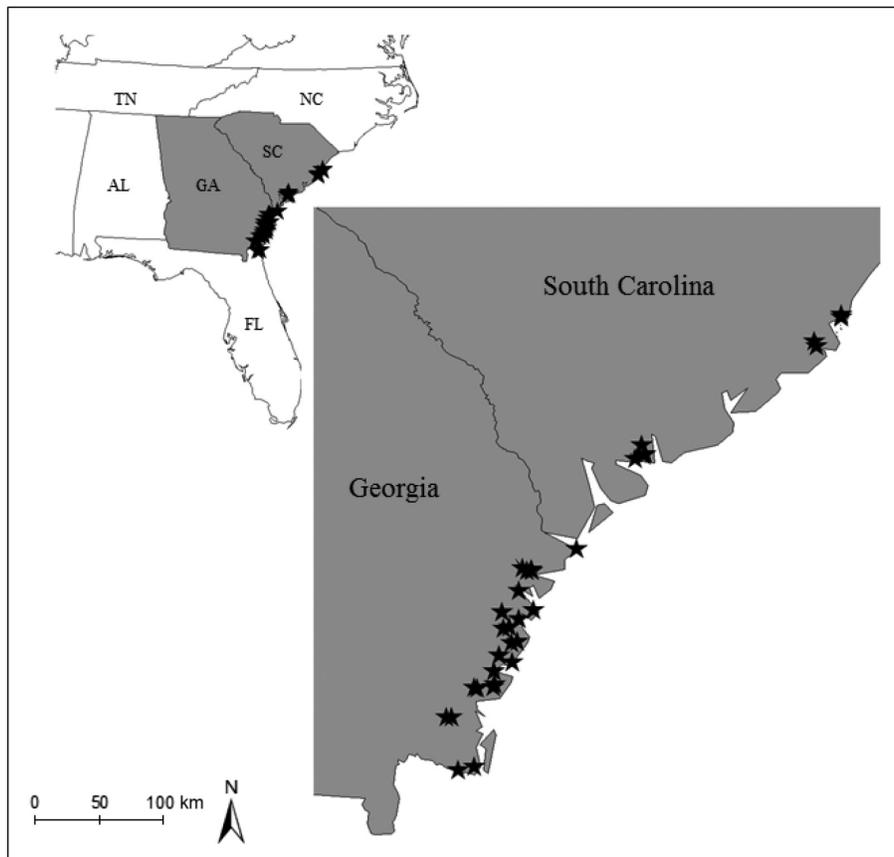
Fig. 1. Starred locations represent areas where Clapper Rails were surveyed during the 2013 breeding season in South Carolina and Georgia, United States.

transferability between the two states because of their similar landscape features, climates, and species. Knowledge of transferability across coastal systems could reduce uncertainties associated with conservation planning risks, as well as help determine suitable habitat for Clapper Rails in the southeast.

MATERIALS AND METHODS

Study area and site selection

We measured Clapper Rail abundance at 286 sites across coastal tidal marsh in South Carolina and Georgia (Fig. 1). We assumed Clapper Rail populations were at equilibrium throughout the study because patches of surveyed habitat included established breeding territories, with little to no prolonged disturbances. There have been no recent (10 yr) extreme climatic events (e.g., hurricanes) in this part of the southeast that

would disrupt the equilibrium of this species. We surveyed points distributed along seven landscape gradients (defined below in *Environmental Variables*) that we hypothesized would affect Clapper Rail abundance and be affected by sea-level rise: patch size (m^2), distance to forest and development (m), elevation (m), proportion of brackish marsh, proportion of marsh landscape (brackish + salt marsh), and edge density (selection of variables described in detail in Hunter et al. 2017). We surveyed 72 points in South Carolina and 214 points in Georgia. Survey points were located along marsh edge, separated by 400 m. All surveys were conducted as close to the initial GPS location as possible but always within 30 m from GPS locale. In South Carolina, research sites were located within 10-km^2 region on the North Santee River and Winyah Bay and within 12 km^2 of tidal marsh in the Ashepoo–Combahee–Edisto (ACE) Basin, one of the largest

intact estuaries on the Atlantic Coast. Sites in Georgia spanned 150 km^2 of salt marsh ranging from Savannah to St. Mary's rivers (Fig. 1).

