

Estimating indices of range shifts in birds using dynamic models when detection is imperfect

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Abstract

There is intense interest in basic and applied ecology about the effect of global change on current and future species distributions. Projections based on widely used static modeling methods implicitly assume that species are in equilibrium with the environment and that detection during surveys is perfect. We used multiseason correlated detection occupancy models, which avoid these assumptions, to relate climate data to distributional shifts of Louisiana Waterthrush in the North American Breeding Bird Survey (BBS) data. We summarized these shifts with indices of range size and position and compared them to the same indices obtained using more basic modeling approaches. Detection rates during point counts in BBS surveys were low, and models that ignored imperfect detection severely underestimated the proportion of area occupied and slightly overestimated mean latitude. Static models indicated Louisiana Waterthrush distribution was most closely associated with moderate temperatures, while dynamic occupancy models indicated that initial occupancy was associated with diurnal temperature ranges and colonization of sites was associated with moderate precipitation. Overall, the proportion of area occupied and mean latitude changed little during the 1997–2013 study period. Near-term forecasts of species distribution generated by dynamic models were more similar to subsequently observed distributions than forecasts from static models. Occupancy models incorporating a finite mixture model on detection – a new extension to correlated detection occupancy models – were better supported and may reduce bias associated with detection heterogeneity. We argue that replacing phenomenological static models with more mechanistic dynamic models can improve projections of future species distributions. In turn, better projections can improve biodiversity forecasts, management decisions, and understanding of global change biology.

Keywords: breeding bird survey, climate change, ecological forecasts, Louisiana Waterthrush, occupancy models, *Parkesia motacilla*, population dynamics, species distribution models

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Introduction

There is widespread interest in contemporary and future effects of climate change on plant and animal distributions because of the relevance for predicting changes in biodiversity (Bellard *et al.*, 2012), developing conservation strategies (Wilson *et al.*, 2005), and selecting effective management actions (Rodríguez *et al.*, 2007). The advent of anthropogenic climate change has lent more urgency to the topic, given the potential for ecological upheaval (Thomas *et al.*, 2004). A common approach for understanding these species–climate relationships is to statistically estimate the relationship between climate covariates and the probability of presence of a species of interest during a specified period of time (Guisan & Thuiller, 2005). Popular methods include MAXENT and ENFA for detection-only data and GLMs, GAMs, classification trees, and neural

networks for detection/nondetection data, among other methods (Heikkinen *et al.*, 2006).

However, various challenges remain when modeling species–climate relationships, two of which we highlight. First, most modeling approaches do not account for imperfect detection even though it is common for individuals and species to go undetected during ecological surveys (Alldredge *et al.*, 2007; Pacifici *et al.*, 2008). If false negatives occur, then statistical models will estimate the probability of obtaining a detection, rather than the probability of presence. In turn, the probability of presence and species–climate relationships will be misestimated (Tyre *et al.*, 2003), especially when detection varies across the study area (Gu & Swihart, 2004). Imperfect detection is especially relevant when we are interested in changes in distribution because such changes are more likely at range margins, where density of individuals is low (Mehlman, 1997) and therefore false negatives more likely (Royle & Nichols, 2003). Whether at range margins or interiors, false negatives also generate biased estimates of

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colonization, local extinction, and turnover rates (Kéry *et al.*, 2013). Although occupancy models that account for imperfect detection have been widely used (MacKenzie *et al.*, 2006), they have rarely been applied to the large-scale, long-term data relevant to climate change because large surveys typically lack the repeated surveys usually required for occupancy modeling (Illán *et al.*, 2014).

Second, most common modeling approaches use static models to correlate the distribution of detections in a time interval to climate characteristics in the same time interval. As such, these models are primarily phenomenological and merely describe the *pattern* of species distributions rather than the *process* generating the distribution (Pearson & Dawson, 2003; Dormann *et al.*, 2012). Projections developed from such correlative models assume that species are in equilibrium with climate both during the period of data analysis and the period targeted by projections (Guisan & Thuiller, 2005; Pagel & Schurr, 2012). However, species are commonly out of equilibrium with the environment (Zhu *et al.*, 2012), whether due to simple environmental and demographic stochasticity or sustained climate change. Such disequilibrium is especially important when we study changes in distribution because local populations are most likely to be in flux at range margins (Mehlman, 1997; Yackulic *et al.*, 2015).

A more mechanistic approach would recognize that the current distribution of a species is a function of previous climate and dispersal constraints, as well as current climate (Dormann *et al.*, 2012; Kéry *et al.*, 2013). Dynamic occupancy models (MacKenzie *et al.*, 2003) can serve as an alternative to static correlative models or data-intensive physiology-based process models (La Sorte & Jetz, 2010; Dormann *et al.*, 2012). These dynamic occupancy models focus on the relationships between covariates and vital rates (colonization and extinction rates), as these permit prediction of range change in the absence of equilibrium. One approach to dynamic species distribution modeling is to model species occurrence as a Markov process in which the probability of occurrence at time t is a function of the probability of occurrence at time $t-1$ (MacKenzie *et al.*, 2003). By modeling a population-level process, these dynamic distribution models can incorporate greater ecological realism. Furthermore, by breaking free of the equilibrium assumption, dynamic models can improve projections of species distributions (Pagel & Schurr, 2012; Yackulic *et al.*, 2015). Although a number of authors have advocated dynamic models (e.g., Guisan & Thuiller, 2005), they have rarely been applied to large-scale, long-term data.

Recent extensions to occupancy models (Hines *et al.*, 2010, 2014) enable estimation of detection probabilities

from certain types of spatially replicated surveys, rather than the temporally replicated surveys usually used in occupancy modeling. Thus, it is now possible to fit dynamic occupancy models to North American Breeding Bird Survey data (BBS; Pardieck *et al.*, 2015). The BBS is one of the most geographically extensive bird surveys conducted today, and it has been widely used to study the effects of climate change on birds (e.g., Robbins *et al.*, 1989; Zuckerberg *et al.*, 2009; Illán *et al.*, 2014). In this paper, we investigate the utility of dynamic correlated detection occupancy models (Hines *et al.*, 2014) for estimating changes in the breeding distribution of Louisiana Waterthrush (*Parkesia motacilla*), while accounting for imperfect detection and dynamic population processes in BBS data. We use the resulting estimates to develop some simple indices to quantify changes in distributions through time. We then compare the dynamic correlated detection occupancy approach to selected alternative approaches that do not account for imperfect detection and/or dynamic processes in order to investigate the value of dynamic models that account for imperfect detection.

