Biological Conservation 298 (2024) 110754

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Predicting the effects of land cover change on biodiversity in Prairie Canada using species distribution models

James E. Paterson *, Lauren E. Bortolotti, Paige D. Kowal, Ashley J. Pidwerbesky, James H. Devries

Institute for Wetland and Waterfowl Research, Ducks Unlimited Canada, P.O. Box 1160, Stonewall, Manitoba R0C 2Z0, Canada

ARTICLE INFO

Keywords:
Conservation planning
Habitat loss
Agricultural conversion
Conservation easements

ABSTRACT

Land cover change is the largest direct driver of global biodiversity loss but often the relationships between habitats and species occurrence are unknown. The conservation community requires tools to assess variation in biodiversity related to land cover for maximizing return on investment. Our objectives were to 1) develop a biodiversity mapping and assessment tool at a fine spatial scale for terrestrial vertebrates, and 2) test how much biodiversity is conserved by retaining natural habitats within agricultural landscapes. We built species distribution models for amphibians, birds, mammals, and reptiles (329 species, > 1.2 million observations) within Prairie Canada. Predicted biodiversity within 805 m × 805 m sites ranged from 0 to 238 species (66 ± 0.1). The proportion of annual cropland at a site had the largest negative effect on biodiversity among predictors. Using simulations of land cover change, we predicted that conserving 20 % of natural habitats would conserve an average of 26.5 % of maximum species richness in fields with annual cropland and 74.3 % of maximum species richness in fields with tame grass (perennial cropland). Our tool predicted that fields with conservation easements (n = 312) had more species (114 ± 2) and natural habitat (48 ± 1 %) compared to nearby unprotected sites (82 ± 3 species; 32 ± 2 % natural habitat). Our results highlight the importance of retaining natural habitats, including wetlands, grasslands, and forests within farms to support biodiversity. In addition, our predictions can be used to target areas for conserving and restoring habitats.

1. Introduction

Global efforts to conserve biodiversity have dramatically increased in recent decades (Brondízio et al., 2019) as species continue to decline (Díaz et al., 2019; Rosenberg et al., 2019; Wagner et al., 2021). The largest direct driver of terrestrial biodiversity loss is land use change (Jaureguiberry et al., 2022), which is largely from land conversion for agriculture (Caro et al., 2022; Foley, 2005; Newbold et al., 2016, 2015; Seibold et al., 2019). As human populations increase, so too does the need to grow more food by increasing the agricultural footprint and intensity per area, with biodiversity loss being an emerging consequence (Lafuite et al., 2018). Land use (humans' intended use of an area) drives changes in land cover (biophysical attributes of an area; Lambin et al., 2001) and we hereafter focus on land cover because it is more tractable to observe.

There have been extensive efforts to identify global biodiversity hotspots for conservation action (Allan et al., 2022; Hoskins et al., 2020; Jenkins et al., 2013; Newbold et al., 2016), but there is also a need for conservation in regions where biodiversity loss and land cover change has already occurred. These areas are often characterized by the juxtaposition of ongoing agricultural activity and a high prevalence of endangered species (Newbold et al., 2015). Well-managed and sustainable agricultural systems can contain rich and diverse ecosystems, which provide many ecosystem services beneficial to agricultural production (Landis, 2017). Biodiversity in agricultural landscapes increases with crop heterogeneity (Sirami et al., 2019), smaller field sizes (Fahrig et al., 2015), and a higher amount of uncultivated land (Estrada-Carmona et al., 2022; Shutler et al., 2000). Conservation in these landscapes presents a significant opportunity to both conserve biodiversity and increase food security (Garibaldi et al., 2021).

A region that exemplifies a large conservation opportunity is the rich agricultural lands in Canada's prairie provinces (Coristine et al., 2018; Kraus and Hebb, 2020). Biodiversity patterns in the Prairies Ecozone of Canada (Prairie Canada) were historically driven by bison (*Bison bison*)

---

* Corresponding author.
E-mail address: j_paterson@ducks.ca (J.E. Paterson).

https://doi.org/10.1016/j.biocon.2024.110754
Received 18 March 2024; Received in revised form 15 July 2024; Accepted 4 August 2024

and fire, but are now driven largely by agriculture, including cattle grazing and growing perennial and annual crops. Historical and continued loss of natural habitats, including native grasslands (Olimb and Robinson, 2019) and wetlands (Bartzen et al., 2010; Watmough et al., 2017), is a primary driver of biodiversity loss in this region. However, by examining relationships between biodiversity and land cover, we can estimate the amounts of natural habitat required for productive agriculture and biodiversity to coexist.

Advancing biodiversity conservation in Prairie Canada requires estimating the relationships between species and habitats to better prioritize conservation activities. Species distribution models constructed from species observations and environmental layers, including land cover, are well suited to this purpose (Elith and Leathwick, 2009; Guisan et al., 2013). The proliferation of citizen and community science observation data and machine learning algorithms make modelling these associations more feasible than ever before (Feldman et al., 2021).

To help the biodiversity conservation community, including land managers, our objectives were to 1) develop a biodiversity mapping and assessment tool with species distribution models at a fine spatial scale for terrestrial vertebrates in Prairie Canada (Fig. 1), and 2) test how much biodiversity is conserved by retaining natural habitats within agricultural landscapes. We used two approaches to meet our second objective. First, we simulated land cover change from natural habitats to increasing cover of either annual cropland or tame grass (perennial cropland). Second, we compared the predicted species richness on farms with conservation easements that protect natural habitats to paired farms without protected habitats.

2. Materials and methods

2.1. Study area

Our study region (Fig. S1) comprises southern Alberta, Saskatchewan, and Manitoba, defined by the Fescue, Mixed, and Moist Mixed Grasslands, and Aspen Parkland ecoregions (Ecological Stratification Working Group, 1996). Land use across the region is largely agricultural, either as annual cropland (predominantly for cereal grain and oil-seed production) or pasture and hay lands (i.e., tame grass perennial croplands and native grass) for cattle production. Areas not in agricultural production include remnant grasslands, shrublands, forests, wetlands, and urban/developed lands.

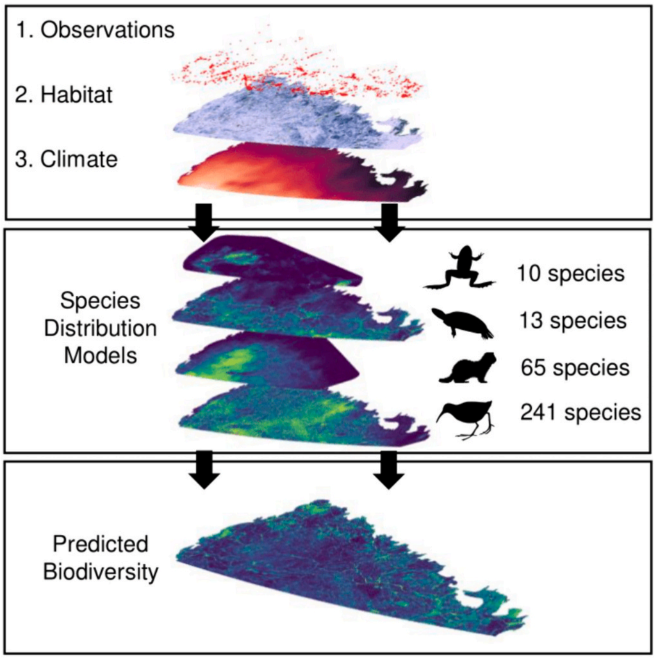

Fig. 1. Conceptual approach for using species observations, habitat data, and climate data to build and stack species distribution models for terrestrial vertebrates (n = 329 species) in Prairie Canada.

