DISTRIBUTION OF THE ENDANGERED AMERICAN BURYING BEETLE AT THE NORTHWESTERN LIMIT OF ITS RANGE

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Abstract

American burying beetle (ABB), *Nicrophorus americanus*, historically occurred in the eastern 35 U.S. States from Canada to Texas and is classified as a habitat generalist. ABB was listed as a federally endangered species in 1989 with remaining distribution in only six U.S. States.. Within these states, populations of ABB are disjunct, occurring in mostly undisturbed habitats associated with multiple soil types and vegetation structure. In Nebraska, the distribution of ABB has been mapped in two ecoregions, the Sandhills and Loess Canyons. In this project, we developed and compared a logistic regression model and a random forest model of ABB distribution at its northern and eastern edge in the Northern Plains ecoregions of Nebraska and South Dakota. We used baited pitfall sampling for 5 trap nights at 482 unique sites to establish presence of ABB at 177 sites. Distribution was not uniform in the plains ecoregion and the random forest model was used predict occurrence. The results show that the ABB population in the northern plains ecoregion is unique from the previous model of the Nebraska Sandhills despite these ecoregions being adjacent. The model results also reduce requirements to survey and conduct habitat mitigation for ABB in approximately 77,938 hectares of Nebraska and South Dakota that was considered potential habitat while prioritizing areas for conservation.

Key words: **endangered, model comparison, predictive map, Silphidae, *Nicrophorus***

Introduction

Species distribution models are becoming increasingly important for conservation of rare and endangered species. This modelling has allowed new populations to be located (e.g. Guisan *et al.* 2006; Jurzenski *et al.* 2014), improve conservation area planning, and predict potential effects of global climate change (e.g. Carvalho *et al.* 2011; Riordan and Rundel 2014). Many threatened and endangered species have limited distribution and specific habitat associations; however, some species once had wide distributions that spanned a multitude of habitats. The use of many habitats may limit the accuracy of predictive models and thus, limit the usefulness of the models for predicting species occurrence and the effects of landscape and climate change on the species.

The American burying beetle (ABB), *Nicrophorus americanus* (Olivier), is a federally endangered species native to North America (USFWS 2008). The ABB's range historically extended into 35 U.S. states and three Canadian provinces (Lomolino and Creighton 1996; Bedick *et al.* 1999). However, the current range is limited to areas within six states: Arkansas, Kansas, Nebraska, Oklahoma, Rhode Island, and South Dakota (Godwin and Minich 2005; USFWS 2008), representing a more than 90% reduction from the historic range of the ABB (Lomolino *et al.* 1995). Within the six states where it still occurs, habitat associations vary and the remaining western populations are disjunct both regionally and within the states (Leasure and Hoback 2017, U.S. FWS 2016).

The ABB is characterized as a habitat generalist, and despite more than 25 years of research since its listing, no critical habitat has been designated because of the variability or contradiction found among variables that are strongly linked with ABB occurrence. Several models of predicted occurrence have been developed for Oklahoma and for two Nebraska populations that occur separately in the Loess Canyons and Sandhills (Crawford and Hogland 2010; McPherron *et al.* 2012; Jurzenski *et al.* 2014). Both the Loess Canyons and Sandhills models included validation and produced an AUC statistic of 0.765 and 0.82, respectively (McPherron *et al.* 2012; Jurzenski *et al.* 2014), suggesting high correlation of the models' ability to predict occurrence of ABB despite differences in predictive variables. Additional modeling of the distribution of western ABB populations by Leasure and Hoback (2017) confirmed differences between habitat associations of ABB in the northern and southern range. However, there are limited data from the farthest north areas in Nebraska and southern South Dakota. Although previous work in South Dakota produced both a distribution and population estimate of ABB (Backlund and Marrone 1997; Backlund *et al.* 2008) this research used variable trap spacing from 0.2-3.22km, a small trap size, rotted beef kidney bait, and longer survey length than standard protocols (USFWS 2014).

In this study, ABB in northern Nebraska and southern South Dakota was sampled and positive and negative trap locations were analyzed based on environmental characteristics that were measured within an 800 m radius around each site. We used GIS to map ecologically-relevant characteristics of climate, soils, land cover, and human impacts. Because our study area is at the extreme northwestern corner of ABB range, we hypothesized that decreasing annual precipitation would limit the western edge of the distribution and colder winter temperatures would limit the northern distribution. The predicted geographic distribution of the ABB and its correlations with environmental covariates were compared using two modeling approaches, a machine learning algorithm (random forest) and a generalized linear model (logistic regression). Validation data were collected both within the model's range and outside of the range to test scalability of the model.

