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Research Article

Climate Change and Nutria Range Expansion in the Eastern United States

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ABSTRACT Nutria (*Myocastor coypus*) are an introduced invasive species expanding their range in North America and may have detrimental effects on wetlands. Little is known about habitat covariates that may limit or enhance range expansion of nutria, especially when combined with predicted changes in climate. We used a hierarchical modeling approach to develop broad- and local-scale maximum entropy (MaxEnt) models based on nutria harvest records in the eastern United States from 2006–2015. We developed models for current conditions and for climate change projections in 2050. At a broad scale, nutria habitat was located in areas with $\leq$80 annual freezing days. At local scales, nutria were found in areas with high proportions of freshwater forested-shrub wetlands close to other wetlands. Managers who are concerned about possible nutria range expansion can use this hierarchical modeling framework to identify areas for surveillance and prioritize control efforts.

KEY WORDS climate change, hierarchical models, invasive species, MaxEnt, nutria, range expansion, species distribution models, wetlands, wildlife-human conflict.

Some invasive species (e.g., nutria [*Myocastor coypus*]) can directly damage the function or structure of an entire ecosystem, which can be problematic for human health or economic wealth (Vitousek et al. 1997). Nutria are large, semi-aquatic rodents that can cause extensive and long-lasting damage to wetland systems with their aggressive foraging habits. Nutria are native to South America but have been introduced globally to every continent except Australia and Antarctica (Carter and Leonard 2002). They were initially introduced unsuccessfully into the United States in California, USA, in 1899 for fur farming (Ashbrook 1948, Jojola et al. 2005). Nutria were introduced again in the 1930s in Louisiana, Michigan, New Mexico, Ohio, Oregon, Utah, and Washington, USA, for fur production (Kinler et al. 1987) and as a biological tool for removal of excessive aquatic vegetation (Carter and Leonard 2002). Nutria escaped or were released when fur farming became unprofitable and established feral populations in nearby wetland systems (Bertolino and Genovesi 2007). Currently, nutria are established in 19 states and are expanding their range (U.S. Geological Survey [USGS] 2017).

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Nutria are generalist herbivores, exhibiting varied diets and preferences depending on availability and season (Wilsey et al. 1991). However, they tend to prefer consuming roots (Willner et al. 1979), rhizomes, and dormant shoots of aquatic and semi-aquatic plants (Ehrich 1962), and have adapted an aggressive foraging behavior of uprooting entire plants to access these nutrient-rich portions (Bertolino et al. 2011). This foraging behavior often transforms healthy emergent marshes into open water habitat and can displace native species that depend on this vegetation. Additional ecological damage caused by nutria includes nest predation on aquatic birds (Bertolino et al. 2012) and burrowing into riverbanks and dykes, which can increase soil erosion or collapse of riverbanks and dykes (Boorman and Fuller 1981).

Controlling nutria populations and their range expansion can be difficult because of their high fecundity and lack of natural predators (Evans 1983); however, lethal control via systematic trapping and hunting appears to be the most successful method of nutria management for local eradication. For example, the Chesapeake Bay Nutria Eradication Project, a federal, state, and private partnership, removed 14,000 nutria from 5 Maryland, USA, counties during 2002–2014 via trapping and hunting (Pepper et al. 2017). Lethal control, although effective, is typically expensive. Early monitoring and detection is critical to effective nutria control. Species distribution models (SDMs) have become a valuable and inexpensive tool that wildlife managers can use to understand species' distributions and predict potential range expansion of invasive species (Yackulic et al. 2013). Species distribution models can be used to predict location, timing, and routes of invasion routes. These results can then be used by wildlife managers to focus control efforts on these estimated areas of concern (Kay et al. 2017). Species respond to habitat covariates across multiple spatial scales (Gehring and Swihart 2003). Thus, SDMs must incorporate a hierarchical approach using a multi-scale modeling framework to address wildlife management issues, such as preventing the range expansion of nutria (Lindenmayer 2000, Pearson and Dawson 2003).

