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# Integrating dynamic processes into waterfowl conservation prioritization tools

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## Abstract

**Aim:** Traditional approaches for including species' distributions in conservation planning have presented them as long-term averages of variation. Like these approaches, the main waterfowl conservation targeting tool in the United States Prairie Pothole Region (US PPR) is based primarily on long-term averaged distributions of breeding pairs. While this tool has supported valuable conservation, it does not explicitly consider spatiotemporal changes in spring wetland availability and does not assess wetland availability during the brood rearing period. We sought to develop a modelling approach and targeting tool that incorporated these types of dynamics for breeding waterfowl pairs and broods. This goal also presented an opportunity for us to compare predictions from a traditional targeting tool based on long-term averages to predictions from spatiotemporal models. Such a comparison facilitated tests of the underlying assumption that this traditional targeting tool could provide an effective surrogate measure for conservation objectives such as brood abundance and climate refugia.

**Location:** US PPR.

**Methods:** We developed spatiotemporal models of waterfowl pair and brood abundance within the US PPR. We compared the distributions predicted by these models and assessed similarity with the averaged pair data that is used to develop the current waterfowl targeting tool.

**Results:** Results demonstrated low similarity and correlation between the averaged pair data and spatiotemporal brood and pair models. The spatiotemporal pair model distributions did not serve as better surrogates for brood abundance than the averaged pair data.

**Main conclusions:** Our study underscored the contributions that the current targeting tool has made to waterfowl conservation but also suggested that conservation plans in the region would benefit from the consideration of inter- and intra-annual dynamics. We suggested that using only the averaged pair data and derived products might result in the omission of 58% - 88% of important pair and brood habitat from conservation plans. [Correction added on 5 February 2021, after first online publication: 'Results' text has been modified and the 'Main conclusions' omission percentages have been corrected.]

KEYWORDS

biodiversity, conservation planning, Prairie Pothole Region, spatiotemporal, waterfowl

## 1 | INTRODUCTION

The traditional approach to including species' distributions in conservation planning has been to pool spatiotemporal variation and create a static snapshot of conditions (Pressey et al., 2007). However, species' distributions and the processes on which they depend are not static, and conservation plans require consideration of the dynamic and highly complex ecological processes that change and maintain the biodiversity within an ecosystem (Pressey et al., 2003, 2007; Soule et al., 2004; Van Teeffelen et al., 2012; Wilson et al., 2009). A highly variable climate, for example, might cause changes in species' habitat use (Groves et al., 2012). Alternatively, natural disturbances can increase the overall habitat needed to support viable populations (Allison et al., 2003). Highly mobile species pose additional challenges for conservation planners, because their natural intra- and inter-annual movements also require consideration (Gilmore et al., 2007; Johnston et al., 2020; Runge et al., 2014; Schuster et al., 2019).

North American waterfowl are perhaps one of the best studied highly mobile groups in the literature with a long history of management and conservation planning (North American Waterfowl Management Plan Committee, 2012, 2018). Species distribution models for waterfowl have helped to support this history of conservation, particularly in the Prairie Pothole Region (PPR: Figure 1), where a disproportionately large number of North American waterfowl breed each year. Most waterfowl modelling efforts have focused on describing patterns of breeding pair abundance and distribution (Barker et al., 2014; Doherty et al., 2015; Feldman et al., 2016; Janke et al., 2017). More recently, there have been efforts to model waterfowl brood abundance and distribution in the PPR as well (Carrlson et al., 2018; Kemink et al., 2019; Walker, Rotella, Schmidt, et al., 2013). Both avenues of investigation have highlighted spatial and temporal trends in both pair and brood distributions (Doherty et al., 2015; Janke et al., 2017; Kemink et al., 2019). However, we know of no studies that have contrasted pair and brood distributions during these different stages of reproduction. Further, the prevailing trend for conservation planning in the PPR still focuses on pooling variation to create a static distribution for targeting purposes (Prairie Habitat Joint Venture, 2014; Barker et al., 2014; Prairie Pothole Joint Venture, 2017, but see Humphreys et al., 2019; Adde et al., 2020).

In the US PPR, the leading tool for supporting decisions about breeding waterfowl conservation is developed through methods that parallel the traditional use of static distributions. The Waterfowl Breeding Pair Accessibility Map, colloquially known as the thunderstorm map (Figure 2; Reynolds et al., 2006, 2007), is used to display categorical ranges of duck pair numbers (mallard [*Anas platyrhynchos*], gadwall [*Mareca strepera*], Northern pintail [*Anas acuta*], Northern shoveler [*Spatula clypeata*] and blue-winged teal [*S. discors*]) that could nest in any given area within the US PPR of Montana, North Dakota and South Dakota. The current version is developed from pair abundance values that used wetland ponding information from >2,000 wetlands that were monitored annually from 1987 to 2016 (Niemuth et al., 2010). These pair abundance values

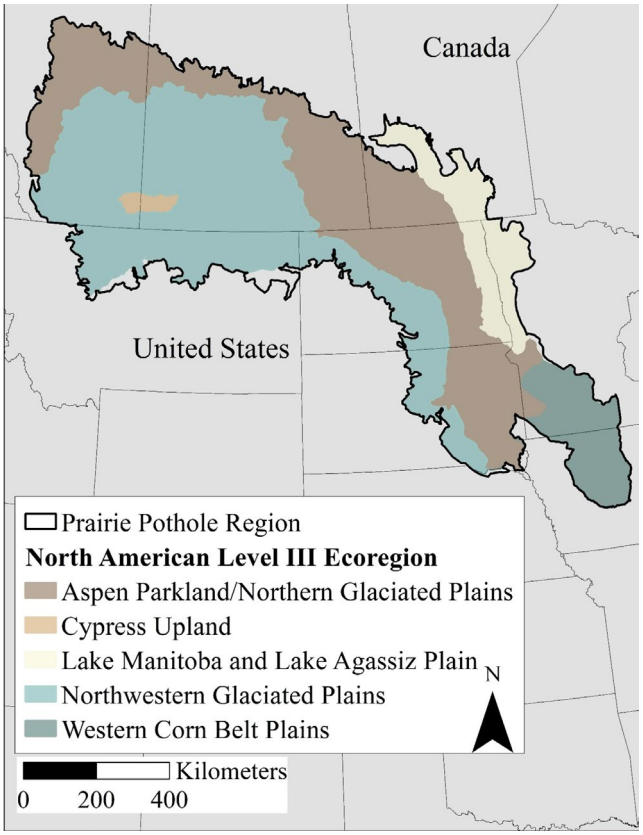


**FIGURE 1** Prairie Pothole Region and the major North American Level III Ecoregions that it encompasses

are scaled to a 0.152 km$^2$ resolution grid and were collected through an annual regional survey known as the "Four Square Mile Survey" (Cowardin et al., 1995). To produce the map of "accessibility," they are adjusted by species-specific constant values of waterfowl hen travel distances from core breeding wetlands to upland nest sites during the breeding season (Reynolds et al., 2006 [Table 1]; Reynolds et al., 2007; personal communication, Chuck Loesch, USFWS).

While these pair abundance values and their derivatives have provided support for decades of valuable conservation work, they preclude the explicit consideration of wetlands' inter-annual wet–dry cycles and ignore any intra-annual changes in wetland ponding across the region. Historically, the US Fish and Wildlife Service (FWS) conducted brood count surveys in the late summer to complement the May breeding population and habitat surveys. However, due to funding cuts and concern about methodology, this data collection was curtailed in the early 2000s. Conservation planners in the PPR might consequently be overlooking areas that have conservation value to waterfowl during periods of extreme weather variation (e.g. drought or deluge: Doherty et al., 2015; Wilson et al., 2009) or during the brood rearing period (Carrlson et al., 2018).

