1-4-2017

Evaluating Simplistic Methods to Understand Current Distributions and Forecast Distribution Changes Under Climate Change Scenarios: An Example With Coypu (Myocastor coypus)

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Citation Details

Jarnevich C.S., Young N.E., Sheffels T.R., Carter J., Sytsma M.D., Talbert C. 2017. Evaluating simplistic methods to understand current distributions and forecast distribution changes under climate change scenarios: An example with coypu (Myocastor coypus). NeoBiota 32(1):107-125.

NeoBiota 32: 107–125 (2017)
doi: 10.3897/neobiota.32.8884
http://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Evaluating simplistic methods to understand current distributions and forecast distribution changes under climate change scenarios: an example with coypu (*Myocastor coypus*)

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Academic editor: *T. Blackburn* | Received 19 April 2016 | Accepted 27 June 2016 | Published 4 January 2017

Citation: Catherine S Jarnevich CS, Young NE, Sheffels TR, Carter J, Sytsma MD, Talbert C (2017) Evaluating simplistic methods to understand current distributions and forecast distribution changes under climate change scenarios: an example with coypu (*Myocastor coypus*). NeoBiota 32: 107–125. https://doi.org/10.3897/neobiota.32.8884

Abstract

Invasive species provide a unique opportunity to evaluate factors controlling biogeographic distributions; we can consider introduction success as an experiment testing suitability of environmental conditions. Predicting potential distributions of spreading species is not easy, and forecasting potential distributions with changing climate is even more difficult. Using the globally invasive coypu (*Myocastor coypus* [Molina, 1782]), we evaluate and compare the utility of a simplistic ecophysiological based model and a correlative model to predict current and future distribution. The ecophysiological model was based on winter temperature relationships with nutria survival. We developed correlative statistical models using the Software for Assisted Habitat Modeling and biologically relevant climate data with a global extent. We applied the ecophysiological based model to several global circulation model (GCM) predictions for mid-century. We used global coypu introduction data to evaluate these models and to explore a hypothesized physiological limitation, finding general agreement with known coypu distribution locally and globally and support for an upper thermal tolerance threshold. Global circulation model based model results showed variability in coypu predicted distribution among GCMs, but had general agreement of increasing suitable area in the USA. Our methods highlighted the dynamic nature of the edges of the coypu distribution due to climate non-equilibrium, and uncertainty associated with forecasting future distributions. Areas deemed suitable habitat, especially those on the edge of the current known range, could be used for early detection of the spread of coypu populations for management purposes. Combining approaches can be beneficial to predicting potential distributions of invasive species now and in the future and in exploring hypotheses of factors controlling distributions.

Keywords
Ecophysiological model, correlative model, coypu, nutria, climate change

Introduction

Understanding species distributions and forecasting potential distributional changes with changing climates is a common goal in ecology. Invasive species provide a unique opportunity to evaluate factors controlling distribution using introduction information to evaluate different hypotheses. Species distribution models (SDM) have a wide range of applications ranging from conservation to invasive species management. There are several different approaches to developing SDMs, including mathematical models, defined a priori, that causally relate a species presence to the environment, and statistical models based on direct correlations between observations of the species and the environment (Dormann et al. 2012).

Correlative models assume that the species being modeled is in equilibrium with its environment, that the current distribution represents basic habitat requirements of the species, and that these requirements are constant through time (Pearson and Dawson 2003). These assumptions are known to be unrealistic, especially for invasive species that are often still spreading in their invaded ranges (Araújo and Peterson 2012; Elith et al. 2010). Correlative models are relatively simple to parameterize, requiring location data for a species and associated environmental data (Kearney and Porter 2009). Ecophysiological based models, on the other hand, are often more difficult to parameterize because they generally require detailed information about the physiological requirements of the species. However, ecophysiological based models may be more appropriate for forecasting species distributions under climate change scenarios due to their causal nature, and the simple and reasonable assumption that physiologically limiting mechanisms are maintained in the models (Dormann 2007).

The coypu (*Myocastor coypus* [Molina, 1782]) is a large, semi-aquatic, invasive rodent native to South America south of 23° latitude (Ehrlich 1967; Woods et al. 1992). The native range includes southern Brazil, Bolivia, Paraguay, Uruguay, Argentina, and central and southern Chile (Gosling and Baker 1991). The coypu has been introduced around the world over the last century for fur farming (Carter and Leonard 2002), but has also been released as a game animal and as a management strategy to control aquatic vegetation (Bounds and Carowan 2000). Feral populations quickly established throughout the introduced range when individuals escaped from farms or were released when fur markets declined. Coypu are now established on every continent except Australia and Antarctica (Carter and Leonard 2002). In the USA, 15 states are considered to have stable or increasing coypu populations (Bounds and Carowan 2000). The global scale introduction, with sufficient time to allow spread in many areas, can be used as an experiment to test if thermal boundaries on coypu distribution exist.

The coypu is a generalist herbivore, with a diet that includes all types of plant material, including leaves, stems, roots, and bark (Willner et al. 1979). Coypu over-utilize preferred species (Borgnia et al. 2000), but are able to change food habits seasonally based on availability of food sources (Abbas 1991; Wilsey et al. 1991). Thus, it is not believed that food or habitat are limiting factors in their distribution. In their introduced range, coypus experience high mortality during periods of sustained freezing temperatures due to both physiological constraints and the lack of available food resources during these events (Doncaster and Micol 1989; Gosling et al. 1981; Willner et al. 1979). There is no evidence of an upper thermal limit for coypus, but we can explore this theory using observed data from the native range and introduction success around the globe.

Using coypu as a test case, we examined and compared the utility of using a very simplistic ecophysiological based model versus a correlative model to predict current and future coypu distribution. We used independent regional and global distribution information to validate the two approaches. Specifically, our objectives were to: 1) evaluate the relationship between known physiological limitations and geographical distribution, 2) evaluate a hypothesized physiological limitation using native range and introduction success information, 3) predict future distribution based on climate change scenarios, and 4) evaluate the benefit of using both modeling approaches. Given the economic and ecological impacts of coypu in invaded ranges, secondary objectives were to develop a current model of potential suitable habitat for coypu within the USA and globally and to investigate possible distribution changes under potential climate change to inform management strategies.