At broad scales, climate is a dominant factor influencing geographic distribution of a species (Pearson and Dawson 2003). Cold winter temperatures have been suggested as a primary factor limiting distribution of nutria (Gosling et al. 1981, Doncaster and Micol 1989). Jarnevich et al. (2017) developed a broad-scale model of nutria habitat based on the number of months with freezing temperatures. Nutria may be able to tolerate cold winter temperatures except when water bodies remain frozen for extended time periods, which would increase mortality rates because of limited access to food resources (Ehrich 1962). For example, Doncaster and Micol (1990) reported nutria densities declined 71% after canals were frozen for 20 days. If global temperatures rise as predicted by climate change, then annual number of freezing days will decrease, possibly opening new areas for potential nutria invasion (Hellman et al. 2008). At local spatial scales, the composition and configuration of habitat can be important in determining nutria establishment, distribution, and abundance.

Our objectives were to identify a threshold number of freezing days that feral nutria populations can tolerate for survival and identify unoccupied areas that are included within this threshold by constructing a broad-scale climate model, identify areas of future concern by using climate change models to predict and model changes in number of freezing days in 2050, identify areas of potential suitable nutria habitat by constructing a habitat suitability model on a local scale, and merge broad- and local-scale habitat models to project current nutria habitat distribution and projected distribution in 2050. At a broad geographic scale, we predicted number of freezing days limited nutria distribution. For our local-scale habitat model, we predicted that proportion of area covered by wetlands, stream density, and wetland size would be positively related to nutria presence and wetland distance would be negatively related to nutria presence.

STUDY AREA

We examined nutria distribution within 18 states in the continental United States that annually experience freezing temperatures and currently have or possibly could be invaded by nutria. Our focus was among states at the northern-most extent of current nutria distribution and predominantly east of the Mississippi River, or in the case of Iowa and Missouri adjacent to the Mississippi River.

METHODS

Broad-Scale Climate Model

We compiled and combined nutria occurrence data for 2006–2015 based on a 10-year nutria harvest data set obtained from United States Department of Agriculture-Animal and Plant Health Inspection Service-Wildlife Services (USDA-APHIS-WS) and a USGS database (nas.er.usgs.gov, accessed 15 Feb 2017) of verified nutria observations. All occurrence data were presence-only and had a spatial resolution to the extent of a United States county. There were 60 counties with nutria occurrences located within the study area. We collected a 10-year (2006–2015) climate data set from Daymet version 3 model output data (Thornton et al. 2017) for all states within the study area. Climate data consisted of daily minimum temperature; we converted this to number of freezing days through Python 3.4 (Python Software Foundation, Wilmington, DE, USA) by summing each day a cell was $\leq 0°C$. We used the Daymet data set because of its ability to overcome restriction of study areas with no or poor meteorological measurements (Thornton et al. 2017). We established interpolation by reducing the search radius of weather stations in data-rich areas and increasing it in data-poor areas (Thornton et al. 2017). These techniques produced a smooth grid surface of 1-km^2 cells. We converted climate data to raster data format and imported data into ArcMap 10.4.1 (Environmental Systems Research Institute [ESRI], Redlands, CA, USA).

We used the maximum entropy method, MaxEnt version 3.4.1 (Phillips et al. 2017), for all SDMs. We chose MaxEnt because it outperforms other SDM approaches when using presence-only occurrence data (Elith et al. 2006, Zlonis et al. 2017). With invasive species this method is often the best option because presence-absence survey data are often not available, as was the case here. Furthermore, the use of county-level data likely reduced any sample selection bias (Phillips et al. 2009). We used ArcMap to establish a centroid georeferenced location of each polygon (county) to serve as each occurrence and created an ASCII layer of annual freezing days for MaxEnt compatibility. We removed 25% of presence points to validate models. We chose the bootstrapping option to guarantee removal of testing points with replacement and used the cloglog output format as a relative habitat suitability index. We ran MaxEnt models with 100 iterations.

We collected climate projection data to 2050 from WorldClim (Fick and Hijmans 2017), which consisted of monthly average minimum temperatures generated from the International Panel on Climate Change (IPCC) fifth assessment on global climate models (IPCC 2014). We used 2006–2015 Daymet annual average minimum temperature data and simple linear regression performed in R version 3.4.0 (R Development Core Team 2017) to forecast number of freezing days based on climate change temperature projections in 2050. We then created an ASCII layer of 2050 data for MaxEnt.