Field methods

We used call-playback surveys to collect abundance data. Count surveys were conducted during the 2013 Clapper Rail breeding season, from sunrise to three hours afterward, during three survey periods: 15 March–15 April, 15 April–15 May, and 15 May–15 June, with a minimum of 10 days between consecutive surveys at the same site. Each site was visited three times by two observers who collected data independently, which resulted in a sampling design with six sampling occasions per site. We broadcasted marsh bird vocalizations using MP3 players and speakers (Radio Shack Mini Audio Amplifier 90 db). We derived our broadcast vocalization sequence from the 2011 Conway Marsh Bird Protocol (Conway 2011). Our playback sequence consisted of five passive minutes followed by three minutes of alternating vocalizations (30 s) and silence (30 s). We broadcasted vocalizations from three species throughout the three-minute call sequence: *kik-kee-doo* and *growl* for Black Rail (*Laterallus jamaicensis*), *tut-tut* and *gack-gack* for Least Bittern (*Ixobrychus exilis*), and *clapper, kek,* and *kek-burr* for Clapper Rail. We included other marsh bird vocalizations in our playback because Clapper Rails are known to vocalize in response to heterospecific calls (Johnson and Dinsmore 1986, Allen et al. 2004, Conway and Nadeau 2010). We used a double observer method when conducting surveys (Bart et al. 2002); during each survey, two observers independently recorded calls and abundance of Clapper Rails. We recorded vocalization type and Clapper Rail abundance at varying distances within a 200 m radius from each point. By separating survey points by 400 m but only recording birds within a 200-m radius, we minimized detection of the same bird at adjacent survey points. We trained surveyors to estimate distances by playing calls throughout the marsh at various distances and having each observer estimate the distance to the playback prior to conducting surveys. During each site visit, we recorded variables believed to influence detectability: wind, background noise, observer, tidal stage, and date. We did not conduct surveys during periods of sustained rain or when wind speed was greater than 25 km/h.

Environmental variables

We collected landscape data from the National Wetlands Inventory (NWI; http://landcover.usgs.gov/), National Land Cover Dataset (NLCD; http://landcover.usgs.gov/), and digital elevation models. Seven landscape variables were measured for the 200 m radius circle around each site and were assessed for the combined coverage of salt (E2EM1N) and brackish (E2EM1P) marsh, designated by NWI. These variables included patch size (total area [m^2] of the marsh which contained the sample point), edge density (interface between marsh and any other land cover), proportion of the landscape that is marsh, proportion of brackish marsh within the 200 m radius, distance to development (m) and forest (m), and average elevation above mean sea level (m) within the 200 m radius. To calculate edge density and proportion of marsh landscape, we applied a FRAGSTATS (McGarigal et al. 2012) analysis with an 8-cell neighborhood rule within a 200-m moving window. We used the Euclidean distance tool (m) in ArcGIS 10.2 (ESRI; Redlands, California, USA) to obtain the closest distance from the buffers (200 m around survey point) to developed or forested areas. We downloaded elevation datasets for South Carolina from the National Elevation Dataset (NED; http://ned.usgs.gov) with a 1/3-arc second (~10 m) resolution. For Georgia, we obtained lidar elevation dataset from the Georgia Department of Natural Resources at a 4-ft resolution that was aggregated to a 28-m cell size. To obtain elevation, we used the resample tool to get a mean elevation within a 200-m buffer of our survey point. To standardize across both states, all raster files were set to the same spatial extent and were analyzed within a 30 × 30 m framework. We extracted values from the rasters to our survey points to get individual survey site landscape information. We standardized all covariates and tested for collinearity. All variables in the analysis had a Pearson's r correlation of <0.5 with the exception of two variables (distance to forest and development in South Carolina [$r = 0.7$]).

Data analysis

We used the unmarked package (Fiske and Chandler 2011) to analyze abundance data using Program R 3.1.0 statistical software (R Core Team 2015, http://www.r-project.org/). We used the

Table 1. Mean and standard error values of predictor variables used in South Carolina (SC) and Georgia (GA), United States.

Environmental variables	SC mean $\pm$ SE	GA mean $\pm$ SE
Proportion of brackish marsh	11.67 $\pm$ 2.60	43.47 $\pm$ 3.30
Distance to forest (m)	450.77 $\pm$ 42.09	644.64 $\pm$ 36.89
Elevation (m)	0.32 $\pm$ 0.034	0.29 $\pm$ 0.0048
Distance to development (m)	2510 $\pm$ 219.09	2011 $\pm$ 106.37
Edge density	86.49 $\pm$ 3.41	82.01 $\pm$ 2.11
Patch area (ha)	738.37 $\pm$ 73.80	910.85 $\pm$ 40.08
Percent of marsh landscape	50.49 $\pm$ 1.97	59.13 $\pm$ 1.057

unmarked function "p-count" to fit N-mixture models to spatially and temporally replicated count data, while accounting for imperfect detection (Royle 2004). We used generalized linear models to assess the influence of detection and landscape covariates on abundance.