Periods of drought and deluge are a well-known characteristic of the PPR (Johnson et al., 2010; Karl & Riebsame, 1984; Larson, 1995; Niemuth et al., 2010; Woodhouse & Overpeck, 1998). These weather patterns are the primary drivers of the region's wetland hydrology

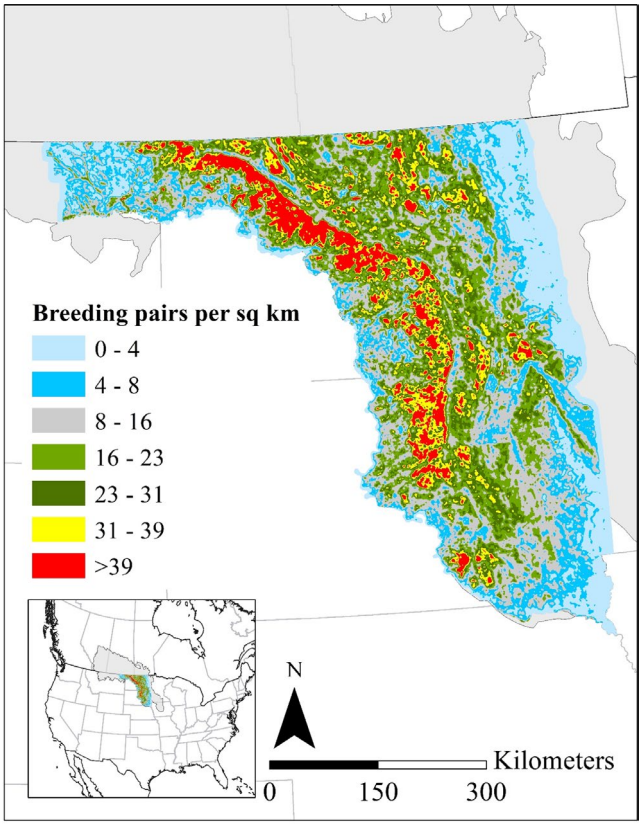


**FIGURE 2** The primary waterfowl conservation targeting tool in the United States Prairie Pothole Region. Data on abundance of waterfowl pairs were generated using GIS modelling techniques utilizing United States Fish and Wildlife Service (USFWS) National Wetland Inventory digital data, the USFWS-Region 6 Four Square Mile Breeding Waterfowl Survey Results, and logistic regression (through 2008) or zero-inflated Poisson regression (post-2008). Equations predicting duck pair/wetland relationships were developed by the USFWS Habitat and Population Evaluation Team and US Geological Survey Northern Prairie Wildlife Research Center. The information presented represents the accessibility of 0.152 $km^2$ landscape units to the combined predicted breeding pairs for mallard, blue-winged teal, gadwall, Northern pintail and Northern shoveler

and thus of aquatic invertebrate abundance and diversity (Euliss & Mushet, 2004; Euliss et al., 1999), which fulfil dietary requirements for breeding duck pairs, nesting hens and growing waterfowl recruits (Cox et al., 1998; Stafford et al., 2016). While both the adults and broods of wetland obligate birds often depend on resources provided by wetlands for survival and growth during the breeding season, the amount and type of habitat available to and used by each group can be quite different (Carrlson et al., 2018; Johnson et al., 2010).

Breeding dabbling duck pairs arrive in the early spring (April–May) to establish territory in the PPR prior to nesting. It is widely accepted that densely ponded areas attract the highest number of pairs. At more local extents, small, seasonal (sensu Stewart & Kantrud, 1971) wetlands tend to provide the best habitat for breeding dabblers (Bartzen et al., 2017; Cowardin et al., 1995; Fields, 2011; Reynolds et al., 2006). These ponds receive most of their water as spring snowmelt running over frozen ground (Hayashi et al., 2016) and thus are available earlier in the spring than their deeper semipermanent counterparts. Dabbling duck pairs feed along the edges of these ponds, concealing themselves from predators and conspecifics (Bartzen et al., 2017; Kantrud & Stewart, 1977; Reynolds et al., 2006). Many of the temporary ponds used by dabbling duck pairs settling in the PPR are dry in the late summer (July–August) by the time waterfowl hens are raising broods (Johnson et al., 2010). Greater numbers of broods are often found on the deeper seasonal or semipermanent ponds (Kemink et al., 2019; Talent et al., 1982). As a result, conservation targeting for successful reproduction requires a diverse mix of wetland types, or hydrologic regimes, ranging from temporary, shallow ponds able to thaw early in the year, to deeper semipermanent wetlands that will remain inundated through hot, dry summers.

In this paper, we develop spatiotemporal models of waterfowl pair and brood abundance that incorporate layers describing water and land use changes on the landscape. Specifically, we seek to use these models to evaluate: (a) whether the pair abundance values scaled to a 0.152 $km^2$ resolution grid (hereafter averaged pair abundance) that are used to develop the thunderstorm map are a good surrogate measure for other conservation objectives including brood abundance and climate refugia and (b) whether spatiotemporal predictions of pair abundance provide a surrogate measure for brood abundance.

## 2 | METHODS

### 2.1 | Study area

The PPR is a 700,000 $km^2$ landscape dominated by small, shallow wetlands and historically covered in perennial grasslands (van der Valk, 1989). The region's major land uses, physiography, geography and climate have been described in detail elsewhere (Cowardin & Golet, 1995; Johnson et al., 1994; Reynolds et al., 2006). The PPR covers five states and three Canadian provinces. However, independently collected brood data and the averaged FWS pair abundance data were available only for the PPR in North Dakota, South Dakota and part of the Montana PPR. Similarly, the annual pair data we used for this analysis were not available for the Iowa and Minnesota portions of the PPR. Consequently, any spatial comparisons made between distributions were limited to the PPR of North Dakota, South Dakota and eastern Montana. The time period for which we modelled pair and brood abundance (2008–2017) is described as one of the wetter periods of the PPR's climatic history since the mid-1900s. However, as was typical for the region, precipitation and temperature varied spatially within and between years (NOAA, 2020).

### 2.2 | Spatiotemporal breeding pair data

We used data from the publicly accessible Waterfowl Breeding Population and Habitat Survey database (WBPHS) to model

**TABLE 1** Description of fixed effects incorporated in pair and brood abundance models with brief justifications for their inclusion as well as the sources of raw data

| Model | Fixed effect | Justification | Data source |
|---|---|---|---|
| Pair | Pond count | Landscapes with more wet area and higher wetland densities overall provide more habitat for breeding duck pairs | Waterfowl Breeding Population and Habitat Survey |
| Pair | Climate moisture index | Landscapes with more moisture on average will tend towards higher wetland densities and more breeding habitat | Doherty et al. (2015); Wang et al. (2016) |
| Pair & brood | Perennial cover | Perennial cover provides the optimal nesting habitat for duck pairs | Cropland data index; annual crop inventory (Natural Resource Conservation Service; Agriculture and Agri-food Canada) |
| Pair | DD5 (Degree days over 5C) | Areas with more growing degree days are more conducive to cropping and will be less likely to have large expanses of perennial cover available for nesting ducks | Wang et al. (2016) |
| Brood | July landscape-level wet area | More wet area available at the landscape scale results in fewer broods per wetland at the individual wetland level | Walker, Rotella, Schmidt, et al. (2013); Carrlson et al. (2018); Kemink et al. (2019) |
| Brood | May wetland count | Higher May pond counts will lead to more duck pairs and subsequently more duck broods | Walker, Rotella, Schmidt, et al. (2013); Carrlson et al. (2018); Kemink et al. (2019) |
| Brood | Emergent cover | Intermediate levels provide optimum amounts of cover for escape and navigation | Walker, Rotella, Schmidt, et al. (2013); Carrlson et al. (2018); Kemink et al. (2019) |
| Brood | Year | Inter-annual variation is a key characteristic of the Prairie Pothole Region | Walker, Rotella, Schmidt, et al. (2013); Carrlson et al. (2018); Kemink et al. (2019) |
| Brood | Wet wetland area | Brood abundance increases at a decreasing rate with wet wetland area | Walker, Rotella, Schmidt, et al. (2013); Carrlson et al. (2018); Kemink et al. (2019) |
| Brood | Regime | Seasonal and semipermanent wetlands tend to hold water later into the summer and thus, provide more habitat for broods than temporary wetlands | Walker, Rotella, Schmidt, et al. (2013); Carrlson et al. (2018); Kemink et al. (2019) |

breeding pair abundance from 2008 to 2017. Since 1955, breeding ducks have been counted along aerial transects in Canada and the United States. The traditional survey area for the WBPHS includes the PPR as well as additional breeding habitat, covering approximately 3.4 million $km^2$. It is broken down hierarchically into strata, then east–west running transects and, finally, segments that are roughly 29 km in length (Smith, 1995: Figure 3a). During the annual survey, the transects are flown by a fixed-wing aircraft 30–45 m above the ground. An observer and the pilot count ducks and ponds 200 m on both sides of the segments (Smith, 1995). Ground counts are also completed simultaneously to allow estimation of detection rates (see Smith, 1995).

The dependent variable in our duck pair analysis was the total number of dabbling duck pairs counted within a segment. We included the dabbling duck species considered in the averaged pair abundance data, which are the five most common dabbling duck species in the PPR: mallard, gadwall, Northern pintail, Northern shoveler and blue-winged teal. These species are the most targeted in wetland and waterfowl management plans in the region (Prairie Pothole Joint Venture, 2017). We calculated the total number of pairs per segment from raw counts such that:

$$\text{Total} = (\text{P} + \text{LM}) \times \text{VIF}$$

where P represents a duck pair (male and female), LM (isolated lone drake) represents an indicated pair, and VIF represents the detection adjustment factor specific to the strata relevant to that segment, year and species (Smith, 1995). We included only counts for segments that were completely within the US or Canadian PPR (Figure 3b).

