

Testing the predictive capabilities of ecological niche models: a case study examining Red-bellied Woodpeckers

ALYSSA M. FITZGERALD ^{1,2,3,†}, NAIMA C. STARKLOFF,^{1,2} AND JEREMY J. KIRCHMAN¹

¹Department of Ornithology, New York State Museum, 3140 Cultural Education Center, Albany, New York 12230 USA

²Department of Biological Sciences, State University of New York at Albany, 1400 Washington Ave., Albany, New York 12222 USA

Citation: FitzGerald, A. M., N. C. Starkloff, and J. J. Kirchman. 2018. Testing the predictive capabilities of ecological niche models: a case study examining Red-bellied Woodpeckers. *Ecosphere* 9(12):e02496. 10.1002/ecs2.2496

Abstract. As humans continue to alter natural habitats indirectly and directly, species' geographic ranges may change as they track shifting climate regimes or changing landscapes. Ecological niche models (ENMs) are frequently used to show modern ranges and forecast future range changes. These models, however, assume that a species will exhibit niche conservatism, though this is rarely tested. Here, we examine a woodpecker species with a well-documented recent range expansion to assess the effectiveness of predictive models by comparing the pre- and post-expansion climate/habitat niche using ENMs and multivariate principal components analysis. Occurrence data for the Red-bellied Woodpecker (*Melanerpes carolinus*) were obtained from the pre-expansion (1910–1939; $n = 299$) and post-expansion (1980–2009; $n = 868$) time periods. Ecological niche models were constructed using GIS layers describing climate data and crop cover for the pre- and post-expansion time periods. We then used the pre-expansion ENM to forecast the distribution of Red-bellied Woodpeckers into the post-expansion time period, and vice versa, and calculated the niche overlap of the projected distributions and the actual distributions in those time periods to determine whether pre- and post-expansion niches were similar. Predictive ENMs did not closely match the actual distributions in the pre- and post-expansion time periods, respectively, and the pre-expansion and post-expansion niches were significantly different from each other (Schoener's $D = 0.745$, $P < 0.001$). Multivariate analyses revealed that the present-day niche encompasses the past niche and that Red-bellied Woodpeckers today have broader temperature and precipitation tolerances and are found in both more- and less-forested areas than they were in the pre-expansion era. Our analyses reveal that Red-bellied Woodpeckers are not exhibiting climate or habitat niche conservatism, explaining why predictive ENMs for this species could not effectively track their range shift. This study emphasizes that predictive models may not be effective for species undergoing niche changes.

Key words: Carolinian avifauna; climate change; ecological niche modeling; land cover change; Maxent; *Melanerpes carolinus*; niche conservatism; niche expansion; predictive modeling; range expansion; Red-bellied Woodpecker.

Received 6 July 2018; revised 6 September 2018; accepted 26 September 2018. Corresponding Editor: Paige Warren.

Copyright: © 2018 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

³Present address: Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 110 McAllister Way, Santa Cruz, California 95060 USA.

† **E-mail:** alyssa.fitzgerald@noaa.gov

INTRODUCTION

Species' range dynamics are inexorably linked with their ecology such that ranges are defined by the complex interplay of a species' fundamental niche, limiting biotic factors in potential habitats, and the species' dispersal capability

(Hutchinson 1957, Hargreaves et al. 2014). The fundamental niche is often constrained by climate aspects, either directly or indirectly, such that climate changes result in species tracking changing conditions if they have the dispersal capacity and if biotic factors do not limit their dispersal (Sexton et al. 2009). Over the last ~70 yr, the climate has

warmed at its fastest rate in over 2 millennia, resulting in range shifts, with some populations moving poleward or uphill (Parmesan 1996, 2006, Parmesan and Yohe 2003). Range changes may also be facilitated by urbanization and other anthropogenic changes to habitats (Robb et al. 2008, Zuckerman et al. 2011). Disentangling the causes of observed range dynamics is a challenge for researchers, but one that has been met by recent advances in niche modeling techniques, the availability of biotic and abiotic geospatial layers, and the availability of long-term datasets on the distributions of species. These new advances have enabled researchers to document range-wide patterns of occurrence, investigate the processes that drive range dynamics, and forecast future range changes.

Ecological niche models (ENMs) are pervasive in ecology and evolution because of their ability to address myriad questions relating to species' ranges and ecological relationships. ENMs are often used to predict future range shifts under different climate change scenarios and to reconstruct past distributions (Elith and Leathwick 2009). Predictive and reconstructive ENMs assume that the niche is conserved, such that if a species is tracking its niche over time, ENM should be able to accurately predict range changes. The assumption that a species exhibits niche conservatism is based on much research that supports the idea that niches are usually conserved over short-to-medium evolutionary timescales (e.g., Peterson et al. 1999, Peterson 2011). Still, ENMs are consistently used to predict future range changes, often without any empirical testing of whether the focal species has displayed niche conservatism in the past (by tracking its niche) and ignoring the ability of that species to change its niche via adaptation or plasticity. Here, we examine the present-day and historic niche of a well-documented woodpecker species in North America that has undergone a range expansion over the last several decades. If this species demonstrates niche conservatism over time, we expect that forecasted models will be able to accurately predict its recent range change.

Focal species and hypothesis testing

We chose to examine the Red-bellied Woodpecker (*Melanerpes carolinus*) as a case study for

three reasons. First, birds comprise the best-documented taxon in North America due to museum collections dating to the 19th century, long-term scientific surveys (e.g., Audubon Christmas Bird Count, an annual count begun in 1900), and citizen observations (e.g., eBird). This woodpecker species, in particular, is large, conspicuous, noisy, and easily identifiable by even novice birders, ensuring the accuracy of observations. Second, the Red-bellied Woodpecker, along with other Carolinian avifauna, has expanded northward (Jackson and Davis 1998, Shackelford et al. 2000) and westward (Kirchman and Schneider 2014) in recent decades, providing an interesting example to test the predictive power of ENM. The comprehensive documentation of its range expansion allows us to define its environmental niche pre- and post-expansion.