Methods

Occurrence data

Global occurrence records for coypu were downloaded from the Global Biodiversity Information Facility (GBIF; gbif.org; March 4, 2011). The data were inspected, and records with a resolution greater than 30 minutes, our model resolution, were removed due to accuracy issues. We also removed presence locations in countries or states with a status of never established or extinct, retaining only those with a status of country of origin, escape or release, range expansion, or eradicated as defined by a global review of coypu distribution (Carter and Leonard 2002).

Environmental data

For the USA, we used monthly mean, minimum and maximum temperature data at a 4-km spatial resolution between 2003 and 2007 for our analyses (PRISM Group 2007). This time frame is biologically meaningful in that it matches the average lifespan of an individual, and is data-driven in that it matches the time frame of the sub-watershed scale (hydrologic unit code [HUC] 12) data used to validate the model in the Pacific Northwest, USA. Global environmental data were obtained from WorldClim (Hijmans et al. 2005). These data were averaged by month between 1950 and 2000 at a 30 arc second resolution. Thus, the national-scale climate data had a fine temporal resolution (monthly data) that matched some data collection whereas the global climate data had a finer spatial resolution with a coarse temporal resolution (50-year average).

Ecophysiological based modeling

We developed ecophysiological based models at the continental USA and the global scale, based on known physiological constraints on coypu. This species has known winter temperature tolerances that are thought to be the primary limiting factors on their distribution, at least in temperate regions (Gosling et al. 1983). Gosling et al. developed a population simulation model based on observed relationships between sequences of freezing days (defined as minimum temperature < 0 °C and maximum temperature < 5 °C) and body fat, litter frequency, litter size, and mortality. This model showed that a sequence of freezing days resulted in population declines due to adverse effects on the four measured characteristics, and Doncaster and Micol (1990) reported a 71% decrease in population density after canals were frozen for 20 consecutive days in France. In addition, coypu heavily depend on aquatic environments and are limited to environments within the transition zone between aquatic and upland environments (D'Adamo et al. 2000; Doncaster and Micol 1989; Guichón et al. 2003). We used this information on known coypu requirements (sensitivity to cold temperatures and need for aquatic environment) to define a model of habitat suitability rather than allowing a statistical model to detect relationships between habitat suitability and coypu presence.

For the continental USA we developed two different ecophysiological based models using monthly climate data from the PRISM data set at 4-km resolution; one using a five-year period (2003 to 2007) and another using a three-year period (2005 to 2007), hereafter referred to as US 5yr and US 3yr. We used two different time periods to assess the importance of inter-annual climatic variability on predicted distribution. We calculated the number of months within each time period that had a minimum temperature of less than 0 °C and a maximum temperature of less than 5 °C. Given the negative relationship between coypu populations and sequences of freezing days, we defined any month with average values meeting these criteria as unsuitable for coypu survival. To address the water limitation we developed a layer of arid locations by identifying locations in the USA with annual precipitation less than 250 mm, based on PRISM average annual precipitation from 2003 to 2007.

For the global ecophysiological model, we used WorldClim monthly data averaged from 1950 to 2000 at a 30 arc second resolution (~1 km), hereafter referred to as Global 50yr. Unsuitable environments were defined as locations with any month meeting the criteria of average minimum temperature less than 0 °C and average maximum temperature less than 5 °C. We again masked out arid regions, defined as areas with annual precipitation less than 250 mm based on the WorldClim average annual precipitation layer.

Correlative modeling

We used the VisTrails software (Freire et al. 2006) with the Software for Assisted Habitat Modeling (SAHM) package (Morisette et al. 2013) to develop correlative models of global coypu distribution using a Generalized Linear Model (GLM). We used GLMs because this technique creates simple models and has been recommended for model generalization (i.e., transferability to novel environment or time periods, Heikkinen et al. 2012). We generated background points using two different methods: a random generation of 10,000 locations within countries from which our data set had location records, referred to as GLM country, and a targeted background approach using location data for muskrats (*Ondatra zibethicus*), referred to as GLM targeted (Suppl. material 1: Figure 1). We downloaded muskrat data from GBIF and cleaned it by dropping records that had a spatial resolution greater than 30 min, removing fossil records and removing records from countries not known to have muskrats. The target background approach of using locations for similar species is recommended when using a presence-background method where the data are likely to have sampling bias (Phillips et al. 2009). Coypu and muskrats are sympatric species because both rodents are aquatic, are herbivores, are burrowers, and have similar global distributions (Ruys et al. 2011). By using a targeted background approach, biases in the presence locations are also assumed to occur in the background and thus cancel each other to some degree, similar to presence and absence data collected using the same methodology.

The number of environmental variables from the global WorldClim data set used in the GLM was limited to six based on the known physiology of coypu and included mean diurnal range, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation seasonality, and precipitation of warmest quarter. Environmental variables were reduced by removing one of each pair of highly correlated environmental variables (maximum of Spearman rank coefficient, Pearson's product moment or Kendall tau rank; $|r| > 0.7$ following the recommendation of Dormann et al. (2013)) and biological knowledge of the species.

Using a threshold defined as maximizing sensitivity plus specificity divided by two, we created binary predictions of suitable and unsuitable habitat for the correlative models.

Liu et al. (2013) recommended this threshold because it is transferable between methods that use presence-absence and presence-background. The binary predictions were then used to create equal-weight ensemble predictions of habitat suitability for coypu. We created two sets of ensemble models, three for the USA and one for the globe. The USA ensembles included an ensemble of the correlative models (GLM country and GLM targeted), another of the three ecophysiological based models (US 3yr, US 5yr, and global 50yr), and another of all five models. The global ensemble model was created using all three global models including the global 50yr, the GLM country, and GLM targeted models.

Model evaluation

The models were evaluated using zonal statics at two scales; sub-watershed hydrologic unit code (HUC12) and the USA state boundaries. Standardized spatial surveys completed by on-the-ground fish and wildlife biologists for Oregon and Washington provided coypu density estimates at the HUC12 level and were used as an independent model validation (Sheffels 2013). Using the binary model predictions, we calculated zonal statistics using ArcGIS version 10.0 (ESRI, 2011) for each HUC12. If any location within a HUC12 was classified as suitable by the model, the entire HUC12 was defined as suitable. HUC12 coypu density estimates were grouped within four density classes, >100, 11–100, 1–10, and 0 individuals, and the percent of HUC12 units that classified as suitable for each model were calculated for each density class. The models were also evaluated using zonal statistics identifying the number of USA states by coypu status (i.e., never established/extinct, present, no data and eradicated) identified by Carter and Leonard (2002). Again, if a state had any locations within it identified as suitable by the model, the state was defined as suitable, while a state was defined as unsuitable if it did not have any suitable habitat (i.e., no suitable locations within entire state).

