Tools and Technology

Presence-Only Species Distribution Models to Predict Suitability Over a Long-Term Study for a Species with a Growing Population

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ABSTRACT We used a long-term data set of black-capped vireo (*Vireo atricapilla*) detection locations collected between May and June of 1990 through 2005 within the Wichita Mountains of Oklahoma, USA, to determine how presence-only distribution models change as a population expands to help focus conservation and management activities. We used MaxEnt to model black-capped vireo habitat suitability for each of 4 years using detection data and several remotely sensed habitat metrics, including soil type, slope, and elevation. We assessed how well each model fit the detection data, what metrics vireos were using, and how well each model predicted occupancy across time. We found that as the vireo population increased, vireos began occupying a wider range of landscape characteristics. As a result, the models predicted more area with high suitability as the population grew. Similarly, we found that a model's ability to predict vireo occupancy in future years decreased with time, with low predictability even 5 years out. The combination of a secluded study site and specific aspects of this species' behavior likely accounted for the poor performance of our models at predicting areas into which vireos would expand over time. We conclude that habitat models should consider population status and be used with caution to predict areas of future occupancy if the population is currently expanding. © 2014 The Wildlife Society.

KEY WORDS black-capped vireo, habitat conservation, MaxEnt, Oklahoma, *Vireo atricapilla*.

Human impacts and changing land uses have decreased species ranges worldwide. In cases where habitat cannot easily be restored or where there is no tangible threat recognized, species recovery can be difficult to accomplish. However, when recovery efforts are able to restore habitat or eliminate the limiting factor or main threat to a species, such as banning pesticides such as dichlorodiphenyltrichloroethane (DDT; Grier 1982); controlling or eliminating overexploitation or collection (Myers and Worm 2005, USFWS 2008); or removing invasive predators, parasites, or competitors (Reardon et al. 2012), then species have the ability to recolonize previously habited areas (Abbitt and Scott 2001). Knowledge of how a species is expected to reinvade previously occupied habitat can lead to more effective management recommendations and conservation of the species.

Predicting areas of potential habitat for a species using remote sensing has become increasingly popular and attainable in the past decade (Gottschalk et al. 2005). Species distribution models (SDMs) predict areas of species' presence by relating known species occurrences to the spatial and ecological characteristics of those locations on the landscape. Species distribution models can project potential habitat outside of the range where a species currently exists or, for growing populations, where they may next colonize. For studies that quantify both presence and absences for a species within a region, regression models, including generalized linear or additive models or ensembles of regression trees (random forests or boosted regression trees), are typically used. However, species records are often only available as locations of species' presence, with no quantifiable absences, as in the case of museum specimens or historical data. Several methods exist for modeling species' distributions using presence-only data, including resource selection functions (Hooten et al. 2013, McDonald et al. 2013, Warton and Aarts 2013). MaxEnt (Phillips et al. 2006, Phillips and Dudik 2008) is one such modeling approach that is commonly used to assess the relative suitability of an area for a species when no definite absences are known (Elith et al. 2011, Phillips and Elith 2013).

The black-capped vireo (*Vireo atricapilla*; hereafter, "vireo") is an endangered migratory songbird with a breeding range concentrated in central Texas, localized regions in southwestern Texas and Oklahoma (USA), and in several states in Mexico (Grzybowski 1995, Farquhar and Gonzalez 2005). In November of 1987, the vireo was listed as Endangered under the Endangered Species Act of 1973, as amended

(Ratzlaff 1987). The vireo has been extirpated from its former range in south-central Kansas (USA), and from much of central Oklahoma and north-central Texas due to habitat conversion, drought, the curtailment of fire, and parasitism by the brown-headed cowbird (*Molothrus ater*; Graber 1961, Grzybowski 1995).