## 2.3 | Spatiotemporal pair models: predictor variables

The predictor variables we tested were supported by previous studies and tied ecological and anthropogenic processes together. They included two variables describing wetlands and moisture and variables describing our hypotheses about human-driven processes (Table 1). The variables describing wetlands included the number of wet wetlands counted per segment in the survey (pond count) and climate moisture index, which is the difference between annual precipitation and potential evapotranspiration on a vegetated landscape. Landscapes with more wet area and higher wetland densities overall generally provide more habitat for breeding duck pairs (Johnson & Grier, 1988). As most wetlands used by pairs in the spring are filled through rainfall and snowmelt, we expected areas with more ponded wetland counts and higher climate moisture indices to coincide with higher pair counts each year (Doherty et al., 2015; Johnson et al., 2010; Zimpfer et al., 2009).

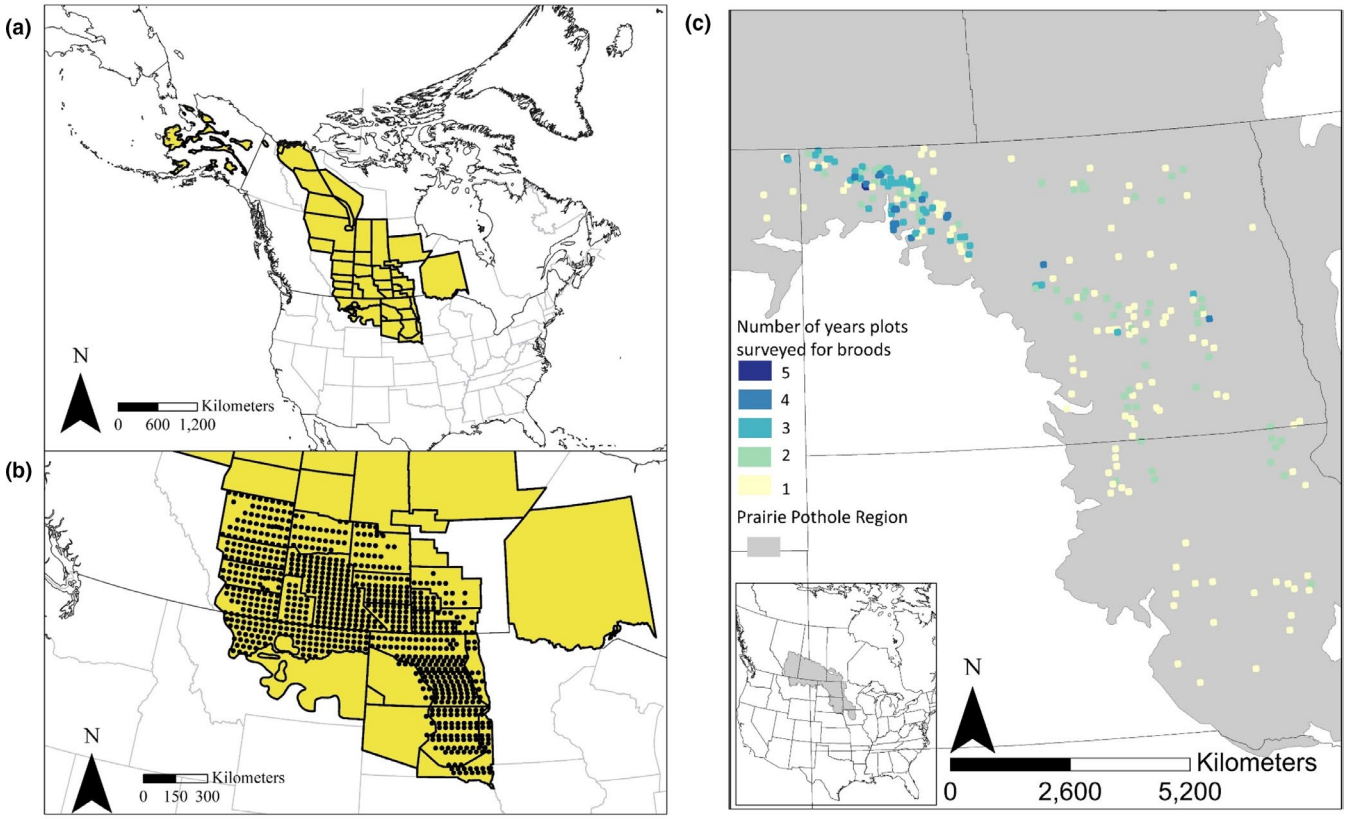


**FIGURE 3** Study areas for waterfowl modelling. (a) United States Fish and Wildlife Service and Canadian Wildlife Service Waterfowl Breeding Population and Habitat Survey. Traditional survey strata are yellow polygons. (b) Centroids of survey segments in traditional strata in the Prairie Pothole Region included in the breeding pair modelling. (c) 10.36 $km^2$ plots used in brood surveys between 2008–2012 and 2013–2017, identified by frequency of years visited

Human-driven processes like agriculture that alter the landscape might also impact pair abundance. Perennial cover surrounding wetlands has been shown to increase nest success and productivity and thus is believed to be the preferred habitat of pairs (Greenwood et al., 1995; Reynolds et al., 2001; Stephens et al., 2005, but see Walker, Rotella, Stephens, et al., 2013). We included a variable to represent the amount of perennial cover surrounding a survey segment as well as the amount of growing degree days (degree days >5°C; Doherty et al., 2015). We expected that perennial cover would demonstrate a positive relationship with breeding pair abundance, while areas with higher growing degree days would be more conducive to cropping and thus have less habitat suitable for breeding duck pairs. Like Doherty et al. (2015), we summarized the climate moisture index, perennial cover and degree day variables using a moving window analysis in ArcMap 10.6 with an area equivalent to the average area of a survey segment (11.52 $km^2$). We extracted the value of the resulting layers to the centroid of each survey segment within the PPR.

## 2.4 | Spatiotemporal pair models: analysis

Preliminary analyses indicated that the Poisson distribution provided the best fit for dabbling duck pair abundance between 2008 and 2017 and that residuals contained spatial and temporal correlation (Zuur et al., 2007). We used Bayesian hierarchical models to examine the data. The hierarchical approach allowed us to test several hypotheses about the structure of spatial and temporal correlation. We binned the data by year and randomly selected 80% of the data for the analysis and withheld 20% of the dataset to test model fit. The remaining analysis contained two stages. We first compared support for different global model structures with regards to the presence or absence of spatial and/or temporal correlation. Global models contained all four fixed effects: pond count, climate moisture index, perennial cover and growing degree days. We assessed support for the fixed effects within the most supported model structure in the second stage of analysis.

In the first stage of our analysis, we considered six model structures to test different hypotheses about how the spatial random field changed over time. The first model contained no spatial or temporal correlation and was an ordinary Poisson model (M1). The second model incorporated a constant spatial correlation over time (M2). Models 3–5 tested three different multiplicative relationships between space and time, while the final model assessed support for additive impacts of space and time on pair abundance. We approximated posterior distributions for covariates in all models using the r-INLA package (Rue et al., 2009). INLA provides an efficient alternative to Markov chain Monte Carlo (MCMC)

for fitting latent Gaussian models, avoiding convergence problems often associated with large spatiotemporal datasets (Rue et al., 2009).

We modelled spatial correlation in M2–M6 using the stochastic partial differential equation (SPDE: Lindgren et al., 2011). The SPDE approach models spatial autocorrelation across a triangular mesh rather than a grid or polygons and has been used to model spatial autocorrelation in a similar manner on waterfowl data from eBird (Humphreys et al., 2019) and Eurasian crane data (Soriano-Redondo et al., 2019) as well as on processes such as tornadoes (Gómez-Rubio et al., 2015) and pollution spread (Cameletti et al., 2013). More recently, a study has also applied the SPDE approach to Canadian WBPHS data to predict the abundance of 15 waterfowl species (Adde et al., 2020). We used a low-resolution mesh (fewer and larger triangles) in the first stage of analysis to speed processing time as recommended by Krainski et al. (2018) and Bakka (2019).