Third, nine potential causes for the range expansion can be classified into three broad hypotheses: climate warming, reforestation (due to aspects of human cultural change that resulted in more trees on the landscape, such as reversion of farms to forests, conversion of farms to landscaped suburbs, shift from wood-burning stoves to regional power plants), and increased supplemental feeding by bird watchers (Jackson and Davis 1998). Here, we test two of these hypotheses that the expansion is due to either climate change or reforestation (Table 1). Data on supplemental feeding do not exist over the timescales examined in this study and could not be tested at this time.

Studies of bird range shifts conducted on decade timescales generally have found movements of species consistent with climate warming in both direction and magnitude (La Sorte and Thompson 2007, Zuckerman et al. 2009, Auer and King 2014, Freeman and Class Freeman 2014, Kirchman and Van Keuren 2017), providing evidence that a single factor like climate change is driving shifts. Counterexamples of species moving downhill or away from the poles have also been reported but are thought to result from species tracking habitat changes or other aspects of climate (Tingley et al. 2012, DeLuca and King 2017). The northern boundaries of many North American bird species, including Red-bellied Woodpeckers, seem to be limited by winter temperature (Root 1988a, b) such that warming winter temperatures may increase the area of suitable temperatures available for

Table 1. Predictions and expected results for two hypotheses proposed to explain the range expansion of the Red-bellied Woodpecker (*Melanerpes carolinus*).

Hypothesis	Prediction	Predictive model results	Multivariate analysis results	Interpretation
Increase in forested habitats	Woodpeckers colonize places associated with a decrease in agricultural habitat, regardless of climate change	Crop cover layer will be a better predictor than climate layers	Woodpeckers are now found in habitats with similar forest cover as pre-expansion, but may occupy a different climatic niche	Habitat niche conservatism
Climate warming	Woodpeckers track shifting geographic climate regimes	Climate layers will be better predictors than crop cover	Woodpeckers are now found in similar climates as pre-expansion, but may occupy a different habitat	Climate niche conservatism
Not climate change or reforestation	Woodpeckers are tracking another factor or have niche plasticity	Predictive models are poor	Pre- and post-expansion niches are dissimilar	Ecological release or niche plasticity

habitation. Indeed, the Red-bellied Woodpecker range expansion seems to be led by winter birds (Kirchman and Schneider 2014), and Red-bellied Woodpeckers and other woodpeckers (*Sphyrapicus* species) are more likely to colonize areas with warming winter temperatures (Zuckerberg et al. 2011, Billerman et al. 2016). We therefore examine changing winter climate, particularly temperature, as the reason for the Red-bellied Woodpecker recent range expansion.

The second hypothesis states that reforestation and the conversion of farms to tree-planted suburbs have resulted in an increase in available habitat. Red-bellied Woodpeckers inhabit mature hardwood forests but also are found in somewhat open habitats as long as large dead trees or even utility poles are present (Shackleford et al. 2000). Reforestation in northeastern North America has been occurring since ~1900 as row-crop agriculture shifted to flatter, more fertile soils in western states. Later in the 20th century, the creation of suburban neighborhoods resulted in the planting of a multitude of yard trees that the Red-bellied Woodpeckers readily utilize (Jackson and Davis 1998). Several 19th-century ornithologists anecdotally observed a range contraction in the mid- to late 1800s and early 1900s as the hardwood forests in eastern North America were cleared in association with human population increases (Wilson 1808, De Kay 1844, Audubon 1849, Forbush 1927). More recently, Koenig et al. (2017) found that the increased abundance of Red-bellied Woodpeckers within the core of their range was weakly correlated with increased forest cover but not with increased temperature. However, this study only included post-expansion occurrences

(1960–2014) and did not include areas into which the Red-bellied Woodpecker range has expanded. Although continental-scale forest cover layers do not exist for both of these time periods for the entire Red-bellied Woodpecker range, we examine cropland instead under the assumption that a decrease in cropland is associated with an increase in forested habitat.

We empirically test the two above hypotheses by examining the pre-expansion and present-day environmental niche. If Red-bellied Woodpeckers have been expanding their range due to shifting climate or reforestation, thus exhibiting niche conservatism, we expect to find that the species occupied similar niches pre- and post-expansion and that ENMs accurately predict distributions under one or both hypotheses (Table 1). In other words, the species has tracked its environmental niche which has shifted geographically, enabling the species to expand into new areas. If, however, the species is not responding to an increase in forested land or following a specific climate regime, niche models may not be similar pre- and post-expansion and predicted distributions will not match actual distributions, indicating that another factor has enabled the expansion of the Red-bellied Woodpecker into new regions, such as niche plasticity or ecological release.

METHODS

Occurrence data

Georeferenced occurrence data were obtained from Kirchman and Schneider (2014). Briefly, in 2010, Kirchman and Schneider (2014) aggregated Red-bellied Woodpecker occurrences by requesting

data from the Audubon Christmas Bird Count (CBC) annual survey, dating back to 1900, and by searching ORNIS (www.ornisnet.org) for museum specimens, dating to the 19th century. We trimmed the dataset to include only occurrences from December and January, and used winter bird occurrence records from 1910 to 1939 to model the pre-expansion niche and from 1980 to 2009 to model the post-expansion niche. After removing duplicate records within a 0.5-degree pixel, 299 occurrences were utilized for 1910–1939, and 868 for 1980–2009.