We began by assessing the role of five covariates hypothesized to influence detection probability: wind (none to minimal wind vs. moderate/high winds), background noise (none/minimal noise vs. moderate/high noise), observer, tide type (low vs. high), and date. These initial models contained no covariates associated with count data. To identify the most important detection covariates, we ran all possible iterations of detection models, allowing detection to vary as a function of one or more of the above variables. The detection covariates present in models with a $\Delta AIC_c < 2$ were included in subsequent abundance models that focused on habitat factors influencing site abundance (Table 1): elevation (m), distance to forest and development (m), patch area (m^2), proportion of brackish marsh, edge density, and proportion of marsh landscape. We ran all univariate models examining count covariates, and retained covariates with high support ($\Delta AIC_c < 2$). We then examined models that allowed for additive or interactive effects to attain a top overall model.

The top model from each state dataset was evaluated for fit both internally (within state) and externally (SC to GA or GA to SC). We used linear regression to compare the model-estimated (predicted) abundance to observed abundance data from the same locations for all four-model-evaluation scenarios. We accounted

for detection probabilities by inflating our observed maximum abundance counts at each site by their respective detection probability determined by the top detection model.

In order to test the hypothesis that transferability across regions is limited by the information contained in local (state-based) datasets, we combined data from South Carolina and Georgia to create a combined dataset. We randomly selected 70% of the data to serve as the training dataset. We followed the same steps for model-ranking and transferability assessments as in the independent state model evaluations outlined in paragraph 2 of *Data analysis*. We used our top-ranked model parameter estimates from our training dataset to predict Clapper Rail abundance for our test data (i.e., the remaining 30%). We then assessed overall model quality by comparing the predicted abundance to the observed abundance.

We also tested the hypothesis that variability between environmental gradients in the different states lowers transferability. We examined any discrepancies among the mean values of our top covariates from South Carolina and Georgia top models. In order to standardize our ranges across environmental gradients between the two regions, we reduced our Georgia dataset by eliminating observations where the top covariates were outside the range of two standard deviations from the mean value of the same covariate in South Carolina. We then re-ran our analyses to test the effect on transferability.

Additionally, we predicted suitable habitat for Clapper Rails in South Carolina using our top model parameter estimates from each state. Our intent with this analysis was to assess on-the-ground consequences of poor transferability (i.e., measures of habitat suitability for a species of management interest). We only evaluated transfer of model parameters from Georgia to South Carolina because it provided the most conservative evaluation given the more robust dataset collected along the Georgia coast. We used each state's top model as an index for habitat quality in South Carolina. We then identified high-quality habitat as the top 25% of tidal marsh habitat predicted by each model within South Carolina. Using ArcGIS 10.2, we applied the analysis to the salt and brackish marsh designated by the initial NWI land cover in our study region.

Table 2. Model selection of Clapper Rail abundance models in South Carolina (SC) and Georgia (GA), United States.†

State	Model name	ΔAIC$_c$	ωi	K	Loglikelihood	Beta estimates ± SE
SC	Distance to forest × elevation	0	1	6	−2174	1.51 ± 0.17; −1.32 ± 1.75
SC	Total landscape variable model (additive)	20.42	3.7E-05	10	−2167	NA
GA	Distance to forest × proportion of brackish marsh	0	1	6	−2146	−0.94 ± 0.12; −0.30 ± 0.11
GA	Total landscape variable model (additive)	50.98	8.5E-12	10	−2167	NA

† Our total landscape variable model was an additive model including all predictor variables measured in our study (Table 2). Our top detection covariate for all models was the presence or absence of wind. AIC$_c$: ΔAIC$_c$ for the ith model is computed as AICi – min (AIC), ωi is the AIC model weight, K is the number of parameters, beta estimates explain the relationship between the parameter and Clapper Rail abundance, and only significant relationships are reported.

RESULTS

Detection probability and habitat variables influencing Clapper Rail abundance

Clapper Rails occupied the majority of sites in both South Carolina and Georgia, and our naïve occupancy estimate was 96% and 88%, respectively. Wind (presence or absence during survey) was the only parameter that influenced detection for both South Carolina and Georgia. Detection probabilities were 0.43 and 0.32 in South Carolina and 0.33 and 0.24 in Georgia with no wind and wind, respectively. In South Carolina, the only competitive model (ΔAIC$_c$ < 2) was the interaction between distance to forest and elevation (Table 2). Distance to forest had a stronger influence on Clapper Rail abundance at lower elevations, where Clapper Rail abundance was generally higher at sites further from forested areas. In Georgia, the only competitive model was the interaction between distance to forest and proportion of brackish marsh (Table 2). Clapper Rail abundance weakly increased with area of brackish marsh at sites that were close to forests; however, for sites that were further away from forests abundance increased at a steeper rate with the proportion of surrounding brackish marsh.