Methods

Field Methods

Presence or absence of the ABB was determined at 456 sites in northern Nebraska and southern South Dakota (Fig. 1) from 2005 to 2015 (mostly post-2008) using federally approved bucket-style baited pitfall traps (Bedick *et al*. 2004). Sites used to generate the models were selected using stratified random sampling methods. Ecoregions in the study area included the Northwestern Great Plains, the Northwestern Glaciated Plains, and a small fragment of Nebraska Sand Hills (USEPA 2013). Sites were spaced at least 1600 meters apart to maintain independence of samples, based on the assumption that the effective sample radius of baited pitfall traps is about 800 meters

(Leasure and Hoback 2017). There is some empirical support for this effective trap radius (Leasure *et al.* 2012, Butler *et al.* 2013), but the trap radius is likely to be influenced by environmental conditions including wind and precipitation. Five nights of trapping were conducted at each site to minimize the chance of false negatives. Previous studies have estimated the probability of detecting an ABB population with baited pitfall traps to be about 50% for a night of trapping and between 85.7 (± 5.3% S.E.) to 93.7 (± 5.1% S.E.) after 5 consecutive trap nights (Leasure *et al.* 2012, Butler *et al.* 2013). This would result in a false negative rate of about 3-10% across five nights of trapping, and we considered this error rate satisfactory for the purposes of this study (Butler *et al.* 2013; USFWS 2014).

Trap locations were selected by identifying areas in the Northwestern Great Plains and Glaciated Plains ecoregions that lacked presence/absence sample data during the last 10 years, were accessible by public roads, and were not within 1600 m of previously sampled areas. Surveys were conducted using federally compliant 18.9 L in-ground bucket pitfall traps (USFWS 2014). These traps were dug into the ground with approximately 3 cm of the bucket lip above ground to prevent the entrance of water during rain events. Soil was packed against the outside of the bucket lip to create a ramp to ease the entrance of beetles into the trap. Approximately 8 cm of moistened soil was added to the bottom of the bucket to reduce competition among individuals, and protect against ABBs overheating or desiccating. Soil moisture was checked daily and water was added if needed. Each trap was baited with an extra-large previously frozen laboratory rat carcass (RodentPro.com®) which had been rotted in a dark colored 18.9L bucket in the sun for 2-4 days, depending on temperature. Traps were covered using 2, 5x5cm sticks cut into 45 cm lengths and a piece of plywood measuring 45x45cm. The sticks were placed on the lip of the bucket in parallel to allow beetles space to enter the trap, and the plywood was then placed on top of the sticks. A large piece of sod was then placed on top of the plywood to prevent removal by scavengers or wind.

Upon capture of an ABB, the individual was aged, sexed, and its pronotum width measured (USFWS 2014). Because open bait allowed direct contact between the ripened rat carcass and the captured beetle, additional handling and feeding time was not required. Beetles were released approximately 100 m away from traps where they were caught to reduce the likelihood of artificially high recapture rates. At the release site, an artificial burrow was created using a stick, and individual beetles were oriented into the hole into which they readily crawled. A small amount of loose soil or vegetation was then placed over the opening. A single capture of ABB resulted in a positive result for the trap site, while no ABB over 5 trap nights resulted in a negative result.

Environmental Covariates

Based on results from previous studies (Hoback and Leasure 2017), we identified 16 environmental covariates to assess as predictors of ABB occurrence including metrics of climate, soil texture, human impacts, and land cover (Table 1). For comparability, an effort was made to use similar predictors to those used in a previous study in the Nebraska Sandhills (Jurzenski *et al.* 2014). A combination of automated GIS scripts and manual GIS processing was used to delineate an 800 m sample area around each trap location and to summarize the underlying GIS layers representing our covariates within the circular sample areas surrounding each trap location (ESRI 2013, Python 2012). This process was repeated for a grid of points spaced 500 m apart to collect covariate data throughout our study area necessary for mapping the expected distribution of the ABB.

Three climate metrics were selected as environmental covariates: annual precipitation, average minimum winter temperature, and average summer temperature (Table. 1). We hypothesized that annual precipitation was related to overall ecosystem productivity and to desiccation risk.

Burying beetles are susceptible to desiccation in dry environments leading to increased risk of mortality (Bedick *et al.* 2006). We also hypothesized that average minimum winter temperature was related to overwintering survival (Schnell *et al.* 2008), and that average summer temperature influenced habitat suitability as related to temperature-dependent flight activity (Merrick and Smith 2004) during summer months when beetles actively search for carcasses to use for reproduction.

Three soil texture covariates were selected: percent sand, silt and clay in the topsoil horizons (O and A) (Table. 1). Soil texture has been identified as an important habitat characteristic for determining suitability of areas for ABB to construct underground brood chambers (Scott 1998). In Nebraska, ABB occurrences appear to be related to the presence of sandy loam soils likely because these soils allow rapid burial of carcasses and formation of stable brood chambers, and retain soil moisture (Lomolino, *et al.* 1995, Scott 1998; Jurzenski *et al.* 2014).

We selected five metrics of human influence: road density, highway density, coverage of developed areas, coverage of crops, and coverage of hayfields (Table. 1). These metrics could all have indirect effects on habitat suitability because of general habitat degradation and fragmentation that could affect availability of carcasses suitable for reproduction across the landscape (USFWS 1991; Jurzenski *et al.* 2014; McPherron *et al.* 2012). In addition to these indirect effects, intensive row crop agriculture, hayfields, and developed areas could have direct negative effects on the ABB from soil disturbance and pesticide applications.

Five land cover metrics were selected: coverage of water, grasslands, wet prairies, wetlands, and forests (Table 1). In dry environments, availability of open water could potentially benefit burying beetles at risk of desiccation, but in general we would expect open water to be negatively related to burying beetle abundance due to decreased availability of terrestrial habitats and potential limits to dispersal. Previous studies have indicated that ABBs were associated with grasslands and wet prairies in Nebraska (Kozol *et al.* 1988; Bedick *et al.* 1999, Jurzenski *et al.* 2014).