Local-Scale Habitat Model

We modeled habitat covariates that best represented the composition and configuration of nutria habitat across the landscape including proportional wetland type, stream density, wetland size, and distance between wetlands. Categorical wetland types included freshwater emergent, freshwater forested-shrub, freshwater pond, lake, and riverine. We downloaded wetland types from the United States Fish and Wildlife Service (USFWS) National Wetlands Inventory (NWI; USFW NWI 2017). We converted this covariate layer and all others to a county-level resolution in ArcMap, using counties as the zone layer. We converted wetland type covariate layers to continuous variables using zonal statistics to determine proportion of each wetland type within all counties in the study area. We then converted all cells within each county to 1-km^2 resolution for all layers because all cells within a county had to be the same resolution for MaxEnt compatibility. We generated the stream density layer from the United States water bodies layer available from ArcGIS Online (ESRI). Using the water body vector data, we selected by attributes to create a vector layer that consisted of only streams, ditches, and canals. We converted this vector layer to raster format with a spatial resolution of 0.01 km^2. We then used focal statistics to calculate the sum of all values within a neighborhood rectangle of 15×15 cells, which we calculated based on an estimated mean dispersal of 1,421 m for male nutria (i.e., 1,500 m/15 cells = 0.01-km^2 resolution; Doncaster and Micol 1989). We calculated mean stream density of counties using the zonal statistics tool in ArcMap. We generated the wetland size layer from USFW NWI (2017) data. We used wetland size in hectares from the attribute table, converted to the raster value, and then used zonal statistics in ArcMap to generate area of wetlands in each county. We used the USFW NWI (2017) wetlands layer to estimate wetland distance. After converting this layer to raster format, we used the raster calculator tool to assign a 1 to all wetlands and zero to the rest of the cells that were not classified as wetlands. We used the Euclidean distance tool to calculate Euclidean distance for each cell to the closest cell classified as a wetland. We calculated the mean distance to wetland within counties using the zonal statistics tool in ArcMap.

We used a Pearson's correlation test in ENMTools (Warren et al. 2010) on all covariates and $r \geq 0.6$ to indicate multicollinearity. We did not find correlations among covariates. We used a backward elimination approach (Parolo et al. 2008, Zlonis et al. 2017) within MaxEnt to create multiple competing models. We first created a full model using all 8 covariates. We ran the model with 100 replicates and eliminated the covariate that was least important to the predictive power of the model. We used the MaxEnt jackknife measure of the area under the curve (AUC) to determine the level of each covariate's relative importance to model prediction. We ran the next model with the remaining 7 covariates over 100 iterations. We repeated this process until a single covariate model remained. For all models, we estimated AUC to evaluate predictive power. Values of AUC range from 0.5 to 1.0, with higher values indicating greater predictive power. An AUC = 0.5 indicates that a model is no better than random in its predictive power (Elith et al. 2006, Phillips et al. 2006). To identify the best model of nutria habitat suitability, we compared competing models with Akaike's Information Criterion corrected for small sample size (AIC*c*; Burnham and Anderson 2002). We calculated AIC*c* values using ENMTools (Warren et al. 2010). We reported all models that we considered and their calculated Akaike weights (w_i) but used $w_i \geq 0.80$ to differentiate the top models (Burnham and Anderson 2002). We used raster calculator in ArcMap and the tenth percentile rule (i.e., a model correctly classified 90% of locations used for training and the lowest 10% of values are deemed unsuitable; Razgour et al. 2011, Bellamy et al. 2013, Zlonis et al. 2017) to estimate total number of counties and percent of study area with suitable nutria habitat.

Multi-Scale Models

We multiplied MaxEnt habitat suitability output for the best broad- and local-scale habitat models to estimate multi-scale habitat suitability. This factored in both number of annual freezing days and composition and configuration of wetland habitat into one multi-scale model. We repeated this process with the 2050 climate projection model. Subsequently, we mapped all habitat suitability model output in ArcMap.