We internally validated model performance by predicting abundance for each state using state-specific top model parameter estimates and compared them to the observed abundance in their respective state. Each internal evaluation was significant (P < 0.0005), although total variance explained by predicted values was low (R^2 = 0.35 and 0.14 in SC and GA, respectively; Fig. 2a, d).

Model transferability

Models did not transfer well from one state to another (Fig. 2b, c); predictions using data from one state had low R^2 values (<0.04) and were not significant (P = 0.15, 0.42). When data from both states were combined in a training dataset and then applied to a randomly selected test data, R^2 values improved to 0.08 (P < 0.05). To evaluate the role of non-analog environments on transferability, we used a reduced dataset that eliminated 21 sites from Georgia where distance to forest values fell outside two standard deviations from the mean distance to forest value in South Carolina. After the reduction of sites, transferability was still poor (R^2 = 0.004).

In order to further assess model fit, we evaluated the suitable habitat (to 25% of predicted tidal marsh habitat) each model predicted in South Carolina and examined the overlap between those two habitats. The South Carolina model identified 73% of the habitat as suitable in South Carolina, whereas the Georgia model predicted 77% of the focal region as suitable in South Carolina. The overlap between the two model-predicted suitable areas was 2% (Fig. 3).

DISCUSSION

Our results indicate that even in a region where the landscape is fairly homogenous, local (state) models of Clapper Rail abundance do not accurately predict Clapper Rail numbers in an adjacent state. Models derived from the same state where abundance is being predicted (internal) performed much better than those models predicting abundance for another state (external). Our top models for South Carolina and Georgia shared one variable, but were not identical. One potential
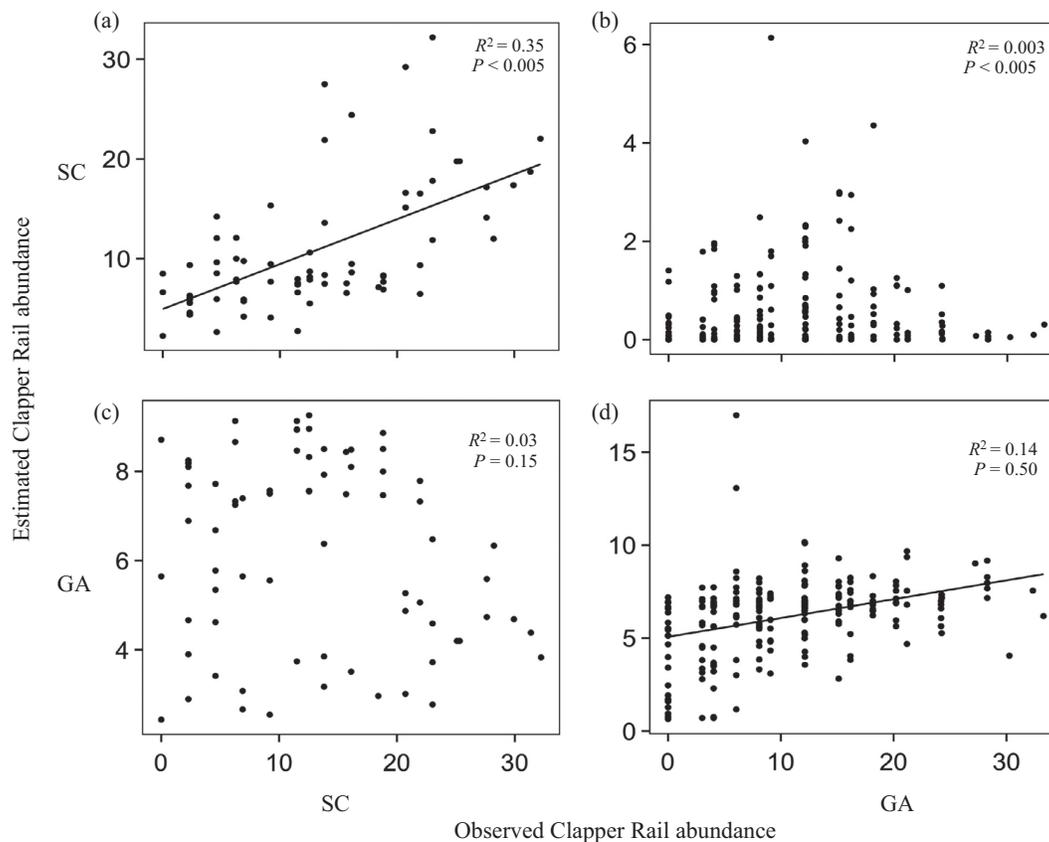
Fig. 2. Comparison of observed and predicted parameter estimates for the top models for Clapper Rail abundance generated in each state. South Carolina estimated abundance (a) significantly predicts observed abundance within South Carolina; however, (b) it does not predict observed abundance in Georgia. Georgia estimated abundance (c) did not predict observed abundance in South Carolina; however, (d) it did significantly predict observed abundance within Georgia.

explanation for poor transferability is a mismatch in the range of values for the top environmental predictors from each state. Nevertheless, when we eliminated outliers from the Georgia dataset, the transferability only increased slightly. Because our results did not show a strong increase in transferability, Clapper Rails in South Carolina and Georgia may be selecting for different habitats.

