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ORIGINAL PAPER

Using species distribution models to guide conservation at the state level: the endangered American burying beetle (*Nicrophorus americanus*) in Oklahoma

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Abstract The goal of the Endangered Species Act is to improve the chances of listed species' survival by increasing population levels (US Fish and Wildlife Service in American burying beetle (*Nicrophorus americanus*) recovery plan. Newton Corner, MA, p 80, 1991). If successful, a species will be delisted, but in order to achieve the goal of species recovery the demography, habitat preferences, reproductive biology, and cause of the species decline must be understood. Like many rare invertebrates, information about the endangered American burying beetle (*Nicrophorus americanus*) prior to listing consisted of the taxonomic description and morphological characterization. Surveys for *N. americanus* provide data that can be integrated into spatial models to help predict suitable habitat. Our objective was to model the potential distribution of *N. americanus* and to evaluate these models ability to generate maps of potential habitat, thus focusing recovering efforts. We chose six modelling algorithms that utilized both presence and absence data from beetle surveys conducted throughout eastern Oklahoma. Using area under the curve (AUC) as our evaluation statistic, we found that ten of the twelve models performed within the AUC index category of "potentially useful" (AUC 0.7–0.9). Models utilizing presence only data performed well compared to models built with presence/absence data. This may indicate the weakness of using absence data to indicate unsuitable habitat. Lack of integration into the model of biotic interactions may also be affecting model performance. To improve model performance, the causes of *N. americanus*'s endangered status and its population shrinkage should be considered. Although the best models were not highly accurate, the map of suitable habitat can help to inform conservation biologists of areas with a likelihood of *N. americanus* presence. Overgenerous models can mislead conservation planners in thinking that more areas are highly suitable. If resources are limited for planning preserves and areas of reintroduction, it may be better to be conservative and to limit consideration to the most suitable habitat.

Keywords Ecological niche model · Habitat model · Maximum entropy · Random forest · CART · Regression models

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Introduction

The goal of the Endangered Species Act is to improve the chances of listed species' survival by increasing population levels, as outlined in an endangered species recovery plan (US Fish and Wildlife Service 1991). If successful, this can result in a species being delisted, but in order to achieve the goal of species recovery the demography, habitat preferences, reproductive biology, and cause of the species decline must be understood. However there are disparities in the level of available knowledge for threatened and endangered species. For example, considerable information has been compiled on the status and life history of species such as the Red-cockaded Woodpecker or Mexican grey wolf, but less in known about the Soccoro springsnail or rock gnome lichen (US Fish and Wildlife Service 2009).

The American burying beetle (*Nicrophorus americanus*) was listed as an endangered species in 1989 (Federal

Register 54(133): 29652–29655). Like many threatened and endangered invertebrates, information about *N. americanus* prior to listing consisted of the taxonomic description and morphological characterization (US Fish and Wildlife Service 1991, 2009). Although thousands of *N. americanus* surveys across the United States conducted since listing have contributed to our knowledge of *N. americanus*'s range and populations, they focused on determining species presence and have minimally contributed to our knowledge of its habitat affinities and reproductive biology. Research conducted since its addition to the endangered species list has focused on the breeding season and over-wintering habitat preferences (Lomolino and Creighton 1996; Lomolino et al. 1994; Schnell et al. 2007), population dynamics (Bedick et al. 1999; Holloway and Schnell 1997; Peyton 2003), and best survey practices (Bedick et al. 2004; Creighton et al. 1993). However, we believe much remains to be discovered about the reproductive and over-wintering requirements of *N. americanus.*

Nicrophorus americanus was once considered common throughout eastern North America (US Fish and Wildlife Service 1991), but at the time of its listing, the known range had been reduced to two disjunct populations; one on an island off the coast of Rhode Island and another in eastern Oklahoma. Surveys throughout the historic range since listing have located extant populations in central Nebraska, south-central South Dakota, southeastern Kansas, western Arkansas, and northeast Texas (US Fish and Wildlife Service 1991). Populations in the historic range east of the Mississippi River have not been found.