Materials and methods

Data

We used data from the North American Breeding Bird Survey (www.pwrc.usgs.gov/BBS/RawData/) and the University of East Anglia Climate Research Unit Time Series Data (CRU; Harris *et al.*, 2014; http://badc.nerc.ac.uk/browse/badc/cru/data/cru_ts/cru_ts_3.22/data/) to estimate the effect of climate on the distribution of breeding Louisiana Waterthrush, a migratory warbler that breeds in North America and winters in Central America. This species nests and forages for insects in riparian habitat. We selected Louisiana Waterthrush for analysis because, as an early breeder (Mulvihill *et al.*, 2009), we expected that detection in late spring might be low, necessitating models that account for imperfect detection. In addition, the Louisiana Waterthrush's breeding range is entirely within the extent of the BBS survey, allowing for estimation of the entire breeding distribution (Barbet-Massin *et al.*, 2010).

The BBS was initiated in 1966 and includes over 5000 survey routes across the United States and southern Canada, approximately 3000 of which are surveyed in a given year. Each route is surveyed by a skilled volunteer on 1 day per year. Surveys are timed to coincide with the peak of territorial behavior, typically late May to early July, depending on latitude. Each route traces approximately 39.4 km along secondary roads. Surveyors stop at regular intervals approximating 800 m, as safety and road conditions allow, and perform a 3-min roadside point count, generating 50 counts per route. We used BBS data because their great geographic and temporal extent is suitable for investigating distributional changes, and we developed a modeling approach that is appropriate for the data structure.

Although BBS data are available from 1966, the digital data that are currently available do not include stop-specific data prior to 1997. Therefore, we used data from 1997 to 2013. From the pool of all BBS routes, we selected 2627 routes from the eastern United States and Canada that have been surveyed since 1997, only using data from acceptable surveys (i.e., acceptable weather, date, time of day, stops; reported by BBS as 'runtype = 1'). On the rare occasions a route had multiple acceptable surveys per year, we used data from the first acceptable survey. The selected routes ranged from Florida to Texas, South Dakota, Ontario, and Nova Scotia. This region encompassed the entire breeding range of the Louisiana Waterthrush with a buffer. We excluded routes outside the states and provinces mentioned above because excessive absences can distort the estimated species–environment relationship and predict presence where the species is certain to be absent (Austin & Meyers, 1996) and to reduce computing time. Finally, we converted counts of birds at each stop along each BBS route to detection/nondetection data suitable for occupancy modeling. This conversion sacrificed data richness, but accounting for imperfect detection in BBS counts of birds typically requires simplifying assumptions (e.g., Illán *et al.*, 2014) or incorporation of additional data sources (e.g., Hooten *et al.*, 2007).

The CRU data set contains high-resolution (0.5°) grid data for common surface climate variables (Harris *et al.*, 2014). The data are obtained from over 6000 weather stations around the globe and interpolated to areas without weather stations. The result is a monthly time series of climate data from 1901 to 2013 covering all land masses except Antarctica. We used CRU data because it covered the entire region of the BBS surveys at a monthly resolution.

While the potential pool of climatic predictors is limitless, we selected five covariates that are reasonably uncorrelated, widely used, and relatively effective for modeling species ranges (Barbet-Massin & Jetz, 2014). In particular, we used a subset of the 'bioclim' variables: annual mean temperature, mean diurnal temperature range, mean temperature of the wettest quarter, annual precipitation, and precipitation of the warmest quarter (Busby, 1991). We calculated the five covariates using CRU data on precipitation, maximum temperature, and minimum temperature as inputs to the 'biovars' function in the 'dismo' package (v. 1.0-5, Hijmans *et al.*, 2014) in program R (v. 3.1.1, R Core Team 2014). We calculated these covariates from the 12 months prior to the BBS survey. For example, the average temperature in each grid cell for 2013 was calculated using data from June 2012 to May 2013. We then related climate covariates to BBS routes by identifying the grid cell containing the first stop on the BBS route and assigning the climate of that cell to the entire route. To improve model convergence, we centered and scaled all covariates by subtracting the mean and dividing by the standard deviation.

Model development

Hines *et al.* (2014) proposed a dynamic correlated detection occupancy model with the following parameters:

ψ = Pr (route occupied during the first season of surveys);
 θ = Pr (species available at stop | route occupied and species unavailable at previous stop);
 θ' = Pr (species available at stop | route occupied and species available at previous stop);
 p = Pr (detection at a stop | route occupied and species available at stop).
 ε_t = Pr (route is not occupied in season $t + 1$ | occupied in season t); and
 γ_t = Pr (route is occupied in season $t + 1$ | not occupied in season t).

Note that if a species is present on a route, it may be absent from stops on that route. To distinguish between these two spatial scales, we use the term 'occupied' when a species is present on a route and the term 'available' when a species is present at a specific stop (Nichols *et al.*, 2009). Hines *et al.* (2010, 2014) developed a model likelihood that allows these parameters to be modeled as functions of route- and year-specific covariates, while detection parameters can also be influenced by stop-specific covariates (MacKenzie *et al.*, 2006). Parameters can then be estimated using maximum-likelihood estimation in program PRESENCE using a quasi-Newton algorithm (Hines, 2006).

Because the BBS is conducted at a large scale, with different observers, habitats, and survey conditions, it seems likely that detection probability could vary among sites despite the standardization in the survey protocol. If unaddressed, such detection heterogeneity can bias occupancy estimates (MacKenzie *et al.*, 2002). Some studies have used random-effects models to account for observer ability (Link & Sauer, 2002), but this is not possible with our computational approach. Therefore, to account for differences in detection probability across routes, we used a finite mixture model on detection (Norris & Pollock, 1996; Pledger, 2000). This approach accommodates greater variance in detection probabilities by replacing the basic binomial detection model with two binomial distributions, p_1 and p_2 , and a mixing parameter, ω , that indicates the relative weight of the two distributions (Royle, 2006). Although a simplification of biological reality, this approximation has been shown to perform well in various applications (Pledger, 2000). Equations developing this new extension to the occupancy model are presented in Appendix S1.

Analysis

Our overall goal was to compare results from models that ignore population dynamics and imperfect detection to models that account for these factors when (i) estimating the relationship between distributional shifts in breeding Louisiana Waterthrush and climate covariates, (ii) summarizing distributional shifts with indices, and (iii) projecting distributional shifts. Specifically, we modeled the relationship between Louisiana Waterthrush presence and climate covariates using a GLM with a logistic link (Heikkinen *et al.*, 2006), a static correlated detection occupancy model (Hines *et al.*, 2010), a dynamic correlated detection occupancy model (Hines *et al.*, 2014), and a Markov process model that assumes detection probability is 1

(Erwin *et al.*, 1998). This set of modeling approaches is not intended to be exhaustive. Rather the methods were selected as representing all combinations of general modeling approaches for dealing with the features of emphasis in this paper (nondetection, dynamics). Specifically, we used one model, dynamic occupancy, that incorporated both features of emphasis (nondetection, dynamics); one, static occupancy, that dealt with nondetection but not dynamics; another (Markov) that included dynamics but not nondetection; and a final one (GLM) that included neither dynamics nor nondetection. We then used results of these four modeling approaches to investigate the effects of imperfect detection and static models on indices of change and projections of future change.