2.2. Species observations

We used observations of species to fit species distribution models using publicly available data and data sharing agreements with organizations collecting those data. We analyzed all data in R (R Core Team, 2021). All observations minimally required the species observed, spatial coordinates accurate to at least 805 m (resolution of prediction; see below), date accurate to the year, and observed between 2000 and 2022. We downloaded observations from the Global Biodiversity Information Facility using the *rgbif* package (Chamberlain, 2017; Chamerlain et al., 2023), and data from the North American Breeding Bird Survey (Ziolkowski Jr. et al., 2022) linked to stops on routes within our study area. We also included regional datasets from NatureCounts, the Alberta Roadkill Database, the Alberta Biodiversity Monitoring Institute (public locations), the North American Bat Monitoring Network, the Manitoba Herp Atlas, and each province's Conservation Data Centre that tracks rare species. We included species with geographic ranges that overlapped our study area and any additional species that had records in one of the data sources we included. We removed duplicate observations of species at the same site to reduce spatial autocorrelation when fitting species distribution models. Our cleaned observation data set included 1,229,701 observations of 329 species (Supplementary information).

2.3. Species distribution models and biodiversity predictions

We fit maximum-entropy (MaxEnt) species distribution models (Phillips et al., 2017; Phillips and Dudík, 2008) for each study species with >20 observations using the *dismo* package (Hijmans et al., 2022). MaxEnt models compare environmental variable attributes of presence locations with background locations and maximize the entropy between the two point-types. We chose MaxEnt because biodiversity observations were presence only for the majority of taxa; that is, our observation data sets did not include structured absence data for all taxa. Below, we outline the major components of the modelling procedure, but further outline our approach in the Supplementary information following the Objectives, Data, Modelling, Assessment, and Predictions (ODMAP) approach (Fitzpatrick et al., 2021; Zurell et al., 2020).

For each species, we used 25 environmental variables within an 805 m × 805 m site that described habitat, soil, elevation, and climate as predictors (Table S1). A site size of 805 m is approximately a quarter-section (half-mile by half-mile) used for farming, which is how most of the study area is parceled for land ownership (i.e., the Dominion Land Survey; McKercher and Bertram, 1986) and relevant to land management decisions. We identified predictor variables that had available data and were likely to affect a significant portion of our study species (Fig. S2). The final set of environmental variables included information on seven major habitat types derived from Agriculture and Agri-Food Canada's Land Use Maps (Agriculture and Agri-Food Canada, 2015) from 2015, the Canadian Wetland Inventory (Canadian Wetland Inventory Technical Committee, 2016; Fournier et al., 2007), and the Alberta Biodiversity Monitoring Institute (ABMI) Wetland Inventory (ABMI, 2021; DeLancey et al., 2019): annual cropland (46.5 % study area), native grassland (16.8 %), tame grass (16.1 %), wetland (9.5 %), forest (4.2 %), open water (2.8 %), and human settlement (1.4 %). For each of the major habitat types, we included a predictor for the proportion of a site and the proportion of area within a moving 10 km window of a focal site it covered. We included predictor variables for the maximum habitat patch size overlapping a site for native grassland, tame grass, forest, and the combination of wetland and open water. We also included the mean and standard deviation of elevation within a site, derived from a digital elevation model (Government of Canada, 2013), to capture differences in terrain (e.g., river valleys). We included a numerical variable for soil texture:

$$Soil\ Texture = ln\left(\frac{sand}{silt + clay}\right)$$

We assigned soil texture values based on the nearest neighbor Soil Landscapes of Canada (Soil Landscapes of Canada Working Group, 2010) polygon for every site.

We used climate data from the 19 WorldClim bioclimatic variables (Fick and Hijmans, 2017), which are based on average values from 1970 to 2000 and represent average recent climatic conditions. To reduce the number of climatic variables, we used Principal Component Analyses and included the top four principal components (4 variables), which cumulatively explained 92 % of variation between sites in the 19 bioclimatic variables (Table S2).

We tested for multicollinearity between environmental variables, using a correlation $\geq$0.7 as a warning of multicollinearity. Unsurprisingly, some of the habitat covariates within a site were correlated with the proportions of the same habitat within a 10 km moving window (native grassland: $r = 0.84$, annual cropland: $r = 0.75$, forest: $r = 0.77$, human settlement: $r = 0.77$; Table S3). Mean elevation was correlated with climate PC1 ($r = 0.73$). All other correlation coefficients were $\leq$ 0.7. We chose to still include the correlated predictor variables because we expected different species to respond to habitat at local versus neighborhood scales.

Species distribution models built with MaxEnt compare presence locations to a set of background points and the extent of the background sample affects inferences (Elith et al., 2011). For each species, we limited model-fitting to an approximation of the species' range within our study area, which we defined as a minimum convex polygon around a species' observations buffered by 50 km. Our buffer was five times the distance of our larger habitat moving window (10 km) but may underestimate a species' range in cases with sparse observations. For species with ranges that were at $\geq$90 % of the study area, we extended their range to the entire study area. We adjusted the number of background points based on a species' range size. For species with ranges <100,000 sites, we sampled 20 % of sites for background points. Where 250,000 sites $\leq$ a species range $\geq$ 100,000 sites, we sampled 10 % of sites for background points. For species with ranges $\geq$250,000 sites, we sampled 5 % of sites for background points. To correct for spatial biases related to survey effort, we sampled background points using a kernel density estimator based on Target Group Sampling (Barber et al., 2022) by summing the total number of observations in a site for each taxonomic group (amphibians, birds, mammals, reptiles). Target Group Sampling can reduce sampling bias in MaxEnt models when survey effort is unknown, as was the case in our study. Thus, background points had a spatial bias that mimicked the spatial bias of the presence points.

Within a species range, we divided the area into 100 blocks and fit five species distribution models using k-fold cross-validation where 80 % of blocks were used for training and 20 % were used for testing (Valavi et al., 2018). For each k-fold, we fit a MaxEnt model using presence points for a species and background points in that fold (80 % of blocks) for training, and the presence and background points in the remaining 20 % of blocks for testing. We used the mean Area Under the Receiver-Operator Curve (AUC) of the five models on test data per species as an indication of model performance. AUC values vary from 0 (perfectly wrong) to 1.0 (perfect prediction), with 0.5 indicating that predictions are no better than random. We considered model performance adequate for species with a mean AUC value $\geq$0.7. For each species, we averaged site scores across the 5 k-folds weighted by AUC. We tested whether mean AUC per species was affected by taxonomic group and the number of presence locations using a general linear model (binomial family). We compared the model predictions of each species to published range maps and habitat associations (Fig. S3).