Endangered species are generally rare for one of two reasons: they were always rare due to habitat specialization or restricted endemism or their population size was substantially reduced due to habitat loss or catastrophic events (Rosenzweig and Lomolino 1997). The cause of *N. americanus* population and range decline over the past 100 years remains uncertain. Sikes and Raithel (2002) presented the following eight possible causes for *N. americanus* decline: pesticide use, artificial lighting, pathogen, habitat loss, vegetation change (both as an old growth woodland specialist or prairie specialist), vertebrate competition, loss of ideal carrion, and congener competition. Of those, they conclude that the most plausible explanation is competition with congeners and vertebrates for carrion and a reduction in optimal prey size. Schnell et al. (2007) suggest that availability of food, in the form of a carcass, during over-wintering will significantly affect the survival of individuals.

Extensive surveys for *N. americanus* within its historic range provide much data that can be integrated into spatial models to help predict suitable habitat. Species distribution models (SDM, also known as habitat suitability or ecological niche models) are used to understand species' distributions (Anderson 2003; Camarero et al. 2005), ecological requirements (Costa et al. 2007; Murphy and Lovett-Doust 2007), locate new populations (Pearson et al. 2007; Peppler-Lisbach and Schräder 2004), plan land conservation (Ortega-Huerta and Peterson 2004; Tole 2006), and predict new habitats associated with climate change (Berry et al. 2002; Pearson et al. 2006). SDMs correlate species occurrence data with environmental data to produce a predictive map of a species' potential distribution or suitable habitat. Different modelling techniques utilize a variety of algorithms to calculate probabilities that a species will occupy a given area. The vast and growing literature on distribution modelling suggest that some techniques are generally more effective, but there is not one algorithm applicable to all species, all data sets, or all research objectives (Elith et al. 2006; Guisan et al. 2006).

A nearly straight north–south line bisecting the eastern third of Oklahoma demarcates the southwest edge of the range for *N. americanus* (Fig. 1). Using specific location information coupled with environmental data, we hope to delineate a less generalized map for potential *N. americanus* habitat and to understand the constraints on the range. Modelling may clarify habitat characteristics and focus conservation efforts. Our objective was to model the potential distribution of *N. americanus* and to evaluate these models' ability to generate maps of potential habitat, thus focusing recovering efforts as well as contributing to the knowledge of this species ecology. Our purpose is to evaluate the ability of current modelling techniques to predict suitable habitat for *N. americanus* using presence-absence data from species observations and surveys. Modelling will facilitate the location of highly suitable habitat, assist in defining and managing conservation lands for *N. americanus*, and help to assess the likely presence of the species prior to surveys. We have chosen to compare six modelling algorithms that utilize both presence and absence data. Although techniques that use absence data have been shown to perform better when absence information is available, we suspect the absence data for the beetle surveys may not truly represent habitat that is unsuitable for *N. americanus*.

Methods

Study area

The study area is the eastern half of Oklahoma, a state in the south-central USA. Elevation within this area ranges from 87 to 806 m with major topographic features including the Ouachita Mountains and the Ozark Plateau. The natural vegetation of this region is primarily

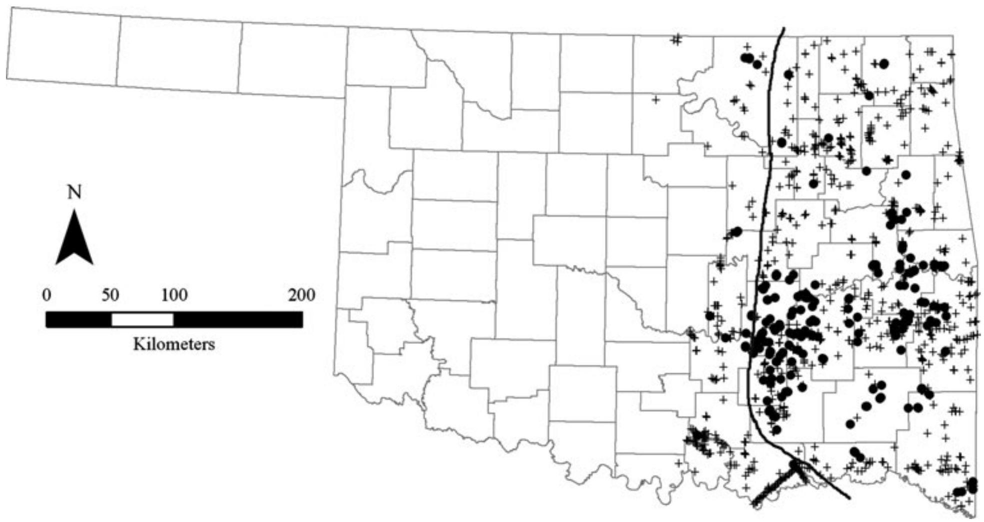

Fig. 1 Occurrence records of *Nicrophorus americanus* in Oklahoma, south-central United States, used in habitat suitability modelling. Presence records are indicated with *circles*, absences with *small crosses* (+). To the east of the *black line* indicates the historic range within Oklahoma