In models M3-M6, spatiotemporal correlation was represented using SPDE in combination with an autoregressive structure AR1 process for residuals (Zuur et al., 2017). Because we used a Bayesian analysis, the models required priors as starting values. For all fixed effects but the intercept, we used normal priors provided by the INLA package (Rue et al., 2009). For the intercept, we provided a prior with a mean of 0 and precision of 0.001 (Kifle et al., 2017). We used penalized complexity (PC) priors for the latent effects in our models as recommended by both Simpson et al. (2017) and Fuglstad and Beguin (2018). These priors penalize departure from a base model and encourage parsimony in model selection. We also used information from the early stages of analysis to inform the prior nominal range of the SPDE mesh in final models. The nominal range is the distance at which residual autocorrelation declines to 0.1 (Krainski et al., 2018). We fitted all models using the INLA package (Rue et al., 2009) in the R statistical environment (R Core Team, 2019). We compared the six described model structures using our hold-out dataset and Spearman's correlation test (Humphreys et al., 2019).

The model that provided the highest *R*-squared values was then used for the second stage of the analysis, in which we applied a remove-one approach to test support for our predictor variables (Chambers, 1992; Walker, Rotella, Schmidt, et al., 2013). In this approach, a variable was removed from the global stage-one model, its Watanabe–Akaike's information criterion recorded, and then the variable put back into the model (WAIC: Gelman et al., 2014; Vehtari et al., 2017). When the removal of a variable decreased the WAIC score of a model by any amount, that variable was not included in the final reduced model. After we applied the remove-one approach to all variables in the model, we ran the reduced model with a high resolution SPDE mesh to acquire parameter estimates.

We assessed the fit of the most supported model from stage 2 using the hold-out data. We compared model-based predictions to actual pair counts using Spearman's correlation test. *R*-squared values over 0.7 with *p*-values below .01 were considered to support correlation and model predictive ability.

## 2.5 | Spatiotemporal brood count data

We used data from several previous studies conducted from 2008 to 2010 (Walker, Rotella, Schmidt, et al., 2013), 2012 to 2013 (Carrlson et al., 2018) and from 2014 to 2017 (Kemink et al., 2019) to develop spatially explicit brood abundance models (Figure 3c). Data were not collected during 2011. The data collection for these surveys was conducted at individual wetland basins. Observers surveyed basins either from a vehicle on the roadside or on foot from the edge of the basin. Each basin was visited two to three times in a 36-hr period. Because the models we intended to use did not permit missing response data, and most of our data were collected via two visits per basin, we selected only two visits from surveys with three visits (Walker, Rotella, Schmidt, et al., 2013). We then had early morning (sunrise—12:00) and late afternoon surveys (15:00—sunset) for comparison. More details on data collection can be found in previously published literature (Carrlson et al., 2018; Kemink et al., 2019; Walker, Rotella, Schmidt, et al., 2013).

## 2.6 | Spatiotemporal brood models: predictor variables

We tested the explanatory strength of a suite of covariates that had significant influence on brood abundance in previous analyses (Table 1). These included perennial cover (Carrlson et al., 2018), log of the basin wet area (Carrlson et al., 2018; Kemink et al., 2019; Walker, Rotella, Schmidt, et al., 2013), May pond counts (Carrlson et al., 2018; Kemink et al., 2019), landscape-level wet area in the summer (Carrlson et al., 2018; Kemink et al., 2019) and basin-level emergent cover (Carrlson et al., 2018; Kemink et al., 2019; Walker, Rotella, Schmidt, et al., 2013). Finally, we included basin regime to separate more ephemeral (typically pair habitat) from more permanent water (typically brood habitat: Johnson et al., 2010; Stewart & Kantrud, 1971). This covariate differentiated between wetlands that were permanent (lakes), experienced strong summer drawdowns (semipermanent), were ponded only through July or August (seasonal) and those that were ponded for only 1–2 months early in the breeding season (temporary: Johnson et al., 2010). We also incorporated several wetland-level variables in the brood detection models. The detection models were, however, not the focus of the analysis, and we included them largely so that we could ensure abundance estimates were being adjusted for imperfect detection rates (Pagano & Arnold, 2009; Royle, 2004).

Two of the landscape covariates we included in our models we expected to have positive relationships with brood abundance. Here, we define landscape as a 10.36 $km^2$ plot on which brood data were collected during the survey. As described previously, we expected higher May pond counts to lead to more breeding duck pairs (Johnson & Grier, 1988) and subsequently greater numbers of broods on surveyed basins. Similarly, we predicted a positive relationship between perennial cover and brood abundance. Hypotheses regarding this relationship have typically stemmed

from the relationship of covariates with pair nesting success (Carrlson et al., 2018; Kemink et al., 2019; Stephens et al., 2005; Walker, Rotella, Schmidt, et al., 2013). In contrast, we predicted that higher amounts of wet area on the landscape in July would provide greater opportunity for birds to spread out, fewer detection opportunities and lower basin-level abundance (Carrlson et al., 2018; Kemink et al., 2019).

During all brood surveys used in our modelling, concurrent flights were used to acquire ponding data on surveyed wetlands and the surrounding landscape. Both technicians and automated software techniques were used in combination to classify the resulting imagery. Specific methodologies can be viewed in previous publications (Carrlson et al., 2018; Kemink et al., 2019; Walker, Rotella, Schmidt, et al., 2013). We used these shapefiles in addition to data collected by observers during the surveys to parameterize the models.

## 2.7 | Spatiotemporal brood models: analysis

We analysed brood count data (2008–2010, 2012–2017) in two stages. Our main impetus was to minimize processing time because the final models we used would have been temporally prohibitive to run through model selection criteria. Prior to any modelling, we stratified the data by year and randomly split them into training (80%) and testing (20%) datasets.

In the first stage of the analysis, we tested the explanatory strength of our selected predictor variables on the training dataset, modelling data within a maximum likelihood framework using N-mixture models in the R package unmarked (Fiske & Chandler, 2011). Applying a remove-one approach, we identified variables that increased the model AIC value and earmarked those to be removed from the final reduced model. We used the reduced model in the second stage of analysis.

We modelled brood abundance in the second stage using Bayesian N-mixture intrinsic conditional autoregressive models (iCAR: Besag, 1974), which allowed us to account for both imperfect detection and spatial autocorrelation (Guélat et al., 2018; Latimer et al., 2006; Vielledent et al., 2015). This model combines an ecological process dealing with the abundance of duck broods due to habitat suitability and an observation process that accounts for the probability of detection being less than one (Pagano & Arnold, 2009). Others have used this modelling approach in a similar manner on shorebirds and pintails (Specht, 2018) and on cetaceans (Vilela et al., 2016).

These models treated the true wetland-level abundance ($N$) as a latent variable with a Poisson distribution and estimated $N$ via a simple reflective random walk algorithm (Hastings, 1970; Vielledent et al., 2015). The observed counts of broods ($y$) on site $i$ during visit $j$ followed a binomial distribution with index parameter $N_i$ and success parameter $p_{ij}$. The ecological process (Abundance: $\lambda_i$) was modelled through a log link as a function of $U$ covariates and the observation process (detection probabilities) through a logit link as a function of $V$ covariates. The ecological process contained an additional term $rho_{ji}$ to account for the spatial autocorrelation between observations wherein the abundance of broods on one wetland depends on the abundance of the broods on neighbouring wetlands. Here, $u_j$ is the mean of $\rho_j$ in the neighbourhood of $j$, $V_\rho$ is the variance of the spatial random effects, and $n_j$ is the number of neighbours for the spatial entity $j$. The models were parameterized with flat priors and fitted using the "hSDM" package (Vielledent, 2019) in the R statistical environment (R Core Team, 2019).

$$N_i = Poisson\left(\lambda_i\right)$$

$$y_{ij} = Binomial\left(N_i p_{ij}\right)$$

$$\log\left(\lambda_i\right) = \beta_0 + \beta_1 x_{i1} + \ldots \beta_U x_{iU} + \rho_{j(i)}$$

$$\text{logit}\left(p_{ij}\right) = \gamma_0 + \gamma_1 x_{ij1} + \ldots \gamma_V x_{ijV}$$

$$p\left(\rho_{j|j'}\right) \sim Normal\left(u_j, V_\rho \mid n_j\right)$$

We assessed model fit in the second stage by conducting Spearman correlation tests between predicted and actual count values for the hold-out dataset (Humphreys et al., 2019; Kendall, 1938). We conducted these tests at both the basin and the plot (10.36 km$^2$) resolution because previous analyses have advised that the plot is the best grain for planning with these data and models (Carrlson et al., 2018). Model fit was considered sufficient if correlation values were over 0.70 with $p$-values less than .01.

## 2.8 | Spatiotemporal model-based predictions

Developing predictions for each year within the time period 2008–2017 required annual PPR-wide layers describing spring and summer ponding as well as overall wetland seasonality. We developed these layers using the Global Surface Water Layer (Pekel et al., 2016). We used layers describing the monthly maximum ponding extent (April–May and July–August) to describe May pond counts (pair and brood models), July wet areas (brood models), basin regime (brood models) and ponded wetland hectares (brood models). We assessed these input variables for accuracy and excluded outliers and data points with missing or invalid predictor data. Other input variables for the pair and brood predictions were obtained from layers used in the original modelling process. In the brood models, the exception to this was the emergent cover variable. Because it was not feasible to obtain region-wide information on the status of this variable, we developed brood predictions at the mean level of this variable observed across all survey years and ponds (2008–2010, 2012–2017: 30.67%).