As part of a state-wide survey for vireos in Oklahoma from 1984 to 1988, surveyors mapped a small, isolated population of black-capped vireos on the Wichita Mountains Wildlife Refuge and adjacent Fort Sill Military Reservation (Grzybowski et al. 1986, Grzybowski 1989). Sampling for the vireo has occurred annually since 1985, with a notable increase in the vireo population, likely as a consequence of management practices. Cowbird trapping was initiated in 1986 on the refuge (Grzybowski 1989), and now occurs on both properties. Parasitism rates on vireo nests by brown-headed cowbirds have been documented at >80% in areas with no cowbird management; this severely limits vireo reproduction (Grzybowski et al. 1986, Grzybowski 1995). However, current research indicates that parasitism rates are now <10% on the Refuge (H. A. Mathewson, unpublished data). Additionally, prescribed burns are performed on the Refuge and on Fort Sill, which, supplemented by recurrent wildfires, create and maintain the early successional habitat with which vireos are associated (Graber 1961, Grzybowski et al. 1994, Juarez 2004).

The expansion of the vireo on the Refuge and Fort Sill over the course of 20 years offers a unique opportunity for testing how well SDM predictions change over time and how well they predict vireo presence in subsequent years. We predicted that in earlier years, when vireo populations were low, their locations would be associated with a narrow range of habitat characteristics; however, as the population increased and expanded across the study area, vireos would be associated with a broader range of habitat characteristics, and this would be reflected in annual SDM predictions. We further predicted that an SDM from a given year would become less reliable at predicting suitability into the future as the population expanded, resulting in an inability to distinguish potential habitat across the area and reduced Receiver Operating Characteristics (ROC) model fit. Here, we first demonstrate that the vireo population experienced growth. We then assessed 1) how vireo detection locations during 4 different breeding seasons (separated by 5-year intervals) affected the MaxEnt probability class proportions within the study area, 2) how ROC model fit of an early model changed as the population increased, and 3) what metrics were associated with areas of increased and decreased suitability. We then assessed how well MaxEnt predicted future areas of species distribution by comparing vireo occupancy in later years to MaxEnt predictions based on an earlier year of data.

STUDY AREA

Our study took place in areas of the Wichita Mountains, Comanche County, Oklahoma on the Wichita Mountains Wildlife Refuge (23,900 ha) and Fort Sill Military Reserva-

tion (20,200 ha). This region was characterized by granite outcrops interspersed with open mixed-grass prairie. Dominant prairie grasses were little bluestem (*Schizachyrium scoparium*), Indiangrass (*Sorghastrum nutans*), big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*), sideoats grama (*Bouteloua curtipendula*), hairy grama (*B. hirsuta*), and blue grama (*B. gracilis*) interspersed with forests and scrub predominantly of post oak (*Quercus stellata*), blackjack oak (*Q. marilandica*) and eastern red cedar (*Juniperus virginiana*). With elevations ranging from 300 m up to 756 m, the Wichita Mountains are a unique, isolated ecosystem in a region that is otherwise composed of flat or rolling grasslands. Prescribed fire was used as a management practice to decrease encroachment of woody species into the grasslands, increase forb growth, and increase diversity of grassland species; wild fires occurred regularly on the properties.

METHODS

Sampling

We conducted annual surveys within the vireo breeding season (May and early Jun) from 1986 through 2007. We detected vireos in 1986 during searches limited to specific areas. We systematically surveyed the entire study area for vireo presence in 1987 and 1988. Following this initial property-wide survey, we varied the amount of area surveyed across the years due to changes in available personnel and funding. We delineated search areas for surveying by using natural topography and vegetation classes containing woody vegetation, but we excluded open grasslands, rocky outcrops lacking vegetation, open water, and mature forests not containing components of vireo habitat. Initially, priority search areas consisted of those sites within which we previously detected vireos and the immediately surrounding areas; we surveyed these areas through the duration of this study. Additionally, we added areas where we had not previously detected vireos on a rotational or random basis; thus, search areas were not consistent across the entire study. Such inconsistencies across large study areas are not uncommon with long-term studies, and we corrected for this bias in our modeling (Kramer-Schadt et al. 2013; see below). We projected our SDM predictions across the majority of the Wichita Mountains.

We systematically surveyed and mapped territories of male vireos within search areas. Surveyors traversed the search area such that they were within hearing distance of all locations within the search area for ≥20 min. We distinguished individual males based on counter-singing with adjacent males. We delineated territory boundaries by marking detection locations on a map or via Global Positioning System and estimated a minimum convex polygon of the extent of their locations. We used the centroid of each territory polygon as a representation of a single detection point for that male. The protocol for searching the areas and mapping vireos did not differ among the years, though, so we assumed that detection probability of vireos in the surveyed areas was constant.