oak-hickory, oak-pine, or post oak-blackjack oak forest (Hoagland 2000). Oklahoma has a strong longitudinal and latitudinal gradient in both precipitation and temperature. Average annual temperature ranges from 16.2°C in the southeastern corner of the study area to 14.4°C in the northwest with the growing season ranging from 201 to 222 days. The coldest month is January with an average temperature in the southeast being 4.1°C and in the northwest being 1.6°C. The warmest month for the study area is July with an average temperature in the southeast being 26.9°C and in the northwest being 27.7°C. Average annual precipitation within the study area ranges from 54.2 cm in the southeast to 33.4 cm in the northwest, with the wettest month being May for all areas (Brock et al. 1995).

Study species and data set

Nicrophorus americanus is the largest species (approximately 2.5–3.5 cm adult length) within the *Nicrophorus* genus, a group of beetles that bury vertebrate carcasses on which to raise their young (Lomolino et al. 1994). The *N. americanus* data set was compiled from records provided by the US Fish and Wildlife Service Tulsa Ecological Services Field Office and the Oklahoma Biological Survey. The data set contained records from both opportunistic collections and standardized transect surveys gathered from 1979 to 2008. Presence of *N. americanus* may have been recorded with either method, but absence was only recorded when the species was not collected during a standardized survey. Standardized surveys are series of carrion traps along a 20 m transect that is maintained for three rainless nights with temperatures above 15.5°C [for survey details see (US Fish and Wildlife Service 1991, 2007)]. Biologists permitted by the US Fish and Wildlife Service conducted the surveys, of which a majority were located in areas of road or pipeline construction.

Multiple surveys were conducted at some locations over the course several years. Surveys at one location may be both positive or negative over time. Therefore records were analyzed to determine the repeatability of the results at one site. Based on the likelihood that a site with a positive observation had subsequent positive observations in following years, a location was considered positive if any survey conducted at the site yielded a positive beetle observation. We tested for spatial autocorrelation in the *N. americanus* data set with Moran's *I* (Rangel et al. 2006).

Because many modelling techniques, especially regression based techniques, are negatively affected by an unequal ratio of presence and absence data (Manel et al. 2001), we randomly removed absence data points until the number of absence and presence was approximately equal. The original data set contained 203 presence locations and 348 absence locations. After random removal, the balanced data set used for modelling contained 426 locations with 203 presence and 223 absence points.

Predictor variables

In previous research, *N. americanus* has been found to be a generalist species (Bedick et al. 1999; Holloway and Schnell 1997; Lomolino et al. 1994), and it is unclear which environmental variables are important in determining its distribution. Therefore, we chose a variety of predictor variables that we believe are likely to affect a burrowing insect. These predictor variables fall into three major categories: topographic, vegetation and landcover, and climatic (Table 1).

We attributed values for all predictor variables to each species data point. To accomplish this, all predictor variables were converted into raster format with 60 m grid cell resolution. Models were run initially with all predictor variables. However, some modelling techniques,

Table 1 Environmental layers used as predictor variables in models of potential habitat suitability of the endangered *Nicrophorus americanus* in eastern Oklahoma

Variable	Range & unit	Source
Elevation	87–806 m	Oklahoma digital elevation model (Cederstrand and Rea 1997; geo.ou.edu)
Slope	0–46°	
Soil association	228 categories	STATSGO (Soil Survey Staff 2005; soildatamart.nrcs.usda.gov)
Surface geology	133 categories	U.S. Geological Survey (Heran et al. 2003; pubs.usgs.gov/of/2003/ofr-03-247)
Vegetation*	34 categories	Oklahoma Gap Project (Fisher and Gregory 2001; www.biosurvey.ou.edu/gap-ok.html)
Potential vegetation*	8 categories	Game type map of Oklahoma (Duck and Fletcher 1945; www.biosurvey.ou.edu/duckflt/dfhome.html)
Landcover	15 categories	National Land Cover Database (Homer et al. 2004; www.mrlc.gov)
Forest cover	0–100%	
Landcover change	48 categories	
Annual temperature	14.4–16.2°C	Oklahoma Climatological Survey and
Number of days below freezing (0°C)*	57–93 days	Oklahoma Mesonet (www.mesonet.org)
Number of days above 32.2°C*	56–85 days	
Length of growing season*	201–222 days	
First growing season day*	87th–97th day of year	
Last growing season day	299th–310th day of year	
Annual precipitation*	32.5–55.5 cm	
May precipitation	4.8–6.7 cm	
September precipitation*	3.4–5.6 cm	