To test the model performance further with an independent data set, we compared the predicted species richness from species distribution models to detected species richness collected from 192 autonomous recording units (ARUs) that were used for separate studies on wetland biodiversity. ARUs were deployed in wetland edges and recorded for 22 min per day from before ice-melt to 31 July in 2022 or 2023; 5 min at 00:00, 3 min at 02:00, 3 min at sunrise, 5 min at 1 h after sunrise, 3 min at 1 h before sunset and 3 min at 1 h after sunset. Bird and anuran species were identified from recordings with BirdNET (Kahl et al., 2021), and we used detections of species with >75 % confidence on at least two days (birds) or one day (anurans) for estimating species richness. We limited our bird analyses to wetland birds using the Avian Conservation Assessment Database (Partners in Flight, 2021) to identify species that breed in wetlands. We used the detected species richness with ARUs as our predictor variable, although ARUs have lower detection probabilities than point counts for some wetland species, such as waterfowl or raptors. However, the ARU data were collected over 90 days and our focus was on relative differences in detected species richness between sites instead of a complete census of all species. We compared estimated species richness from our species distribution models to detected species richness with ARUs using generalized linear models. We fit separate models for wetland birds (negative-binomial distribution) and anurans (Poisson distribution).

2.4. Species distribution models and biodiversity predictions

We stacked species distribution model outputs to get spatial predictions of biodiversity and test the effects of land cover change on biodiversity. For each species, we converted the weighted habitat suitability score of each site to a binary presence or absence prediction using a threshold that maximized the sum of the specificity (true negative rate) and sensitivity (true positive rate; Florkowski, 2008). We chose to use thresholding to convert continuous model output into a binary prediction so that our estimate of relative biodiversity was an interpretable scale of species richness. We summed the number of species predicted to have suitable habitat in each site as a proxy for predicted biodiversity (α-diversity, species richness). We estimated total species richness (γ-diversity) for each site based on species' ranges. There are many approaches to quantify biodiversity hotspots, and as one illustration of using our species distribution models to do this, we identified sites with a predicted species richness in the top 5 % of the distribution for each taxonomic group. Alternate methods, such as the number of rare or threatened species, would identify different areas.

2.5. Most important variables affecting biodiversity

We tested which predictors had the largest effects on biodiversity by identifying which variables had the highest median percent drop in accuracy when they were removed from a species' model (variable importance). For the top four most important variables, we fit generalized additive models (GAMs) to the relationships between predicted species richness and the predictor variables using the *mgcv* package (Wood, 2023, 2004).

2.6. Effects of land cover change on biodiversity

To test how land cover change affects biodiversity, we used our species distribution models to predict how habitat conversion affects species richness. We focused on two major land cover changes: 1) conversion of natural habitat to annual cropland and 2) conversion of natural habitat to tame grass, typically used for haying and pasture. We randomly sampled 100 sites within our study area to include variation from other sources (climate, soil texture, elevation). For every site, we started with an approximation of a site with natural habitats using the mean levels of our habitat predictors at sites with <5 % annual cropland, tame grass, and human settlement. Thus, we started with a site that was 66 % native grassland, 12 % wetland, 10 % forest, and 8 % open water, totaling 96 % of a site's area. We set the amount of habitat within a 10 km moving window using the same approach and values. We varied the focal variable (proportion annual cropland or tame grass) from 0 to 1.0 (by 0.01) and predicted species richness using our species distribution models. We modelled the response of total species richness (% of maximum value) to proportion annual or tame grass (predictor variables) using GAMMs. We included a random intercept term for site to account for multiple data points per site. To test the effects of conserving natural habitats within agricultural fields, we predicted the species richness (% of maximum value) supported by conserving 10 % or 20 % of natural habitats within each scenario. To test how land cover change affected the biological community, we used nonmetric multidimensional scaling (NMDS) fit with the *vegan* package (Jari Oksanen et al., 2020) to compare predicted communities at natural and relatively converted (90 % annual cropland or 90 % tame grass) states. We used a minimum of 50 random starts for the NMDS to find solutions that were repeated at least once (k = 2 dimensions).

2.7. Effects of conservation lands on predicted biodiversity

We compared the predicted biodiversity in places with conservation easements (protected areas under private ownership) to random points outside of protected areas. We used conservation easements delivered by Ducks Unlimited Canada completed prior to 31 March 2016, which corresponds to imagery used for land cover classification. For each conservation easement (n = 312), we selected a random point within 10 km that fell outside of the conservation easement and Canada's Protected and Conserved Areas Database (Environment and Climate Change Canada, 2021) for comparison. We chose 10 km to compare places with similar species pools and land cover. We fit a generalized linear mixed-effects model (GLMM; Poisson family) comparing the predicted species richness at each site (response) between the protection categories (conservation easement or no protection, fixed-effect) using the *lme4* package (Bates et al., 2015). We included a random intercept term for project because of our paired sampling design. We also extracted the proportion of each site with natural habitats (summed proportion wetland, open water, native grassland, and forest). We compared the proportion of natural habitat (response) at each site using a GLMM (binomial family) with protection category (fixed effect) and project (random intercept term) as predictor variables.

3. Results

3.1. Species distribution models and biodiversity predictions

Overall, our species distribution models performed well using AUC as a benchmark (mean ± SE; 0.80 ± 0.01, Fig. S4). Of the 329 modelled species, 46 were below our benchmark AUC of 0.70 (Table S4). There was no effect of taxonomic group on a species' AUC ($\chi^2 = 2.28$, df = 3, P = 0.52) and there was a marginal negative effect of the number of observations on a species' AUC ($\chi^2 = 3.75$, df = 1, P = 0.05). Species with AUC < 0.70 included rare or difficult to detect species with very few observations (e.g., Arctic Shrew, *Sorex arcticus*, n = 22) and ubiquitous common species (e.g., Mallard, *Anas platyrhynchos*, n = 18,521; Coyote, *Canis latrans*, n = 8952).

The wetland bird species richness predicted by species distribution models was positively associated with the species richness of wetland birds detected by ARUs ($\chi^2 = 14.80$, df = 1, $P = 1.2 \times 10^{-4}$, n = 192, Fig. S5A). The wetland bird species richness predicted by species distribution models overpredicted the species richness of wetland birds detected by ARUs, but there was only one ARU at each 805 m × 805 m site and some species may have been present elsewhere within the site. The anuran species richness predicted by species distribution models was not associated with anuran species richness detected by ARUs ($\chi^2 = 0.29$, df = 1, P = 0.59, n = 192); however, the species pool was small (Fig. S5B).