RESULTS

Our broad-scale MaxEnt model identified suitable nutria habitat in 8 states and 10% of the total study area (136 of 1,360 counties), an increase from the 60 counties recorded in our dataset. Model results predicted greater habitat suitability in areas with $\leq$80 annual freezing days (Fig. 1). Most of the Atlantic coast was forecasted as suitable habitat, reaching as far north as lower New Jersey. With climate

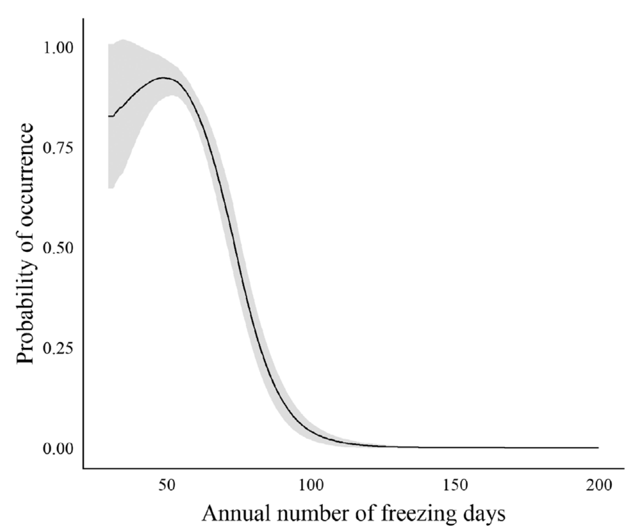

Figure 1. Response curve for number of annual freezing days estimated for nutria habitat suitability from a broad-scale climate MaxEnt model using North American climate data from 2006–2015. Curve shown is the average of 100 iterations, and the shaded area is ±1 standard deviation around the mean response.

change projections in 2050, we predicted suitable nutria habitat in 13 states (i.e., 5 additional states) and 23% of the study area (312 of 1,360 counties).

For the local-scale habitat analysis, a single-covariate model with proportion of freshwater forested-shrub wetlands ranked the highest based on AUC, ΔAIC_c, and w_i values (Table 1). However, a competing 2-covariate model with proportion of freshwater forested-shrub wetlands and distance between wetlands ranked nearly identical based on AUC, ΔAIC_c, and w_i (Table 1). We chose to interpret results of the 2-covariate model because it incorporated composition and configuration dimensions that better reflected the ecological niche of nutria and it demonstrated predictive power (AUC = 0.878), whereas the single-covariate model had a lower AUC value and only included habitat composition. Proportion of freshwater forested-shrub wetlands was positively associated with nutria presence, with the most suitable nutria habitat in landscapes with ≥18% freshwater forested-shrub wetlands (Fig. 2a). Distance between wetlands was negatively associated with nutria presence, with the most suitable nutria habitat characterized by landscapes with wetlands ≤400 m apart (Fig. 2b). The selected model predicted suitable nutria habitat in 18 states (260 of 1,360 counties) and 19% of the study area. A large portion of the Atlantic coast and portions of Illinois, Indiana, Kentucky, Missouri, Ohio, and Tennessee contained suitable habitat.

Under current conditions, the combined broad- and local-scale model predicted suitable nutria habitat in 5 states (57 of 1,360 counties) and 4% of the study area (Fig. 3a). The model predicted large areas of suitable nutria habitat along the Atlantic coast ranging as far north as Delaware and southern New Jersey, and into western Tennessee, western Kentucky, and southern Illinois counties adjacent to the Mississippi River (Fig. 3a; Table A1). With estimated rate of climate change factored in, by 2050 nutria habitat was predicted in 8 states (93 of 1,360 counties) and 7% of the study area (Fig. 3b). By 2050, nutria range is predicted to have expanded along the Atlantic coast states into the southern quarter of New Jersey and continentally within the western quarter of Tennessee, western Kentucky, southern Illinois, and southern Indiana (Fig. 3b; Table A2).