The eight environmental variables marked with * were removed from the second round of model building due to high correlation

particularly regressions, are significantly affected by correlation among the predictor variables. Therefore we ran bivariate correlations to determine which variables were highly correlated prior to a second round of model building. Among those variables that were highly correlated, we conducted logistic regressions of each variable with the species data set to determine which variable had a greater effect on *N. americanus* occurrence. The variable within each correlated group that had the greatest effect on the species was kept for a second round of model building.

Modelling techniques

We used six modelling techniques to create predictive models of habitat suitable for *N. americanus*. Many researchers suggest comparing the results of several techniques because no one method has proven to be the best for all species and study areas (Elith et al. 2006; Guisan et al. 2006). We wanted to compare methods that were based on traditional statistics and machine learning; and methods that utilized absence data and generated pseudo-absence data.

Generalized linear models (GLMs) and generalized additive models (GAMs) are applied extensively in species distribution modelling because of their statistical power (Austin 2002; Guisan et al. 2002; Yee and Mitchell 1991). GLM and GAM models require absence data and results can be affected by an uneven ratio of presence and absence points. For our model building, it was necessary to reduce the number of absence points from the data set to achieve an appropriate presence–absence ratio. Both models were implemented in R using the BIOMOD package (Thuiller 2003).

Classification and regression tree (CART) methods construct a tree by dichotomous division of the data that best reduces the variance in the response variable (De'ath and Fabricius 2000). CART was implemented in R using the BIOMOD package (Thuiller 2003). Random Forest is a form of CART that increases the power of the classification tree by generating multiple models from repeatedly sub-sampled training data sets (bootstrapping). The multiple models grow a "forest" of trees of which each tree is "grown" from a randomized subset of environmental variables (Breiman 2001). Random Forest was implemented in R using the BIOMOD package (Thuiller 2003). The generalized boosted method (GBM, also known as boosted regression trees) is another advanced CART method that incorporates the regression tree algorithm with a boosting algorithm (Elith et al. 2008). We implemented GBM using 'gbm' in the BIOMOD package in R (Ridgeway 2006; Thuiller 2003).

Maximum entropy (Maxent) is a machine learning method that is able to make predictions using presence only data. Although Maxent was designed to use presence-only data, it also performs well when compared to presence–absence procedures that utilize both real and pseudo-absence data (Elith et al. 2006; Hernandez et al. 2006; Pearson et al. 2007). We implemented Maxent with stand-alone software (Phillips et al. 2006; Phillips and Dudik 2008).

All models were built using 75% of the presence-absence balanced data set. The remaining 25% was used to evaluate the model described below.

Model evaluation

We used the threshold independent method, receiver-operating characteristic curve (ROC) to evaluate all models. The area under the curve (AUC) of a ROC plot has been widely recommended to assess the predictive performance of species distribution models (Elith et al. 2006; Fielding and Bell 1997; Rushton et al. 2004). An index has been developed for AUC values: 0.5–0.7 = low accuracy; 0.7–0.9 = potentially useful; and >0.9 high accuracy (Swets 1988). Models were evaluated by calculating the AUC for the evaluation data set which was 25% of all the species data points (both presence and absence) held out from the original species data set.

Results

Species data set

From 1979 to 2008, 1,182 surveys for *N. americanus* were conducted across the eastern third of Oklahoma with 1,089 surveys conducted in the past 10 years (Fig. 1). Of those, 230 (20%) of the surveys collected at least one *N. americanus* specimen. Of the total number of surveys, 72 locations were surveyed more than once, representing 173 survey events (15%). Of the 72 locations, 29 were negative for all surveys; 28 were positive for all surveys; 15 of the locations had surveys of both negative and positive results. We considered the 15 locations with conflicting survey results as positive. Spatial autocorrelation of presence and absence was weak for neighboring data points and became 0 at a distance of 84 km (Table 2; Fig. 2).