Predicted species richness (α-diversity) in our study area varied from 0 to 238 per site (66 ± 0.1 species; Figs. 2, S6A), including 2 ± 0.002 amphibians, 50 ± 0.05 birds, 13 ± 0.01 mammals, and 1 ± 0.002 reptiles per site. The predicted γ-diversity varied from 231 to 304 (278 ± 0.02; Fig. S6B). There were 2543 of 715,946 sites with ≥75 % of available species, using our estimates of γ-diversity (164,792 ha; 0.35 % of study area). Hotspots of predicted species richness differed between major taxonomic groups (Fig. S7) and included major rivers and river valleys, such as the Assiniboine River and the South Saskatchewan River.

3.2. Most important variables affecting biodiversity

The four variables with the largest median effect on habitat suitability per species were proportion human settlement, proportion forest within a 10 km moving window, climate PC1, and proportion annual cropland (Fig. 3A). Considering current variation in environmental covariates, the predicted species richness had an approximately quadratic relationship with the proportion of human settlement (Fig. 3B). The predicted species richness had an approximately quadratic relationship with the proportion of forest within a 10 km moving window (Fig. 3C). Although climate PC1 was one of the most important variables affecting habitat suitability, there was no relationship between predicted species richness and climate PC1 (Fig. 3D). Finally, the predicted total species richness decreased substantially from 50 % to 100 % annual cropland within a site (Fig. 3E). The four most important variables differed between taxonomic groups (Table S5), with amphibian species' habitat suitability strongly influenced by climate and less by land cover.

3.3. Effects of land cover change on biodiversity

When simulating changes from natural land cover to annual cropland, there was a clear decline in predicted species richness overall and for each taxonomic group (Fig. 4A). The species richness (% of maximum) declined from 96.8 % (± 0.1 %) when there was no annual cropland to 6.8 % (± 0.2 %) when the whole site was annual cropland (GAM prediction; adjusted-$R^2 = 0.98$). The decline in species richness with more annual cropland was approximately linear, but the response was dominated by birds (241 of 329 species). The decline in species richness with more annual cropland was steepest at high proportions of cropland for amphibians and mammals. The model predicted retaining 20 % of a site as natural habitat would retain 26.5 % (± 0.5 %) of species richness and retaining 10 % would retain 17.5 % (± 0.4 %) of species richness (Fig. 4C). The NMDS analyses showed when sites contained natural habitat, the communities were relatively similar. As more land was converted to annual cropland, the species distribution models predicted that communities diverged in community composition (Fig. S8).

When simulating changes in land cover from natural land cover to tame grass, there was a decline in predicted species richness (% of maximum) overall and for each major taxonomic group that was less steep than the decline from changing natural land cover to annual cropland (Fig. 4B). Amphibian species richness (% of maximum) showed a bimodal relationship with the proportion tame grass, but the community size was relatively small (9 modelled species) so changes in 1–2 species had high proportional responses. The total species richness (% of maximum) declined from 90.5 % (± 0.3 %) when there was no tame grass to 38.0 % of maximum (± 0.7 %) when the whole site was tame grass (GAM prediction; adjusted-$R^2 = 0.87$). The decline in species richness with more tame grass was most steep when there were very low amounts of natural habitats, and the model predicted retaining 20 % of a site as natural habitat would still retain 74.3 % (± 0.5 %) of species richness and retaining 10 % would retain 67.8 % (± 0.6 %) of species richness. As more land was converted to tame grass, the communities shifted in composition but were more similar to sites with natural habitats than when land was converted to annual cropland (Fig. S8).

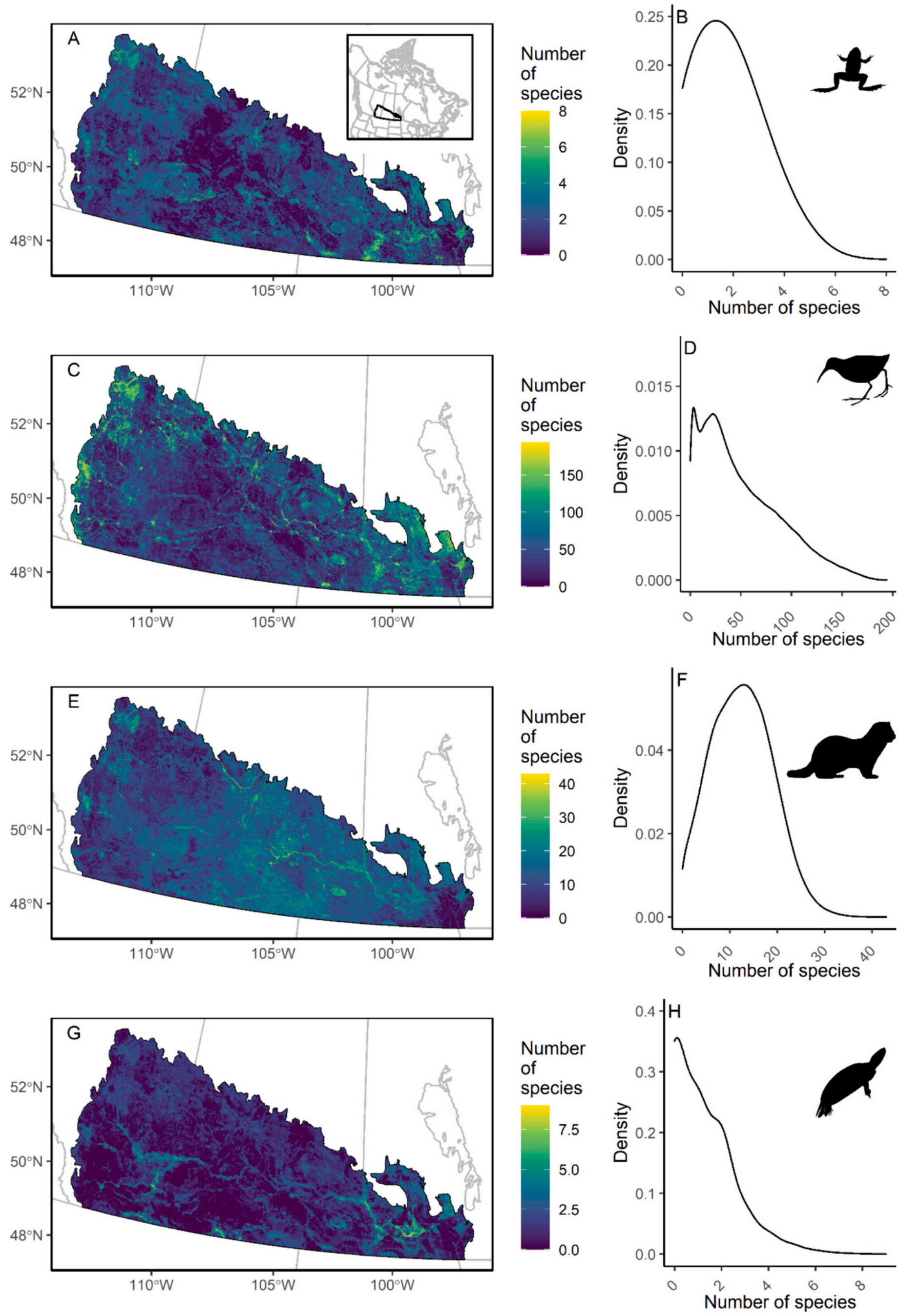

Fig. 2. The predicted species richness of terrestrial vertebrates (n = 329 species) in Prairie Canada (inset in A) using individual species distribution models for amphibians (A, B), birds (C, D), mammals (E, F), and reptiles (G, H).