Our combined analyses yielded the highest fit to an external dataset. The top model from our combined analysis maintained the same parameter as previous models (distance to forest) and one new parameter (proportion of marsh landscape). While every top model for individual analyses was different, distance to forest appeared in each model as an important parameter. However, because the other top parameters varied between

states, it is still imperative to consider the local-scale (in this case at a state level) environmental variables when predicting abundance for species in areas with regional differences or varying environmental conditions. Lastly, the South Carolina and Georgia top models did not identify similar suitable marsh habitat in South Carolina (Fig. 3). The lack of overlap from the two models demonstrates that non-transferability can have big consequences; using the Georgia-derived model to predict suitable habitat for Clapper Rails in South Carolina would result in poor habitat assessment for conservation planning.

There are a number of factors that may have led to the poor transferability we observed between states. Previous studies have shown that habitat relationships may exhibit regional
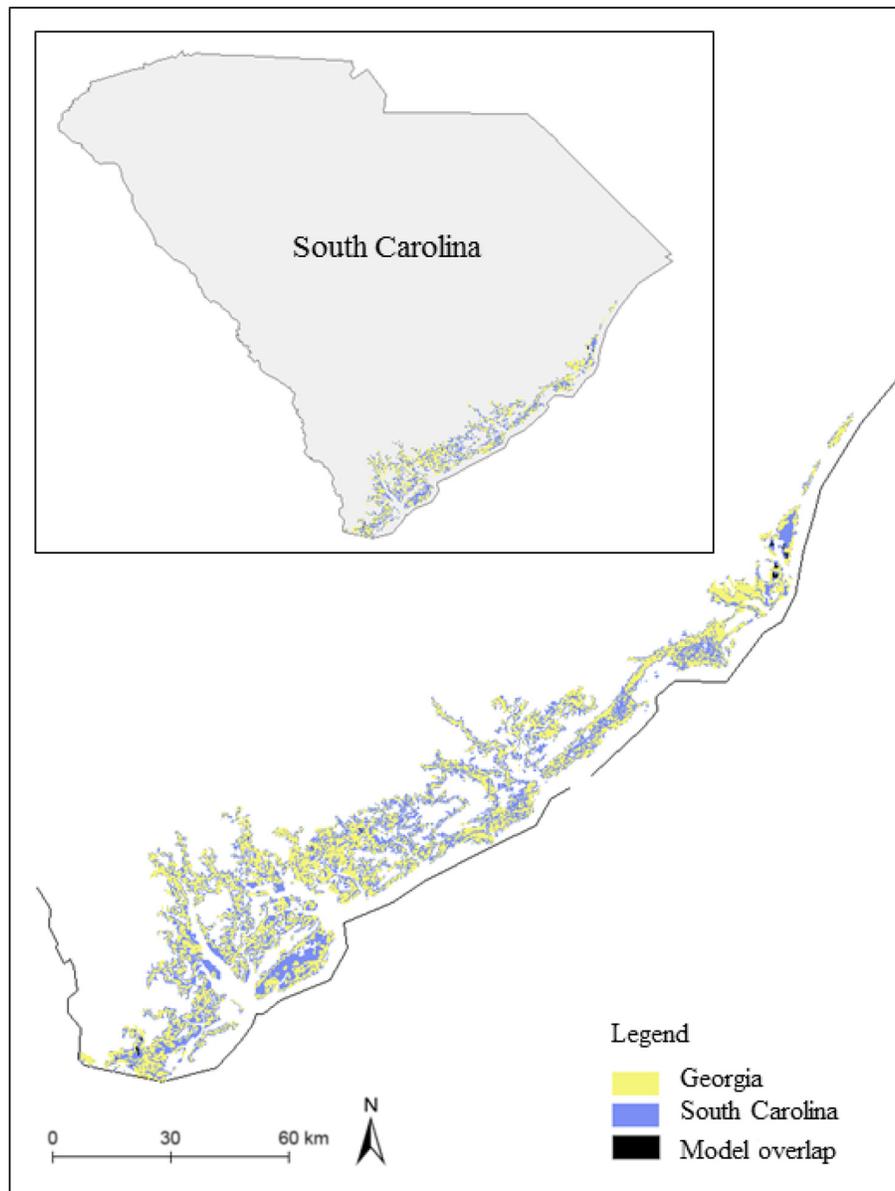
Fig. 3. The predicted top 25% suitable Clapper Rail habitat for the top South Carolina and Georgia-derived models and the overlap between the two.