Timing and rate of range expansion

We first re-examine the timing of range expansion with a quantitative diffusion analysis of range size change. Linear regression determined whether range expansion followed a linear relationship between dispersal and colonization as expected under a quantitative diffusion scenario (Skellam 1951). We calculated the square root of the total area occupied by Red-bellied Woodpeckers in each decade of the 20th century using minimum convex polygons around occurrences in ArcMap 10.3 (ESRI). We calculated the linear expansion of forested land as the square root of the total forested area in states occupied by Red-bellied Woodpeckers using data (reported as total acres of forest per state) from Oswalt et al. (2014), and compared this with the pattern of woodpecker range expansion over the same interval. Forested area data were available for 1907, 1920, 1938, 1953, 1963, 1977, 1987, 1997, and 2007.

Pre- and post-expansion niche comparison

Few individuals were reported west of the Rocky Mountains or in Canada during the time periods examined, and so December and January monthly climate data for the conterminous United States east of the Rocky Mountains for 1910–1939 and 1980–2009 were obtained through PRISM (PRISM Climate Group, Oregon State University, Corvallis, Oregon, USA). Monthly data were combined for each 30-yr period, resulting in seven climate variables: (1) precipitation, (2) mean temperature, (3) maximum temperature (the maximum temperature of December/January recorded during all years), (4) minimum temperature (the minimum temperature of December/January recorded during all years), (5) minimum

vapor pressure deficit (VPD, minimum difference between the amount of air moisture before water condenses, a measure of humidity), (6) maximum VPD, and (7) mean dewpoint temperature. Two snapshots of cropland cover from 1910 and 1990 were included to represent changes in available habitat before and after range expansion (Ramanakutty and Foley 1999). All eight environmental layers were moderated to a pixel size of 0.5 degrees, matching the resolution of the cropland dataset and encompassing the geographic uncertainty (12 km) from the CBC occurrences. A Pearson correlation analysis run in ArcMap 10.3 (ESRI) confirmed that cropland was not highly correlated with any climate variable (range: -0.22 to 0.37).

Ecological niche modeling, projection, and assessment

The ENM program MAXENT 3.3.3K uses a maximum entropy algorithm to assess the niche conditions associated with presence-only occurrences, and a habitat suitability model is created based on where those same conditions are found in geographical space (Phillips et al. 2006). We chose to utilize MAXENT because this software has been demonstrated to accurately portray modern distributions (Phillips et al. 2006, Elith et al. 2011). Models were run for 100 replicates with 25% of occurrences bootstrapped to assess the model's accuracy using the area under the curve (AUC) criterion. In general, AUC values below 0.7 are considered inaccurate and no better than random, while values above 0.9 indicate that the model is good at determining suitable vs. unsuitable habitat for the given data (Fielding and Bell 1997, Phillips et al. 2006, Baldwin 2009, Elith et al. 2011). We tested multiple regularization values (0.1, 0.5, 1, 5, and 10) and found that higher regularization values (5 and 10) had lower AUC values and over-projected actual distributions for both time periods whereas lower regularization values (0.1 and 0.5) had higher AUC values, but under-projected actual distributions. Therefore, a regularization value of 1 (default) was employed. A jackknife test determined which variables contributed the most to each model. For each jackknife test, one variable was removed from the model and the results were compared to the complete model; the removed variables that caused the highest drop in model

performance were the variables that contributed the most to the model (Phillips et al. 2006).

We determined whether pre- and post-expansion niches were similar using four different assessments. First, the pre-expansion (1910–1939) MAXENT model was forecasted to the post-expansion time period (1980–2009), and the post-expansion model was hindcasted to the pre-expansion time period, and these projected models were compared to actual occurrences in each time period. Niche overlap between all actual and projected models was calculated using Schoener's D in ENMTools (Warren et al. 2010).

Next, to calculate niche similarity between the pre-expansion and post-expansion time periods, we employed the niche identity test in ENMTools (Warren et al. 2010). For the niche identity test, all pre-expansion and post-expansion occurrences were pooled and then randomly partitioned into two pseudo-populations. Niche overlap was then calculated between the ENMs of the pseudo-populations, and this was replicated with 100 random divisions, resulting in a null distribution of overlap values representing the range of overlap under the assumption that past and present niches are not significantly different from each other. The niches were significantly different if

actual overlap was less than 95% of the null distribution based on a one-tailed t -test.

Third, we examined the pre- and post-expansion niche axes defined by a principal components analysis (PCA) of environmental layer values extracted from each occurrence point using ArcMap 10.3 (ESRI). Covariates were centered and scaled, and then, the PCA was run with correlation matrix for each time period in R v. 3.3.4 (R Development Core Team 2017). Loadings on the top three niche axes were plotted with the packages ggplot2 (Wickham 2009) and ggbiplot (Vu 2011). Finally, kernel density estimate plots were made using R for each environmental variable for both time periods.

RESULTS

The quantitative diffusion analysis indicated that the Red-bellied Woodpecker range was fairly stable until ~1950, when a dramatic expansion began (Fig. 1). Prior to 1950, gradual, linear increases in range size radius of <60 km per decade occurred. After 1950, the range size radius increased an average of 190 km per decade, with the largest increase occurring between the 1950s and 1960s (388.5 km). In comparison, the total