Analysis

Initially, we examined the response of ABB based on presence or absence to the sixteen GIS-based environmental covariates within the 800 m buffer surrounding each trap site. We collected data from a total of 456 sites. Covariates were centered and scaled prior to analysis, except percentages that were remained unscaled. We compared results from two modeling approaches, a generalized linear model and a random forest model (Breiman 2001).

The generalized linear model (logistic regression) was implemented using the R statistical programing language (R Core Team 2014). To avoid collinearity among predictors in the model, environmental covariates were screened based on Spearman correlation coefficients greater than 0.6. Ten of the 16 environmental covariates were selected for logistic regression (Table 1). Predictors were centered and scaled prior to analysis. Regression coefficients and p-values were used to infer the strength and direction of correlations among ABB occurrence and environmental covariates in the model. The influence of each observation on model parameters (leverage) was assessed graphically using the 'glm diag plots' and 'influence measures' functions from the R package boot (Canty and Ripley 2014). We focused on the Cook's D and hat statistics. High leverage observations were removed to avoid a small number of points having a large pull on the predictions produced.

The random forest model was implemented using the R package "randomForest" (Liaw and Wiener 2002). Random forest is a machine learning algorithm that produces ensemble predictions from a large number of classification trees trained on bootstrap samples of the data. We used 10,000 trees in our model. To build each tree, the algorithm first selected four predictors at random and searched for a threshold that could be applied to one of them to best separate our samples into ABB presence versus absence sites. The best predictor and threshold were retained as the first node in the tree, and the algorithm moved to the next node in each branch (i.e., above and below the selected threshold) to randomly select a new set of four predictors to assess. We included all 16 predictors in the random forest model because the algorithm handles correlations among predictors. Model fit was assessed based on the "out-of-bag" classification error rate. Out-of-bag error rates are produced by the random forest algorithm by making predictions at each site using only those trees in the model that did not include that site in their training data (see Breiman 2001 for more). These error rates are considered conservative estimates that reflect expected error when extrapolating the model to new sites within the study area. The importance of predictors was assessed based on decreases in the Gini index (a measure of homogeneity in predicted presence and absence bins) resulting from random permutations of each predictor (Breiman 2001, Liaw and Wiener 2002).

To compare fit between the random forest model and the logistic regression, the area under curve (AUC) statistic was calculated using the R package ROCR (Sing *et al.* 2005). AUC is a measure of how well predicted probabilities of the ABB occurrence fit our presence-absence observations. It is a threshold-independent fit statistic, meaning that we do not arbitrarily select a threshold for inferring presence or absence based on predicted probabilities of occurrence. We used AUC to compare model fit between our logistic regression and random forest models. AUC greater than 0.8 is considered a good fit (Franklin 2010). We identified a threshold for each model to convert probabilities of occurrence into binary presence-absence predictions that balanced false positive and false negative rates using R package ROCR (Sing *et al.* 2005).

To validate the model and to test the models' transferability to new regions (both GLM and random forest), we assessed predictive performance at 151 new sites in 2016. We converted predicted probabilities of ABB occurrence to discrete presence-absence predictions using the thresholds identified above that balanced rates of false negative and false positives. Predictor variables for validation sites were collected using the same GIS process described above.

Results

Of the 456 trap sites, 177 sites were positive, with a total of 1,201 ABB captured (Fig. 1). Both models had relatively good fits to the data within our study area. The logistic regression model had an AUC of 0.83 and a non-significant chi-square deviance test ($p = 0.529$). Five false negative trap sites were removed due to high leverage based on Cook's D and hat statistics. This is not surprising based on previous studies that have shown five percent or more beetles present in an area cannot be caught even under ideal conditions after five trap nights (Butler *et al.* 2013). The random forest model had an AUC of 0.82 and an out-of-bag classification error rate of 25.6%. A threshold of 0.4 to convert probabilities of occurrence to discrete presence-absence predictions balanced the false positive and false negative rates for both models. The predicted distributions of ABB from the two models also agreed closely (Fig. 2).

Although both models fit relatively well within our study area, neither model performed well outside of our study area (47% error rate; Fig. 3). The random forest model had far better predictive accuracy than logistic regression within the study area at sites with original training data (Fig. 3). It should be noted that predictions in Fig. 3 are from the full random forest model, whereas AUC for random forest (above) were more conservative assessments based on "out-of-bag" model predictions.

The importance of predictors in each model were noticeably different, except that minimum average winter temperature (twinter) was always a strong predictor. For the random forest model the most important predictors (Fig. 4) were minimum average winter temperature, average precipitation (which was negatively correlated with minimum average winter temperature), clay, which was correlated with sand and silt, grasslands which were negatively correlated with crops, and roads. In the logistic regression, minimum average winter temperature and percent coverage of wet-grasslands had significant positive relationships with the presence of ABB, while the presence of water and forest had significant negative relationships (Table 2, Fig. 5).