We evaluated the global models using two additional methods. Similar to the state level evaluation, we used country level zonal statistics compared to the coypu status identified by Carter and Leonard (2002) for countries. Countries were classified into two coypu occurrence statuses: present (status of present or eradicated) and absent (status of never established or extinct). A country was classified as suitable habitat if any location within the country was predicted suitable based on the model. In addition, we used independent georeferenced locations as another evaluation metric. These independent records were compiled by searching the social media site 'YouTube' for the keywords: 'bieberratte' and 'wasserratte' (German), 'beverrat' (Dutch), 'castorino' (Italian), 'coypu' (British English, Spanish), 'nutria' (American English, Italian), 'ragondin' (French), Нутрия (Russian, Kyrgyzstani, Uzbekistani). The coypu in the videos had to be a naturally occurring population and the location of where the video was taken provided. Videos were examined to make certain that other species were not being misidentified as coypus. Videos where coypu were held as pets or in other confined situations such as fur farms, zoos or aquaria or for which location could not be determined were excluded. For videos not in English or French we used 'Google Translate' as an approximate translation tool to determine the circumstances and location. Since our focus was documenting the range of coypu, once presence was determined in a particular location we excluded videos from those regions on future searches. Finally, we used documents from national reports such as the 'Red Book Data and Invasive Species Korea' or personal communications from trusted researchers to verify regional presence. We used R version 2.15 (R Core Team, 2012) and the caret package (Kuhn, 2013) to calculate sensitivity, specificity and percent correctly classified for each global model based on the model predictions and either the classification by Carter and Leonard (2002) or the independent locations.

Forecasting distributions

We applied our ecophysiological based rule-set to future climate data. We obtained historic data from the Maurer data set (Maurer et al. 2007), which covers the USA at 1/8th degree (~12km). These data were the reference data set used to downscale the global climate projections (GCMs) from the World Climate Research Programme's Coupled Model Intercomparison Project phase 5 (CMIP5) projections using the monthly bias correction spatial disaggregation (BCSD) technique (Reclamation 2013). These downscaled GCMs (listed in Suppl. material 1: Table 1) provided monthly projections of total precipitation and monthly average temperature. We quantified the amount of suitable habitat (i.e., the number of pixels meeting the criteria of monthly minimum temperature >0 °C or monthly maximum temperature >5 °C) for the Maurer dataset (1950 to 2013) and the 12 downscaled GCMs available (1950 to 2013 for historic comparison; 2014 to 2100 as climate forecasts). We calculated the forecasts for all four representative concentration pathways (RCPs), which describe four different greenhouse gas concentration trajectories. We also generated maps of suitable habitat based on the Maurer dataset for 2003 to 2013 and an ensemble of downscaled GCMs for 2006 to 2016 to assess how well the GCMs performed currently when compared to the observations on which they were calibrated. Because the forecasted GCMs began in 2006, we were unable to have complete overlap in the decades for comparison. We applied our criteria for suitable habitat to the GCMs for the period 2040 to 2050 to assess how coypu distribution may change in the future. For this forecast we only used the 4.5 RCP, as RCPs do not begin to diverge significantly until after mid-century.

Results

Model results

For the ecophysiological based models, we produced layers with the number of months for each cell that did not meet the required temperature criteria. For the US 5yr model, the number of months with unsuitable temperature conditions ranged from 0 to 41, while for the US 3yr model the maximum number of unsuitable months was 28.

The GLM country model retained all six environmental variables in model fitting, while the GLM targeted model dropped average annual precipitation and mean diurnal range. Average minimum temperature of the coldest month was the most important predictor in both models, with a logistic shape where suitability began to steeply increase from zero around -10 °C and climbing to 1.3 °C before reaching an index value defined as suitable. Both models retained temperature of the warmest month, with a generally positive relationship when considered with other variables. However, a function considering that predictor alone revealed a hump shaped relationship. Internal cross validation produced good assessment metrics for both models. The GLM country model had a cross-validation area under the receiver operating characteristic curve (AUC) of 0.94 and a true skill statistic (TSS) of 0.76, while the GLM targeted model had a cross-validation AUC value of 0.91 and TSS of 0.70. To produce binary maps, the GLM country threshold was 0.14 and the GLM targeted threshold was 0.44.

USA Assessment

All models performed well when compared to the HUC12 coypu density data (Table 1). All HUC12 sub-watersheds with a coypu density greater than 100 individuals per sub-watershed were predicted by all models to contain suitable habitat. The percentage of coypu density HUC12 classes of 11-100 and 1-10 predicted as suitable by the models were also high (> 87%), while HUC12 areas with a reported density of 0 had a much lower percentage predicted as suitable (Table 1). Model predictions compared to USA state-level classifications showed the models were better at correctly identifying states with established coypu populations than in predicting states that had populations that are now extinct or states where coypu have never been established (Fig. 1). Only the US 3yr and US 5yr models predicted a state classified as having an established coypu population as unsuitable (state of Delaware), while the other three models correctly classified all states with coypu status as present. For states with no data on population status, three to 12 of them were predicted to contain suitable habitat.

The ecophysiological based ensemble model results show greatest agreement in suitability in the southeastern USA from Texas to North Carolina and along the Pacific coast from Washington to southern California (Fig. 2a). Currently, coypu are not in California. We hypothesize this is due to a geographic barrier to their expansion south from Oregon. The waterways containing coypu in Southwestern Oregon are not hydrologically connected to the ones in Northern California and mountain ranges separate the two. The greatest area of model discrepancy was along the border between Tennessee and Arkansas, where the US 3yr model predicted a more northern distribution limit compared to the US 5yr and global 50yr models (Fig. 2a). These

Table 1. Model correct classification by coypu density class. Numbers represent the percent of sub-watersheds (Hydrologic Unit Code 12s) in Washington and Oregon classified as suitable by each model (generalized linear models [GLM]; row) and coypu density class (>100, 11–100, 1–10, and 0 individuals; column).