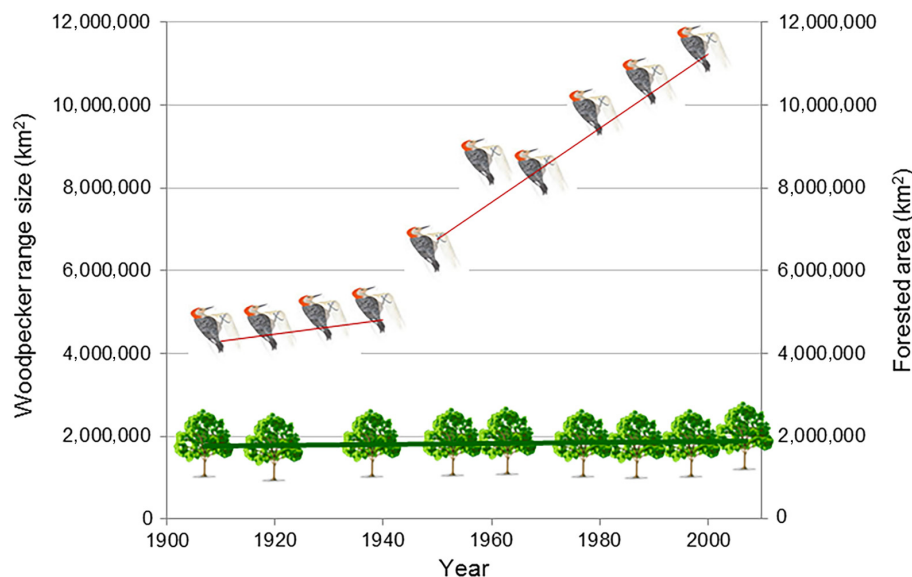


Fig. 1. Timing of range expansion and comparison with forested area. The pace of the Red-bellied Woodpecker (*Melanerpes carolinus*) range expansion increased dramatically beginning in 1950. Prior to 1950, the population was fairly stable with small, gradual increases in range size per decade. Forested area in states where Red-bellied Woodpeckers currently reside does not show a similar dramatic increase (forest data from Oswalt et al. 2014).

area of forested land summed for all states occupied by Red-bellied Woodpeckers has remained relatively stable over the last century (Fig. 1). This reforestation pattern was not substantially changed when removing data from Montana, which has been recently colonized by only a few woodpeckers in the eastern part of the state. Forested area in the Northeast (CT, ME, MA, NH, NY, RI, and VT) also has not changed dramatically since 1907 when compared to the woodpecker range expansion.

The ENMs for pre-expansion (1910–1939) and post-expansion (1980–2009) had moderate AUC scores of 0.821 (± 0.017) and 0.710 (± 0.016), respectively, but we note that AUC scores are often lower for broadly distributed, generalist species (Stockwell and Peterson 2002) and that these

non-projected models closely match the actual distributions of Red-bellied Woodpeckers at those time periods (Fig. 2). Conversely, the forecasted model underestimated the actual Red-bellied Woodpecker range in the post-expansion period, and the hindcasted model indicated much more suitable habitat, especially in the Northeast, than was actually occupied from 1910 to 1939 (Fig. 2).

Niche overlap was 88.7% between the pre-expansion ENM and its forecast model and 92.3% between the post-expansion ENM and its hindcast model (Fig. 2, Appendix S1: Fig. S1), and actual models and their projections were not significantly different ($P > 0.05$). In contrast, niche overlap between models of the same time period (i.e., pre-expansion vs. hindcast, and post-expansion vs. forecast) was lower than the null distribution and

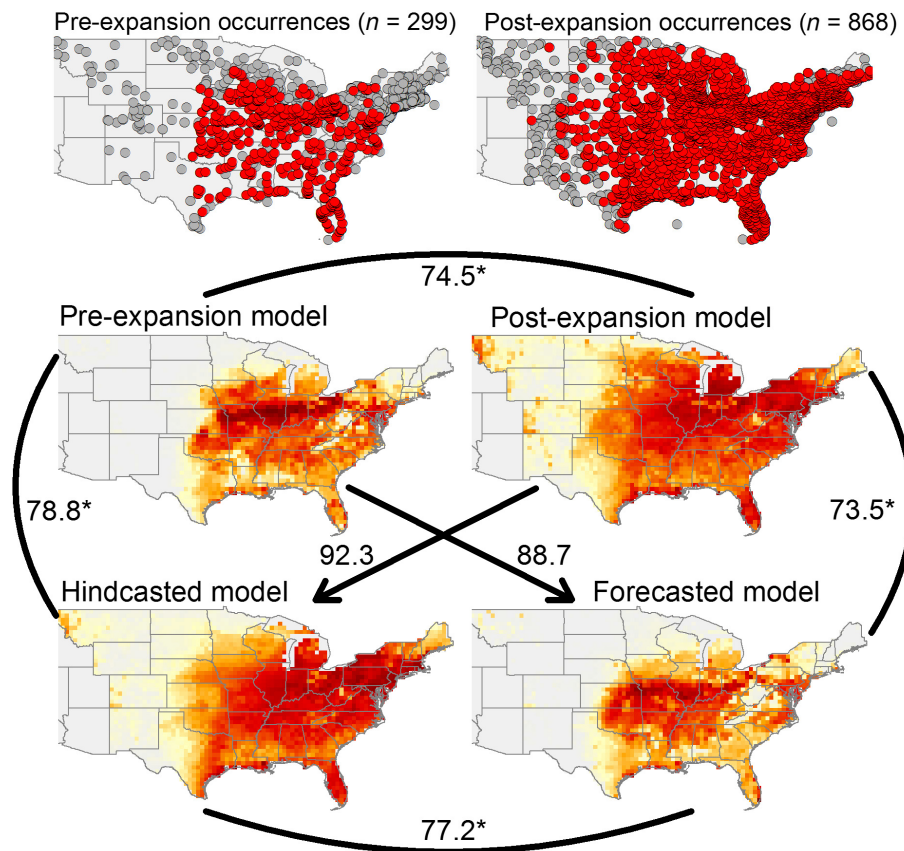


Fig. 2. Red-bellied Woodpecker pre- and post-expansion occurrences, models, and niche overlap values. Occurrence data (red dots) obtained from Audubon Christmas Bird Count and museum specimen locality information via Kirchman and Schneider (2014); CBC locations where Red-bellied Woodpeckers were not reported are shown by gray dots. Warmer colors indicate a higher probability of species occurrence. The values indicate the percentage of niche overlap between specified models, and asterisks indicate significant differences.