The response variable in our models was presence or absence of birds in the area sampled by each BBS route during a specific year. In contrast, many analyses of BBS data use detection of birds over the previous 5 or 10 years as a response variable (e.g., Barbet-Massin & Jetz, 2014; Illán *et al.*, 2014), which appears to be an *ad hoc* method for dealing with imperfect detection. However, combining survey years does not eliminate the problem of nondetection, reduces the size of the data set, obscures population dynamics occurring within the 5 or 10 year window, and can distort species–climate relationships because models relate presence in one year with climate in different (possibly subsequent) years. With occupancy modeling, we can estimate presence from annual data, or, if there is a genuine ecological interest in the presence of a species over an extended time period, occupancy models could estimate this state variable as well.

Our predictor variables were annual climate measurements. Many studies of the ecological effects of climate change use longer time periods, such as 5 or 30 years of climate data (e.g., Illán *et al.*, 2014). Combining multiple years of data reflects research interest in long-term climate trends as well as a strategy to accommodate combining years of species surveys. Although long-term climate is a reasonable predictor variable, we used an annual time period for climate data because we expected that recent climate might affect birds more strongly than temporally distant climate. If recent climate is important, combining years of data could obscure the effect of climate on bird distributions. Although analyzing species and climate data on an annual interval differs from some other studies, it focuses on the state variable of interest, annual occupancy, and it facilitates comparison of the models evaluated here.

Our analysis was guided by the general hypothesis that niches of species, including Louisiana Waterthrush, are bounded by intolerable environmental extremes (Kendeigh, 1934) and therefore we included quadratic terms in models. Our expectation was that moderate climate would be associated with higher values for ψ , γ , and lower values for ε . Beyond this general paradigm, we did not develop specific hypotheses about how individual covariates affected Louisiana Waterthrush, or the mechanisms involved (e.g., direct mortality, resource availability, competitor abundance). Instead, we fit models sequentially and identified the best supported models using Akaike's information criterion (AIC). For many purposes, we would favor a more hypothesis-driven approach to single-species modeling. However, in this investi-

gation, we focused on comparative modeling approaches and on indices that could be applied across a wide range of species.

Static, single-season models. For each of the 17 years of data, we fit a GLM relating presence of Louisiana Waterthrush to climate covariates using the 'glm' function in program R. These models ignored detection probabilities as well as stop-level observations so that birds were either detected (1) or undetected (0) on each route. We did not consider climate covariate interactions because the large number of coefficients could not be estimated. By treating the linear and quadratic terms as a unit (both included or both excluded), we were able to fit 32 models each year. We used AIC to identify the best supported model each year. However, rather than using different models for each year, we selected one well-supported model structure to use in all 17 years. Although using a single set of covariates caused some loss of parsimony, it simplified comparison of occupancy across years and is consistent with the general concept of a species niche. Furthermore, projecting occupancy required selecting one covariate set for use in all future years.

Next, we used program PRESENCE to fit static correlated detection occupancy models to the Louisiana Waterthrush data for each of the 17 years. We note that in occupancy modeling, static models are typically called 'single-season' models. A season can last any length of time, but all data are combined into a single time period for analysis. As described above, these models analyzed detection (1) and nondetection (0) observations from each stop to estimate parameters associated with the data-observation process. This model included sampling process parameters for detection, p_1 , p_2 , ω , and local availability, θ , θ' , as well as our parameter of interest, ψ . Initially, we considered models with climate covariates included on the sampling process parameters. However, these models did not converge on stable estimates in most years. This estimation problem may have been due to the low number of detections in the data. Specifically, of all routes with Louisiana Waterthrush detections, most (62%) had detections at only one stop. These sparse data likely made it difficult to fit sensible models of observations at the stop level. Therefore, we only estimated intercepts for p_1 , p_2 , ω , θ , and θ' , while we fit different models relating ψ to climate covariates. As with the GLMs, we used AIC to identify the best model in each year, but then selected a single model structure to use in all 17 years to simplify interpretation of results and enable projections.

Dynamic, multiseason models. We also used program PRESENCE to fit a multiseason correlated detection occupancy model. Because this model included more parameters and was informed by 17 years of data, we were able to consider more complex models. Fitting all possible models would be time prohibitive, so we considered parameters sequentially. Initially, we fit general models, including all climate covariates, for the sampling process parameters p_1 , p_2 , θ , and θ' , as well as ψ for 1997, while we considered alternative models for γ and ε . We fit a model including all five covariates for γ and ε , and then we fit additional reduced models, selecting the

model with the lowest AIC. We then considered ψ , θ , θ' , p_1 , and p_2 in turn, maintaining the model structure on γ and ε . We constrained the covariates on p_1 and p_2 to be identical, and we did not consider covariates on ω because such a model would not be identifiable. Our expectation was that moderate climate would be associated with higher values for ψ , γ , and lower values for ε . We did not expect that climate would directly affect the ability of surveyors to detect birds, but rather that climate would affect habitat and abundance, which would affect detection probabilities. Because bird activity often varies with time of day, we also modeled detection as a quadratic function of stop number, which we consider to be a proxy for time of day. (We did not include stop number in the static correlated detection model due to convergence problems).

Finally, we fit a Markov process model, which is a multiseason model that ignored imperfect detection. As with the GLM, we ignored the stop-level observations and assumed the data included no false negatives. As with the other multiseason model, we estimated the probability of presence in the first year and then estimated the probability of colonization and extinction in subsequent years. We did this by fitting a standard multiseason model in program PRESENCE while fixing detection probability equals to 1. We used the same covariates on ψ , γ , and ε as in the multiseason correlated detection occupancy model to facilitate comparison.

Evaluation of models. One common approach to comparing model performance is to perform some type of cross-validation, such as an area under the receiver operating characteristic curve (AUC) calculation (Heikkinen *et al.*, 2006). However, AUC and other test statistics evaluate the ability of models to predict observations, rather than our state variable of interest, probability of occupancy. Given that empirical field studies demonstrate that conditional detection of Louisiana Waterthrush is low (0.08–0.33; Buskirk & McDonald, 1995; Reidy *et al.*, 2011), observations may be weakly related to occupancy. Because it treats false absences as classification errors rather than observation errors, AUC may favor models that ignore imperfect detection and observation errors. However, ignoring imperfect detection can bias estimates of occupancy and species–habitat relationships (Tyre *et al.*, 2003; Gu & Swihart, 2004). Therefore, we elected not to rely on AUC or similar statistics to judge model performance. Instead, we made an *a priori* decision that multiseason correlated detection occupancy models are an appropriate choice for analysis of BBS data because these models account for imperfect detection and focus on population dynamics, rather than patterns. Accordingly, we rely on this model for inferences about Louisiana Waterthrush distributions. Our purpose in comparing dynamic occupancy models to other models is not to determine which modeling approach best fits the data, but to assess the magnitude of differences between the modeling approaches.