3.4. *Effects of conservation lands on predicted biodiversity*

Sites with conservation easements had a higher species richness (114 ± 2 species) than paired random points outside of protected and conserved areas (82 ± 3 species; $\chi^2 = 1610.2$, df = 1, $P < 0.001$; Fig. 5A). Sites with conservation easements had higher proportions of natural habitat (mean = 0.48 ± 0.01) than paired random points outside of protected and conserved areas (0.32 ± 0.02; $\chi^2 = 14.09$, df = 1, $P < 0.001$; Fig. 5B).

4. Discussion

We found substantial variation in predicted terrestrial vertebrate biodiversity across Prairie Canada, and much of it was explained by the amount of natural habitats. However, we assert that it is possible to conserve biodiversity in this working landscape while still producing food and supporting the livelihoods of agricultural producers. First, despite being the most important and largest agricultural region in Canada (Campbell et al., 2002; Government of Canada, 2021), there are still many sites with high predicted biodiversity relative to the number of species whose range overlaps a site. Second, we found evidence that conserving natural habitats within agricultural landscapes can support a substantial subset of biodiversity. These results provide evidence to support policies and programs that conserve remaining natural habitats on farmland through incentives in long-term programs, such as conservation easements (Rissman et al., 2007) and shorter-term

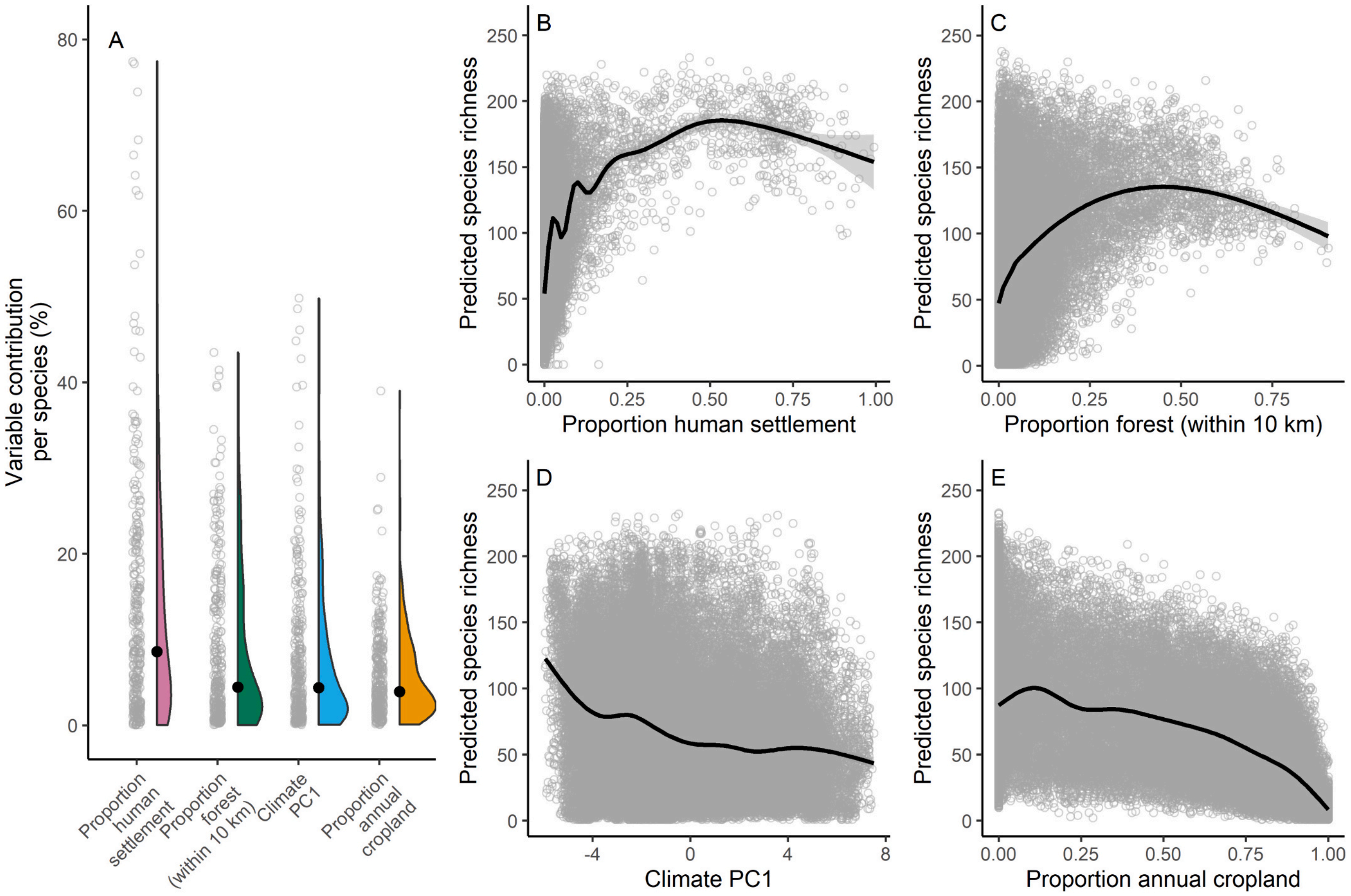

Fig. 3. Species distribution models for terrestrial vertebrates (n = 329 species) in Prairie Canada were A) most influenced by proportion human settlement, proportion forest within 10 km, and proportion annual cropland. Each species is represented by a gray point and the black points are the variable medians among species. B) The effect of proportion human settlement on the predicted species richness. C) The effect of proportion forest within a 10 km moving window on the predicted species richness. D) The effect of climate PC1 on the predicted species richness. E) The effect of proportion annual cropland on the predicted species richness. In B, C, D and E: Gray points are a random selection of 50,000 sites (805 m × 805 m), and black lines are predictions from a General Additive Model.

conservation agreements (e.g., Paterson et al., 2023). In addition, our results provide evidence that areas planted with tame grass for forage or haying such as through crop rotations or longer-term incentive programs for conservation will support more biodiversity than annually cropped areas.

4.1. Species distribution models and biodiversity predictions

Our spatial predictions of biodiversity can be used for prioritizing areas and estimating consequences of land cover change in this region. For example, by targeting habitat conservation at sites with the highest predicted species richness overall or by region. Further, by quantifying the relationship between species habitat suitability and land cover across large regions, tools of this type are well suited to quantify the impact of policy decisions pertaining to biodiversity conservation. Because our approach uses species-specific layers, it also is well suited for targeting conservation for important species subsets (e.g., species at risk) and informing the mitigation hierarchy in land development planning (avoid, mitigate, offset; Phalan et al., 2018).