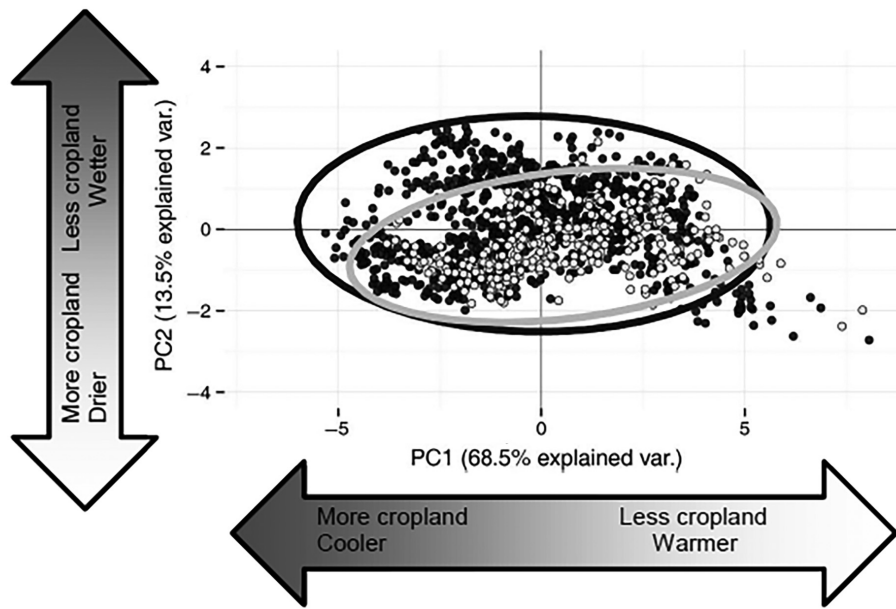


Fig. 3. Comparison of pre- and post-expansion niche. The multivariate principal components analysis shows that the post-expansion (dark) niche of the Red-bellied Woodpecker (*Melanerpes carolinus*) is larger than the pre-expansion niche (light).

significantly different ($P < 0.001$) from one another. Niche overlap was also low and significantly different ($P < 0.001$) when comparing the two time periods, both in terms of non-projected models (pre-expansion vs. post-expansion) and projected models (hindcast vs. forecast). These results indicate that (1) projected models that assume niche conservatism over time do a poor job describing the actual distribution of Red-bellied Woodpeckers, and (2) the pre-expansion and post-expansion niches are significantly different from each other.

In our multivariate plot of pre-expansion and post-expansion occurrences in the niche space (Fig. 3), the post-expansion niche is broader than and encompasses the pre-expansion niche. PC1 (explaining 68.5% of the variance) is an axis of cropland and temperature, and PC2 (13.5%) is an axis of cropland and precipitation (Table 2). These results are consistent with the jackknife tests from the ENMs that showed that precipitation, cropland, and dewpoint were the highest contributors for both pre- and post-expansion models (Appendix S1: Fig. S2). Kernel density plots for these covariates revealed that post-expansion birds are more often found in areas with both higher and lower cropland percentage, less precipitation, and

Table 2. Variable loadings for the top three principal components (PC). The proportion of variance explained by each PC is shown in parentheses.

Variable	PC1 (0.685)	PC2 (0.135)	PC3 (0.100)
Cropland	-0.114	-0.791	0.525
Dewpoint	0.410	-0.084	0.219
Precipitation	0.247	0.525	0.508
Temp maximum	0.419	-0.077	0.009
Temp mean	0.424	-0.077	0.058
Temp minimum	0.416	0.010	0.112
Vapor maximum	0.398	-0.157	-0.169
Vapor minimum	0.266	-0.235	-0.612

slightly lower dewpoint temperatures compared to pre-expansion birds (Fig. 4). Present-day birds are also found in areas with lower maximum, mean, and minimum winter temperatures and higher humidity (lower VPD).

DISCUSSION

Can ecological niche models accurately predict range changes?

Because the historic and current ranges of the Red-bellied Woodpecker are so well documented,