Model-based predictions of pair abundance were developed through a posterior bootstrapping method described in Fuglstad and Beguin (2018). Using 10,000 posterior samples, we developed predictions for each cell in a 1 km × 1 km grid across the traditional waterfowl breeding population and habitat survey sampling area in the PPR. Since models were developed for 11.52 km$^2$ areas, results

were scaled by this amount to obtain per km values. This process was completed for each year of the analysis (2008–2017), to obtain 10 raster layers.

Brood abundance predictions and population estimates were developed using 110,000 bootstrapped samples created during the modelling process following methods described by Vielledent et al. (2015). Because sampling was not completed for broods in Canada, Iowa or Minnesota, we limited our predictions for broods to the US PPR of North Dakota, South Dakota and eastern Montana. Using ArcMap 10.6 focal statistics, we summarized the results within a 10.36 $km^2$ neighbourhood as suggested by Carrlson et al. (2018). This process was completed for each year of the analysis (2008–2010; 2012–2017) until we had nine 1 km × 1 km layers wherein each cell represented the total number of predicted broods within the surrounding 10.36 $km^2$.

### 2.9 | Comparison of distributions

To facilitate comparison to the brood data, we applied similar methods to both the averaged pair data and our pair prediction raster layers. We aggregated the averaged pair abundance data to a 1 km × 1 km raster layer. Then, we applied focal statistics using a 10.36 $km^2$ neighbourhood to both the averaged pair data layer and the 10 modelled pair abundance layers. We clipped the spatiotemporal pair distributions to the extent of the spatiotemporal brood and averaged pair abundance data. Next, we used the Spearman correlation statistic to test for similarities between the averaged pair, and spatiotemporal pair, and brood data distributions in these areas. All raster comparisons were completed using the stats package in program R (cor: R Core Team, 2019). For all correlation results, we considered values greater than 0.70 to be significant, indicative of highly similar distributions and to suggest the potential for surrogacy as a conservation measure.

Finally, we examined the overlap among our predicted pair and brood distributions and the averaged pair abundance data (Reynolds et al., 2006). We considered larger proportional areas of overlap to be more indicative of similar distributions and to suggest the potential for surrogacy as a conservation measure. We examined only the most abundant 7,203.41 $km^2$ of our predicted pair and brood distributions for similarities with each other and with the highest 7,203.41 $km^2$ of the averaged pair abundance data. We chose this figure because it was the remaining high priority wetland habitat area in need of protection under the current Prairie Pothole Joint Venture Implementation Plan (2017). The same averaged pair abundance data layer was used for each year.

## 3 | RESULTS

### 3.1 | Spatiotemporal pair models

The two stages of our modelling process for the breeding duck pair data provided support for a reduced model with spatial and temporal autocorrelation. In the first stage of our analysis, we found most support for a model structure demonstrating an additive relationship between spatial and temporal autocorrelation (Appendix S1: Table S1). In the second stage, the remove-one analysis showed support for the removal of all variables except adjusted pond count (Appendix S1: Table S2).

The final reduced model consisted of an SPDE mesh of 27,862 vertices, an AR1 temporal structure and contained ponded basin count (log-scale median of the posterior distribution = 0.32, 95% CI: 0.31–0.32) and an intercept term (log-scale median of the posterior distribution = 5.23, 95% CI: 5.00–5.46). This model explained 78% ($p < .01$ CI: 76%–80%) of the variation in our testing dataset. Model-based estimates for latent effects revealed support for low autocorrelation among years (Table 2) and a high spatial autocorrelation with a median nominal range of 78 km (CI: 70–88 km: Appendix S1: Figure S1).

**TABLE 2** Log-scale median posterior estimates of AR-1 lag effects

| Year | 2.50% | 50% | 97.50% |
|---|---|---|---|
| 2008 | −0.25 | −0.08 | 0.10 |
| 2009 | −0.19 | −0.02 | 0.16 |
| 2010 | −0.37 | −0.20 | −0.02 |
| 2011 | −0.17 | 0.00 | 0.18 |
| 2012 | 0.03 | 0.20 | 0.38 |
| 2013 | −0.16 | 0.02 | 0.19 |
| 2014 | −0.12 | 0.06 | 0.23 |
| 2015 | −0.10 | 0.07 | 0.25 |
| 2016 | −0.18 | 0.00 | 0.17 |
| 2017 | −0.15 | 0.03 | 0.20 |

*Note:* 2.50% and 97.50% represent the lower and upper 95% credible intervals.

### 3.2 | Spatiotemporal brood models

Our initial remove-one analysis did not support the removal of any predictor variables in the brood abundance or detection models. Thus, we used a global model in the Bayesian analysis to obtain parameter estimates. Results supported the major conclusions of previous studies, indicating that wetland area is a strong driver of duck brood abundance in the PPR. Further, variables at a larger spatial resolution had both positive (May pond count, perennial cover) and negative (July wet area) associations with brood abundance. However, the credible intervals for the perennial cover relationship crossed zero, suggesting some ambiguity in this effect (Table 3). We also saw support for inclusion of variables describing the seasonality of ponds. The largest difference was between the "Lake" category and the more ephemeral pond types. Finally, model parameter estimates suggested that abundance varied significantly across years and that spatial correlation was relatively high (Appendix S1: Figure S2).

**TABLE 3** Log-scale median posterior estimates of brood spatial model parameters

| Covariate | 2.50% | 50% | 97.50% |
|---|---|---|---|
| Abundance model | | | |
| Intercept | −2.76 | −2.08 | −1.24 |
| log(basin wet area) | 1.16 | 1.20 | 1.23 |
| July wet area (10.36 $km^2$) | −0.14 | −0.07 | −0.01 |
| Regime—seasonal | 0.79 | 1.59 | 2.34 |
| Regime—semipermanent | 0.73 | 1.52 | 2.27 |
| Regime—temporary | 0.39 | 1.19 | 1.96 |
| May wetland count (10.36 $km^2$) | −0.01 | 0.06 | 0.13 |
| Basin emergent cover | 0.04 | 0.11 | 0.20 |
| Basin emergent cover$^2$ | −0.48 | −0.43 | −0.39 |
| Perennial cover (10.36 $km^2$) | −0.07 | 0.01 | 0.08 |
| Year 2009 | −0.93 | −0.72 | −0.51 |
| Year 2010 | −0.56 | −0.19 | 0.17 |
| Year 2012 | 1.06 | 1.42 | 1.79 |
| Year 2013 | −0.22 | 0.12 | 0.46 |
| Year 2014 | −0.17 | 0.29 | 0.67 |
| Year 2015 | −0.02 | 0.43 | 0.81 |
| Year 2016 | 0.38 | 0.82 | 1.19 |
| Year 2017 | 0.26 | 0.71 | 1.09 |
| Detection model | | | |
| Intercept | −1.06 | −0.96 | −0.87 |
| Basin wet area | −0.16 | −0.13 | −0.10 |
| Date | 0.57 | 0.60 | 0.63 |
| Basin emergent cover | −0.27 | −0.16 | −0.05 |
| Survey mode (walk-in = 0/ vehicle = 1) | 0.88 | 1.14 | 1.39 |
| Variance of spatial random effects | 2.01 | 2.24 | 2.48 |

*Note:* 2.50% and 97.50% represent the lower and upper 95% credible intervals.

Spearman tests of hold-out data revealed moderate correlation with actual count data at the resolution of individual basins (0.53, $p < .001$) but high correlation at the 10.36 $km^2$ resolution (0.80, $p < .001$).

## 3.3 | Spatiotemporal pair and brood predictions

Using the top models from each analysis, we provided year-specific pair and brood predictions of abundance for all years 2008–2017, except for year 2011 when no data were collected on broods. Median bootstrapped estimates of pair abundance for the traditional WBPHS area within the US and Canadian PPR varied annually and ranged from 12,188,879 (2008: 95% CI 10,753,552 - 13,861,340) to 16,898,488 (2014: 95% CI 14,915,348 - 19,204,329; Appendix S1: Figure S3a). Predicted distributions at the 10.36 $km^2$ resolution reflected these temporal changes but did not change dramatically across the study period, with the highest densities of pairs remaining concentrated in the western PPR each year (Appendix S1: Figure S4).