We evaluated model goodness-of-fit of the best supported models using a Hosmer–Lemeshow test (Hosmer & Lemeshow, 2000). For static models, we predicted the unconditional probability of detecting Louisiana Waterthrush at each BBS route. We divided the routes into deciles based on the

unconditional probability of detection and compared the predicted number of detections to the observed number. For dynamic models, we compared the predicted rate of turnover in detections and compared this to the observed rate at each site. Turnover, which is the proportion of occupied sites that is newly occupied, is a more appropriate statistic for dynamic models, because these models estimate changes in occupancy. We used a χ^2 test to determine whether the predictions deviated significantly ($\alpha = 0.05$) from observations. If necessary, we combined deciles to ensure that the predicted number of detections in a decile was >5 .

We also checked for overfitting with a parametric bootstrap analysis (MacKenzie and Bailey, 2004). We used the parameter estimates from the best supported model to simulate a new data set and then fit a model with the original structure to the simulated data to obtain new parameter estimates. If the confidence intervals of the new parameter estimates did not contain the original parameter estimates, we took this as evidence of overfitting and discarded the model.

Route-level detection probability. Detection probability, p , is sometimes considered a nuisance variable and of less interest than ψ . However, there are few estimates of species detection probability for the BBS, even though the survey is widely used in ecological studies (but see Sauer *et al.*, 2001). Therefore, we calculated the stop-level probability of detection across the study area from the output of the multiseason correlated detection occupancy model. Because analysis and inference often occur at the route level, we also calculated p^* , route-level detection probability. In standard occupancy studies, where sites are closed across surveys, $p^* = 1 - (1 - p)^R$, where R is the number of repeat surveys. However, with correlated detection occupancy models, our target species may be available at only a few stops on occupied routes so that R would overstate the opportunities for detection. A better approximation of the opportunities for detection is π , the average number of stops where birds are available. However, the distribution across routes of the number of stops with available Louisiana Waterthrush also affects p^* . The greater the correlation between stops, the more overdispersed the distribution of stops-with-available-birds-per-route will be. Such overdispersion yields more routes with few available birds and therefore a lower overall p^* . Similarly, heterogeneity in p produces more routes with no detections, relative to a constant p^* , which also reduces p^* . It is possible to calculate p^* from our parameter estimates, but the number of potential detection histories is vast ($>10^{15}$), so we used simulation methods to estimate p^* in each 0.5° grid cell. We used parameter estimates from the multiseason correlated detection model analysis to simulate the number of stops with available Louisiana Waterthrush on each occupied route and then the number of these routes with at least one detection. We repeated this simulation 1000 times and used the average number of simulations with at least one detection as an estimate of p^* at each route.

Displaying results: range maps and indices. The above models generated coefficient estimates relating climate covariates to a year-specific probability of occupancy by Louisiana

Waterthrush. In program R, we applied these coefficients to 0.5° resolution climate data for the eastern United States and southeastern Canada to estimate the unconditional probability of occupancy in all 0.5° cells in the study area. We then displayed these occupancy probabilities in a map. However, for many purposes, it is useful to summarize the detailed information provided by a map into one or two summary statistics, for example, when we wish to compare range-wide occupancy across multiple years and models. Therefore, we also calculated indices of range size and location from the maps. First, we estimated the proportion of area occupied by the focal species (MacKenzie *et al.*, 2002) in the study area. We isolated the area between longitude 60°W and 102°W and latitude 24°N and 49°N and averaged the occupancy estimates of all 0.5° map cells each year. We estimated standard errors from the variance–covariance matrix of parameter estimates using the delta method. This yielded an estimate of the proportion of area occupied through time for each modeling approach. This index could be used, for example, to tell whether species are expanding or contracting their ranges. Such information could be useful if we have hypotheses about whether climate change will have positive or negative impacts on range size of species.

We also estimated an occupancy-based mean latitude for Louisiana Waterthrush (e.g., La Sorte & Thompson, 2007). Again, we isolated the area between longitude 60°W and 102°W and latitude 24°N and 49°N. We then weighted the latitude of each map cell by the probability of occupancy in that cell and divided by occupancy summed over all cells to estimate the mean latitude. Again, we used the delta method to estimate standard errors. This generated a time series for mean latitude for each modeling method. This index could be used to estimate range shifts relative to the equator. Such estimates could be useful if we have hypotheses about how climate change will affect the location of species ranges.

The described modeling thus resulted in range maps and range indices for each year of data based on the preferred methodology (dynamic occupancy modeling) as well as static occupancy modeling, a static GLM, and a Markov process model. We then compared maps and index estimates across the different modeling approaches. We expected that models accounting for imperfect detection would indicate a higher probability of occupancy (e.g., larger range size) than models that do not. We expected that estimates of mean latitude might differ across modeling approaches, but we could not predict the direction of differences. We also expected that static models would produce higher annual variation in index values.

Projections of species distributions. The motivation for much recent species distribution modeling is the projection of distributions into the future in response to climate or land-use change (Pearson & Dawson, 2003). Thus, we compared projected species distributions under the different modeling approaches. To generate projections, we fit models using bird and climate data from only the first half of the study period (1997–2005 for multiseason models; 2005 for single-season models). We then projected bird distributions into the second half of the study period (2006–2013) using only coefficient estimates and climate data, as in typical projections of climate

change effects on species distributions (Peterson *et al.*, 2002; Pearson & Dawson, 2003). To evaluate these projections, we fit new models using bird and climate data from the second half of the study period (2006–2013) to estimate the species distribution. These estimated distributions should be more reliable than projections because they are based on bird observations and not just climate data. Although we computed estimates based on each of the four models, those produced by the dynamic occupancy models were viewed as closest to ‘truth’, as these models were developed to deal with the two focal modeling features considered in this investigation (nondetection, dynamics). We used the same indices, proportion of area occupied and mean latitude, to summarize the estimates and projections. We generated projections for all four modeling approaches and noted whether projected confidence intervals contained the estimated index values. We expected that projections from multiseason correlated detection occupancy models would be more similar to estimates.

Results

For the static GLM relating presence of Louisiana Waterthrush to climate covariates, the best supported model was the global (all five covariates) model in three years, various models with four covariates in seven years, and various models with three covariates in seven years. The single model we selected for our final analysis of all 17 years was the global model (Table S1). In 15 years, mean temperature squared had the most negative coefficient, suggesting that extreme temperature was most associated with the limits of the species range. As with the GLMs, the best supported single-season occupancy models each year tended to include four or five covariates on ψ , so the single model we used in the final analysis included all five covariates (Table S2). For the occupancy component of this model, mean temperature squared had the most negative coefficient, again indicating that the limits of the species range were most associated with extreme temperature.