Predictor variables

Eight environmental variables were removed for a second round of model building due to high correlation (Table 1). Three of the categorical landcover and vegetation layers were highly correlated and two were removed. Landcover

Table 2 Analysis of spatial autocorrelation of *Nicrophorus americanus* occurrence records in Oklahoma

Average paired distance (km)	Moran's I	I (max)
15.4	0.23 ± 0.012*	0.592
39.3	0.176 ± 0.013*	0.523
55.7	0.054 ± 0.013*	0.401
70.5	0.065 ± 0.013*	0.371
84.1	0.01 ± 0.013	0.333
96.8	−0.001 ± 0.013	0.343
108.3	0.011 ± 0.013	0.323
119.0	−0.051 ± 0.013*	0.324
129.9	−0.093 ± 0.013*	0.360
141.2	−0.124 ± 0.013*	0.391
153.1	−0.142 ± 0.013*	0.439
167.0	−0.157 ± 0.013*	0.456
183.7	−0.118 ± 0.013*	0.468
204.6	−0.093 ± 0.013*	0.486
233.7	−0.011 ± 0.012	0.500
320.7	0.206 ± 0.011*	0.717

The average Moran's I is given for 16 distance classes. Values for I can range from −1 to 1; values close to 1 indicate a positive spatial autocorrelation and negative values a negative spatial autocorrelation. Spatial autocorrelation is low at the closest distances and approaches 0 at 84 km

* $P < 0.001$

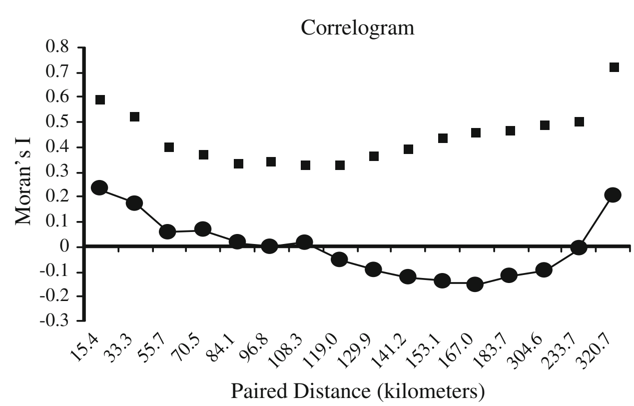

Fig. 2 Spatial correlograms of *Nicrophorus americanus* occurrences in Oklahoma. *Circles* indicate the Moran's I for each distance pair. *Squares* are the highest Moran's I value for each distance class

was retained. Six climatic variables were removed leaving annual temperature, days below freezing, and May precipitation.

Model comparison

Ten of the twelve models performed within the AUC index category of "potentially useful" with an AUC value

Table 3 Performance of different modelling techniques for *Nicrophorus americanus* using all available predictor variables and a reduced set of variables based on variable correlations

	All predictors	Correlated predictors removed
CART	0.726	0.688
GAM	0.780	0.802
GBM	0.765	0.813
GLM	0.674	0.731
Maxent	0.857	0.831
Random forest	0.792	0.834

AUC value of 0.5–0.7 is considered low accuracy; 0.7–0.9 is considered useful; and 0.9 and above is considered high accuracy. Models were evaluated with 25% holdout data from the occurrence data set

CART classification and regression tree; *GAM* generalized additive model; *GBM* generalized boosted model; *GLM* generalized linear model; *Maxent* maximum entropy

between 0.7 and 0.9 (Table 3). As expected, removing correlated variables improved the performance of GLM, GBM, and GAM, and also improved the Random Forest model. The model with the best performance was Maxent using all the predictor variables (AUC 0.857). Other models with AUC values in the "useful" category were Random Forest, GBM, and Maxent—all which used the smaller set of predictor variables (Table 3).

The map of the best Maxent model indicates that *N. americanus* is more likely to be present in the northern part of the southern half of the study area (Fig. 3), with small areas in the far north and southeast. May precipitation, geology, days below freezing, annual temperature, and last day of growing season were accounted for the highest gain in AUC in the Maxent jackknife test of variable importance. Slope was the only variable responsible for reducing model performance.