	>100	11–100	1–10	0
GLM country	100	100	93	16
GLM targeted	100	100	95	18
Global 50yr	100	98	87	15
US 3yr	100	99	91	12
US 5yr	100	99	89	12

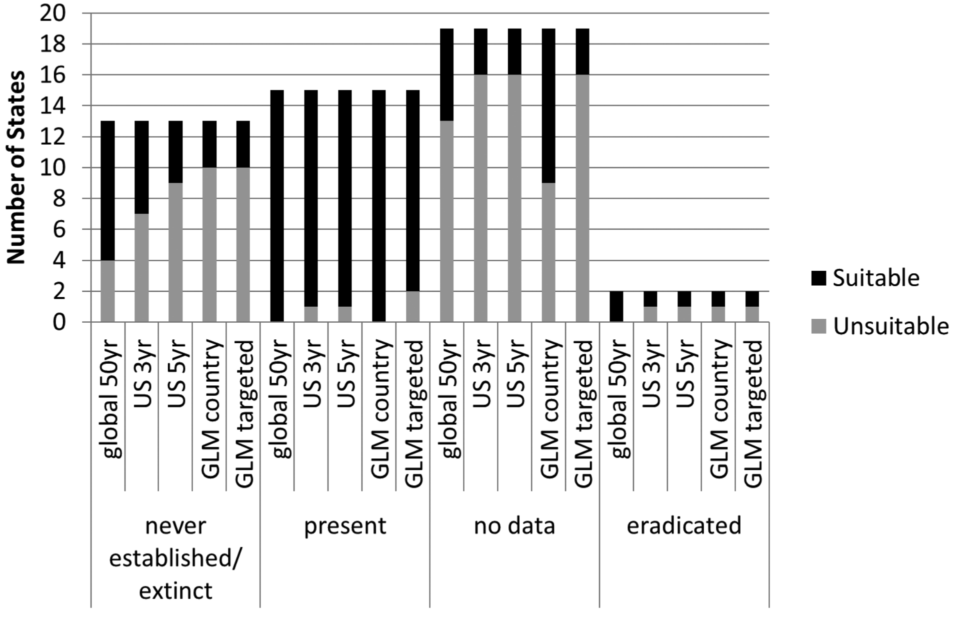

Figure 1. USA state assessment of the five models. The assessment includes the number of USA states classified with at least some suitable (1) or no suitable (0) coypu (*Myocastor coypus* [Molina, 1782]) habitat for each coypu status class (never established/ extinct, present, no data, or eradicated) as defined by Carter and Leonard (2002) for each model of the five models.

models agreed on suitable/ unsuitable classification 92% of the time. The GLM targeted model predicted a much greater amount of suitable habitat across the southern USA than the GLM country model (Fig. 2b). The ensemble of all five models for the USA revealed that the addition of the correlative models to the ecophysiological based models resulted in a more restricted distribution of agreement (Fig. 2c). Model agreement on habitat suitability was more confined to east Texas, Louisiana, Mississippi, and Alabama, mainly following the restricted distribution of the GLM country model. On the Pacific coast, model agreement was restricted to areas in Washington, Oregon and the northern half of California.

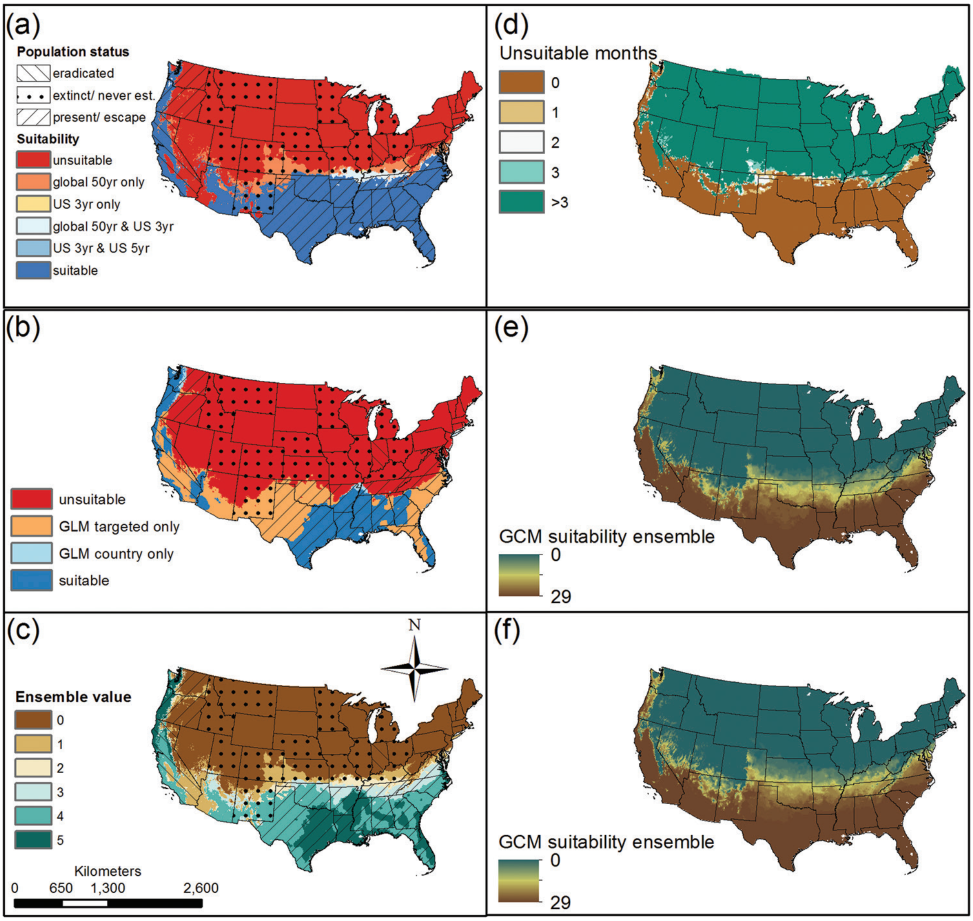

Figure 2. Model predictions for *Myocastor coypus* [Molina, 1782] for **a** an ensemble of US 3yr, US 5yr, and global 50yr **b** an ensemble of GLM country and GLM targeted **c** an ensemble of all five models **d** number of months classified as unsuitable using the Maurer observed climate data for 2001 to 2010 **e** the number of GCMs defining each pixel as suitable (ensemble of the 29 binary downscaled GCMs using the Maurer dataset as the reference) **f** ensemble of the 31 downscaled GCMs average from 2040 to 2050. All maps are overlaid with USA state population status according to Carter and Leonard (2002). Unsuitable habitat is defined as areas where no models predicted the area as suitable, while suitable areas are defined according to which model(s) predicted suitable habitat. Maps are in Albers Equal Area projection.