Depicting Growth

To verify that vireo populations within the study area increased over the course of the study, we calculated the density of vireo territories within the sections of the search areas that overlapped between study years. Because overlapping areas were not consistent across the study years, we created polygons of the search areas that were the same between 1990 and 1995, 1995 and 2000, and 2000 and 2005. We then calculated the change in vireo density (no. of territorial males/ha) between the 2 years of each subsequent 5-year interval. Density calculations were to show population growth only and were not used in modeling.

Modeling Presence

We used the mapped vireo territory centroids from each year as our sample of presence records for that year. To correct for our sampling bias (Kramer-Schadt et al. 2013), we created a bias grid for each year depicting sampling effort that was included in each model. Areas that were searched were assigned a value of 1, while unsearched areas were assigned a value of 0.001. These numbers indicate relative sampling effort, implying that areas searched (value = 1) were 1,000 times more likely to be searched than non-searched areas (value = 0.001; Elith et al. 2011).

Predictor variables.—We chose predictor variables that influence broad-scale vireo distribution (McFarland et al. 2013), can be acquired using remote-sensing techniques across the landscape, and that would not vary across 20 years. These included variables that we assumed to be static over time: land-cover class, elevation, slope, profile curvature, and soil type. Profile curvature is the rate of change of slope gradient in the direction of greatest change, where positive values are vertically concave and negative values are vertically convex; a zero value indicates the slope has a flat profile (Carson and Kirkby 1972, Schmidt et al. 2003).

We used the U.S. Geological Survey National Elevation Dataset 1/3 arc-second digital elevation models (30-m resolution) and ArcMap to derive elevation (meters), slope (degrees), and profile curvature (degrees/100 m) across the study site. We used the Soil Survey Geographic database (soils.usda.gov) digital soils data produced and distributed by the Natural Resources Conservation Service (NRCS) to determine soil type, and converted this shapefile to a 30-m-resolution raster data set. Comanche County has 60 recognized soil types (NRCS 2013), 33 of which occur in our study area.

Further, we used ENVI version 4.8 (Exelis Visual Information Solutions, Boulder, CO) to perform a supervised classification to define all areas within our study site as water, rock, or grassland and mixed shrubland–woodland to create a land-cover classification from 1995 Landsat (30-m resolution) imagery, from a clear scene in July (4 Jul). Because of the grouping of shrubland and woodland together, and the nature of the ecosystems on the refuge, we did not expect land-cover classes to change across the 20-year study period. We used Landsat from other years to visually confirm our assumption of no major changes in land-cover class. We clipped all land-cover layers to the same extent and snapped them to the same pixel locations using ArcMap. On a 30-m grid, we extracted the values of each predictor variable for each cell containing a vireo location and across all background grid cells within the Wichita Mountains.

Species distribution model.—We developed a MaxEnt model (version 3.3.3) for 1990, 1995, 2000, and 2005 by fitting the probability distribution of covariate data acquired from vireo locations for each focal year to a single probability distribution of background data for the covariates of interest, while accounting for sampling bias (Phillips et al. 2006, Elith et al. 2011). For each model, we used a background of 10,000 pseudo-absence pixels randomly selected from all pixels across the study region. We used a jackknife test of variable importance to determine which covariates to retain for model prediction. We retained variables in our final model that obtained a regularized training gain of ≥ 0.02 and a positive test gain. We then reran each model to ensure that all remaining variables contributed to model fit.

For each study year, we used MaxEnt default settings but used a subsample replicate run type. We set max iterations to 5,000. We ran 15 random partitions of the presence locations by selecting 75% of the presence data for model training, with the remaining 25% used for model testing. We used the average coefficients from all 15 individual runs to predict vireo occurrences across the study site based on the covariates estimated at each pixel (Elith et al. 2011).

We binned the predicted suitability values in increments of 10% and calculated the percent of the total study area identified by our models in each binned estimate, such that we could examine comparisons within annual models and among annual models. To examine how different annual SDMs altered the amount of predicted suitable habitat, we compared the frequency distribution within binned predicted suitability estimates among the 4 focal study years from 1990 to 2005.