Initially, AIC scores supported a dynamic occupancy model that included climate covariates on detection probability and the correlation between stops. However, the parametric bootstrap indicated this model was overfitted. We suspected that the problem was due to sparse data at the stop level, so we fit additional models with fewer stop-level covariates until we identified a well-supported model with no evidence of overfitting. In this model, initial year occupancy and annual colonization rates were each affected by four climate covariates, while extinction was only affected by annual mean temperature (Table 1). The correlation between stops was modeled as a constant, while detection was affected by stop number, as well as climate. Based on the large coefficient on the quadratic term, the limit of the species range in the initial year was most strongly

Table 1 Estimated coefficients (and standard errors) for multiseason correlated detection occupancy model. Coefficients are on the logit scale. Parameters include probability of occupancy (ψ), probability of availability at a stop given occupancy but no availability at the previous stop (θ), probability of availability at a stop given occupancy and availability at the previous stop (θ'), probability of colonization (γ), probability of extinction (ε), probabilities of detection, given availability (p_1 or p_2), and probability that detection is p_1 (ω). Covariates include annual mean temperature (TEMP), mean diurnal temperature range (DTR), mean temperature of the wettest quarter (TWET), annual precipitation (PREC), precipitation of the warmest quarter (PWARM), BBS route stop number (Stop), and quadratic terms for each. 'NA' indicates the covariate was not considered for that parameter, while '-' indicates the covariate was considered, but not included in the best supported model

	ψ	θ	θ'	γ	ε	p_1	p_2	ω
Intercept	-1.82 (0.23)	-2.28 (0.05)	1.06 (0.15)	-5.08 (0.43)	-3.55 (0.17)	-3.49 (0.11)	-1.94 (0.11)	1.09 (0.11)
TEMP*	0.93 (0.27)	-	-	1.00 (0.35)	-2.39 (0.38)	-0.12 (0.18)	1.08 (0.16)	NA
DTR	-0.63 (0.33)	-	-	1.11 (0.31)	-	0.29 (0.09)	0.11 (0.06)	NA
TWET	0.42 (0.11)	-	-	-	-	-	-	NA
PREC	3.41 (0.36)	-	-	3.98 (1.12)	-	-	-	NA
PWARM	-	-	-	1.09 (0.70)	-	-	-	NA
TEMP ²	-1.35 (0.22)	-	-	-0.57 (0.24)	2.12 (0.28)	-0.23 (0.15)	-1.20 (0.12)	NA
DTR ²	-1.77 (0.38)	-	-	-1.01 (0.44)	-	-0.01 (0.12)	-0.21 (0.10)	NA
TWET ²	0.04 (0.10)	-	-	-	-	-	-	NA
PREC ²	-1.16 (0.17)	-	-	-2.19 (0.88)	-	-	-	NA
PWARM ²	-	-	-	-0.72 (0.36)	-	-	-	NA
Stop	NA	NA	NA	NA	NA	0.06 (0.03)	-0.33 (0.03)	NA
Stop ²	NA	NA	NA	NA	NA	0.05 (0.03)	-0.04 (0.03)	NA

*All covariates centered and scaled. TEMP adjusted by mean = 9.9 °C, SD = 6.3. DTR adjusted by mean = 12.1 °C, SD = 2.4. TWET adjusted by mean = 13.4 °C, SD = 8.3. PREC adjusted by mean = 902.2 mm, SD = 442.2. PWARM adjusted by mean = 249.0 mm, SD = 144.3. Stop adjusted by mean = 24.5, SD = 14.6.

associated with extreme diurnal temperature ranges. In subsequent years, extinction from routes was associated with extreme temperature, while colonization of routes was limited by extreme precipitation. The Markov process model included the same covariates for ψ , γ , and ε as the dynamic occupancy model, while excluding p_1 , p_2 , θ , and θ' (Table S3). In this model, extreme temperature was associated with the limits of initial occupancy and colonization, and was positively associated with extinction from routes.

Goodness-of-fit was adequate for the GLM in 13 years. However, there was some divergence between observed and expected values of summary statistics in 2006 ($X^2 = 14.01$, $df = 4$, $P = 0.01$), 2007 ($X^2 = 16.14$, $df = 5$, $P = 0.01$), 2011 ($X^2 = 17.21$, $df = 4$, $P < 0.01$), and 2012 ($X^2 = 13.57$, $df = 5$, $P = 0.02$). Under the static occupancy model, goodness-of-fit was adequate in all years except 2011 ($X^2 = 22.06$, $df = 5$, $P < 0.01$). For multiseason models, goodness-of-fit was poor for the Markov process model ($X^2 = 131.35$, $df = 8$, $P < 0.01$), but adequate for the dynamic occupancy model ($X^2 = 10.30$, $df = 8$, $P = 0.24$).

Maps generated from each of the models indicated that Louisiana Waterthrush breed in the eastern United States, north of Florida, and south of the Great Lakes (Fig. 1). However, the maximum probability of occupancy was much higher (70–100%) in the occu-

pancy models, relative to the other models (~40%). For the multiseason correlated detection model, annual probabilities of changes at a site with average climate were modest, with $\gamma = 0.0062$ (SE = 0.0026) and $\varepsilon = 0.0280$ (SE = 0.0046) (Table 1). Furthermore, γ was highest and ε was lowest near the range center, as expected.

The multiseason correlated detection occupancy model provided evidence for detection heterogeneity among routes: A model without a finite mixture received no AIC weight, and variance in number of detections across routes with average climate was 43% higher in the finite mixture model. Stop number also affected detection probability, estimated to be 0.069 (SE = 0.007) at the first stop and 0.045 (SE = 0.005) at the last, given average climate. In 2005, between 35°N and 40°N and 70°W and 93°W, the core of the Louisiana Waterthrush range, detection probability at the first stop, given the species was available, ranged from about 0.05 to 0.08, depending on climate at each location (Fig. 2a).