Median bootstrapped estimates of brood abundance for the surveyed areas of Montana, North and South Dakota ranged from 81,070 (2009: 95% CI 60,802 - 108,727) to 754,767 (2012: 95% CI 560,666 - 1,033,458; Appendix S1: Figure S3b). Predicted distributions at the 10.36 $km^2$ resolution reflected these temporal changes (Appendix S1: Figure S5). Brood density appeared to concentrate in similar areas to the predicted pair distributions of the western PPR along the Northwestern Glaciated Plains. However, portions of the Northern Glaciated Plains and the Lake Agassiz were highlighted as well. [Correction added on 5 February 2021, after first online publication: the data results have been corrected in this section.]

## 3.4 | Distribution comparisons

The strongest correlations occurred between the averaged pair distribution (Appendix S1: Figure S6) and our predicted pair distributions. Spearman correlation coefficient values exceeded 0.70 in the comparison of the averaged pair distribution with our predicted pair distributions from 2011 ($\rho = 0.71$, $p < .001$) and 2017 ($\rho = 0.71$, $p < .001$: Figure 4; Appendix S1: Figure S7). We did not see strong correlations between either the predicted brood distributions and the averaged pair distribution or our predicted pair distributions (Figure 4; Appendix S1: Figures S8 and S9).

The most abundant 7,203.41 $km^2$ in the averaged pair abundance data overlapped similar areas of our predicted pair and brood distributions (Figure 5). The overlap between the averaged pair distribution and our predicted pair distribution ranged from 18.05% in 2008 to 35.69% in 2016. Likewise, the overlap between the averaged pair distribution and our predicted brood distribution ranged from 12.34% in 2008 to 41.59% in 2015. For both the pair and brood distributions, more overlap with the averaged pair data occurred consistently in the Northwestern Glaciated Plains of North Dakota.

Our predicted duck pair and brood distributions' areas of overlap changed annually with the lowest amount appearing in 2009 (8.23%) and the highest in 2014 (37.69%: Figure 5). The highest percentage overlap occurred consistently in the Northwestern Glaciated Plains of North Dakota and in small areas of the Northern Glaciated Plains of northeast North Dakota and South Dakota.

Over the time series, neither the averaged pair distribution nor the spatiotemporal predicted distributions represented more than 41.59% and 37.69% of high abundance brood areas, respectively. Put another way, over 55% of high priority brood habitat was not represented by the most abundant 7,203.41 $km^2$ in the averaged pair abundance data from 2008 to 2017 and similar amounts would have still been unrepresented even if our spatiotemporal

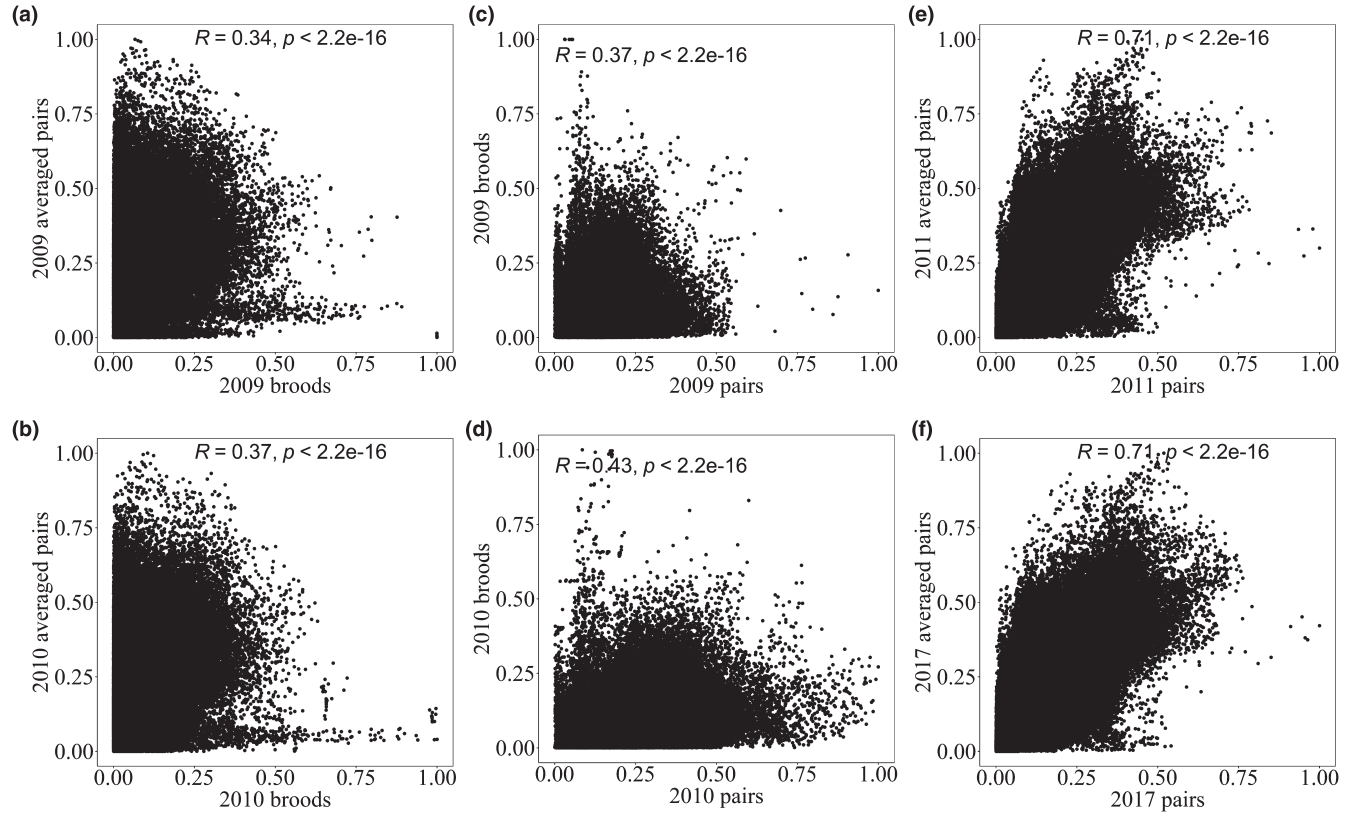


**FIGURE 4** Scaled correlation plots with Spearman correlation coefficients (*R*) and associated *p*-values. Graphs show correlations between: (a) predicted brood abundance layer and averaged pair layer in 2009; (b) predicted brood abundance layer and averaged pair layer in 2010; (c) predicted brood abundance layer and predicted pair abundance layer in 2009; (d) predicted brood abundance layer and predicted pair abundance layer in 2010; (e) predicted pair abundance layer and averaged pair layer in 2011; and (f) predicted pair abundance layer and averaged pair layer in 2017. Additional years' plots are in Appendix S1: Figures S7-S9 [Correction added on 5 February 2021, after first online publication: figure 4 has been replaced and the legend has been updated.]

pair models were used. [Correction added on 5 February 2021, after first online publication: the data results have been corrected in this section.]

## 4 | DISCUSSION

Our results underscore the contributions that current conservation targeting tools have made to waterfowl conservation to date but also suggest that conservation plans in the PPR would benefit from the additional consideration of intra- and inter-annual dynamics of habitat use by breeding duck pairs and broods. We used advanced modelling techniques to assess the extent to which average pair abundance is a good surrogate measure for other conservation measures and to assess whether spatiotemporal predictions of pair abundance provide a surrogate measure for brood abundance. Our predictions also supported previous waterfowl distribution modelling in the region.

The comparison of the averaged pair data distribution with our spatiotemporal pair and brood distributions suggested higher and more consistent overlap between the averaged pair and our predicted breeding pair distributions than between the former and our predicted brood distributions. This relationship provided corroboration for the overall robustness of our modelling approach because the averaged pair data, despite being collected through a different survey, should in theory have represented the same population as our breeding pair models (Prairie Pothole Joint Venture, 2017) although our surveys represented a much shorter period of time. Overall though, results of the comparison between our annual pair and brood predictions, and the averaged pair data distributions suggested that relying only on the averaged data and products produced from it might give undue low priority to important areas that could provide refugia to waterfowl during periods of climate variation.

In the PPR, the cyclic weather patterns of drought and deluge drive many of the changes in annual carrying capacity for waterfowl. Evidence of these dynamics has been displayed in other studies (Doherty et al., 2015; Janke et al., 2017; Johnson & Grier, 1988) and is most obvious in our pair predictions from 2008 to 2012. Low densities of breeding pairs were predicted from 2008 to 2010 in the northernmost portions of the US PPR. This distribution shifted in 2011 and 2012 due to a higher concentration of pairs in these areas,

which parallels reports of improved pond conditions in that area and period (USFWS, 2008, 2009, 2010, 2011). The averaged pair data identified the Northwest Glaciated Plains as an area that was consistently important for breeding pairs. However, in portions of the Northern Glaciated Plains there were areas where our distributions predicted higher densities than the averaged pair data because of changes in wetland numbers.