Global assessment

At the global scale, global 50yr, GLM targeted, and GLM country models had varying levels of performance when compared to country level classification by Carter and Leonard (2002; Table 2). For country level comparison, all models had high sensitivity values (>0.85) and low specificity values (<0.25) with the number of countries correctly classified > 70% (Table 2). When comparing global model performance to independent coypu locations, sensitivity values decreased to 0.73 for all models and specificity values and percent correctly classified increased (Table 2).

An ensemble of the three global models had high agreement in coypu suitability for regions with established invasions (Fig. 3), although all three models only agreed on classification as suitable or unsuitable across 59% of the globe. The GLM targeted and global 50yr models were more similar with 81% agreement between predictions. The GLM targeted model predicted much more of the earth's surface as suitable (59%) compared to the other models (GLM country = 32%; global 50yr = 45%). All models predicted suitable coypu habitat in Western Europe and portions of the USA where coypu populations are known to exist – and where occurrence data were available to fit the models. At least a portion of all countries reporting coypu as native were predicted as suitable by all models. Evaluation of the models in the native range is difficult, however, as range maps that do exist do not provide information on how they were derived, and the rigor with which they were created is questionable.

The GLM country model predicted the least amount of tropical areas as suitable, with the GLM targeted model and the global 50yr model being more similar. However, many of these areas had novel environmental conditions. In dry areas such as North Africa, however, the global 50yr model did not predict suitable habitat due to the added arid region mask. The GLM country model excluded some of these dry areas, while the GLM targeted model included almost all of them.

Ecophysiological based versus Correlative

Model evaluations from HUC coypu density for the northwestern USA show very little difference between ecophysiological based and correlative models (Table 1). The same was true for evaluations at the state level. The greatest difference was for the 'no data' category where the GLM country model predicted suitable habitat in only ten states while the other models predicted suitable habitat in three to six states (Fig. 1).

Table 2. Evaluation metrics for global extent models. Evaluation metrics include percent correctly classified, sensitivity and specificity for global models of coypu (*Myocastor coypus* [Molina, 1782]) habitat suitability (global 50yr: ecophysiological based model based using average monthly temperature for 1950 to 2000, generalized linear model [GLM] country: GLM model using coypu presence locations and random background locations from countries containing coypu locations, and GLM targeted: GLM model using coypu presence locations and targeted background consisting of muskrat locations), evaluated using country level classification according to Carter and Leonard (2002; 'country' columns) and independent coypu location data ('independent' columns).

	Global 50yr		GLM country		GLM targeted	
	Country	**Independent**	**Country**	**Independent**	**Country**	**Independent**
Percent correctly classified	0.7	0.76	0.76	0.76	0.67	0.68
Sensitivity	0.85	0.73	0.97	0.73	0.82	0.73
Specificity	0.25	1	0.17	1	0.25	0.33

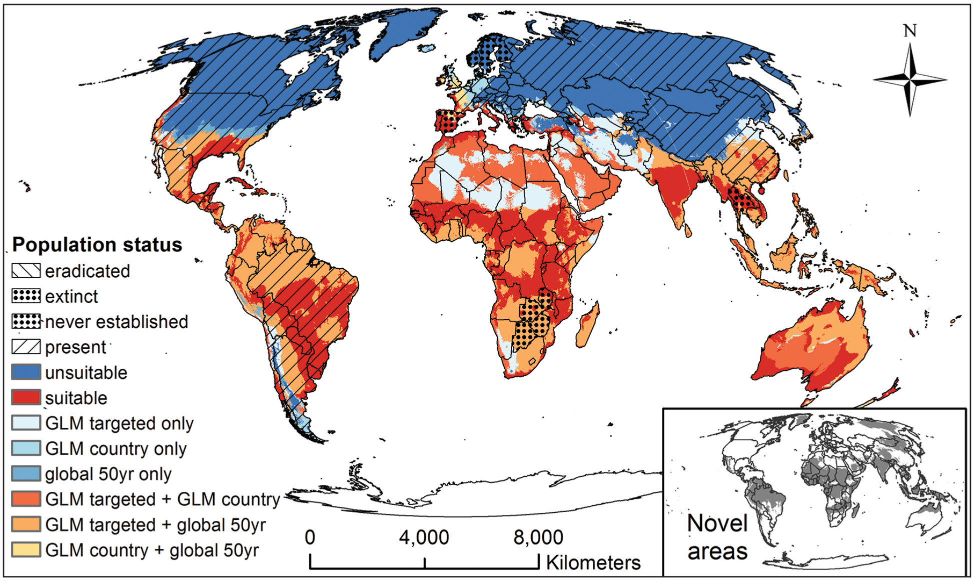

Figure 3. Global predictions of habitat suitability for coypu (*Myocastor coypus* [Molina, 1782]). Ensemble predictions using three models at the global scale including an ecophysiological based model based on average monthly climate data from WorldClim, a correlative model using country background and a correlative model using a taxonomically targeted background approach. Maps are in Mollweide projection.

For the global models, predictions between the correlative models and the ecophysiological based model were again very similar for both country level evaluations and independent location evaluations.

Potential future distribution

There is substantial variation in potential future climate from year to year as well as between GCMs and RCPs (Fig. 4). RCPs do not vary greatly until after mid-century. Comparing predictions of suitability between the modeled climate for current conditions (2006-2016) and the observed climate on which it is based (Maurer 2001-2010) revealed some discrepancies, with a mean disagreement in predictions (over or under prediction) of 6.1% of the area of USA (range of 3.2 to 10.6%). The Maurer dataset defined 34% of the USA as suitable (Fig. 2d). Extremes among the GCMs ranged from giss-e2-r-cc predicting 27% to canesm2 predicting 40% of the USA as suitable during the 2006-2016 period, though both had higher than average levels of disagreement (7.4% and 10.6%, respectively). The average amount of suitable area (32.4%) was comparable to the Maurer reference dataset. The range was similar for 2040 to 2050, with a minimum of 27.5% (ACCESS1-0), a maximum of 44.1% (CSIRO-MK3-6.0) and an average of 35.5%. Only three of the 29 GCMs predicted a decrease in suitable habitat (-3.7%, -0.2%, and -0.2%) and the maximum predicted increase in suitable habitat was 9.4% by HADGEM2-AO. The average increase in suitable habitat was an additional 3.1% of the USA. There was more discrepancy among GCM predictions for the eastern USA than the western USA (Fig. 2e and f).