We examined how predicted habitat suitability changed during the study period relative to the values of the landscape covariates included in the SDM. We calculated the change in predicted suitability between 1990 and 2005 for each background pixel and binned these into <-0.5, -0.5 to -0.3, -0.3 to -0.1, -0.1 to 0.1, 0.1 to 0.3, 0.3 to 0.5, and >0.5 change in estimated suitability. We provide box plots of the values of slope and elevation by change in suitability between 1990 and 2005. We calculated the proportion of the main soil types that fell into each of the binned measures of change in suitability.

To assess model fit from the MaxEnt SDMs, we compared vireo locations from the model year and each of the following study years with the predicted habitat suitability estimate for each location. This allowed us to assess the ability of the 1990, 1995, and 2000 SDMs to predict future vireo locations.

RESULTS

Depicting Growth

Although we searched larger areas in 2000 and 2005 than in 1990 and 1995, the density of male vireos within search areas

Table 1. Total area searched, count of male individuals, and density of black-capped vireo males detected each year at the Wichita Mountains in Oklahoma, USA.

Year	Search area (ha)	No. individuals	Males/ha
1990	3,936.5	117	0.030
1995	2,791.3	114	0.041
2000	8,666.6	477	0.055
2005	7,497.2	1,234	0.165

steadily increased across all years. In 2005, the number of birds per ha was three times the value in 2000 (Table 1). Similarly, density of vireos increased when we compared only the overlapping search areas between the 4 focal study years (Fig. 1). In 1990 and 1995, the overlapping search area was 1,926 ha and the number of male vireos increased from 81 to 100. In 1995 and 2000, the overlapping search area was 2,573 ha, and the number of male vireos more than doubled from 107 to 230. In 2000 and 2005, we searched 5,557 ha of overlapping area and the number of male vireos almost tripled from 338 to 999.

Modeling Suitability

Predictor variables.—The jackknife tests for determining which predictor variables to retain for the final predictive models indicated that land-cover type did not contribute to the model prediction in any year, because it did not obtain a regularized training gain >0.02 in 1990, 2000, or 2005, and had a very negative test gain in 1995. Profile curvature also did not obtain a training gain >0.02 in 1995 or 2000, and contributed a negative test gain in 1990. Slope did not obtain a training gain >0.02 in 1995. Thus, our final models included elevation, slope, and soil type for 1990 and 2000; elevation and soil type for 1995; and elevation, slope, soil type, and profile curvature for 2005.

Between sample years, the minimum elevation that vireos occupied decreased, while the maximum generally remained consistent (Fig. 2). The average elevation at which we found vireos decreased over study years, from 590 m in 1990 to 523 m in 2005. Elevation ranged from 337 m to 751 m for
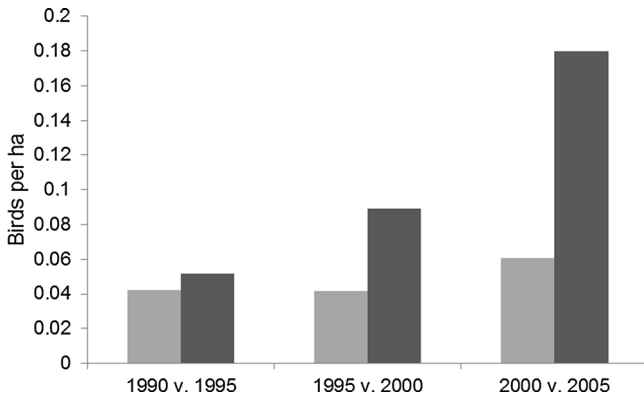
Figure 1. Density of male black-capped vireos (birds/ha) within overlapping search areas between consecutive years on the Wichita Mountains in Oklahoma, USA. Each pair of bars represents overlapping search areas within the paired study years; density of the first year is in light gray and the second year in dark gray.
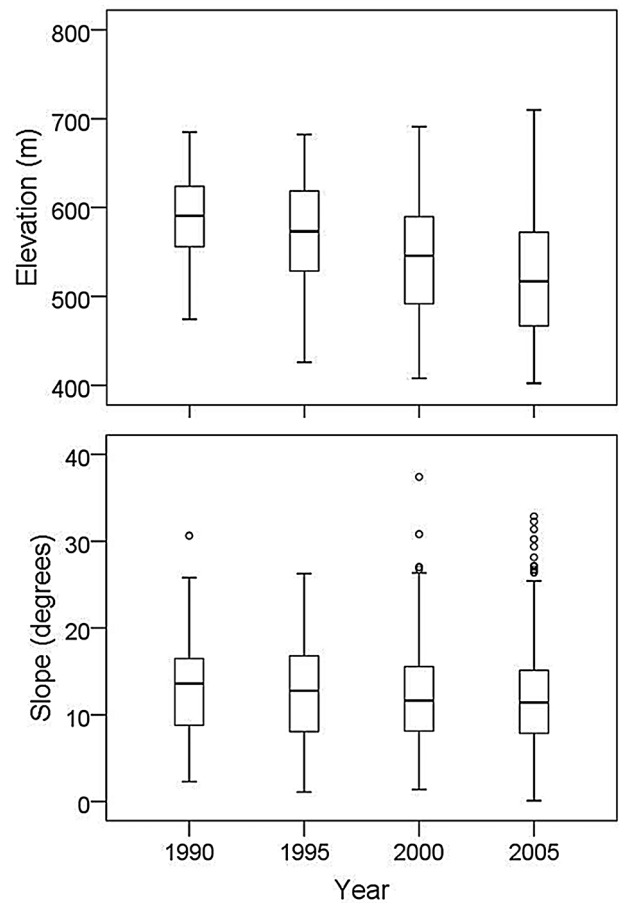