Of the other model predictions, the spatial representation of CART and Random Forest appear to have the most agreement with the best Maxent model. Both CART and Random Forest predict greatest habitat suitability in the lower middle of the study area, but also indicate suitable habitat in the far north and southeastern corner. None of the model predictions were obviously different from the Maxent predictive map (Fig. 3).

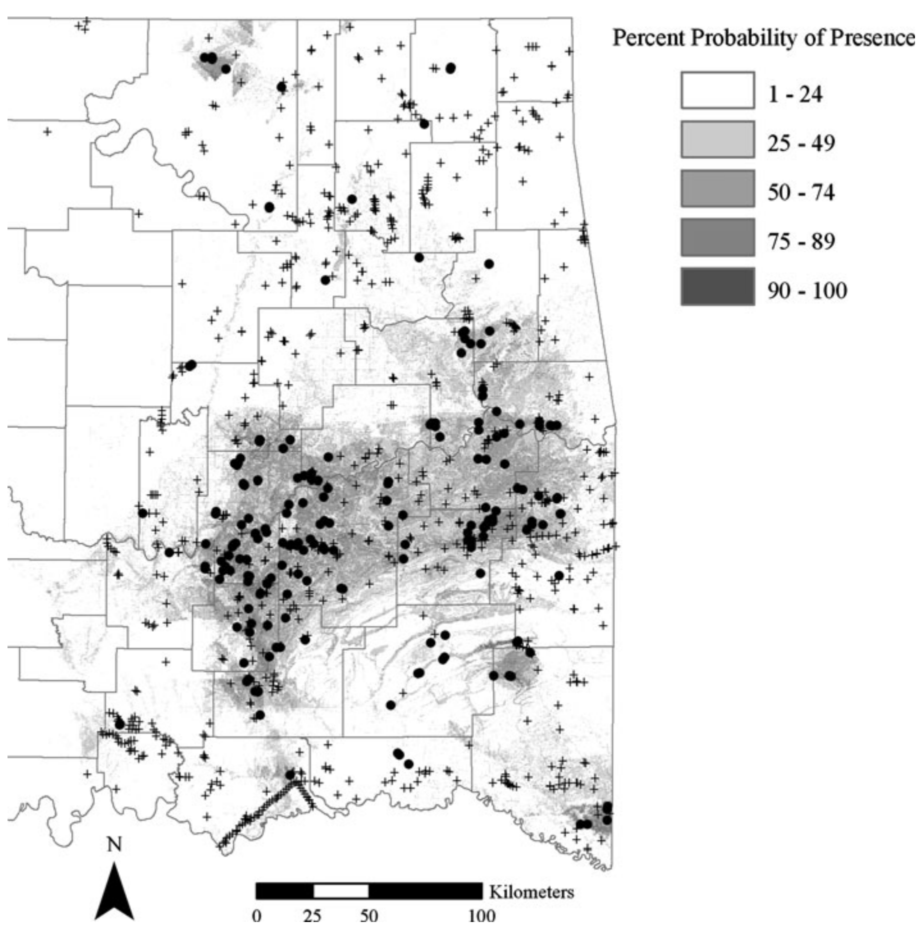

Fig. 3 Predicted habitat of *Nicrophorus americanus* in eastern Oklahoma based on the Maxent model using all predictor variables. This modelling technique produced the most accurate model of all techniques tested, with an AUC value of 0.857. *Circles* indicate known presence locations of *Nicrophorus americanus* and *small crosses* (+) indicate surveys that found no *Nicrophorus americanus*

Discussion

Even the best performing models did not fall into the highly accurate category (AUC $\geq$ 0.9). Several factors may have inhibited predictive performance. Errors in model building generally fall into two categories: data deficiencies, in both species and predictors, and incorrect model specifications (Barry and Elith 2006). The variation in model output for *N. americanus* is consistent with other studies comparing these modelling techniques (Elith et al. 2006; Hernandez et al. 2006; Meynard and Quinn 2007). GAM and GLM were two of the worst performing models—both techniques utilized absence data from the *N. americanus* surveys and are known to be significantly affected by spatial autocorrelation (Austin 2002; Diniz-Filho et al. 2008; Segurado et al. 2006). The spatial autocorrelation for the species data set was low (Table 2), but may have been high enough to affect the model algorithm. It has been suggested that when using these regression techniques that a covariate term be added to account for spatial autocorrelation (Segurado and Araújo 2004). Autoregressive techniques designed to account for spatial autocorrelation can also be used, but have mixed results with models built with presence/absence data sets as compared to those using abundance values. The addition of covariates or using autoregressive techniques do not consistently improve the results of models from binary data (Dormann et al. 2007). The use of ensemble or consensus methods may improve model predictions. By comparing, averaging, and measuring variation in the predictions of multiple modelling techniques, ensemble methods can draw out the correctly predicted areas from several models and indicate areas of uncertainty (Marmion et al. 2009). Ensemble methods have been used for other analyses, but only recently applied to SDM by a few researchers (Araújo and New 2007; Marmion et al. 2009).