Discussion

Despite the fact that our ecophysiological based model is relatively simplistic and is based on physiological data from one location, it showed overall agreement with current knowledge of coypu distribution in local regions (e.g., the Pacific Northwest of the USA) and globally. For endotherms, prolonged exposure to thermal stress can decrease fitness and our relatively coarse temporal scale of monthly climate data accounts for extended periods of potentially stressful cold temperatures. There are also likely microclimatic factors that influence coypu distribution at local scales, especially in arid regions where there may be narrow suitable habitat along riparian areas. These results concur with previous research that winter temperatures may limit coypu distribution, at least in the invaded range (Gosling et al. 1983, Doncaster and Micol 1990).

While minimum temperature thresholds have been identified for coypu, thermal tolerance at high temperature has not been studied. This tolerance could be another limiting factor in locations such as the Amazon and portions of Africa where the models did not match known distributions. Examining tropical climate designation using WorldClim climate data to hypothesize an upper thermal limit matched well with known coypu distribution (Fig. 5 and Suppl. material 1: Figure 2). In South America the northern native range boundary has been described as -23 degrees latitude which matches the southern boundary of the tropics (Fig. 5a). Despite their widespread introduction globally, the sole successful establishment in the equatorial region is Lake Naivasha, Africa (Fig. 5b; Carter and Leonard 2002). Lake Naivasha is equatorial (latitude 0°46'S), but its climate, according to WorldClim average monthly temperature data (Hijmans et al. 2005), does not meet the Koppen climate criteria for tropical climatic designation (each month's average temperature >= 18 C; Peel et al. 2007). For our area of interest, the USA, this tolerance is likely not a factor with the exception of the southern tip of Florida, where coypu are absent (Fig. 5c). Location data in the Non-indigenous Aquatic Species database, which is the best source of location data for the southeastern USA, indicates coypu are found throughout Florida north of the tropical designation area (Suppl. material 1: Figure 2 and Fig. 5c). Thus, observational data support the hypothesis of an upper thermal limit, but physiological studies are required to further evaluate this hypothesis.

The baseline dataset (PRISM or WorldClim) and time frame used (3 year, 5 year, 10 year) made a difference in the predictions of current suitable habitat. Climate is not in equilibrium (Fig. 4), and therefore we expect the edges of distributions to be dynamic. An unusually cold winter could negatively affect coypu populations in otherwise suitable areas, which could be re-inhabited later when temperatures are again

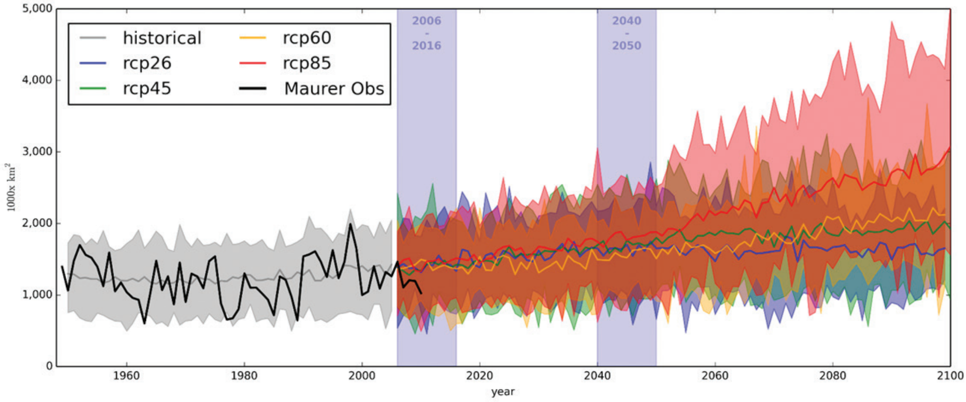

Figure 4. Amount of suitable habitat for coypu by year starting in 1950 and extending to 2100. Amount of suitable habitat is defined as thousands of km² within the continental USA without any months where average minimum temperature was <0 °C while average maximum temperature was also <5 °C. The solid black line from 1950 to 2013 is the Maurer observed dataset, the historical data is the 12 General Circulation Models (GCMs) calibrated between 1950 and 2013 using the Maurer dataset, and the projected climate by the GCMs with the average amount of predicted suitable habitat (solid line) and variation in predicted suitable habitat (solid colored area) for the four different representative concentration pathways (RCPs) describing possible climate futures by the GCMs. The solid vertical bars indicate the time periods for which we created geographic maps of predicted suitable habitat.

favorable. The US 5yr model contained less suitable habitat along the northern border of predicted suitable habitat in the USA due to colder winter temperatures in 2003 to 2004 compared to 2005 to 2007. For Delaware, Carter and Leonard (2002) based their classification of 'present' on reports from 2000. Coypu were not detected in Delaware between 2002 and 2009, but they were again found in 2010. While there are relatively large differences in GCM predictions, the models generally agree that there will be more suitable coypu habitat in the future. Examining a suite of GCMs highlighted the uncertainty that exists in future climate projections. The areas of suitable habitat highlighted by the models, especially those on the edge of the current known range, could be used for early detection of the spread of coypu populations for management purposes.

The model comparisons also are consistent with other studies that produced both ecophysiological based and correlative models (e.g., Martínez et al. 2014). The ecophysiological based models predict more suitable habitat than the correlative models. This pattern is expected as correlative models may capture factors not included in ecophysiological based models such as biotic interactions and unknown physiological limits. Movement restrictions and the biotic and abiotic environment define where a species occurs (Soberon and Peterson 2005). For invasive species, such as the coypu, understanding physiological limits of a species is desirable because constraints on native range distribution imposed by movement restrictions or biotic interactions may