We estimated $\theta = 0.09$ (SE = 0.005) and $\theta' = 0.74$ (SE = 0.029), indicating that only 9% of stops where Louisiana Waterthrush were unavailable were followed by stops where they were available, while 74% of stops with available birds were followed by stops where birds were also available. These correlation estimates

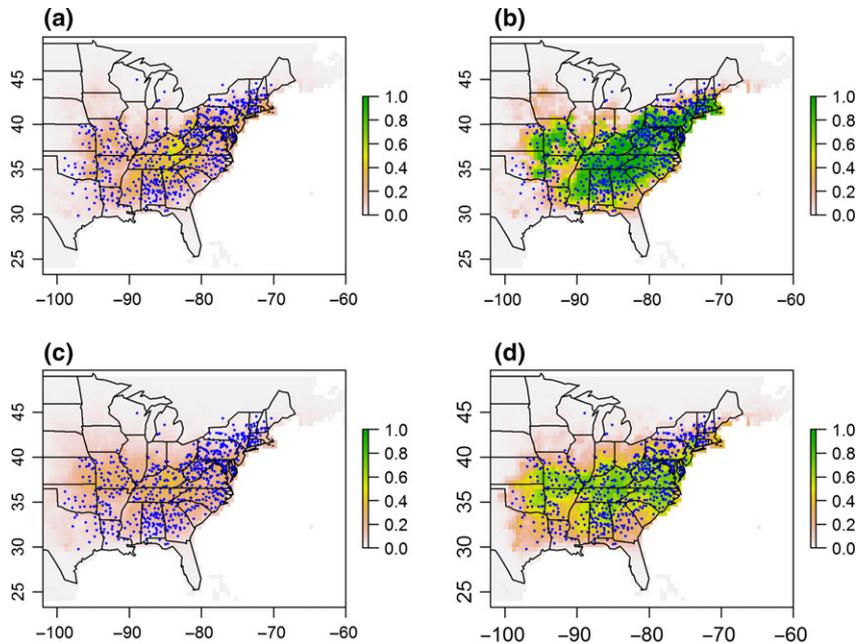


Fig. 1 Probability of presence in 2005 estimated under four different models. (a) Single-season GLM with $p = 1$, (b) single-season correlated detection occupancy model, (c) Markov process model with $p = 1$, and (d) multiseason correlated detection occupancy model. Dots show Louisiana Waterthrush records between 1997 and 2013.

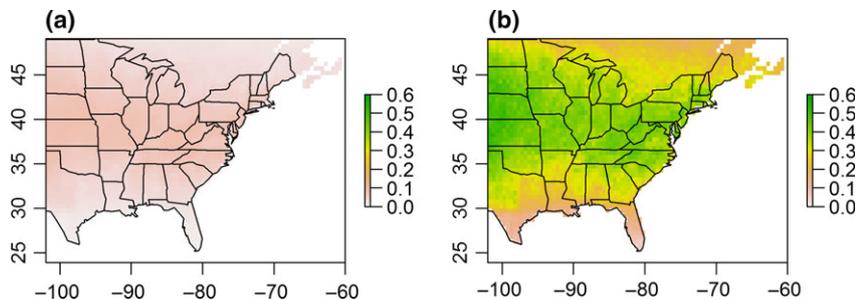


Fig. 2 Estimated conditional detection probabilities in BBS surveys for Louisiana Waterthrush, 2005. (a) Average detection probability at the first stop on a route, given that Louisiana Waterthrush is available at the stop. (b) Route-level detection probability, p^* , given the route is occupied by Louisiana Waterthrush.

mean that Louisiana Waterthrush were available at an average of 26.5% of stops (13.3 stops) per occupied route. Because each route presented surveyors with several opportunities to detect birds, route-level detection was higher than stop-level detection (Fig. 2b). In 2005, between 35°N and 40°N and 70°W and 93°W, detection probability on a route, given it was occupied, ranged from about 0.33 to 0.45, depending on the climate at each route. Estimates outside the range of the bird (Fig. 1) are based on very little data and thus are not reliable.

We used proportion of area occupied and mean latitude as summary indices to examine trends. None of the model estimates appeared to show a strong trend in the proportion of area occupied between 1997 and 2013

(Fig. 3). The estimated proportion of area occupied was much higher (20–30%) under the occupancy models, relative to the other models (~10%), and the single-season correlated detection occupancy model showed greater annual variation than the other models. Mean latitude also showed little trend over the time period examined (Fig. 4). The estimate of mean latitude under the multiseason occupancy model was approximately 0.6° (67 km) further south than under the single-season GLM.

Multiseason parameter estimates used for projections differed from estimates in Table 1 because the former used only 1997 to 2005 data (Tables S3–S5). Annual projections of the proportion of area occupied during 2006–2013 showed little overall trend, consistent with

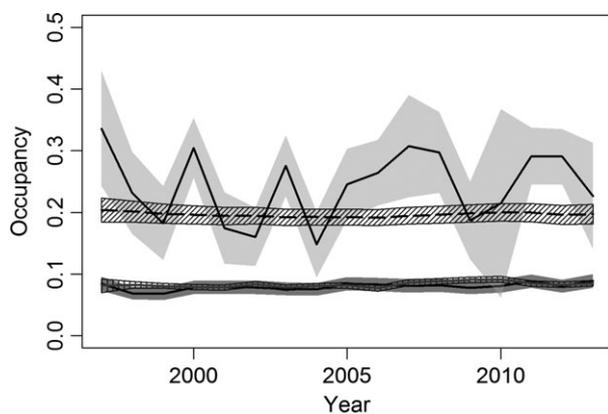


Fig. 3 Proportion of area occupied by Louisiana Waterthrush (and confidence intervals) from 1997 to 2013, estimated using four different models: a single-season GLM with $p = 1$ (gray), a single-season correlated detection occupancy model (light gray), a Markov process model with $p = 1$ (vertical hatching), and a multiseason correlated detection occupancy model (diagonal hatching).

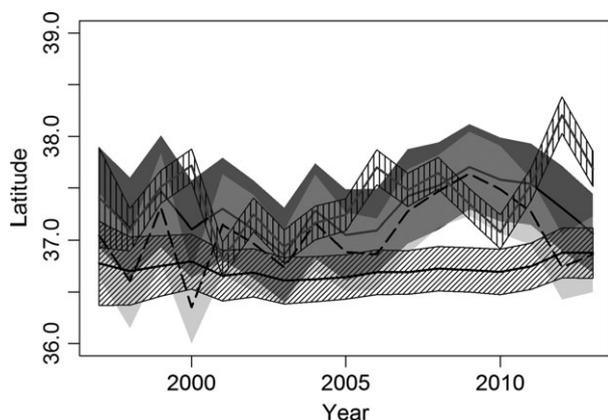


Fig. 4 Mean latitude for Louisiana Waterthrush (and confidence intervals) from 1997 to 2013, using four different models: a single-season GLM with $p = 1$ (gray), a single-season correlated detection occupancy model (light gray), a Markov process model with $p = 1$ (vertical hatching), and a multiseason correlated detection occupancy model (diagonal hatching).

estimates using data from 2006 to 2013 (Fig. 5). Projections from static models showed higher annual variation within the study period, and in one year, projected confidence intervals did not contain the estimated area occupied (Fig. 5). Dynamic models projected almost no change in occupancy, and confidence intervals contained the estimated proportion of area occupied (Fig. 5). Annual projections of mean latitude also showed annual variation, but little trend (Fig. 6). Projections from static models again showed larger annual changes in latitude than the mean latitude estimated from the 2006 to 2013 data and projected confidence

intervals did not contain estimated latitude in several years (Fig. 6). Multiseason model projections diverged from estimated latitude initially, when the estimates are most informed by the static initial occupancy parameter, ψ . Projections converged on estimates in later years, especially for the dynamic correlated detection model (Fig. 6).