Discussion

This study represents the first model created specifically for predicting occurrence of ABB in the northwestern limit of its known current range. Our results showed minimum average winter temperature, which was not included in either the Loess Canyons or Sandhills models, as the strongest single predictive factor in both the random forest and linear regression models (McPherron *et al.* 2012; Jurzenski *et al.* 2014). The average minimum winter temperature was obtained for the average from 1950-2000. Correlation with warmer average winter temperatures may suggest that areas with a lower amount of temperature fluctuation during the winter months increase the likelihood of ABB occurrence along with areas with a warmer climate. The Northern Plains lacks large bodies of open water; however, the Ogallala Aquifer is close to the surface (McMahon *et al.* 2007). The areas with highest likelihood of ABB occurrence in both the random forest and generalized linear models are also close to the surface groundwater from the Ogallala Aquifer (McMahon *et al.* 2007). This would suggest that minimum average winter temperature may be acting as a surrogate for proximity to subsurface water rather than minimum average winter temperature alone and may relate to avoidance of overwintering desiccation (Bedick *et al.* 2006).

This correlation between ABB occurrence and proximity to subsurface water may also partly explain the differences in habitat association between Nebraska and Oklahoma populations of ABB. Lomolino and Creighton (1996) noted that in its southern range, the ABB appeared to be a forest specialist. The results of this study contradict their finding because ABB had negative correlations with forest and open waters, which were often surrounded by trees in this study region. The correlation may be another product of an association of Nebraska ABBs with the Ogallala Aquifer as a source of soil moisture and temperature stability. ABBs in Oklahoma cannot access aquifer moisture and likely depend on forestation and tree cover to help retain soil moisture (Lomolino and Creighton 1996; Mcmahon *et al.* 2007; Walker and Hoback 2007). ABBs present in the Loess Canyons were also found to associate with water features and trees, and in these areas, the Ogallala Aquifer is deep underground and inaccessible to the beetles (Mcmahon *et al.* 2007; McPherron *et al.* 2012).

Precipitation was a strong predictor of ABB occurrence in the random forest model, which is in agreement with Jurzenski *et al.* (2014) who found precipitation to be the strongest predictive factor. ABB was negatively associated with clay in the random forest model, which also agrees with the Sandhills model. In the Sandhills, ABBs appear to prefer a more sand dominant soil texture, but will avoid areas without trace amounts of silt and clay as the soil is likely unstable for maintaining a brood chamber (Jurzenski *et al.* 2014). In contrast, the Loess canyon soil is fine silt and sandy soils are limited in the region (Bedick *et al.* 1999; McPherron *et al.* 2012). The Sandhills and Loess canyons differ in suitability for rowcrop agriculture with the Sandhills having unstable or saturated soils that limits crops and the Loess canyons having steep topography.

The presence of human development represented by crops and roads were negative predictors in the random forest model, while areas with high percentages of grassland were positive predictors of ABB presence. These findings are consistent with past models and literature that show ABBs to avoid areas of developed land such as agriculture (Sikes and Raithel 2002; McPherron *et al.* 2012; Jurzenski *et al.* 2014). As crop values increase, marginal lands are often developed (Lichtenberg

1989) leading to both direct (mortality from pesticides, soil disturbance) and indirect (changes in vertebrate species, habitat fragmentation) impacts on ABB.

Areas in this model designated 70 - 100% probability of presence should be considered for additional conservation measures and preservation as they may be especially suitable ABB habitat. However, caution must be used because the predictive power of this and other predictive occurrence models is limited to predicted absence or predicted presence on average over a period of years. This long-term trend prediction is not translatable into density estimation data as predictive occurrence models are based on long term climate trends and general habitat characteristics. The ABB is a highly mobile animal that is able to routinely travel 1.23 km per night, as far as 2.9 km in a single night, and up to 10 km in 6 nights (Creighton and Schnell 1998). This gives the ABB the ability to move into areas with better conditions in terms of climate, food availability, and mate availability. These types of year-to-year fluctuations would render any density models built upon long term temperature or precipitation trends unacceptably inaccurate. Thus, future studies contributing to the conservation and recovery of the ABB should include population density distribution over an area to better manage potential disturbances from land use and climate change coupled with the impacts of these changes on vertebrates used as food and reproductive resources.

Future studies should also seek to utilize or generate detailed distribution data of not only the ABB but also common carrion sources. Carrion availability is likely the single most important factor in determining presence of ABBs, but due to the lack of fine scale distribution data across a broad range of possible carrion sources, such modeling efforts remain out of reach at the time of this study. While the of the passenger pigeon (*Ectopistes migratorius* L.) and subsequent loss of suitable carrion source has been widely implicated as a driving force in the endangerment of ABB, the wide-scale suppression and loss of black-tailed prairie dog (*Cynomys ludovicianus* Ord) towns has not been suggested as a contributing factor to the loss of ABB. Populations of black tailed prairie dogs are currently about 2 percent of their historical population size (Summers and Linder 1978). Black-tailed prairie dog towns support a rich diversity of vertebrates as potential carrion sources of appropriate size for use by ABBs, but such an association has yet to be properly evaluated (Sikes and Rathel 2002; Whicker and Detling 1988; Lomolino and Smith 2003).

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Tables.

Table 1. Predictive variables used in the logistic regression (GLM) and random forest (RF) models to create distribution maps for American burying beetle in northeastern Nebraska and South Dakota.