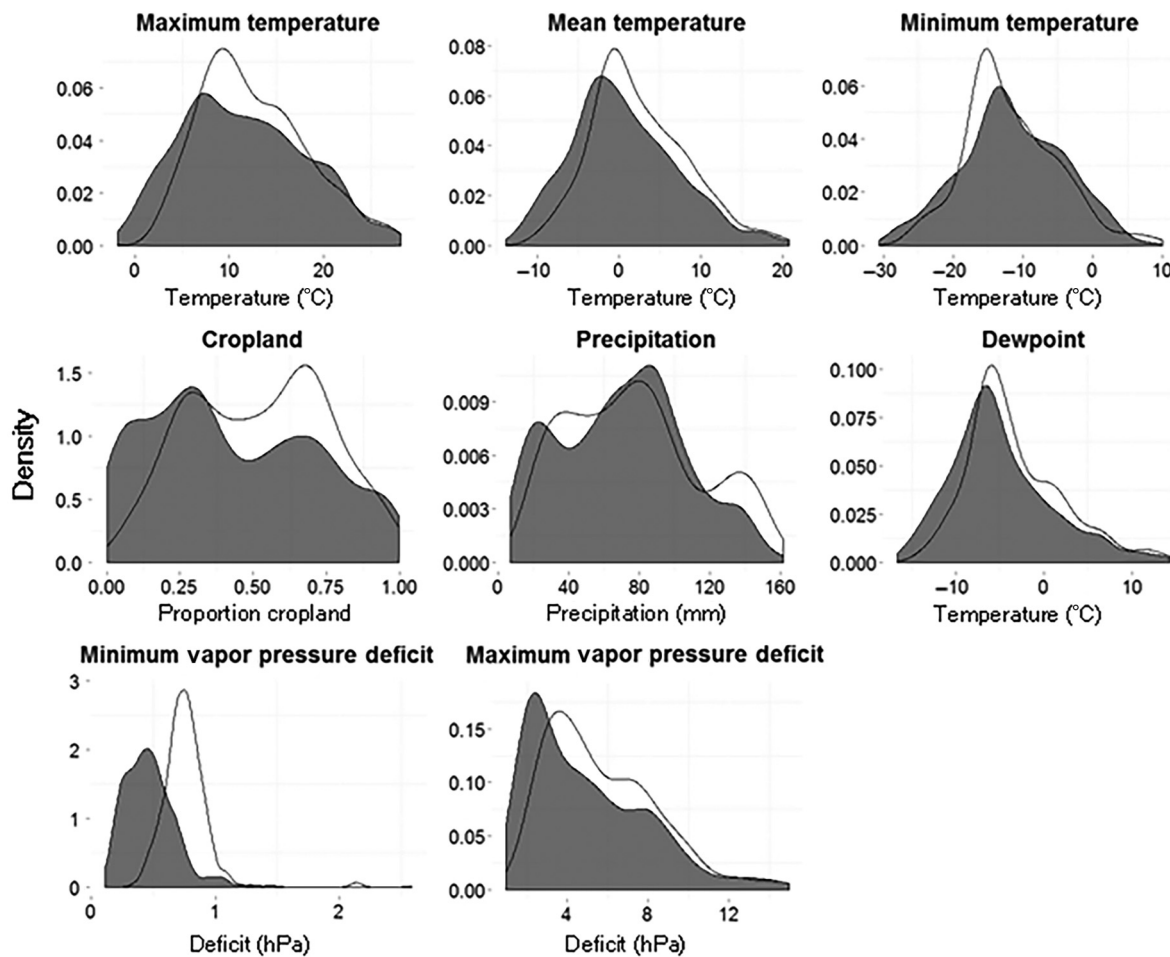


Fig. 4. Pre- and post-expansion comparison of covariates. Kernel density estimate plots illustrate how Red-bellied Woodpeckers (*Melanerpes carolinus*) utilized each covariate pre-expansion (light) and post-expansion (dark).

we were able to assess whether forecasted models could accurately predict the recent range expansion. Although both the pre- and post-expansion ENMs accurately portrayed distributions at those respective time periods, the forecasted and hind-casted models did not closely match actual occurrences and showed low overlap with actual models, especially on the periphery of the Red-bellied Woodpecker range. The projected (hind-casted and forecasted) models in this project were poor for Red-bellied Woodpeckers because this species did not exhibit climatic or habitat niche conservatism. Similarly, our multivariate analyses showed expansion along both climate and habitat niche axes, indicating that the Red-bellied Woodpecker's climate and habitat niches, based on the

covariates used in this study, were not conserved over the last century.

Ecological niche models assume niche conservatism and generally do not account for a species' adaptive capabilities, evolution potential, or plasticity, attributes which may affect a species' propensity to colonize new areas. As a generalist, the Red-bellied Woodpecker has the potential to adapt to rapidly changing environments. Kirchman and Schneider (2014) found that the northernmost individuals are larger post-expansion, perhaps indicating that a shift in body size has enabled expansion into colder regions. This supports the idea that generalist species can expand their environmental breadth and range due to adaptation or plasticity. In contrast, specialist

species are more likely to show niche conservatism (Peterson 2011).

Predictive niche models based solely on a single time period or a single set of niche conditions (i.e., climatic factors) will not be able to accurately determine species' range changes or shifts unless that species is exhibiting niche conservatism, which is not the case in our study of the Red-bellied Woodpecker. Testing temporal predictive models is extremely difficult unless, like here, the species is well documented over a long period of time. However, spatial predictive models, which are often used to predict biological invasions, can be compared with actual occurrences from the invaded range to assess predictive accuracy (Guisan et al. 2014). Still, these spatial predictive models assume niche conservatism such that any differences between the native and invaded ranges may be interpreted as either niche expansion or niche unfilling; that is, the invaded niche is smaller than native niche (Guisan et al. 2014). Further, niche differences may be confounded by underlying differences in abiotic or biotic factors between native and invaded ranges. If unable to test predictive models using actual occurrences, we strongly advocate caution when projecting niche models into novel spaces or times. Our study emphasizes that testing for niche conservatism is paramount when using predictive models, as they are only effective if a species is tracking its niche.

Have Red-bellied Woodpeckers tracked climate or reforestation?

We examined two hypotheses regarding the cause of the Red-bellied Woodpecker range expansion. Expanding populations of Red-bellied Woodpeckers have not tracked warming winter temperatures, but have actually expanded their climate niche and are now tolerating colder winter temperatures (Figs. 3, 4). Although many bird species have shifted their ranges poleward or upward in elevation in the era of rapidly warming temperatures (La Sorte and Thompson 2007), this pattern is not consistent across all bird species. Range-shift studies have revealed varied responses among taxa, indicating that rising temperature is not the only factor contributing to range determination (Tingley et al. 2012). A recent re-survey of high-elevation bird species in montane New York found a predominant pattern

of uphill movement over the past 40 yr (Kirchman and Van Keuren 2017), but in nearby New Hampshire, nine of 11 montane bird species had lower elevational boundaries over a 16-yr period, possibly because they were tracking the downhill movement of fir trees (*Picea*) rather than changes in climate (DeLuca and King 2017). Further, although warming winter temperatures may correlate with the northward expansion of Red-bellied Woodpeckers, latitudinal temperature shifts do not explain the observed westward expansion of Red-bellied Woodpeckers.

Anecdotal 19th- and early 20th-century records support the hypothesis that Red-bellied Woodpeckers have been tracking the recent trend of increasing forest abundance (Wilson 1808, De Kay 1844, Audubon 1849, Forbush 1927), and the species showed small, gradual increases in range size (Fig. 1) similar to patterns of reforestation (Oswalt et al. 2014) prior to the onset of the ongoing, rapid range expansion. However, whereas the reforestation trend continued slowly after 1950, the range of the Red-bellied Woodpecker expanded dramatically. We found evidence for an expansion of the habitat niche, such that woodpeckers are now found in low-density cropland (forested) habitats but also in high-density cropland (open) habitats (Figs. 3, 4). This suggests that reforestation is also not the primary cause of the Red-bellied Woodpecker range expansion.