Discussion

Species distribution models are widely used to investigate the ecological niches of species and to project future changes in distribution. Until recently, there were few options for accounting for imperfect detection in continental-scale surveys, such as the BBS. Using correlated detection occupancy models (Hines *et al.*, 2010, 2014), we estimated that detection probabilities for Louisiana Waterthrush during 3-min point counts in June were low, which doubled estimates of the proportion of area occupied, relative to estimates from GLM and Markov process models that ignored detection. Although we do not know ‘true’ detection probability in this system, our estimates are consistent with previous field work estimating the probability of detecting an individual Louisiana Waterthrush during 10-min point counts as 0.08 to 0.33 (Reidy *et al.*, 2011) and the ‘detection frequency’ (percent of surveys with detections, at sites with detections) for the species during repeated 3-min point counts as 0.18 (Buskirk & McDonald, 1995). Although Louisiana Waterthrush may have below-average detection probabilities, our results suggest that the implicit assumption of $p = 1$ used by the GLM is invalid and that it is important to account for imperfect detection in species distribution models (Kéry *et al.*, 2013).

We also found a strong correlation ($\theta = 0.09$, $\theta' = 0.74$) between successive stops in the probability of local availability of Louisiana Waterthrush. This correlation is presumably caused by adjacent stops having similar habitat so that both stops are either suitable or unsuitable for Louisiana Waterthrush. Simulation studies have shown that even a weaker correlation ($\theta = 0.10$, $\theta' = 0.50$) could significantly bias estimates of ψ (Hines *et al.*, 2010), indicating the importance of considering correlation along linear transects of point counts. Detections in the BBS are also correlated for the Brown-headed Nuthatch (*Sitta pusilla*) and Eastern Wood-Pewee (*Contopus virens*), but not for the Red-headed Woodpecker (*Melanerpes erythrocephalus*), indicating that correlated detection occupancy models may often, but not always, be preferred over standard occupancy models (Iglecia *et al.*, 2012; Hines *et al.*, 2014).

We extended the correlated detection occupancy models of Hines *et al.* (2010, 2014) to include a finite

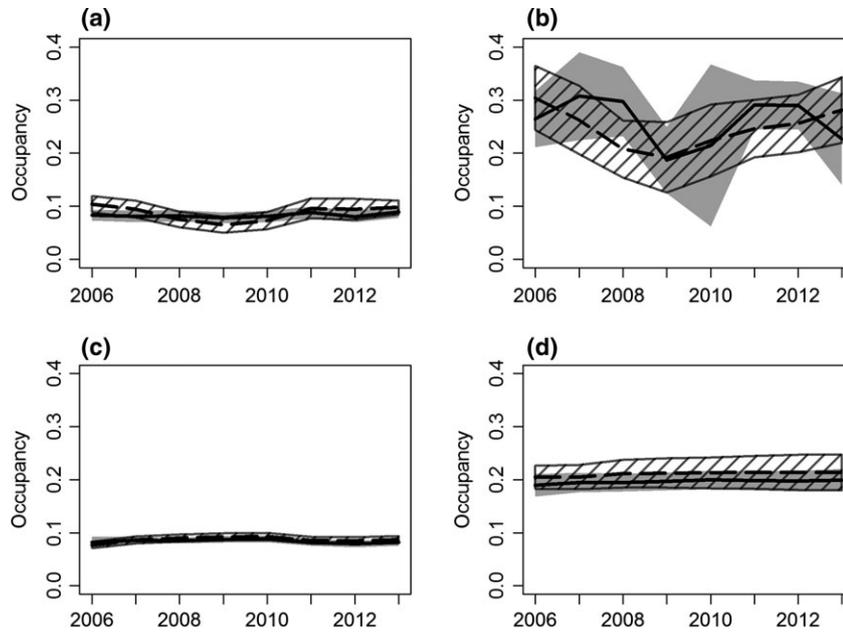


Fig. 5 Projected area occupied (dashed line) and estimated area occupied (solid line) from 2006 to 2013 under different models. Projections developed from 1997 to 2005 data. (a) Single-season GLM with $p = 1$, (b) single-season correlated detection occupancy model, (c) Markov process model with $P = 1$, and (d) multiseason correlated detection occupancy model.

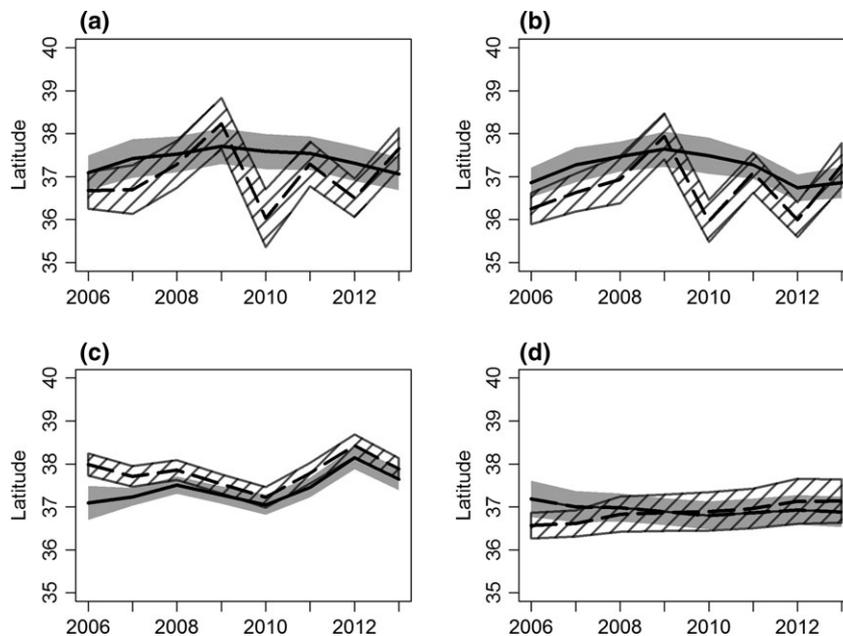


Fig. 6 Projected mean latitude (dashed line) and estimated mean latitude (solid line) from 2006 to 2013 under different models. Projections developed from 1997 to 2005 data. (a) Single-season GLM with $p = 1$, (b) single-season correlated detection occupancy model, (c) Markov process model with $p = 1$, and (d) multiseason correlated detection occupancy model.

mixture model on detection to account for detection heterogeneity. Any unmodeled detection process that causes detection to differ among routes can cause detection heterogeneity. Examples include differences in abilities among observers (Sauer *et al.*, 1994), differ-

ences within an observer through time (Kendall *et al.*, 1996), habitat features and background noise (Pacifi *et al.*, 2008), and differences in bird abundance across routes (Alldredge *et al.*, 2007). In theory, suitable covariates or random-effects models could account for

detection heterogeneity, but we judged these were not practical in the current application. The mixture model accounted for the relatively high variance in p across routes, and models with the mixture were strongly supported over models without it. Although we provide estimated coefficients for the two components of the mixture, it is not advisable to assign biological meaning to the two sets of coefficients (Pledger, 2000). Given that unmodeled detection heterogeneity can bias occupancy estimates, especially when detection is low (MacKenzie *et al.*, 2002; Royle, 2006), we suggest that this extension may improve model estimates in many applications. However, we also caution that when p is low, model estimates may be quite sensitive to the mixture used (e.g., finite, logit normal, beta), yet model selection may not distinguish among these heterogeneity models (Link, 2003; Royle, 2006).