Figure 2. Box plots for elevation and slope at black-capped vireo locations during each year of our study on the Wichita Mountains in Oklahoma, USA (1990: $n = 117$ location points, 1995: $n = 114$, 2000: $n = 477$, and 2005: $n = 1,234$). Search areas varied each year.

background pixels ($n = 487,501$, mean = 482 m, SD = 87); in all study years, vireos inhabited elevations greater than the mean elevation available across the study area.

Between sample years, average slope decreased from 13.3° in 1990 to 11.7° in 2005, while the range stayed consistent (Fig. 2). Across the study area, for the 487,501 background pixels, slope ranged from 0° to 49° ($n = 487,501$, mean = 6.2°, SD = 5.8); vireos occupied locations with greater slopes than the mean across the study area.

We found vireos primarily on 2 soil classifications. The Brico Soils and Rock outcrop (St) occurs on slopes of 15–50°, and bedrock outcrops comprise approximately 40% of the area. The second soil type—Rock outcrop–Brico complex (Ro)—occurs on less steep slopes, typically 3–20°, and approximately 70% is composed of rocky outcrops interspersed with Brico soils (which are well-drained soils of cobbly loam; NRCS 2013). Background pixels were composed of 19% St ($n = 487,501$) and 31% Ro. In 1990, 88% ($n = 117$) of the vireos were detected on St soils, while only 8% were found on Ro. By 2005, the percent on St had decreased to 70% ($n = 1,234$), and the detections on Ro rose to 20%.

Model outputs.—Habitat suitability (predicted >0.5) increased across the study area from 20.8% of the study
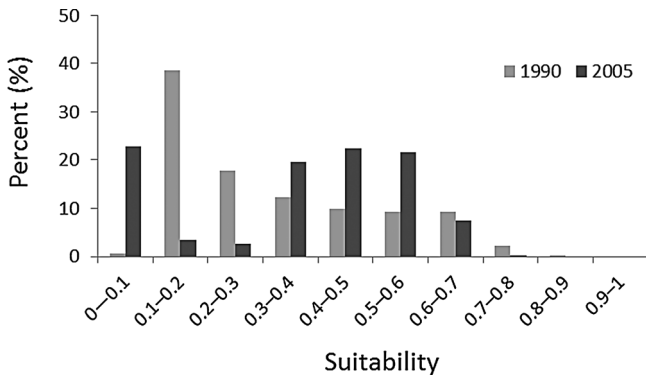
Figure 3. Percent of the study area (43,875 ha) within predicted suitability bins based on the 1990 MaxEnt model and the 2005 model for black-capped vireos in the Wichita Mountains of Oklahoma, USA.