variation for similar species in fairly homogenous-seeming landscapes (Whittingham et al. 2007). Varying management strategies and historical land uses in each state can create local-scale differences between the landscapes we examined. For instance, South Carolina has a highly impounded coastline (managed wetlands) due to a history of rice harvest until the early 20th century, whereas Georgia does not maintain impoundments at such

a high frequency. This variability in local-scale habitats could influence habitat selection of Clapper Rails and drive variability between South Carolina and Georgia. Model transferability can also be impaired for logistical reasons. In the southeastern United States, there are few congruent regional datasets, making it difficult to assess models across large regions. Additionally, some datasets in one location may be more current than

others, leading to mismatches in future projections of habitat models.

Previous studies of model transferability have had mixed results, and accuracy of model predictions has varied across taxa (McPherson and Jetz 2007, Pöyry et al. 2008, Dobrowski et al. 2011) and modeling frameworks (Rapacciuolo et al. 2012, Wenger and Olden 2012). Studies using resource-based models, models incorporating phenological metrics, and models containing multi-year data have demonstrated high transferability (Vanreusel et al. 2007, Tuanmu et al. 2011). Often, the primary reason transferability efforts fail is due to high variability in relevance among the environmental predictors (Fielding and Haworth 1995, Guay et al. 2003, Zharikov et al. 2007, Gray et al. 2009, Sundblad et al. 2009, Wenger and Olden 2012). Even when relevant environmental predictors are used, generalist species, such as Clapper Rails, pose additional challenges. Clapper Rails inhabit a wide range of marsh types across the southeast, which makes transferability models for these species problematic since either the species has broad habitat tolerances or habitat selection varies geographically.

We argue it is important to understand and adequately sample environmental variation across a region of interest and then assess transferability in order to enact effective conservation measures across geographic scales. While our initial models did not transfer well across space, the information we gathered can still be useful to local conservation planners and help reduce uncertainties of species response to habitat loss associated with current and future anthropogenic disturbances. In the southeastern United States, many federal and regional wildlife agencies and land managers are interested in understanding the potential impacts sea-level rise has on wildlife populations. Sea-level rise is expected to alter habitats significantly in South Carolina and Georgia with rapid tidal marsh loss of 20–45% projected for 2100 (Craft et al. 2009, Hunter et al. 2015). Evaluating environmental variables that influence abundance of Clapper Rails in South Carolina and Georgia provides conservation planners information on key habitats for monitoring and protection. Species distribution models are often used in large-scale conservation planning, but they may not be as effective if the habitat relationships or predictor variables are not appropriately understood. Transferability will likely be most effective when the training area is similar to the test area; however, such conveniences may not be realistic in the context of real-world conservation efforts spanning large regions or long time periods. This study demonstrates that there is a need to continue monitoring populations at a local scale because both abundance and habitat–abundance relationships differed in South Carolina and Georgia. Ecological systems are complex, so in addition to data collected across broad spatial scales we will also likely need long-term datasets to untangle some of those complexities.

Predictive models can be powerful tools for forecasting species occurrences in poorly documented areas, selecting sites for species reintroduction and preservation, predicting species responses to environmental changes, and reducing uncertainties associated with anthropogenic change (Fielding and Haworth 1995). Few studies have evaluated relationships of species and environments well beyond the areas where training data were collected (Fielding and Haworth 1995, Rodríguez and Andren 1999, Morris et al. 2001, Whittingham et al. 2003). Independent model transferability should be assessed when there is an interest in making inferences outside the data used for fitting (Wenger and Olden 2012). The ability to use general models when making conservation decisions is particularly useful on larger scales. More statewide cooperation, regionally standardized protocols, and better regional datasets could greatly enhance the ability to more effectively assess model transferability. In regions that are particularly susceptible to land-use and climate impacts, predictive models can have important management implications, but the impact of such models will be stronger when transferability has been robustly assessed.

Acknowledgments

thank the Baruch Institute and the McKenzie field station in Bennett's point South Carolina for housing, field assistance, and access to field sites. In addition, we would like to thank the two anonymous reviewers; their edits helped greatly improve this manuscript.

Literature Cited

Allen, T., S. L. Finkbeiner, and D. H. Johnson. 2004. Comparison of detection rates of breeding marsh birds in passive and playback surveys at Lacreek National Wildlife Refuge, South Dakota. Waterbirds 27:277–281.

Araújo, M. B., M. Cabeza, W. Thuiller, L. Hannah, and P. H. Williams. 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Global Change Biology 10:1618–1626.