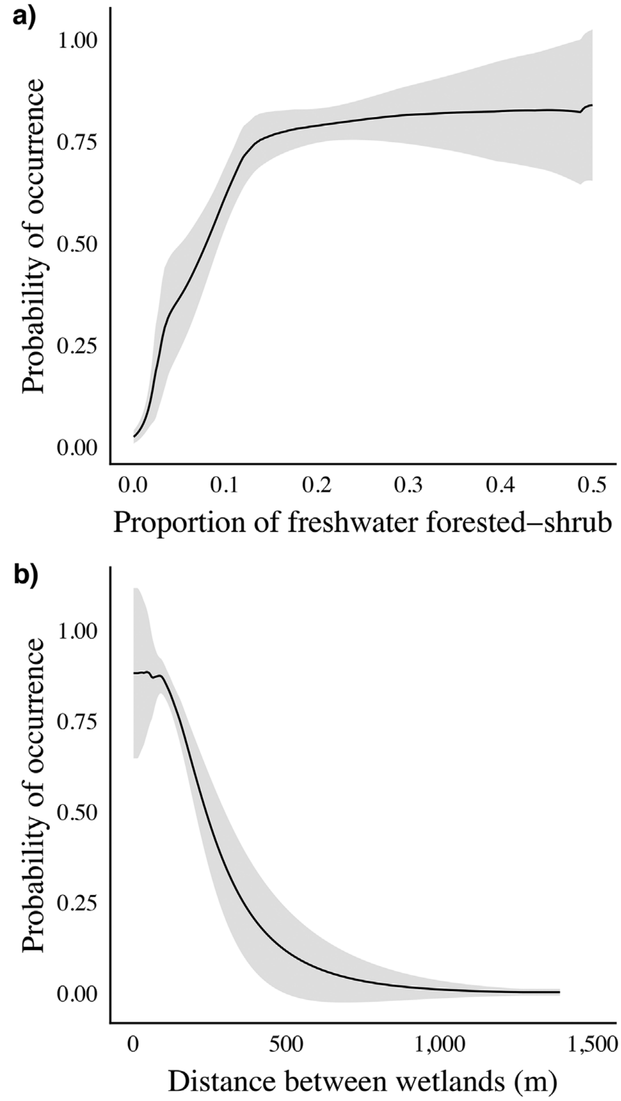

Figure 2. Response curves for model habitat covariates a) proportion of freshwater forested-shrub wetland, and b) distance between wetlands, for the best local-scale MaxEnt model identifying suitable nutria habitat in the eastern United States, 2006–2015. Curves shown are the average of 100 iterations. The shaded area is ±1 standard deviation around the mean response.

Table 1. Competing MaxEnt habitat suitability models for predicting nutria presence in the eastern United States, 2006–2015. We created models using a backward elimination approach, with 100 iterations, and ranked models on difference from the top model in Akaike's Information Criterion corrected for small sample sizes (ΔAIC_c) and Akaike weight (w_i).

Model[a]	AUC[b]	AIC_c	ΔAIC_c	w_i
Freshwater forest	0.864	1,643.95	0.00	0.518
Freshwater forest+wetland distance	0.878	1,644.10	0.15	0.480
Freshwater forest+wetland distance+stream density	0.892	1,654.85	10.90	0.002
Freshwater forest+stream density+wetland distance+area	0.913	1,704.40	60.45	<0.001
Freshwater forest+lake+stream density+wetland distance+area	0.925	1,798.04	154.09	<0.001
Freshwater forest+lake+river+stream density+wetland distance+area	0.931	1,928.12	284.17	<0.001
Freshwater forest+pond+lake+river+stream density+wetland distance+area	0.932	2,025.66	381.71	<0.001
Freshwater forest+emergent+pond+lake+river+stream density+wetland distance+area	0.955	2,392.70	748.84	<0.001

[a] Covariates included proportion of freshwater forested-shrub wetland (freshwater forest), lake, riverine (river), freshwater pond (pond), and freshwater emergent wetland (emergent); distance to nearest wetland (wetland distance); stream density; and wetland area (area).
[b] Area under the curve.