area ($n = 487,501$ pixels, 43,875 ha) in 1990 to 21.9% in 2005 (Fig. 3; 23.0% in 1995, 30.0% in 2000). Percent of the study area with a suitability value ≤ 0.2 decreased from 39.2% in 1990 to 26.2% in 2005. Overall, 50.9% of the area did not change in predicted suitability (change between -0.1 and 0.1) between 1990 and 2005, and only 11.3% of the area decreased in suitability (change < -0.1) between those years. Predicted suitability increased over 37.8% of the study area (change > 0.1), but only 2.6% of the study area increased in suitability by > 0.3. Areas where the predicted suitability remained similar or increased from 1990 to 2005 were characterized by lower slopes and lower elevations, while areas where predicted suitability decreased from 1990 to 2005 were areas with steep slopes and high elevations (Figs. 4 and 5).

Model fit.—As predicted, ROC curve model fit decreased across study years (1990, area under curve [AUC] = 0.876; 1995, AUC = 0.809; 2000, AUC = 0.788; 2005, AUC = 0.762). The 1990 SDM predicted 91% of vireo locations ($n = 117$) in 1990 within the 0.5–0.8 predicted suitability range (Fig. 6). However, the ability of the 1990 model to predict habitat suitability for vireo locations in future years decreased over time. By 2005, only 43% of the vireo locations ($n = 1,234$) were located in areas where the 1990 model predicted suitability > 0.5 (Fig. 6).

DISCUSSION

Using a long-term data set, we demonstrated how habitat suitability models change as a species' population size increased and that there is a potential for error when predicting areas into which a species will expand. In the early years of our study, vireos concentrated in a narrow range of landscape conditions, resulting in a predictive model that suggested that much of the landscape within our study area was not of high predicted suitability. However, as the vireo population expanded, we detected vireos settling in areas with broader landscape conditions. For instance, we observed that vireos began occupying areas with less-steep slopes and across a wider range of elevations. Understandably, this increase in distribution across broader habitat conditions resulted in models that predicted more area as suitable habitat. We saw a clear trend across all 4 years of study; as the
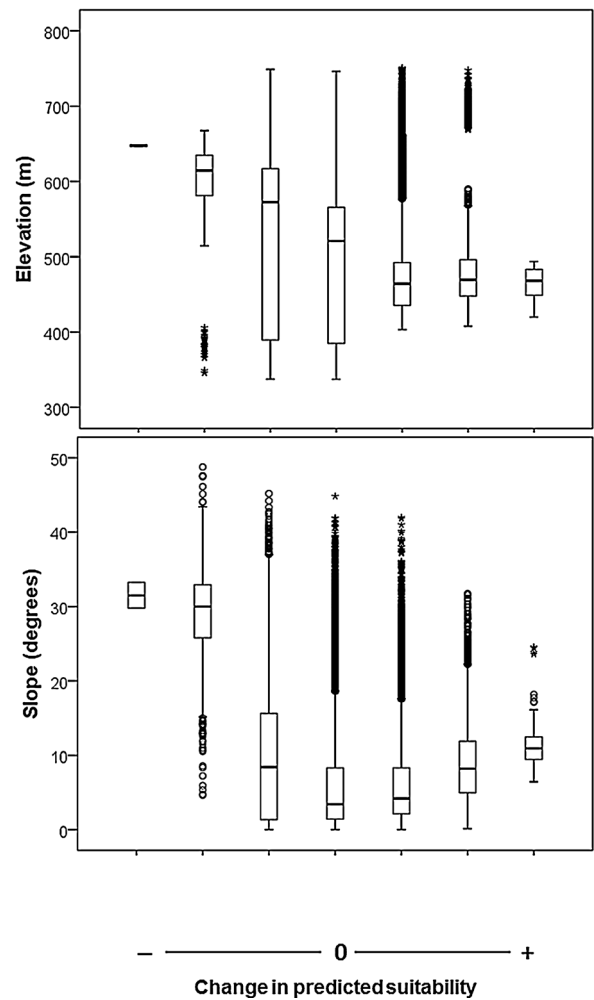

Figure 4. Values of slope and elevation at each pixel ($n = 487,501$ pixels) in the Wichita Mountains in Oklahoma, USA, in relation to the change in predicted suitability of black-capped vireo habitat from 1990 to 2005.

population increased each year, so did the area predicted as suitable.