While there are many existing and emerging tools for prioritizing and planning conservation actions (Hanson et al., 2019b; Sarkar et al., 2006; Watts et al., 2009), the predicted biological responses (e.g., species richness) are typically at coarse spatial scales. Our results advance biodiversity conservation by providing predictions of biodiversity response based on species-specific associations with land cover at the scale where land use decisions are made. Our approach is applicable in other regions and for other taxonomic groups. Ultimately, we see this approach being used in combination with data on the economic and societal costs of biodiversity loss and conservation to identify cost-effective sites and approaches for maintaining and restoring biodiversity (Asare et al., 2022; Naidoo et al., 2006; Rashford and Adams, 2007). Our approach is consistent with numerous Essential Biodiversity Variables proposed to monitor global biodiversity (Pereira et al., 2013), including ecosystem distributions, species distributions, and community composition.

4.2. Most important variables affecting biodiversity

The three land cover variables with the largest median effect on species' distribution models were proportion human settlement, proportion forest within 10 km, and proportion annual cropland. The proportion of human settlement was the single most important predictor for many species associated with urban and suburban areas, including Chimney Swift (*Chaetura pelagica*) and Eastern Gray Squirrel (*Sciurus carolinensis*). The proportion of human settlement was generally positively associated with species richness, which is partly explained by a subset of species associated with human settlement. Not as many species had strong negative relationships with the proportion of human settlement, but this habitat type was rare in our study area (mean proportion = 0.01). The proportion forest within 10 km had a large effect on biodiversity. Many species are dependent on treed habitats, such as cavity nesting birds and large mammals. The relative rarity of this habitat meant species richness was associated with this variable and conserving treed habitat will support a subset of species within Prairie

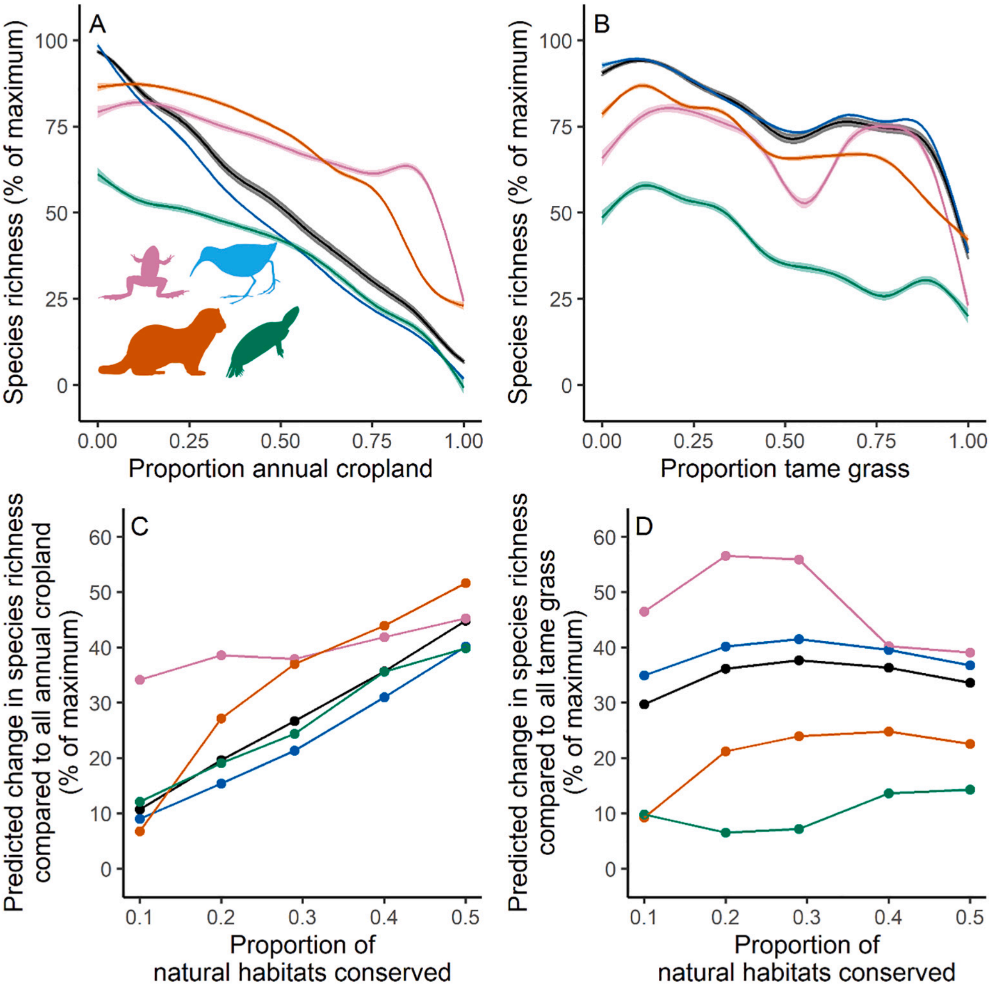

Fig. 4. The predicted effects of land cover change from mostly natural habitats on a gradient of increasing A) annual cropland and B) tame grass (perennial cropland) at 805 m × 805 m sites using species distribution models for all species of terrestrial vertebrates (black; n = 329 species), amphibians (pink), birds (blue), mammals (orange), and reptiles (green) in Prairie Canada. Lines are predictions from General Additive Models from simulations at 100 sites and ribbons represent 95 % confidence intervals. The predicted change in species richness from conserving natural habitats within C) annual cropland and D) tame grass.

Canada. The proportion of annual cropland had a negative relationship with biodiversity and all the species' models where cropland was an important predictor displayed negative associations with the proportion annual cropland. The negative association between annual cropland and biodiversity is supported by studies in Prairie Canada (Mantyka-Pringle et al., 2019), other regions (Fahrig et al., 2015) and for other taxonomic groups (Raven and Wagner, 2021).

The maximum patch sizes of natural habitats were important predictors for some species even though they had low median effects among species. Maximum patch size was especially influential on native grassland specialists (Swift Fox, *Vulpes velox*, variable importance = 61.4 %; Sprague's Pipit, *Anthus spragueii*, variable importance = 45.3 %) and species associated with large water bodies (Western Grebe, *Aechmophorus occidentalis*, variable importance = 46.7 %; Piping Plover, *Charadrius melodus*, variable importance = 46.9 %). The high variable importance of maximum patch size highlights that conserving remaining contiguous blocks of habitat is critical for many species in our study area, including multiple species at risk.

4.3. *Effects of land cover change on biodiversity*

Our simulations of land cover change from natural habitats to annual cropland or tame grass support two conclusions. First, initiatives that conserve remnant patches of habitat within farm fields are valuable because we found retaining 10–20 % natural habitat within fields can support terrestrial vertebrate biodiversity. The negative association between agricultural land cover change and species richness occurred in each taxonomic group and overall richness, despite some species being positively associated with these habitats. Although retaining natural habitat within fields can support biodiversity, our results also strongly support conserving large patches of remaining natural habitats because of the negative association between agricultural land cover and species richness. In addition to a decrease in total species richness, we observed a shift in community composition, based on which species we predicted to be present (Fig. S8), as found in other biodiversity hotspots with high land cover change (Vargas Soto et al., 2022).