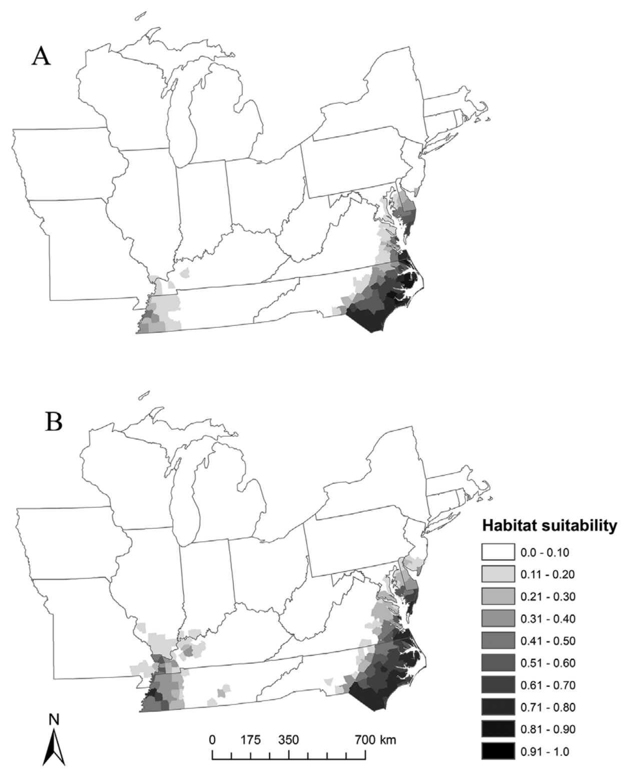

Figure 3. Output maps from multi-scale suitability models, broad- and local-scale models combined, identifying nutria habitat for a) 2015 conditions, and b) 2050 projection with climate change. Darker colors represent areas of high habitat suitability, whereas lighter colors represent lower suitability.

DISCUSSION

At a broad spatial scale, nutria habitat was isolated to areas with ≤80 annual freezing days. Climatic factors are commonly a dominant influence on species distribution at broad spatial scales (Pearson and Dawson 2003). Past studies suggested distribution of nutria was influenced by cold winter temperatures (Gosling et al. 1981, Doncaster and Micol 1989). Ehrich (1962), however, observed nutria could survive cold temperatures during severe winters in Patagonia, which is part of their native range, but sheet-ice formation on water bodies caused high mortality. Thus, we chose to isolate and model nutria habitat at a broad spatial scale, given the increased likelihood of sheet-ice formation as annual number of freezing days increased.

Our model based solely on annual number of freezing days is similar to other bioclimatic envelope models, whereby an association is inferred between a species' occurrence data and climate variables (Brandt et al. 2017). Bioclimatic envelope models can be useful for predicting potential change in distribution of species, but they can be limited because they do not consider specific details of a species' ecology important in determining distribution (Araújo and Peterson 2012, Real et al. 2013).

Bioclimatic envelope models can be useful as the first assessment to identify the location and timing of invasive species range expansion (Garcia et al. 2016). Once climate conditions are satisfied, however, local-scale features can become dominant factors influencing the presence of invasive species (Pearson and Dawson 2003). Our local-scale model suggests areas with high proportions of freshwater forested-shrub wetlands (i.e., swamps) near other wetlands are likely to support nutria populations. Freshwater swamps possess an overstory of trees, an understory of shrubs and young trees, and a dense herbaceous layer (Cowardin et al. 1979) that may provide nutria thermal and foraging habitat during cold winter temperatures. Swamps are productive systems that provide a high diversity of plant species (Lugo et al. 1988) suitable for nutria. In Louisiana swamps, nutria diets varied among sites and seasons; however, common duckweed (*Lemna minor*) and common duckmeat (*Spirodela polyrrhiza*) were preferred food items during all seasons (Bertolino et al. 2012). Borgnia et al. (2000) found duckweed (*Lemna* sp.) was the most consumed food source in the summer and fall in the Pampas region of Argentina, which is a native area of nutria. Wilsey et al. (1991) also reported nutria consumed multiple sedge (*Carex* spp.) and rush species (*Schoenoplectus* spp.) in emergent wetlands during spring. Emergent wetlands are frequently close to freshwater swamps and could be ideal for nutria foraging. Freshwater swamps are typically fed by groundwater or an outside water source, such as a flooded river or lake (Mitsch and Gosselink 2015), which may be beneficial to nutria because they prefer foraging near edges of slow-flowing water (Borgnia et al. 2000).

Freshwater rivers or lakes connecting swamps could also maintain high connectivity in the landscape and allow nutria to disperse between wetlands. We included stream density as a covariate in our competing models to more directly include wetland connectivity, but it was not included in our best models. We suggest this may be due to both the coarseness of the occurrence data used (i.e., county level) and the classification system of wetland vector data used (e.g., streams were included within the borders of forested-shrub wetland shapefiles). Nutria dispersal rates and home-range sizes vary considerably in literature. Annual minimum convex polygon home ranges in the United States ranged from 2.7 ha (Denena et al. 2003) to 28.8 ha (Nolfo-Clements 2009). Movement patterns of nutria vary based on location of site, wetland type, and time of year (Doncaster and Micol 1989). The wetland distance covariate overall had minimal contribution to the best MaxEnt model, but it was maintained through the backward elimination process and ranked high in relative importance to model prediction based on the MaxEnt jackknife measure of test AUC.