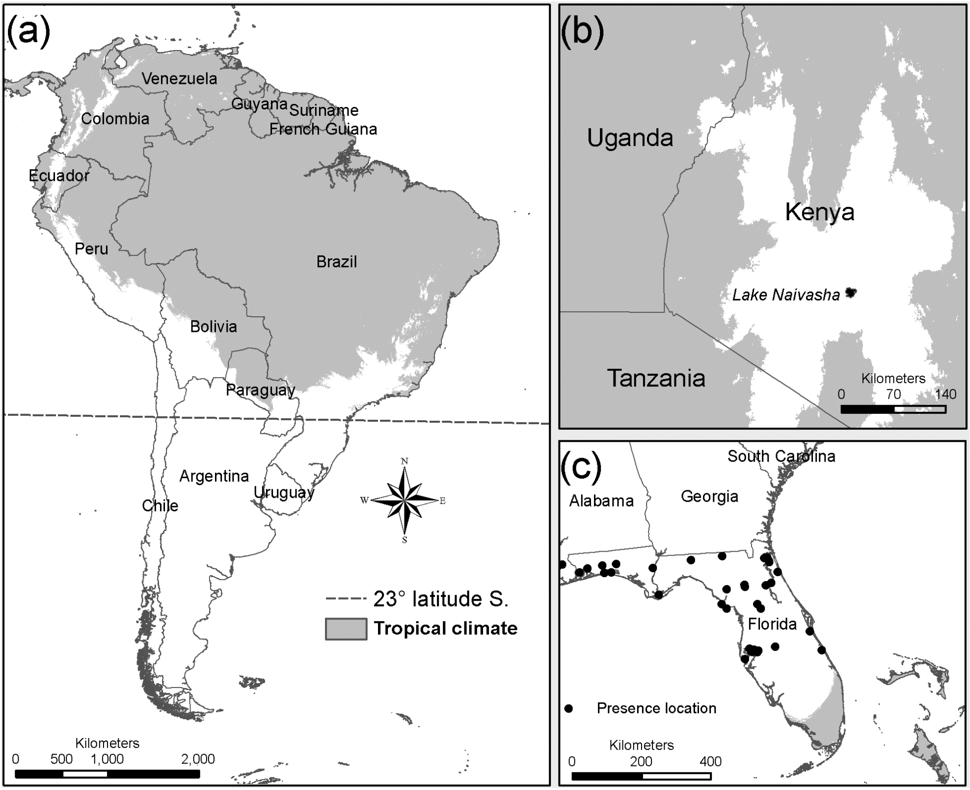

Figure 5. Tropical areas in relation to coypu presence. Areas defined as tropical are shown in **a** South America where coypu are native south of -23° latitude **b** Kenya where coypu have only been reported around Lake Naivasha, and **c** Florida, USA where coypu have not been reported in the southern part. Maps are in Mollweide projection.

not be expected to remain in the invaded range. Having information on physiological tolerances of a species to climate may better define potential distributions beyond a species' native range (Jiménez-Valverde et al. 2011). Additionally, information on the global distribution of invasive species that are widely distributed can assist development of hypotheses about physiological tolerances. These direct linkages to environmental conditions are needed for predicting species' distributions to novel locations or times (Jiménez-Valverde et al. 2011).

Future research could incorporate additional factors into the ecophysiological based model, such as an upper thermal limit. For the correlative model, obtaining more locations from the native range may improve model performance. We know there was particularly poor coverage in our observation data for this region. Finer temporal resolution of global climate data may improve all global models, as 50 year averages do not capture the extremes that may be important for species with distributions limited by thermoregulatory processes.

Conclusions

Overall, the national and global models for suitable coypu habitat performed well. By utilizing two different approaches (correlative and ecophysiological based) that produced similar projected distributions, we have more confidence in our results than we would using a single method. With these models we can now predict where coypu are likely to invade given climatic changes and regional hydrologic networks. These predictions can help focus early detection efforts by identifying areas to monitor for and potentially eradicate nacent coypu populations. Furthermore, the models can provide specific information about which areas might be invaded based on recent weather trends and hydrologic pathways. This is important because it has been demonstrated that the costs of early intervention with respect to a coypu invasion are much less than the costs of the damage they do and control efforts once their populations become established (Bertolino and Viterbi 2010; Panzacchi et al. 2007). Although our ecophysiological based model was rather simplistic and did not require a lot of detailed information about coypu, it still proved useful, especially in conjunction with correlative models. Using combined techniques, even with a simplistic ecophysiological based model such as we used here, could be useful in modeling potential distributions of invasive species now and in the future.

Acknowledgements

The authors would like to thank the U.S. Geological Survey Invasive Species Program for support. We acknowledge the World Climate Research Programme's Working Group on Coupled Modelling, which is responsible for CMIP, and we thank the climate modeling groups (listed in Suppl. material 1: Table 1 of this paper) for producing and making available their model output. For CMIP the U.S. Department of Energy's Program for Climate Model Diagnosis and Intercomparison provides coordinating support and led development of software infrastructure in partnership with the Global Organization for Earth System Science Portals. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

Abbas A (1991) Feeding strategy of coypu (Myocastor coypus) in central western France. Journal of Zoology 224: 385–401. doi:10.1111/j.1469-7998.1991.tb06033.x

Araújo MB, Peterson AT (2012) Uses and misuses of bioclimatic envelope modeling. Ecology 93: 1527–1539. doi:10.1890/11-1930.1

Bertolino S, Viterbi R (2010) Long-term cost-effectiveness of coypu (Myocastor coypus) control in Piedmont (Italy). Biological Invasions 12: 2549–2558. doi: 10.1007/s10530-009-9664-4

Borgnia M, Galante ML, Cassini MH (2000) Diet of the coypu (Nutria, Myocastor coypus) in agro-systems of Argentinean pampas. Journal of Wildlife Management 64: 354–361. doi:10.2307/3803233

Bounds D, Carowan GAJ (2000) Nutria: A nonnative nemesis. Transactions of the North American Wildlife and Natural Resources Conference 65: 405–413.