What factors in the species data set may have confounded model predictions? Absence data points from the *N. americanus* surveys may not truly represent unsuitable habitat. Habitat suitability models work on the principle that the observed occurrences of a species reflects the species ecological requirements. Most models rely on the assumption that the organism will be present in suitable habitat and absent from unsuitable habitat—that the species is in equilibrium with its environment. Unfortunately that assumption is often fallacious because organisms can be found and recorded in apparently unsuitable breeding habitat or not found in highly suitable areas. The current distribution of *N. americanus* is almost certainly not at equilibrium with the environment or the species would occupy more of its historic range. Knowing the cause of the range reduction would help to choose predictor variables that directly affect the current distribution. Methods relying on these absence data will therefore have errors. Techniques that use presence and absence data usually have higher AUC values than presence only methods, but only when true absence data is available (Brotons et al. 2004; Pearson et al. 2006). However, we argue that the absence data for *N. americanus* do not represent true absence, and using it to build the models introduced error into the predictions. If false absences are suspected it is better to use a presence-only method (Chefaoui and Lobo 2008; Hirzel and Le Lay 2008). Consequently, Maxent may have performed better because it does not rely on absence data, but uses pseudo-absences or "background" data that characterizes the environment of the entire study area (Phillips et al. 2006).

Although the majority of the data come from standardized surveys conducted over the past 20 years, we believe there are some problematic features of the data set. The survey method relies on rotten meat to lure insects to a pit fall trap and is likely to attract *N. americanus* to suboptimal habitat. The USFWS provides trap specifications and notes that beetles within a 8 km radius could be attracted to the bait (US Fish and Wildlife Service 2007). For other flying invertebrates, such as butterflies, distribution model performance decreases as mobility and flight period increases (Pöyry et al. 2008). Although *N. americanus* are attracted to carrion traps, this does not necessarily signify that the trap location is suitable reproductive habitat.

Because survey locations were not placed randomly on the landscape or in a strict grid pattern covering the entire region, some geographic biases are apparent in the data. Many of the *N. americanus* survey data were collected in roadside or pipeline right-of-ways because surveys were commissioned by agencies prior to construction projects. Therefore a pronounced bias exists in the *N. americanus* data set that may affect model results. However, Kadmon et al. (2004) found that even though woody plant records in Israel had a strong roadside bias, they were able to produce accurate models from the data set.

Species life history characteristics can affect the accuracy of a model. *N. americanus* is considered a generalist species and thus has no specialized habitat requirements (Bedick et al. 1999; Holloway and Schnell 1997; Lomolino et al. 1994). Generalist species have proven difficult to model because environmental requirements are not simply correlated to predictor variables unlike species with strong habitat or host specificity (Brotons et al. 2004; Evangelista et al. 2008; Guisan et al. 2007).

The predictive performance of our models may be reduced by not including predictors that directly affect the distribution of *N. americanus*. We used a variety of predictor variables that should influence the distribution of *N. americanus* at several ecological scales. Climatic variables are known to determine the continental or regional distribution of a species. Topographic and landcover variables often affect the species at a finer scale. However, we need to have greater emphasis on predictor variables that directly affect the organism at the sub-state scale. Derived bioclimatic variables, such as evapotranspiration, may make more ecological sense and are more appropriate to the smaller scale than precipitation or temperature considered separately.