Araújo, M. B., R. G. Pearson, W. Thuiller, and M. Erhard. 2005. Validation of species–climate impact models under climate change. Global Change Biology 11:1504–1513.

Bart, J., S. Earnst, and M. Murphy. 2002. Double sampling to estimate density and population trends in birds. Auk 119:36–45.

Conway, C. J. 2011. Standardized North American marsh bird monitoring protocol. Waterbirds 34:319–346.

Conway, C. J., and C. P. Nadeau. 2010. Effects of broadcasting conspecific and heterospecific calls on detection of marsh birds in North America. Wetlands 30:358–368.

Conway, C. J., and C. Sulzman. 2007. Status and habitat use of the California black rail in the Southwestern USA. Wetlands 27:987–998.

Craft, C., J. Clough, J. Ehman, S. Joye, R. Park, S. Pennings, H. Guo, and M. Machmuller. 2009. Forecasting the effects of accelerated sea-level rise on tidal marsh ecosystem services. Frontiers in Ecology and the Environment 7:73–78.

Dobrowski, S. Z., J. H. Thorne, J. A. Greenberg, H. D. Safford, A. R. Mynsberge, S. M. Crimmins, and A. K. Swanson. 2011. Modeling plant ranges over 75 years of climate change in California, USA: temporal transferability and species traits. Ecological Monographs 81:241–257.

Dormann, C. F. 2007. Promising the future? Global change projections of species distributions. Basic and Applied Ecology 8:387–397.

Eddleman, W. R., F. L. Knopf, B. Meanley, F. A. Reid, and R. Zembal. 1988. Conservation of North American Rallids. Wilson Bulletin 100:458–475.

Elith, J., and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics 40:677–697.

Engler, R., A. Guisan, and L. Rechsteiner. 2004. An improved approach for predicting the distribution of rare and endangered species from occurence and pseudo-absence data. Journal of Applied Ecology 41:263–274.

Ferrier, S. 2002. Mapping spatial pattern in biodiversity for regional conservation planning: Where to from here? Systematic Biology 51:331–363.

Fielding, A. H., and P. F. Haworth. 1995. Testing the generality of bird-habitat models. Conservation Biology 9:1466–1481.

Fiske, I., and R. Chandler. 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Graf, R. F., K. Bollmann, S. Sachot, W. Suter, and H. Bugmann. 2006. On the generality of habitat distribution models: a case study of capercaillie in three Swiss regions. Ecography 29:319–328.

Gray, T. N. E., R. Borey, S. K. Hout, H. Chamnan, N. Collar and P. M. Dolman. 2009. Generality of models that predict the distribution of species: conservation activity and reduction of model transferability for a threatened bustard. Conservation Biology 23:433–439.

Greenberg, R., J. E. Maldonado, S. Droege, and M. V. McDonald. 2006. Tidal marshes: a global perspective on the evolution and conservation of their terrestrial vertebrates. BioScience 56:675–685.

Guay, J. C., D. Boisclair, M. Leclerc, and M. Lapointe. 2003. Assessment of the transferability of biological habitat models for Atlantic salmon parr (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 60:1398–1408.

Guisan, A. et al. 2013. Predicting species distributions for conservation decisions. Ecology Letters 16:1424–1435.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8:993–1009.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological modelling 135:147–186.

Hunter, E. A., N. P. Nibbelink, C. R. Alexander, K. Barrett, L. F. Mengak, R. K. Guy, C. T. Moore, and R. J. Cooper. 2015. Coastal vertebrate exposure to predicted habitat changes due to sea level rise. Environmental Management 56:1528–1537.

Hunter, E. A., N. P. Nibbelink and R. J. Cooper. 2017. Divergent forecasts for two salt marsh specialists in response to sea level rise. Animal Conservation 20:20–28.

Johnson, R. R., and J. J. Dinsmore. 1986. The use of tape-recorded calls to count virginia rails and soras. Wilson Bulletin 98:303–306.

Loehle, C., and D. LeBlanc. 1996. Model-based assessments of climate change effects on forests: a critical review. Ecological Modelling 90:1–31.

Mac Nally, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: the distinction between – and reconciliation of – 'predictive' and 'explanatory' models. Biodiversity and Conservation 9:655–671.

McGarigal, K., S. A. Cushman, and E. Ene. 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. University of Massachusetts, Amherst, Massachusetts, USA. http://www.umass.edu/landeco/research/fragstats/fragstats.html

McPherson, J. M., and W. Jetz. 2007. Effects of species ecology on the accuracy of distribution models. Ecography 30:135–151.