Model-based predictions of brood abundance also suggested disagreement with the averaged pair data, supporting our hypothesis and the research of others (Carrlson et al., 2018; Talent et al., 1982; Walker, Rotella, Schmidt, et al., 2013) that the habitats used by duck pairs and duck broods would not always coincide. The lowest amount of overlapping area between averaged pair data and brood distribution occurred in 2008 when our models predicted relatively low brood numbers as well. We suspect this type of mismatch is related to the underlying carrying capacity of the landscape as driven by pond availability throughout the breeding season. Most of the US PPR in 2008 experienced moderate to severe drought conditions in the spring (NOAA, 2020), forcing pairs to settle in more concentrated areas of available habitat. Cooler summer temperatures

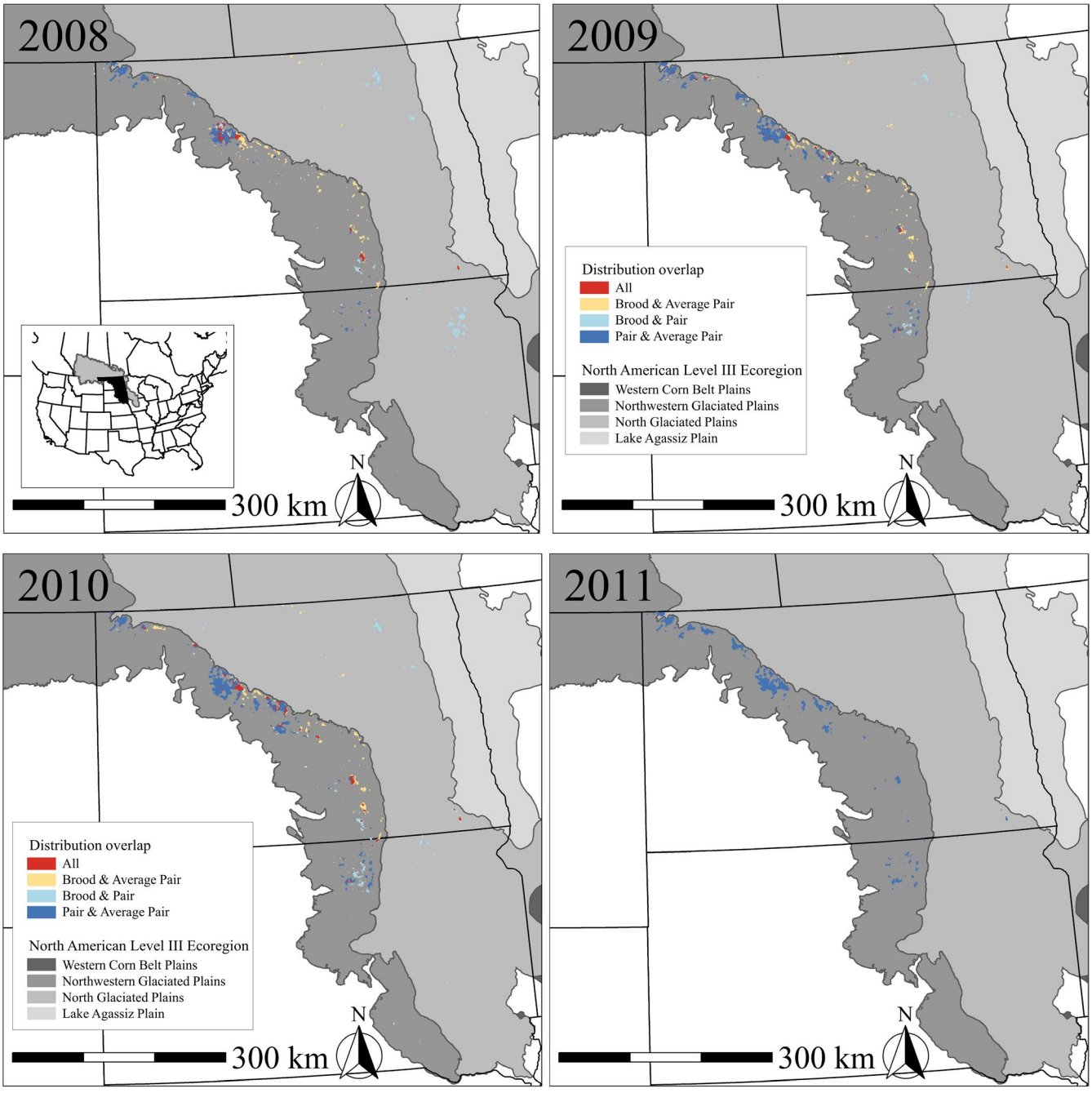


**FIGURE 5** Most abundant 7,203.41 km$^2$ of averaged pair, predicted pair and predicted brood distributions. Areas of overlap between averaged pair and predicted pair (royal blue), averaged pair and predicted brood (yellow), predicted pair and predicted brood (light blue), all three distributions (red), superimposed on major level III North American ecoregions

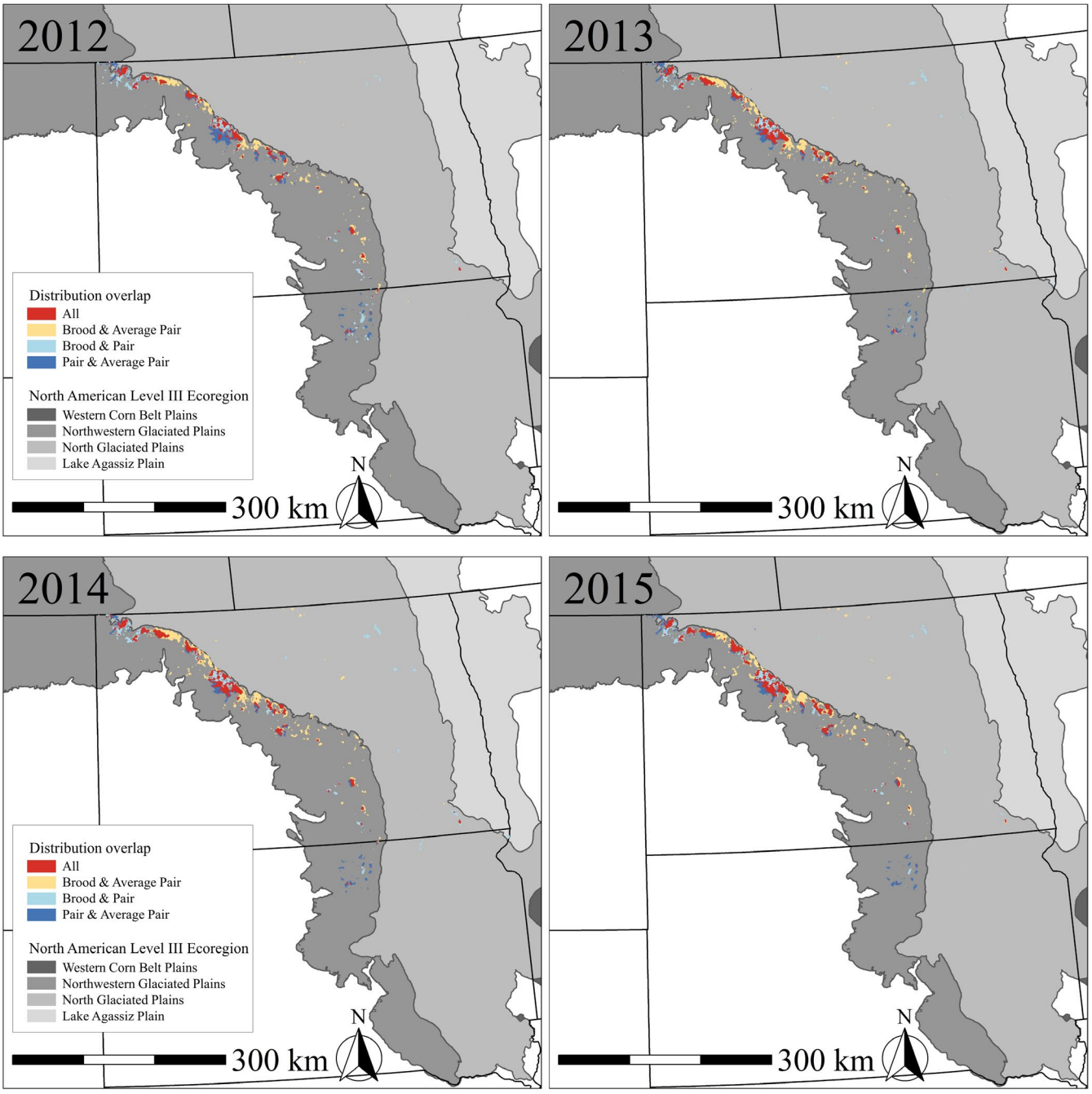


**FIGURE 5**

coupled with moderate levels of precipitation, particularly in the glaciated plains of southeast South Dakota and eastern North Dakota, provided pockets of brood-rearing habitat that might not have been available or as attractive to pairs earlier in the season (USFWS, 2008). [Correction added on 5 February 2021, after first online publication: this paragraph has been corrected.]