GLM	RF	Covariate	Description	Citation
	•	precip	Average annual precipitation 1950-2000	Hijmans *et al.* 2005
•	•	twinter	Avg. min. winter temperature 1950-2000	Hijmans *et al.* 2005
•	•	tsummer	Avg. summer temperature 1950-2000	Hijmans *et al.* 2005
•	•	sand	% sand in top soil horizon	USDA 2006
	•	silt	% silt in top soil horizon	USDA 2006
	•	clay	% clay in top soil horizon	USDA 2006
•	•	road	Road density in 2011 (km / km^2)	USDC 2011
	•	hwy	Highway density in 2011 (km / km^2)	USDC 2011
•	•	develop	% coverage of developed areas	Homer *et al.* 2015
	•	crop	% coverage of crops	Homer *et al.* 2015
	•	hay	% coverage of hayfields	Homer *et al.* 2015
•	•	water	% coverage of open water	Homer *et al.* 2015
•	•	grass	% coverage of grasslands	Homer *et al.* 2015
•	•	wetgrass	% coverage of wet prairies	Homer *et al.* 2015
•	•	wetland	% coverage of wetlands	Homer *et al.* 2015
•	•	forest	% coverage of forests	Homer *et al.* 2015

Table 2. Regression coefficients for each predictor in the logistic regression model of American burying beetle occurrence in northeastern Nebraska and South Dakota. Asterisks indicate statistical significance when alpha = 0.05 (*) or alpha = 0.01 (**).

Coefficient	Estimate	SE	p	
(Intercept)	0.812	0.132	< 0.001	**
tsummer	0.084	0.151	0.579	
twinter	1.25	0.146	< 0.001	**
sand	0.07	0.138	0.61	
develop	-0.041	0.145	0.779	
road	-0.169	0.151	0.265	
grass	0.201	0.15	0.179	
wetgrass	0.378	0.146	0.01	**
water	-0.605	0.293	0.039	*
forest	-0.75	0.216	< 0.001	*

Figures.

Figure 1. Study area and recovery data for *Nicrophorus americanus* in Nebraska and South Dakota (2005-2015).

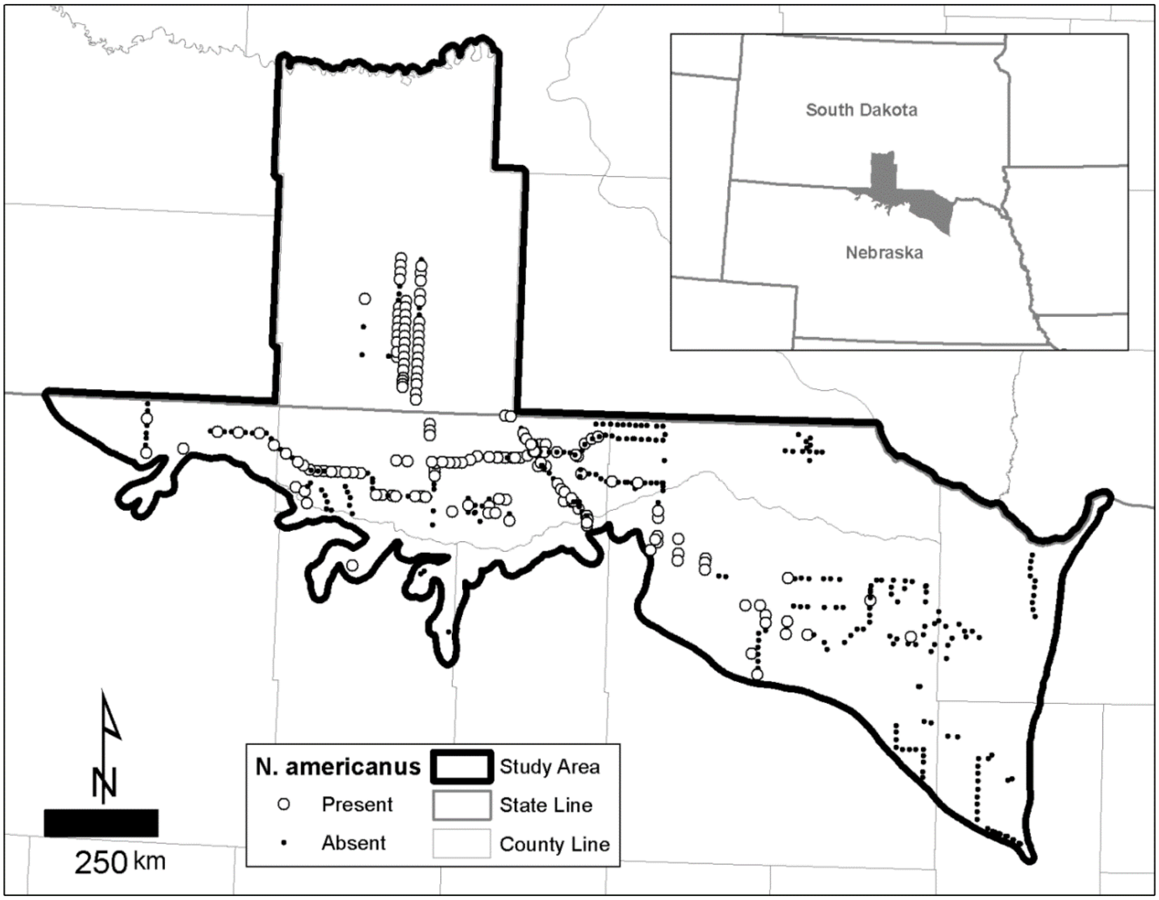


Figure 2. Model predictions throughout study area. Color schemes use a probability of occurrence of 0.4 as the threshold to distinguish a presence versus an absence site because this balances the rates of false positives and false negative in both models of ABB probability of occurrence.