Carter J, Leonard BP (2002) A Review of the Literature on the Worldwide Distribution, Spread of, and Efforts to Eradicate the Coypu (Myocastor coypus). Wildlife Society Bulletin 30: 162–175. http://www.jstor.org/stable/3784650

D'Adamo P, Guichon ML, Bo RF, Cassini MH (2000) Habitat use by coypu Myocastor coypus in agro-systems of the Argentinean pampas. Acta Theriologica 45: 25–33. doi: 10.4098/AT.arch.00-3

Doncaster CP, Micol T (1989) Annual cycle of a coypu (*myocastor coypus*) population: male and female strategies. Journal of Zoology 217: 227–240. doi: 10.1111/j.1469-7998.1989.tb02484.x

Doncaster CP, Micol T (1990) Response by coypus to catastrophic events of cold and flooding. Ecography 13: 98–104. doi: 10.1111/j.1600-0587.1990.tb00594.x

Dormann CF (2007) Promising the future? Global change projections of species distributions. Basic and Applied Ecology 8: 387–397. doi: 10.1016/j.baae.2006.11.001

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36: 027-046. doi: 10.1111/j.1600-0587.2012.07348.x

Dormann CF, Schymanski SJ, Cabral J, Chuine I, Graham C, Hartig F, Kearney M, Morin X, Römermann C, Schröder B, Singer A (2012) Correlation and process in species distribution models: bridging a dichotomy. Journal of Biogeography 39: 2119–2131. doi: 10.1111/j.1365-2699.2011.02659.x

Ehrlich S (1967) Field studies in the adaptation of nutria to seasonal variations. Mammalia 31: 347–360. doi: 10.1515/mamm.1967.31.3.347

Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. Methods in Ecology and Evolution 1: 330–342. doi: 10.1111/j.2041-210X.2010.00036.x

Freire J, Silva C, Callahan S, Santos E, Scheidegger C, Vo H (2006) Managing Rapidly-Evolving Scientific Workflows Provenance and Annotation of Data. In: Moreau L, Foster I (Eds) Springer, Berlin & Heidelberg, 10–18. doi: 10.1007/11890850_2

Gosling LM, Baker SJ (1991) Coypu. In: Corbet GB, Harris S (Eds) The handbook of British mammals. Blackwell, Oxford, England, 267-275

Gosling LM, Baker SJ, Skinner JR (1983) A Simulation Approach to Investigating the Response of a Coypu Population to Climatic Variation1. EPPO Bulletin 13: 183-192. doi: 10.1111/j.1365-2338.1983.tb01597.x

Gosling LM, Watt AD, Baker SJ (1981) Continuous Retrospective Census of the East Anglian Coypu Population Between 1970 and 1979. Journal of Animal Ecology 50: 885–901. doi: 10.2307/4144

Guichón ML, Borgnia M, Righi CF, Cassini GH, Cassini MH (2003) Social Behavior and Group Formation in the Coypu (Myocastor coypus) in the Argentinean Pampas. Journal of Mammalogy 84: 254–262. doi: 10.2307/1383653

Heikkinen RK, Marmion M, Luoto M (2012) Does the interpolation accuracy of species distribution models come at the expense of transferability? Ecography 35: 276–288. doi: 10.1111/j.1600-0587.2011.06999.x

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965–1978. doi: 10.1002/joc.1276

Jiménez-Valverde A, Peterson AT, Soberón J, Overton JM, Aragón P, Lobo JM (2011) Use of niche models in invasive species risk assessments. Biological Invasions 13: 2785–2797. doi: 10.1007/s10530-011-9963-4

Kearney M, Porter W (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12: 334–350. doi: 10.1111/j.1461-0248.2008.01277.x

Liu C, White M, Newell G (2013) Selecting thresholds for the prediction of species occurrence with presence-only data. Journal of Biogeography 40: 778–789. doi: 10.1111/jbi.12058

Martínez B, Arenas F, Trilla A, Viejo RM, Carreño F (2014) Combining physiological threshold knowledge to species distribution models is key to improving forecasts of the future niche for macroalgae. Global Change Biology 21(4): 1422–1433. doi: 10.1111/gcb.12655

Maurer EP, Brekke L, Pruitt T, Duffy PB (2007) Fine-resolution climate projections enhance regional climate change impact studies. Eos, Transactions American Geophysical Union 88: 504–504. doi: 10.1029/2007eo470006

Morisette JT, Jarnevich CS, Holcombe TR, Talbert CB, Ignizio D, Talbert MK, Silva C, Koop D, Swanson A, Young NE (2013) VisTrails SAHM: visualization and workflow management for species habitat modeling. Ecography 36: 129–135. doi: 10.1111/j.1600-0587.2012.07815.x

Panzacchi M, Cocchi R, Genovesi P, Bertolino S (2007) Population control of coypu Myocastor coypus in Italy compared to eradication in UK: a cost-benefit analysis. Wildlife Biology 13: 159–171. doi: 10.2981/0909-6396(2007)13[159:pcocmc]2.0.co;2

Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12: 361–371. doi: 10.1046/j.1466-822X.2003.00042.x

Peel MC, Finlayson BL, McMahon TA (2007) Updated world map of the Köppen-Geiger climate classification. Hydrol Earth Syst Sci 11: 1633–1644. doi: 10.5194/hess-11-1633-2007

Oregon State University. http://www.prism.oregonstate.edu/ [accessed: February 2008]

Reclamation (2013) Downscaled CMIP3 and CMIP5 Climate and Hydrology Projections: Release of Downscaled CMIP5 Climate Projections, Comparison with preceding Information, and Summary of User Needs. Denver, Colorado, 47 pp.

Ruys T, Lorvelec O, Marre A, Bernez I (2011) River management and habitat characteristics of three sympatric aquatic rodents: common muskrat, coypu and European beaver. European Journal of Wildlife Research 57: 851–864. doi: 10.1007/s10344-011-0497-y

Sheffels T (2013) Status of Nutria (Myocastor coypus) Populations in the Pacific Northwest and Development of Associated Control and Management Strategies, with an Emphasis on Metropolitan Habitats. Dissertation, Portland, Oregon: Portland State University.

Soberon J, Peterson AT (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiversity Informatics 2: 1–10. doi: 10.17161/bi.v2i0.4

Willner GR, Chapman JA, Pursley D (1979) Reproduction, Physiological Responses, Food Habits, and Abundance of Nutria on Maryland Marshes. Wildlife Monographs: 3–43. doi: 10.2307/3830722

Wilsey B, Chabreck R, Linscombe RG (1991) Variation in nutria diets in selected freshwater forested wetlands of Louisiana. Wetlands 11: 263–278. doi: 10.1007/bf03160853

Woods CA, Contreras L, Willner-Chapman G, Whidden HP (1992) *Myocastor coypus*. Mammalian Species 398: 1–8. doi: 10.2307/3504182

Supplementary material 1

Supplementary figures and table

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Data type: Adobe PDF file

Explanation note: Supporting information including global location data used to create models (Supplementary figure 1), global distribution of tropical environments (Supplementary figure 2), and Global circulation model climate data used for forecasts of *Myocastor coypus* distributions (Supplementary table 1).