Brood abundance is often influenced by environmental factors like pond abundance, pond size, weather and climate (Amundson & Arnold, 2011; Bloom et al., 2012; Carrlson et al., 2018; Kemink et al., 2019; Walker, Rotella, Schmidt, et al., 2013). The inter-annual variation we observed could reflect these environmental factors as well as high nest survival rates. As with the pair models, we saw evidence of spatial correlation in brood abundance, possibly suggesting that areas with broods already present signals to others that these areas are "good" to inhabit (whether true or false: Hobbs & Hanley, 1990). Although the spatial effect within our model was heterogeneous, on average, we observed more positive spatial correlation among smaller basins than larger basins. Previous studies of brood abundance have emphasized the importance of small, shallow wetlands as habitat and a food resource (Carrlson et al., 2018; Gleason & Rooney, 2017; Kemink et al., 2019; Walker, Rotella, Schmidt, et al., 2013).

The consideration of spatial and temporal effects in both our pair and brood abundance predictions did not lead to higher

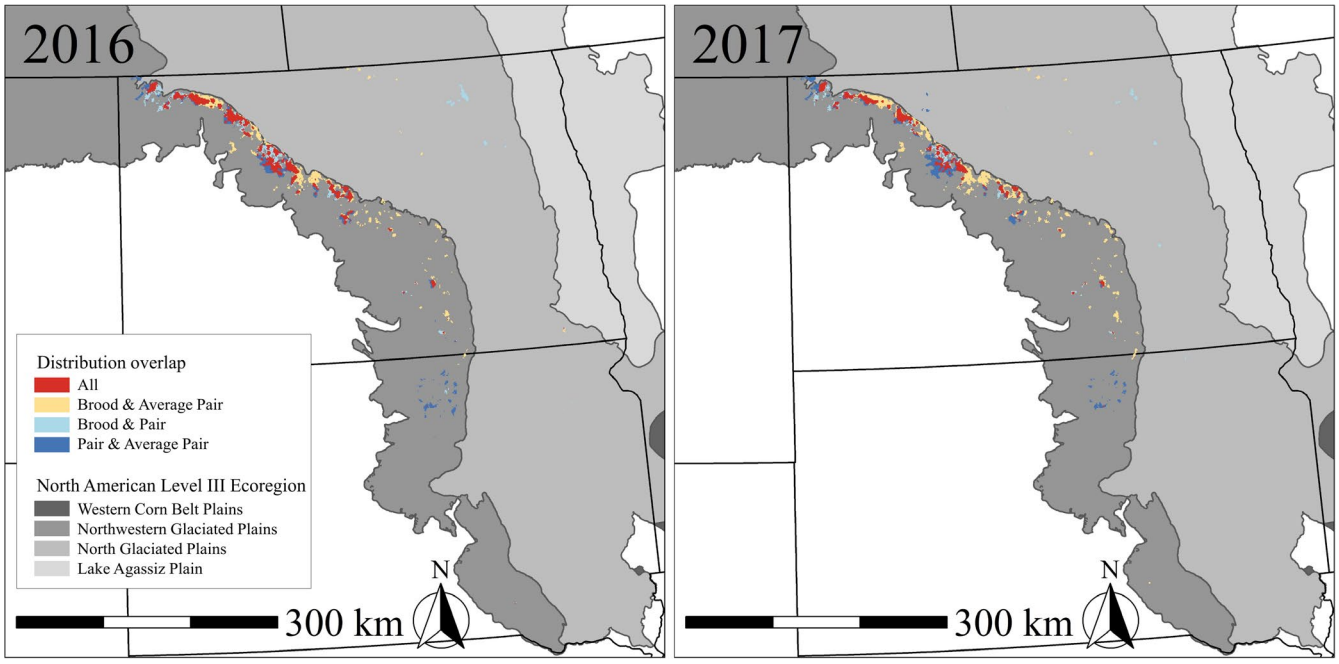


**FIGURE 5**

extents of overlap when compared to the overlap between the brood distributions and the averaged pair data. The overall dissimilarities between the two sets of distributions still outweighed any spatiotemporal similarities across all years. In drier years (2009, 2010) we observed the least overlap between the highest abundance areas of pair and brood distributions (8.23%, 12.27%). This result supports our hypothesis of intra-annual variation in habitat use. Further, we suggest that the differences in distribution might be more pronounced during drier years when temporary and seasonal ponds are less available during the brooding period. Targeted surveys of these pond types during more variable climatic conditions would be needed to support this hypothesis though. According to our results, if a primary goal of waterfowl conservation planning in the PPR is sustaining a persistent regional breeding population, achieving this goal requires not only attention to habitat needed by breeding pairs but also to habitat important to brood survival and recruitment (Hoekman et al., 2002; Prairie Pothole Joint Venture, 2017). [Correction added on 5 February 2021, after first online publication: this paragraph has been corrected.]

Based on the spatiotemporal variability we observed in both the pair and brood distributions, we suggest that conservation prioritization for waterfowl in the PPR would benefit from considering both intra- and inter-annual variation. Other studies have made similar recommendations based upon pair modelling that displayed highly clustered and spatiotemporally heterogeneous distributions of breeding waterfowl in the PPR (Doherty et al., 2015; Janke et al., 2017). Both Doherty et al. (2015) and Janke et al. (2017) advised that areas capable of consistently attracting large numbers of waterfowl should be considered high value habitat for conservation purposes. While we agree with this advice, we also suggest that targeted areas will be highly dependent on whether an organization's conservation goal is minimizing poor, increasing average or facilitating excellent production in good years. If the latter is true, a conservation strategy that targeted areas with consistently high brood numbers would be most appropriate. However, if the goal was to minimize poor production, areas used less often but during drought years might be equally if not more important because of their value as refugia (Bino et al., 2015; Murray et al., 2012; Stralberg et al., 2020).

Even with the addition of pair and brood spatiotemporal distributions, the efficacy of a conservation prioritization tool for the PPR would depend, in part, on the uncertainty and error accompanying the predictions. The noisy nature of the input data and the questions we asked resulted in uncertainty in our predictions, particularly for the pair data which were modelled at a coarser spatial resolution than the brood data (Hermoso & Kennard, 2012). While we feel the results presented herein are robust given the spatial and temporal resolution of the data used, we also note that the datasets incorporated for developing annual predictive surfaces could be improved. The Global Surface Water layer we used had a 30 × 30 m resolution and was not developed for identifying wetlands obscured by vegetation (Pekel et al., 2016). As a result, we expect that abundance was underestimated in some areas, most likely the abundance of pairs because of their preference for small, temporary and seasonal wetlands (Cowardin et al., 1995; Johnson & Grier, 1988; Reynolds et al., 2006). However, preliminary correlation analyses indicated that the layers developed from the data were positively correlated with both May pond counts from the WBPHS and brood survey wetland data. Thus, we were comfortable using these data for predictions and maintain that, until an easily accessible data source at a comparable spatiotemporal scale

is made publicly available, the Global Surface Water data might represent the best option for regional geospatial wetland data in the PPR (Davidson, 2014; Guo et al., 2017). Further, we emphasize the importance of addressing uncertainty in any conservation planning strategy (Langford et al., 2009).

## 5 | CONCLUSION

Waterfowl conservation is perhaps one of the oldest fields of conservation management but has yet to adopt many of the new conservation practices such as the integration of spatiotemporal processes addressed in this analysis (Prairie Pothole Joint Venture, 2017). Future studies will need to improve upon our work here by incorporating better remote sensing data for predictions (more geared towards the PPR), brood data from Canada so that predictions can be expanded to that area and sensitivity analyses regarding uncertainty that include cost data.

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### PEER REVIEW

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### DATA AVAILABILITY STATEMENT

Analysis and modelling were performed using the open-source R language for statistical computing (R Core Team, 2019) and the licensed software ArcMap 10.6. Pair abundance data are available at no cost from the US Fish and Wildlife Breeding Population and Habitat Survey database (https://migbirdapps.fws.gov/mbdc/databases/mas/maydb.asp?opt=maydb). Brood abundance data are available at no cost from the public repository Dryad [https://doi.org/10.5061/dryad.37pvmcvhv].

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## BIOSKETCHES

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1: Integrating dynamic processes into waterfowl conservation prioritization tools

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