Why have Red-bellied Woodpeckers expanded?

If Red-bellied Woodpeckers are not tracking winter climate or reforestation, why are they expanding? Interspecific interactions may have facilitated the range expansion of the Red-bellied Woodpecker via ecological release. In particular, the Red-bellied Woodpecker has expanded its range and increased in abundance as its congener, the Red-headed Woodpecker, declines throughout its range. Aggressive interactions have been observed between the species in battles over nesting cavities (Shackleford et al. 2000), and a decline in Red-headed Woodpeckers may have resulted in more nesting habitat for Red-bellied Woodpeckers. However, a recent study by Koenig et al. (2017) found that interspecific competition with Red-bellied Woodpeckers was not a significant cause of Red-headed Woodpecker declines; instead, they found that warming winter temperatures and reforestation have contributed directly

or indirectly to their declining numbers. In contrast, our study did not find that Red-bellied Woodpeckers tracked warming temperature or reforestation. The results from Koenig et al. (2017) and ours (indirectly) do not support the hypothesis that the Red-bellied Woodpecker is expanding because of its declining congener, the Red-headed Woodpecker.

Red-bellied Woodpeckers may be tracking other aspects of climate or habitat not included in our models. One possibility suggested by Jackson and Davis (1998) is that Dutch elm disease created new nesting and roosting habitat that allowed the woodpeckers to expand into new regions. The increased presence of bird feeders may also have resulted in expansion into formerly inhospitable geographic areas (Jackson and Davis 1998). Supplemental feeding experiments have demonstrated direct links to increased reproductive output and behavioral changes in birds (Robb et al. 2008), but there are no studies quantifying the effect of feeding on Red-bellied Woodpecker survivorship or that establish a spatial correlation between supplemental feeding and range expansion of bird species. However, Red-bellied Woodpeckers were observed visiting bird feeders more frequently on abnormally cold winter days (Zuckerberg et al. 2011), perhaps indicating that supplemental feeding might help them survive colder temperatures. Increased survival due to supplemental feeding could explain our data showing that Red-bellied Woodpeckers are now found in colder areas than pre-expansion (Fig. 4). Establishing a causal link between range expansion and supplemental bird feeding, Dutch elm disease, or another factor is difficult at large geographic scales over long time periods, precluding an examination of these hypotheses in our study. Still, the addition of biotic factors results in a more accurate representation of the realized niche (FitzGerald 2017) and should be included when data are available to have better explanatory and predictive models.

Other members of the Carolinian avifauna, species that historically inhabited the hardwood forests found in the southeastern United States, have expanded northward and westward in recent decades (Beddall 1963). Warming climate is usually suspected as the root cause, as for the Carolina Wren (*Thryothorus ludovicianus*; Haggerty and

Morton 2014). Other factors, however, are sometimes implicated. For example, the Northern Mockingbird (*Mimus polyglottos*) is suspected to have expanded as human-mediated habitats—particularly, suburbs and secondary growth—increase (Farnsworth et al. 2011). The Tufted Titmice (*Baeolophus bicolor*) and Northern Cardinals (*Cardinalis cardinalis*) often visit feeders, but climate warming may also have contributed to their range expansions (Halkin and Linville 1999, Ritchison et al. 2015). Although beyond the purview of this study, our methods could be applied to examine whether similar factors resulted in the parallel expansions of these species.

CONCLUSIONS

For the Red-bellied Woodpecker, a generalist species that has undergone a recent and dramatic range expansion, predictive niche models do a poor job of forecasting and hindcasting its range change. This could be because this species has expanded its niche or because we have not captured the particular covariates it is tracking. Regardless, this study provides important implications for all researchers using predictive modeling. Unless the focal species is exhibiting niche conservatism, ecological niche modeling will not accurately predict future or past distributions in a changing environment. Although not explicitly tested here, our study hints at the idea that specialist species are more likely to show niche conservatism and to track changing habitats, and may therefore be better candidates for predictive modeling than generalist species. Still, we recommend testing for niche conservatism, using methods such as those in this study, before running predictive models in order to obtain accurate predictions. This warning is particularly timely as predictive ecological niche modeling becomes simpler to implement, more widespread, and necessary in the era of rapid environmental change.

ACKNOWLEDGMENTS

We thank Kathryn J. Schneider for georeferencing the Red-bellied Woodpecker occurrence dataset. George Robinson provided several helpful comments that improved analyses and interpretation, and we thank two anonymous reviewers for their comments and suggestions.