Despite the low predictive success of our models, the work we have done suggests future avenues of research that will improve our understanding of the *N. americanus*'s biology and ecology. Maxent's test of variable importance identifies variables that were most responsible for improving the model's performance: May precipitation, geology, days below freezing, annual temperature, and last day of growing season. Number of days below freezing and last day of growing season indicate that environmental conditions during over-wintering may account for part of the species' suitable habitat. Over-wintering survival has been studied with regard to habitat type, carrion availability, and depth in soil (Schnell et al. 2007), but another factor may be soil temperature. Although we were able to see a signal on a large scale, the affect of soil temperature on *N. americanus* distribution may be better studied at a smaller scale while taking into consideration the microclimate variation in small study areas. The importance of geology in contributing to model performance indicates that substrate may limit what *N. americanus* finds to be suitable habitat. Substrate will affect the insect's ability to bury carrion and successfully raise a brood. Preliminary results from Smith's (2007) research indicates that brood carcasses were most likely to be buried in loose soil with low clay content. Future habitat models may be enhanced by the addition of an accurate soil texture layer, rather than soil association, which is a group of soils forming a pattern of soil types within geographical region.

The model results that indicate increased habitat suitability with increased May precipitation could suggest a physiological effect with over-wintering or brooding carcass decay or may simply be a surrogate for a predictor variable that we did not use. Because of the strong southeast-northwest precipitation gradient in Oklahoma, precipitation may be a surrogate for the distribution of a competitor or prey item. Research into the direct effect of precipitation on *N. americanus* reproduction and over-wintering might prove useful in understanding the current distribution of the species and the possible reasons for the historic range collapse.

Inclusion of biotic interactions such as overlap with competitor distribution and shared resources improve model performance at small and macroscales for a variety of organisms (Araújo and Luoto 2007; Heikkinen et al. 2007; Preston et al. 2008). Indeed, Sikes and Raithel (2002) have hypothesized that competition with congeneric and other scavengers and a reduction in suitably sized carrion affects the distribution and abundance of *N. americanus*. The effect of congeneric competitors on distribution models has been demonstrated for mammals (Anderson et al. 2002) and plants (Leathwick and Austin 2001). While work needs to be done, the most plausible cause for *N. americanus* decline is likely related to a change in these biotic interactions. Holloway and Schnell (1997) suggest that habitat fragmentation has caused an increase in vertebrate scavengers and a reduction in carrion supply. Bedick et al. (1999) agree with fragmentation as a possible cause, but also found that not all land-cover change is detrimental.

Another challenge for modelers is the inclusion of processes that affect the distribution of a species (Austin 2002; Guisan and Thuiller 2005). *N. americanus* may be directly affected by processes ongoing on the landscape, such as: fire, dispersal, and succession. Woody plant encroachment is affecting the *N. americanus* population in the grasslands of Nebraska (Walker and Hoback 2007). Revising the 48 categories of landcover change by grouping types of change that are more likely to *N. americanus* could improve the variable importance in the models.

Modelling *N. americanus* only in Oklahoma has allowed us to use a finer scale of environmental variables, but we may have compromised the predictive ability of the model by looking at the species at the western edge of its historic range. More sophisticated algorithms have been developed recently that may be better for modelling species at the edge of the range, where habitat may be suboptimal and the species-environment relationship is skewed compared to the whole range (Braunisch et al. 2008).

Conclusions

Other researchers have repeatedly encouraged better links from ecological theory and biology of the organism to the model building process (Austin 2007; Guisan et al. 2006). To improve model performance, we should think more carefully about the cause of *N. americanus*'s endangered status and its population shrinkage. Sikes and Raithel's (2002) review concludes that the most plausible explanation for *N. americanus*'s decline is a combination of factors associated with biotic interactions including congener and vertebrate competition and a reduction in optimally sized prey. To improve the models and consequently the recovery effort for the species, we need to take into account these important variables. Creating an accurate spatial layer of this data will be a future challenge.

Our objective was to produce a map of potentially suitable habitat for *N. americanus* that would guide conservation efforts within the state of Oklahoma. Although the best model was not highly accurate, our map of suitable habitat can help to inform conservation biologists of areas that may have suitable foraging habitat for the *N. americanus*. Overgenerous models can mislead conservation planners in thinking that more areas are highly suited to the species. Also, overgenerous models will greatly increase the number of surveys with beetles absent. It is better to be conservative and find the best areas if resources are limited for planning preserves or looking for areas of reintroduction (Loiselle et al. 2003). Therefore, we urge caution in interpreting the predictive map. We offer it as a suggestion from which additional research can be done to support or refute our suitability map.

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