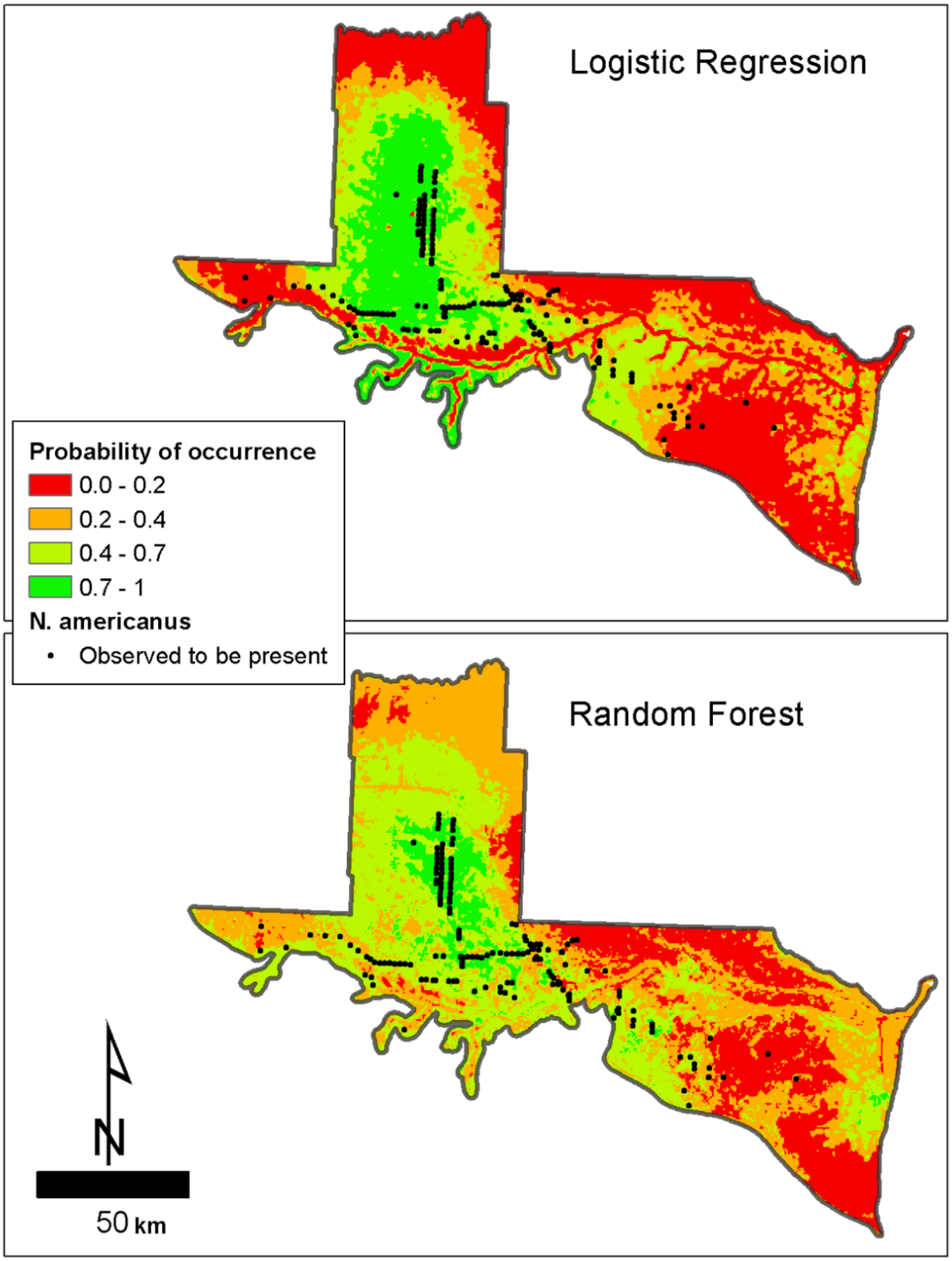


Figure 3. Assessment of model prediction accuracy inside and outside the original study area. Predictions inside the study area are for the sites used to fit the model, while predictions outside the study area are new sites. The random forest model had better predictive accuracy within the study area. Both models performed poorly outside the original study area when predicting probability of occurrence of ABB.