As the numbers of vireos increased between 1990 and 2005, we also found that the habitat suitability models created by MaxEnt for 1 year of vireo detection data did not reliably predict areas that vireos occupied in future study years. The predictive ability of the models decreased over time, and in each year of study after 1990, vireos settled in areas that the 1990 model predicted to have low suitability. After just 10 years, the 1990 model designated almost 50% of the 2000 vireo locations as having low (< 0.5) predicted suitability.
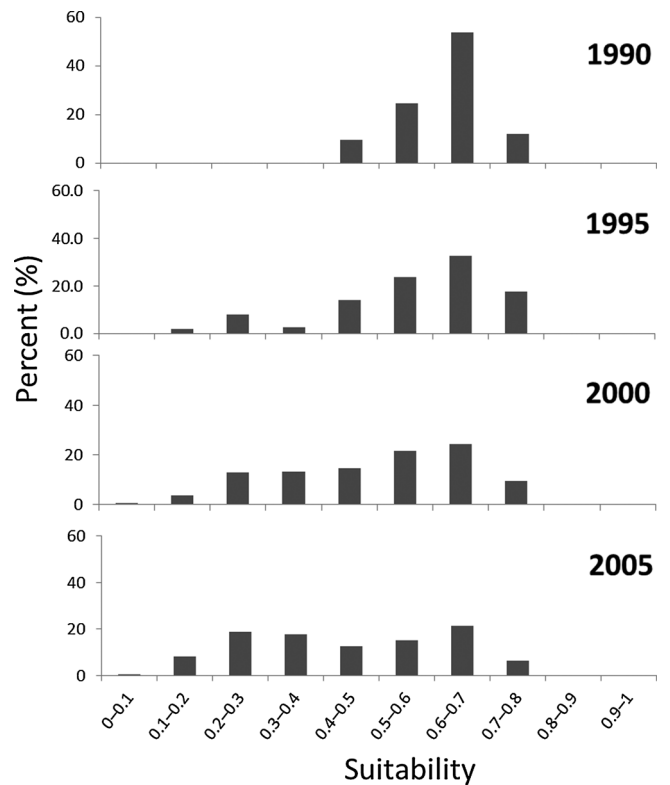
The vireo population expanded into areas with a broader range of landscape characteristics as it grew; therefore, it makes sense that the decrease in model ROC fit was a byproduct of the growing population. The Wichita Mountains are small and localized, surrounded by areas that contain no potential vireo habitat (i.e., croplands and grasslands). Thus, we can imagine that as the vireo population grew, vireos moved into areas with different landscape characteristics, eventually saturating all potential habitat. The Wichita Mountains are isolated from other
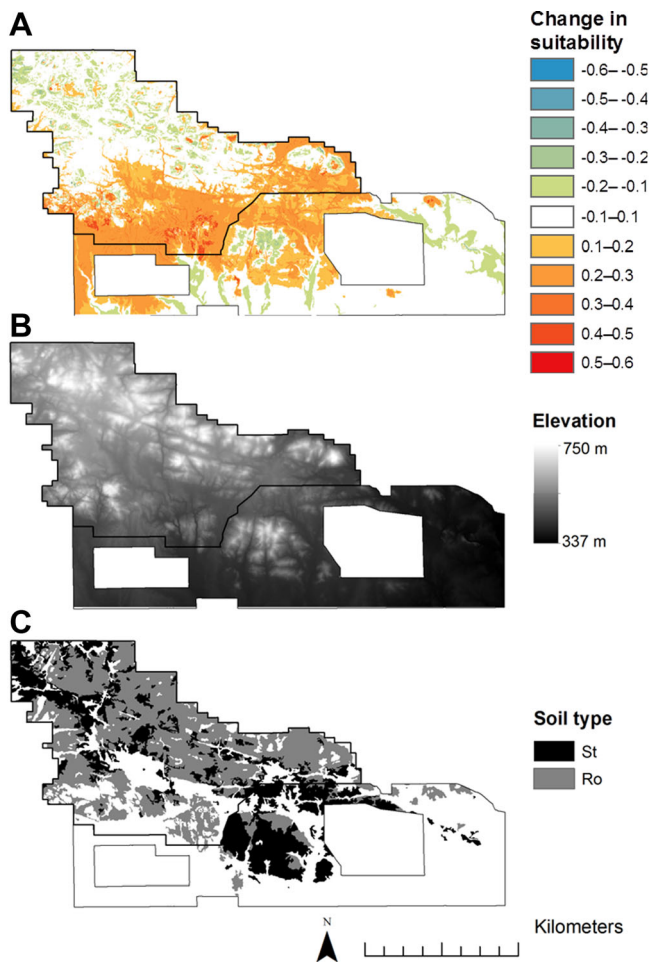
Figure 5. Distribution of (A) the change in predicted suitability for black-capped vireos from 1990 to 2005, (B) high and low elevations, and (C) major soil types within the Wichita Mountains of Oklahoma, USA.