Our models are likely conservative in predicting potential distribution of nutria habitat and range expansion. The rate of climate change is not certain and may accelerate beyond IPCC (2014) estimates used here, which would further increase nutria range projections. Nutria may adapt to an increased duration of freezing conditions, allowing them to expand their range farther north. Ehrich (1962) reported some nutria populations were able to use stands of herbaceous vegetation adjacent to wetlands as refugia when wetlands froze over, thus surviving extended freezing conditions. Additionally, the coarseness of our broad-scale model likely did not identify local phenomena (D'Adamo et al. 2000), such as thermal pollution associated with industrial and urban centers. Thermal pollution would likely decrease the annual number of freezing days and provide viable habitat for nutria beyond the projected range of our models.

MANAGEMENT IMPLICATIONS

We suggest a hierarchical modeling approach, as presented in this study, may be more beneficial to management for forecasting potential distribution of invasive species and is recommended for future nutria control efforts. Managers who are concerned about possible nutria range expansion can use this hierarchical modeling framework to identify areas for surveillance and prioritize control efforts. At a broad scale, managers should identify areas with ≤80 annual freezing days, and then examine amount of freshwater forested-shrub wetlands and proximity to other wetlands as local-scale components of nutria habitat. Riverine and freshwater emergent systems without continuous sheet-ice formation and close to forested-shrub wetlands also may important areas to monitor for nutria presence.

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APPENDIX A . COUNTIES CONTAINING SUITABLE NUTRIA HABITAT

Table A1. Counties in the eastern United States that contain suitable nutria habitat in 2015 based on multi-scale suitability models, broad- and local-scale models combined.

State	County
Delaware	Sussex
Maryland	Dorchester, Somerset, Wicomico, Worcester
North Carolina	Beaufort, Bertie, Bladen, Brunswick, Camden, Carteret, Chowan, Columbus, Craven, Cumberland, Currituck, Dare, Duplin, Edgecombe, Gates, Greene, Halifax, Harnett, Hoke, Hyde, Johnston, Jones, Lenoir, Martin, Nash, New Hanover, Onslow, Pamlico, Pasquotank, Pender, Perquimans, Pitt, Richmond, Robeson, Sampson, Scotland, Tyrrell, Washington, Wayne, Wilson
Tennessee	Haywood, Lauderdale, Shelby
Virginia	Accomack, Chesapeake, Gloucester, Isle of Wight, Mathews, Poquoson, Suffolk, Virginia Beach, York

Table A2. Counties in the eastern United States that are projected to contain suitable nutria habitat in 2050 based on multi-scale suitability models, broad- and local-scale models combined, and forecasted number of freezing days based on climate change temperature projections in 2050.

State	County
Delaware	Kent, Sussex
Illinois	Alexander, Pulaski
Kentucky	Ballard, Carlisle, Fulton, Hickman, Hopkins, Marshall, McCracken
Maryland	Dorchester, Somerset, St. Mary's, Wicomico, Worcester
New Jersey	Cape May
North Carolina	Beaufort, Bertie, Bladen, Brunswick, Camden, Carteret, Chowan, Columbus, Craven, Cumberland, Currituck, Dare, Duplin, Edgecombe, Franklin, Gates, Greene, Halifax, Harnett, Hertford, Hoke, Hyde, Johnston, Jones, Lenoir, Martin, Moore, Nash, New Hanover, Northampton, Onslow, Pamlico, Pasquotank, Pender, Perquimans, Pitt, Richmond, Robeson, Sampson, Scotland, Tyrrell, Washington, Wayne, Wilson
Tennessee	Carroll, Chester, Crockett, Dyer, Fayette, Gibson, Hardeman, Haywood, Lake, Lauderdale, Madison, McNairy, Obion, Shelby, Tipton, Weakley
Virginia	Accomack, Charles City, Chesapeake, Gloucester, Hopewell, Isle of Wight, James City, Mathews, Poquoson, Prince George, Southampton, Suffolk, Surry, Sussex, Virginia Beach, York