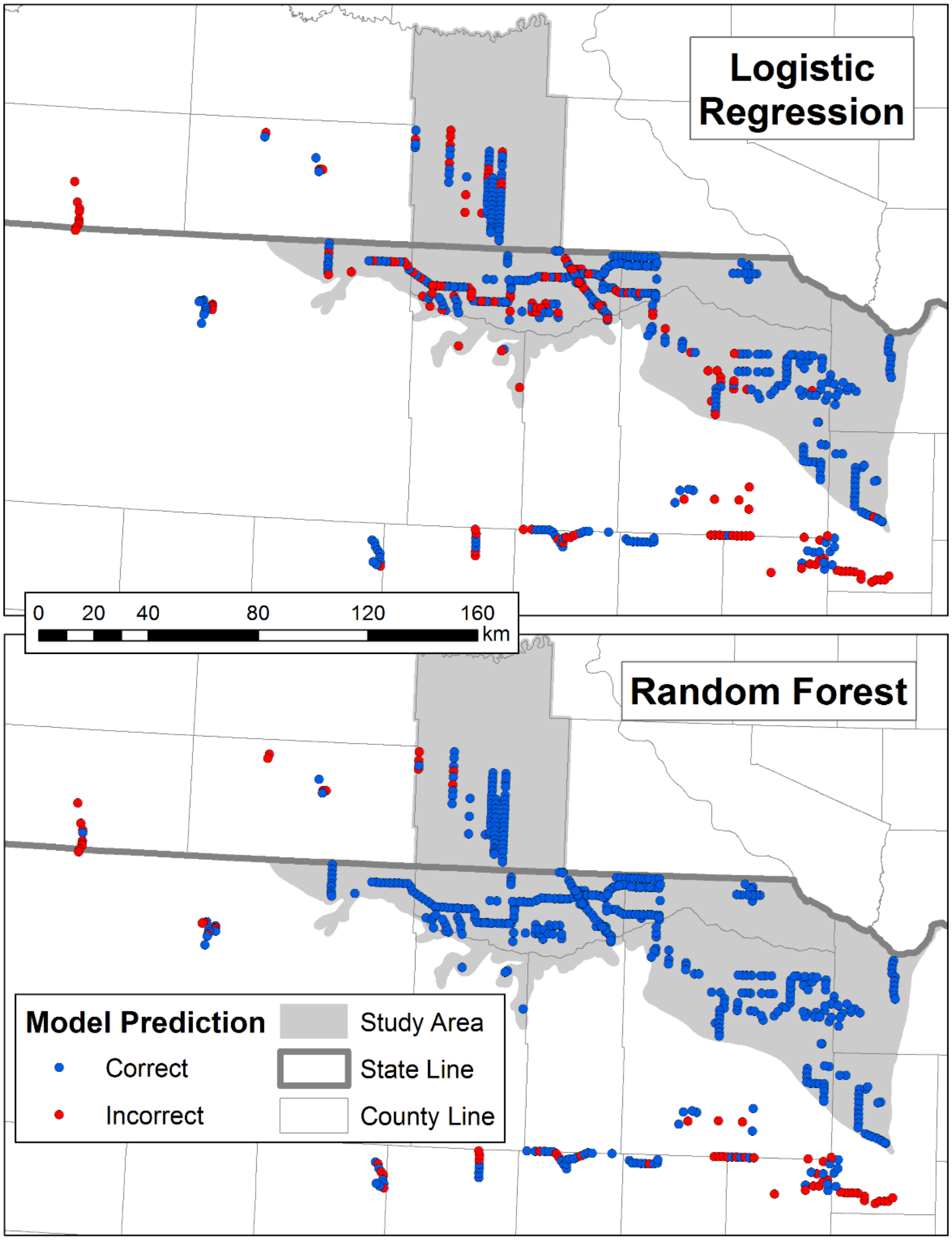


Figure 4. Importance of predictor variables in the random forest model of American burying beetle occurrence in northeastern Nebraska and South Dakota.