The second conclusion from our land cover change analyses is that tame grass fields for hay or pasture support an intermediate proportion of vertebrate biodiversity within agricultural landscapes between natural habitats (highest diversity) and annual croplands (lowest diversity). This is consistent with previous findings that tame grass provides habitat for biodiversity, including nesting waterfowl (Arnold et al., 2007) and pollinators (Carvell et al., 2006). For supporting biodiversity in Prairie Canada, conserving existing native grasslands should be a high priority because they continue to be lost (Gage et al., 2016), support specialist species in long-term decline (Mahony et al., 2022) and are challenging to restore (Knight and Overbeck, 2021). However, converting annual croplands to tame grass represents a relatively efficient restoration activity that 1) keeps land within agricultural operation, as opposed to land 'sparing' and 2) can support a substantial proportion of

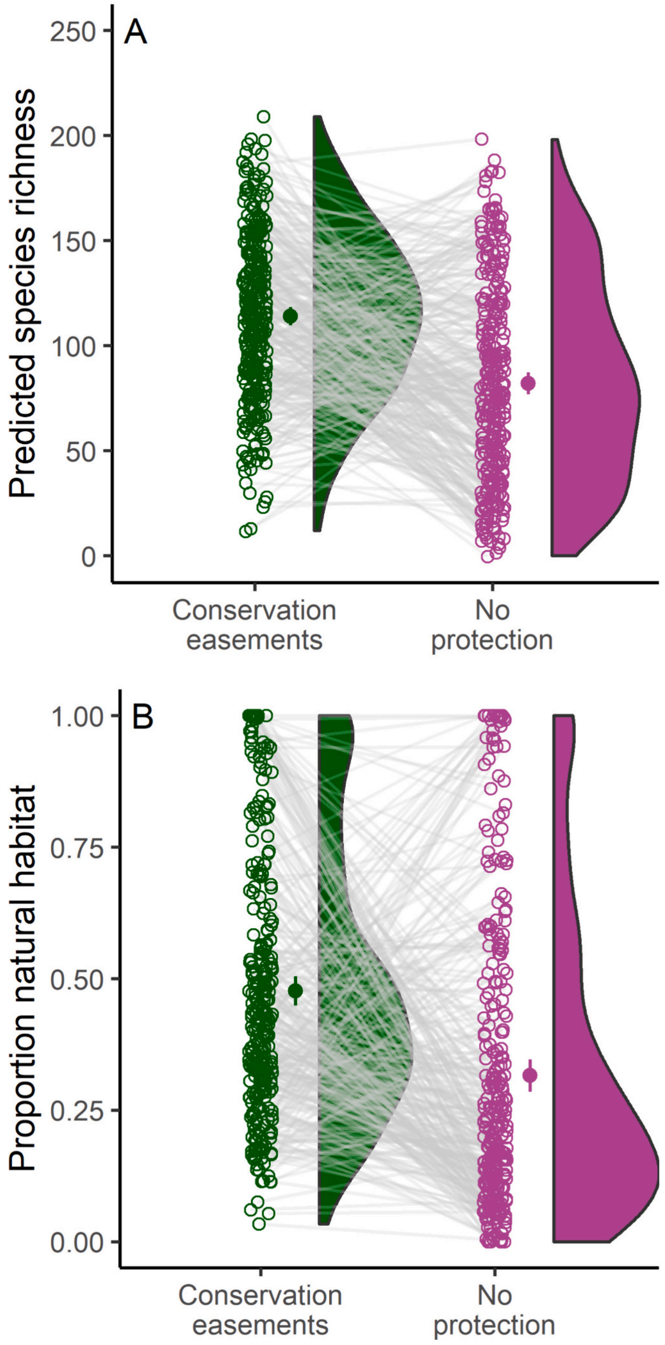

Fig. 5. The predicted species richness of terrestrial vertebrates (n = 329 species) with species distribution models (A) and proportion natural habitats (B) at conservation easements and paired random points within 10 km outside of protected and conserved areas (n = 312) in Prairie Canada. Hollow points are individual sites, filled points are group means, and vertical lines are 95 % confidence intervals of group means. Gray lines connect paired sites of conservation easements and random points. Filled curves are the density distributions of each category.

biodiversity.

4.4. Limitations

Despite generally good model performance indicators and detecting biologically plausible (and predicted) relationships between species and habitats, our approach does have some limitations from the type of species observations we used and the accuracy of remotely sensed land cover data. Most observation sources we used are 'presence only' which prevents direct estimation of detection probability or survey effort, minus some structured bird data, such as the North American Breeding Bird Survey. Thus, we used MaxEnt species distribution models that compared presence locations to background points, which risks spatial biases in observation data. While we estimated and corrected for spatial bias in observation data using Target Group Sampling, it is possible our corrections were inadequate. Besides the observation data, our land cover habitat predictors are from remotely sensed data and some habitats are difficult to distinguish using satellite data. For example, the classification of native grassland may have some errors because the focus of the land cover product is to separate grasslands managed with grazers, unmanaged grasslands (e.g., right-of-ways) and perennial cropland (haylands). Given the habitat associations we observed between native grassland amount with native grassland specialists, the error is unlikely to strongly affect our inferences. Future land cover products should focus on distinguishing native and tame grasslands in this region. Next, we used species observations centered on the land cover classification dates (2015–2016), but we recognize that this choice likely contributed statistical noise when land cover at the time of a species observation did not match the land cover in the 2015–2016 data. Finally, we limited the number of predictor variables by grouping major land cover classifications, such as annual crop type. Species likely respond differently to different annual crops, and future work should separately estimate how different annual crop field types affect biodiversity.

5. Conclusions

Land use change is the largest direct driver of terrestrial biodiversity loss, and estimating the relationship between biodiversity and major categories of land cover change allowed us to test how species are responding to change. Our results highlighted local biodiversity hotspots within Prairie Canada and supported the hypothesis that conserving natural habitats within farm fields can support substantial portions of this landscape's biodiversity in combination with conserving larger blocks of natural habitats for species sensitive to connectivity and patch size. In the future, species distribution models incorporating fine-scale habitat data can be used to build and expand on conservation tools that estimate return-on-investment of different actions (Carwardine et al., 2019; Hanson et al., 2019a; Silvestro et al., 2022; Watts et al., 2009), including habitat conservation, restoration efforts, biodiversity policy, and land use planning.

CRediT authorship contribution statement

James E. Paterson: Conceptualization, Methodology, Funding acquisition, Formal analysis, Data curation, Writing – original draft, Visualization, Project administration. **Lauren E. Bortolotti:** Conceptualization, Methodology, Funding acquisition, Writing – review & editing. **Paige D. Kowal:** Methodology, Formal analysis, Data curation, Writing – review & editing. **Ashley J. Pidwerbesky:** Methodology, Formal analysis, Data curation, Writing – review & editing, Visualization. **James H. Devries:** Conceptualization, Methodology, Funding acquisition, Writing – original draft, Project administration.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: James Paterson reports financial support was provided by Royal Bank of Canada Tech for Nature program, the United States Fish and Wildlife Service, Ducks Unlimited Inc., and Ducks Unlimited Canada. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Most data is available from the original source or linked in the manuscript. Some data (sensitive species observations) are unavailable for sharing.