LITERATURE CITED

- Audubon, J. J. 1849. Ornithological biography. Volume 5. Adam and Charles Black, Edinburgh, UK.
- Auer, S. K., and D. I. King. 2014. Ecological and life-history traits explain recent boundary shifts in elevation and latitude of western North American songbirds. *Global Ecology and Biogeography* 23:867–875.
- Baldwin, R. 2009. Use of maximum entropy modeling in wildlife research. *Entropy* 11:854–866.
- Beddall, B. G. 1963. Range expansion of the cardinal and other birds in the northeastern states. *Wilson Bulletin* 75:140–158.
- Billerman, S. M., M. A. Murphy, and M. D. Carling. 2016. Changing climate mediates sapsucker (*Aves: Sphyrapicus*) hybrid zone movement. *Ecology and Evolution* 6:7976–7990.
- De Kay, J. E. 1844. Zoology of New York, or the New York Fauna, Part II, Birds. Carroll and Cook, Printers to the Assembly, Albany, New York, USA.
- DeLuca, W. V., and D. I. King. 2017. Montane birds shift downslope despite recent warming in the northern Appalachian Mountains. *Journal of Ornithology* 158:493–505.
- Elith, J., and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* 40:677–697.
- Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee, and C. J. Yates. 2011. A statistical explanation of Maxent for ecologists. *Diversity and Distributions* 17:43–57.
- Farnsworth, G., G. A. Londono, J. U. Martin, K. C. Derrickson, and R. Breitwisch. 2011. Northern Mockingbird (*Mimus polyglottos*), version 2.0. In A. Poole, editor. *The Birds of North America*. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24:38–49.
- FitzGerald, A. M. 2017. Division within the North American boreal forest: ecological niche divergence between the Bicknell's Thrush (*Catharus bicknelli*) and Gray-cheeked Thrush (*C. minimus*). *Ecology and Evolution* 7:5285–5295.
- Forbush, E. H. 1927. *Birds of Massachusetts and other New England States, Part II*. Norwood Press, J. S. Cushing Co., Berwick & Smith Co., Norwood, Massachusetts, USA.
- Freeman, B. G., and A. M. Class Freeman. 2014. Rapid upslope shifts in New Guinean birds illustrate strong distributional responses of tropical montane species to global warming. *Proceedings of the National Academy of Sciences, USA* 111:4490–4494.
- Guisan, A., B. Petitpierre, O. Broennimann, C. Daehler, and C. Kueffer. 2014. Unifying niche shift studies: insights from biological invasions. *Trends in Ecology and Evolution* 29:260–269.
- Haggerty, T. M., and E. S. Morton. 2014. Carolina Wren (*Thryothorus ludovicianus*), version 2.0. In A. Poole, editor. *The Birds of North America*. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Halkin, S. L., and S. U. Linville. 1999. Northern Cardinal (*Cardinalis cardinalis*), version 2.0. In A. Poole and F. B. Gill, editors. *The Birds of North America*. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Hargreaves, A. L., K. E. Samis, and C. G. Eckert. 2014. Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *American Naturalist* 183:157–173.
- Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology 22:415–427.
- Jackson, J. A., and W. E. Davis Jr. 1998. Range expansion of the Red-bellied Woodpecker. *Bird Observer* 26:4–11.
- Kirchman, J. J., and K. J. Schneider. 2014. Range expansion and the breakdown of Bergmann's rule in Red-bellied Woodpeckers (*Melanerpes carolinus*). *Wilson Journal of Ornithology* 126:236–248.
- Kirchman, J. J., and A. E. Van Keuren. 2017. Altitudinal range shifts of birds at the southern periphery of the boreal forest: 40 years of change in the Adirondack Mountains. *Wilson Journal of Ornithology* 129:742–753.
- Koenig, W. D., E. L. Walters, and P. G. Rodewald. 2017. Testing alternative hypotheses for the cause of population declines: the case of the Red-headed Woodpecker. *Condor* 119:143–154.
- La Sorte, F. A., and F. R. Thompson III. 2007. Poleward shifts in winter ranges of North American birds. *Ecology* 88:1803–1812.
- Oswalt, S. N., W. B. Smith, P. D. Miles, and S. A. Pugh. 2014. *Forest resources of the United States, 2012*. Washington Office. Forest Service, U.S. Dept. Agriculture, Washington, D.C., USA.
- Parmesan, C. 1996. Climate and species' range. *Nature* 382:765–766.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics* 37:637–669.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.

- Peterson, A. T. 2011. Ecological niche conservatism: a time-structured review of evidence. *Journal of Biogeography* 38:817–827.
- Peterson, A. T., J. Soberón, and V. Sánchez-Cordero. 1999. Conservatism of ecological niches in evolutionary time. *Science* 285:1265–1267.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231–259.
- R Development Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ramankutty, N., and J. A. Foley. 1999. Estimating historical changes in global land cover: croplands from 1700 to 1992. *Global Biogeochemical Cycles* 13:997–1027.
- Ritchison, G., T. C. Grubb Jr, and V. V. Pravosudov. 2015. Tufted Titmouse (*Baeolophus bicolor*), version 2.0. In P. G. Rodewald, editor. *The Birds of North America*. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Robb, G. N., R. A. McDonald, D. E. Chamberlain, and S. Bearhop. 2008. Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Frontiers in Ecology and the Environment* 6:476–484.
- Root, T. L. 1988a. Energy constraints on avian distributions and abundances. *Ecology* 69:330–339.
- Root, T. L. 1988b. Environmental factors associated with avian distributional boundaries. *Journal of Biogeography* 15:489–505.
- Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics* 40:415–436.
- Shackleford, C. E., R. E. Brown, and R. N. Conner. 2000. Red-bellied Woodpecker *Melanerpes carolinus*. No. 500. In A. Poole and F. Gill, editors. *The Birds of North America*. The Birds of North America, Philadelphia, Pennsylvania, USA.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* 38:196–218.
- Stockwell, D. R. B., and A. T. Peterson. 2002. Effects of sample size on accuracy of species distribution models. *Ecological Modelling* 148:1–13.
- Tingley, M. W., M. S. Koo, C. Moritz, A. C. Rush, and S. R. Beissinger. 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Global Change Biology* 18:3279–3290.
- Vu, V. Q. 2011. ggbiplot: a ggplot2 based biplot. R package version 0.55. <http://github.com/vqv/ggbiplot>
- Warren, D. L., R. E. Glor, and M. Turelli. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography* 33:607–611.
- Wickham, H. 2009. *ggplot2: elegant graphics for data analysis*. Springer, New York, New York, USA.
- Wilson, A. 1808. *American Ornithology: or, the Natural History of the Birds of the United States*. Volume 1. Porter & Coates, Philadelphia, Pennsylvania, USA.
- Zuckerberg, B., D. N. Bonter, W. M. Hochachka, W. D. Koenig, A. T. DeGaetano, and J. L. Dickinson. 2011. Climatic constraints on wintering bird distributions are modified by urbanization and weather. *Journal of Animal Ecology* 80:403–411.
- Zuckerberg, B., A. M. Woods, and W. F. Porter. 2009. Poleward shifts in breeding bird distributions in New York State. *Global Change Biology* 15:1866–1883.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2496/full>