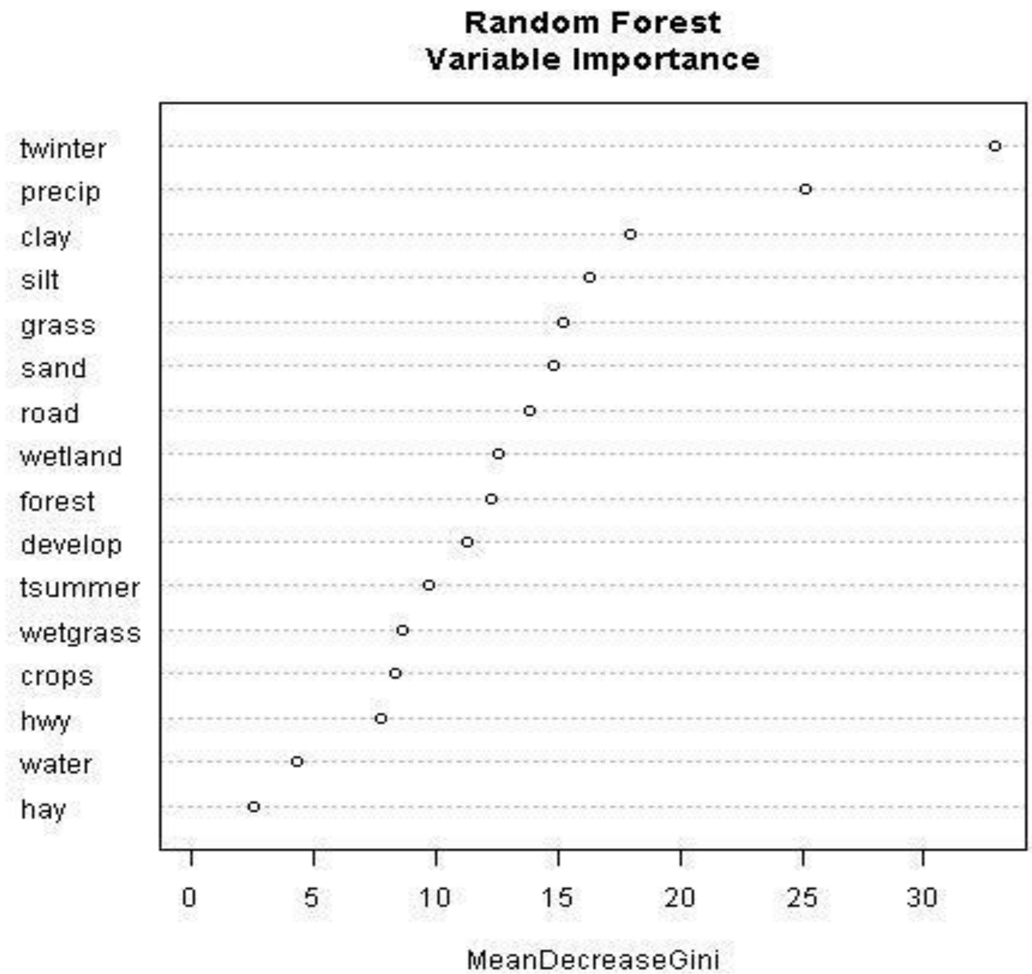
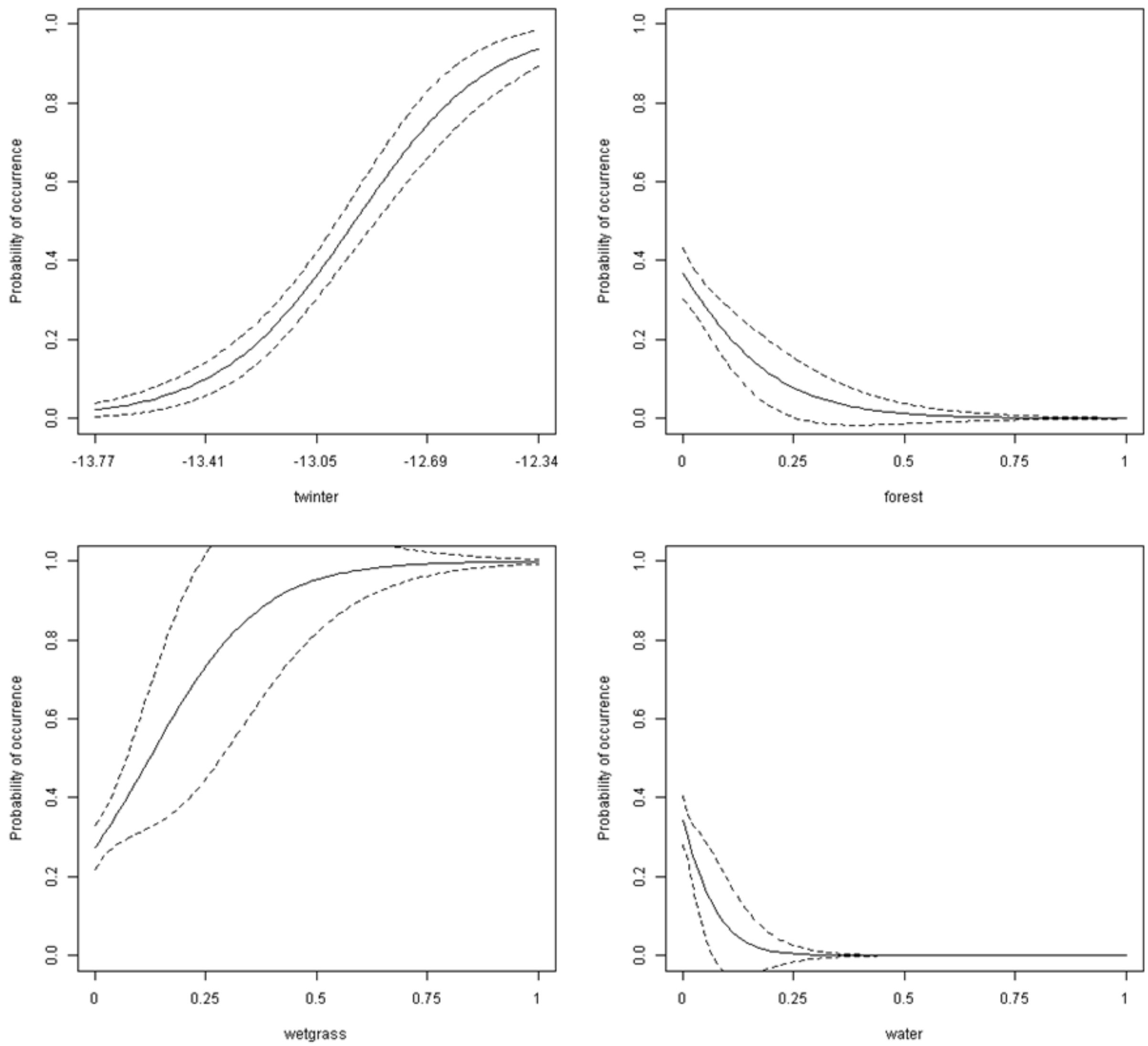


Figure 5. Partial regression plots of significant predictors in the logistic regression model for American burying beetle occurrence in northeastern Nebraska and South Dakota.



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