Morris, A. J., M. J. Whittingham, R. B. Bradbury, J. D. Wilson, A. Kyrkos, D. L. Buckingham, and A. D. Evans. 2001. Foraging habitat selection by yellowhammers (*Emberiza citrinella*) nesting in agriculturally contrasting regions in lowland England. Biological Conservation 101:197–210.

Norgues-Bravo, D. 2009. Predicting the past distribution of species climatic niches. Global Ecology and Biogeography 18:521–531.

Pearce, J., and D. Lindenmayer. 1998. Bioclimatic analysis to enhance reintroduction biology of the endangered helmeted honeyeater (*Lichenostomus menalops cassidix*) in southeastern Australia. Restoration Ecology 6:238–243.

Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? Global Ecology and Biogeography 12:361–371.

Peterson, A. T., and Y. Nakazawa. 2008. Environmental data sets matter in ecological niche modelling: an example with *Solenopsis invicta* and *Solenopsis richteri*. Global Ecology and Biogeography 17:135–144.

Pöyry, J., M. Luoto, R. K. Heikkinen, and K. Saarinen. 2008. Species traits are associated with the quality of bioclimatic models. Global Ecology and Biogeography 17:403–414.

Randin, C. F., T. Dirnböck, S. Dullinger, N. E. Zimmermann, M. Zappa, and A. Guisan. 2006. Are niche-based species distribution models transferable in space? Journal of Biogeography 33:1689–1703.

Rapacciuolo, G., D. B. Roy, S. Gillings, R. Fox, K. Walker, and A. Purvis. 2012. Climatic associations of British species distributions show good transferability in time but low predictive accuracy for range change. PLoS ONE 7:e40212.

Raxworthy, C. J., E. Martinez-Meyer, N. Horning, R. A. Nussbaum, G. E. Schneider, M. A. Ortega-Huerta, and A. T. Peterson. 2003. Predicting distributions of known and unknown reptile species in Madagascar. Nature 426:837–841.

Rödder, D., and S. Lötters. 2010. Explanative power of variables used in species distribution modelling: an issue of general model transferability or niche shift in the invasive Greenhouse frog (*Eleutherodactylus planirostris*). Naturwissenschaften 97:781–796.

Rodríguez, A., and H. Andren. 1999. A comparison of Eurasian red squirrel at the landscape scale: a combined GIS and population dynamics approach. Journal of Applied Ecology 36:649–662.

Royle, A. J. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60:108–115.

Rush, S. A., E. C. Soehren, M. S. Woodrey, C. L. Graydon, and R. J. Cooper. 2009. Occupancy of select marsh birds within northern Gulf of Mexico tidal marsh: current estimates and projected change. Wetlands 29:798–808.

Rush, S. A., M. S. Woodrey, and R. J. Cooper. 2010. Variation in the nesting habits of clapper rails in tidal marshes of the Northern Gulf of Mexico. Condor 112:356–362.

Sundblad, G., M. Härmä, A. Lappalainen, L. Urho, and U. Bergström. 2009. Transferability of predictive fish distribution models in two coastal systems. Estuarine, Coastal and Shelf Science 83:90–96.

Tuanmu, M.-N., A. Viña, G. J. Roloff, W. Liu, Z. Ouyang, H. Zhang, and J. Liu. 2011. Temporal transferability of wildlife habitat models: implications for habitat monitoring. Journal of Biogeography 38:1510–1523.

Vallecillo, S., L. Brotons, and W. Thuiller. 2009. Dangers of predicting bird species distributions in response to land-cover changes. Ecological Applications 19:538–549.

Vanreusel, W., D. Maes, and H. Van Dyck. 2007. Transferability of species distribution models: a functional habitat approach for two regionally threatened butterflies. Conservation Biology 21:201–212.

Varela, S., J. Rodríguez, and J. M. Lobo. 2009. Is current climatic equilibrium a guarantee for the transferability of distribution model predictions? A case study of the spotted hyena. Journal of Biogeography 36:1645–1655.

Wenger, S. J., and J. D. Olden. 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. Methods in Ecology and Evolution 3:260–267.

Whittingham, M. J., J. R. Krebs, R. D. Swetnam, J. A. Vickery, J. D. Wilson, and R. P. Freckleton. 2007. Should conservation strategies consider spatial generality? Farmland birds show regional not national patterns of habitat association. Ecology Letters 10:25–35.

Whittingham, M. J., J. D. Wilson, and P. F. Donald. 2003. Do habitat association models have any generality? Predicting skylark *Alauda arvensis* abundance in different regions of southern England. Ecography 26:521–531.

Zharikov, Y., D. B. Lank, and F. Cooke. 2007. Influence of landscape pattern on breeding distribution and success in a threatened Alcid, the marbled murrelet: model transferability and management implications. Journal of Applied Ecology 44:748–759.