Figure 6. Percent of black-capped vireo locations relative to habitat suitability estimates predicted by the 1990 MaxEnt model for each of 4 study years in the Wichita Mountains of Oklahoma, USA. We binned predicted habitat suitability estimates into increments of 10%.

areas into which the vireos could expand; therefore, we can imagine saturation would happen more quickly here than in study sites that are adjacent to additional areas of potential habitat. As the population grew over the course of our study, the differences between areas where vireos settled and what was available (i.e., all the background pixels) decreased. Thus, we see in our data that as the birds move into more of the available habitat, the model fit becomes worse. Similarly, the 1990 model, which we built using vireo locations from a narrow range of landscape characteristics, lost predictive ability as the vireo population expanded into areas with broader landscape characteristics.

The goal of our MaxEnt models to predict vireo habitat suitability was based on landscape characteristics; however, the modeling approach does not consider behavior aspects associated with vireo territory settlement. Settlement patterns by some birds are associated with proximity of conspecifics, which act as indicators of local habitat quality (Valone 1989, Danchin and Doligez 2001). Black-capped vireos have been shown to cluster on the landscape, attracted to conspecific cues (Ward and Schlossberg 2004, McFarland et al. 2013). When the population was small and clustered across the refuge, the vireos would not have occupied all

potential habitat. As the population grew, however, the vireos began filling in more habitat, occupying areas with landscape characteristics that they previously had not. This clustering behavior would increase the effect of vireos using particular landscape characteristics first. By packing in closely, more vireos would occur in one set of conditions, whereas a more secluded species that was not drawn to conspecifics might use more varying conditions, even at the same population size. Thus, clustering would account for the change in predicted suitability as the population grew, even if the amount of available habitat did not change across years (Aarts et al. 2013).

Our study does not indicate whether vireos prefer some landscape characteristics over others. If vireos cluster with conspecifics, then vireo locations in the early years of this study would be more attributed only to proximity of other vireos, and not necessarily to a preference for certain habitat conditions. However, over the course of our study, we saw that vireos moved from occupying only areas of the refuge, where the elevation is higher, to occupying more areas of the fort, where the elevation is lower. Occupied areas of the fort are also largely made up of the St soil type. However, we found that areas where predicted suitability increased occurred on both Ro and St soil types.

However, if the landscape conditions that vireos are first occupying is the habitat that allows for the highest productivity (e.g., quality), then as the population grows and the best habitat becomes saturated, they would

eventually get pushed into less desirable habitat. Therefore, for the vireos detected in 1995, 2000, and 2005 in areas where the predicted suitability in the 1990 model is low, we are unable to determine whether the 1990 model is predicting poorly and those areas were misidentified as potential habitat in the 1990 model, or whether some of those vireos are actually occupying less desirable habitat due to conspecific attraction, and are choosing this habitat over habitat where their chances of successfully reproducing are better as a trade-off to be closer to other vireos.

Our study indicates that SDMs like MaxEnt may not be a reliable tool to predict suitability of a species' habitat into the future during periods of population growth and expansion. Furthermore, our study species demonstrates conspecific attraction, which can create complication for SDM predictions. In addition, our study site is an isolated ecosystem within the region, resulting in a discrete area in which birds have settlement options. Without including consideration of conspecific interactions and demographic variation across predicted suitable habitat, models like these should be used with caution when predicting areas for conservation work.

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