Under static models, occupancy may be estimated separately during each season, supporting potentially different conclusions about species–climate relationships each season. For example, t-tests indicated that GLM coefficients were significantly ($\alpha = 0.05$) related to precipitation-squared in 12 years, but not in 5 years (Table S1). If we ignore issues such as uncertainty in sampling and model selection, these estimates might suggest the relationship between Louisiana Waterthrush and precipitation abruptly changed several times during the study period. However, such an interpretation creates difficulties both for our understanding of a species niche and our ability to project distributional responses to future precipitation changes. The single-season occupancy model appeared to be particularly sensitive to annual changes in the data (Fig. 3). Low detection rates in this data set combined with the inverse sampling correlation between ψ and p and the flexibility of the finite mixture on detection may make the single-season correlated detection occupancy model more prone to overfitting, although our parametric bootstrap did not indicate overfitting.

In contrast, multiseason models estimate *changes* in occupancy, recognizing that species may be out of equilibrium. This approach can parse climate covariates that cause changes in the distribution of a species from covariates that are simply spatially co-occurring with a species (Yackulic *et al.*, 2015). Accordingly, dynamic models also provide a sensible approach for projecting range responses to climate or habitat change (Pagel & Schurr, 2012). Specifically, our dynamic models were structured to estimate time-invariant relationships between colonization and climate and between extinction and climate, an approach that is more consistent with the niche concept. This approach led to different conclusions about how climate affects Louisiana Waterthrush. In particular, the dynamic occupancy model

indicated that initial occupancy was limited by extreme diurnal temperature range and colonization was limited by extreme precipitation, while all other models indicated that occupancy was limited by extreme temperature.

We summarized distributional changes for Louisiana Waterthrush with two indices, proportion of area occupied and mean latitude. By converting a distribution map to a single value, the indices contain less information than the full model results. However, communicating the changes in 17 years of maps is difficult without simplifying metrics (Gregory *et al.*, 2005). Furthermore, investigation of more species and years of data would only increase the need for indices. Indices used for monitoring should be related to motivating hypotheses and conservation decisions (Nichols & Williams, 2006). We selected proportion of area occupied because it is a measure of range size, and it is often hypothesized that climate change (or other environmental change) will cause range contractions (McDonald & Brown, 1992) or expansions (Ogden *et al.*, 2006). We selected mean latitude because it is often hypothesized that warmer temperatures will cause species distributions to shift poleward (Thomas & Lennon, 1999). We note that other indices could be appropriate for other hypotheses. For example, a turnover rate index could be used to test the hypothesis that climate change is increasing local colonization and extinction events. An index tracking the poleward distributional boundary could be appropriate because the poleward boundary may be more strongly affected by abiotic factors (e.g., climate change), while the equatorial boundary is affected by biotic factors (Brown *et al.*, 1996). With the current data set, accounting for imperfect detection doubled the level of one index, the proportion of area occupied. Although index levels differed among models, the overall trends were similar regardless of the model used. Our expectation was that model performance would differ more when projecting future distributions because of the equilibrium assumption inherent in static models. Static model projections were poor in some years, but the overall trend was similarly flat under all modeling approaches. A data set with greater variation in climate or species distribution might yield more differences among the modeling approaches. Most importantly, comparison of estimates and projections from the dynamic occupancy model with those of models that did not deal with either nondetection (Markov model) or dynamics (static occupancy model) or both features (GLM) showed substantive differences.

Much effort has been invested into modeling the effects of climate change or other ecological changes on species distributions (Heikkinen *et al.*, 2006). Frequently, these models predict huge changes in range

size or location (e.g., Peterson *et al.*, 2002). In turn, differences in projected distributions can have large impacts on management decisions, such as the size and location of reserve networks (Wilson *et al.*, 2005). Several authors have advocated more mechanistic, dynamic species distribution models (Pearson & Dawson, 2003; Guisan & Thuiller, 2005), and here, we have fit more mechanistic models to BBS data. While some proposed mechanistic models envision parameterizing models with experimental data on physiological and behavioral responses of individual organisms (La Sorte & Jetz, 2010), our approach relies on simple detection/nondetection data. Spatially explicit models are another relatively mechanistic approach to species distribution models (Hooten *et al.*, 2007; Yackulic *et al.*, 2012, 2015). In these models, colonization and extinction rates depend on the distance to other populations. For invasive species, such spatial models may be well supported (Hooten *et al.*, 2007; Yackulic *et al.*, 2015), while spatial effects may be muted for species in equilibrium (Yackulic *et al.*, 2012). In contrast, our model follows the more typical approach of allowing unlimited dispersal, although we acknowledge that this simplifying assumption is rarely true (Guisan & Thuiller, 2005). We did not use a spatially explicit model because the species distribution remained compact without a spatially explicit model (Fig. 1) and because we suspect it would be difficult to estimate the additional parameters.

Because our study was observational, it is difficult to demonstrate a causal relationship between climate and distribution, and we acknowledge that other factors, such as habitat change or species competition, could also affect the distribution of Louisiana Waterthrush. More generally, we argue that accounting for imperfect detection can reduce bias of estimates of occupancy (Tyre *et al.*, 2003) and that dynamic models can better project species distributions, especially in the face of disequilibrium (Pagel & Schurr, 2012; Yackulic *et al.*, 2015). Broader use of dynamic models accounting for imperfect detection will require surveys to be designed to collect data sufficient for estimation and possibly further model development for systems with different survey protocols.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Model development.

Table S1 Estimated coefficients (and standard errors) on probability of occupancy for single-season GLMs for each of 17 years.

Table S2 Estimated coefficients (and standard errors) for single-season correlated detection occupancy models for each of 17 years.

Table S3 Estimated coefficients (and standard errors) for Markov process models that ignore detection, during three overlapping time periods (1997–2013, 1997–2005, 2006–2013).

Table S4 Estimated coefficients (and standard errors) for multi-season correlated detection occupancy model for the period 1997–2005.

Table S5 Estimated coefficients (and standard errors) for multi-season correlated detection occupancy model for the period 2006–2013.