Acknowledgements

This work was supported with funding from Royal Bank of Canada's Tech For Nature program, an anonymous donor, the United States Fish and Wildlife Service through the North American Wetland Conservation Act, Ducks Unlimited Inc., and Ducks Unlimited Canada. Data was contributed from Alberta Biodiversity Monitoring Institute, Alberta Fish and Wildlife Management Information System, the Saskatchewan Conservation Data Centre, and the Manitoba Conservation Data Centre. Llwellyn Armstrong provided advice and code for analyses of soil texture.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110754.

References

ABMI, 2021. ABMI Wetland Inventory. https://abmi.ca/home/data-analytics/da-top/da-product-overview/Advanced-Landcover-Prediction-and-Habitat-Assessment–ALPHA–Products/ABMI-Wetland-Inventory.html.

Agriculture and Agri-Food Canada, 2015. AAFC land use maps. https://open.canada.ca/data/en/dataset/b9c89625-d7dc-43fd-b5f0-d993c3f8a35f.

Allan, J.R., Possingham, H.P., Atkinson, S.C., Waldron, A., Marco, M.D., Butchart, S.H.M., Adams, V.M., Kissling, W.D., Worsdell, T., Sandbrook, C., Gibbon, G., Kumar, K., Mehta, P., Maron, M., Williams, B.A., Jones, K.R., Wintle, B.A., Reside, A.E., Watson, J.A.E., 2022. The minimum land area requiring conservation attention to safeguard biodiversity. Science 376, 1094–1101. https://doi.org/10.1126/science.abl9127.

Arnold, T.W., Craig-Moore, L.M., Armstrong, L.M., Howerter, D.W., Devries, J.H., Joynt, B.L., Emery, R.B., Anderson, M.G., 2007. Waterfowl use of dense nesting cover in the Canadian Prairie Parklands. J. Wildl. Manag. 71, 2542–2549.

Asare, E., Mantyka-Pringle, C., Anderson, E., Belcher, K., Clark, R., 2022. Evaluating ecosystem services for agricultural wetlands: a systematic review and meta-analysis. Wetl. Ecol. Manag. 30, 1129–1149. https://doi.org/10.1007/s11273-022-09857-5.

Barber, R.A., Ball, S.G., Morris, R.K.A., Gilbert, F., 2022. Target-group backgrounds prove effective at correcting sampling bias in Maxent models. Divers. Distrib. 28, 128–141. https://doi.org/10.1111/ddi.13442.

Bartzen, B.A., Dufour, K.W., Clark, R.G., Caswell, F.D., 2010. Trends in agricultural impact and recovery of wetlands in prairie Canada. Ecol. Appl. 20, 525–538. https://doi.org/10.1890/08-1650.1.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Brondízio, E.S., Settele, J., Díaz, S., Ngo, H.T. (Eds.), 2019. The Global Assessment Report of the Intergovernmental Science-policy Platform on Biodiversity and Ecosystem Services. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), Bonn.

Campbell, C.A., Zentner, R.P., Gameda, S., Blomert, B., Wall, D.D., 2002. Production of annual crops on the Canadian prairies: trends during 1976–1998. Can. J. Soil Sci. 82, 45–57. https://doi.org/10.4141/S01-046.

Canadian Wetland Inventory Technical Committee, 2016. Canadian Wetland Inventory (Data Model).

Caro, T., Rowe, Z., Berger, J., Wholey, P., Dobson, A., 2022. An inconvenient misconception: climate change is not the principal driver of biodiversity loss. Conserv. Lett. 15 https://doi.org/10.1111/conl.12868.

Carvell, C., Westrich, P., Meek, W.R., Pywell, R.F., Nowakowski, M., 2006. Assessing the value of annual and perennial forage mixtures for bumblebees by direct observation and pollen analysis. Apidologie 37, 326–340. https://doi.org/10.1051/apido:2006002.

Carwardine, J., Martin, T.G., Firn, J., Reyes, R.P., Nicol, S., Reeson, A., Grantham, H.S., Stratford, D., Kehoe, L., Chadès, I., 2019. Priority threat management for biodiversity conservation: a handbook. J. Appl. Ecol. 56, 481–490. https://doi.org/10.1111/1365-2664.13268.

Chamberlain, S., 2017. R Python, and Ruby Clients for GBIF Species Occurrence Data. https://doi.org/10.7287/peerj.preprints.3304v1.

Chamerlain, S., Barve, V., McGlinn, D., Desmet, P., Geffert, L., Ram, K., 2023. rgbif: Interface to the Global Biodiversity Information Facility API.

Coristine, L.E., Jacob, A.L., Schuster, R., Otto, S.P., Baron, N.E., Bennett, N.J., Bittick, S.J., Dey, C., Favaro, B., Ford, A., 2018. Informing Canada’s commitment to biodiversity conservation: a science-based framework to help guide protected areas designation through Target 1 and beyond. Facets 3, 531–562. https://doi.org/10.1139/facets-2017-0102.

DeLancey, E.R., Simms, J.F., Mahdianpari, M., Brisco, B., Mahoney, C., Kariyeva, J., 2019. Comparing deep learning and shallow learning for large-scale wetland classification in Alberta. Canada. Remote Sensing 12, 2. https://doi.org/10.3390/rs12010002.

Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Agard, J., Arneth, A., Balvanera, P., Brauman, K.A., Butchart, S.H.M., Chan, K.M.A., Garibaldi, L.A., Ichii, K., Liu, J., Subramanian, S.M., Midgley, G.F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Chowdhury, R.R., Shin, Y.-J., Visseren-Hamakers, I., Willis, K.J., Zayas, C.N., 2019. Pervasive human-driven decline of life on Earth points to the need for transformative change. Science 366, eaax3100. https://doi.org/10.1126/science.aax3100.

Ecological Stratification Working Group, 1996. A National Ecological Framework for Canada. Centre for Land and Biological Resources Research, Research Branch, Agriculture and Agri-Food Canada, Ottawa.

Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. 40, 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. Divers. Distrib. 17, 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x.

Environment and Climate Change Canada, 2021. Canadian Protected and Conserved Areas Database. URL. https://www.canada.ca/en/environment-climate-change/services/national-wildlife-areas/protected-conserved-areas-database.html. (Accessed 25 August 2023) (WWW Document).

Estrada-Carmona, N., Sánchez, A.C., Remans, R., Jones, S.K., 2022. Complex agricultural landscapes host more biodiversity than simple ones: a global meta-analysis. Proc. Natl. Acad. Sci. USA 119, e2203385119. https://doi.org/10.1073/pnas.2203385119.

Fahrig, L., Girard, J., Duro, D., Pasher, J., Smith, A., Javorek, S., King, D., Lindsay, K.F., Mitchell, S., Tischendorf, L., 2015. Farmlands with smaller crop fields have higher within-field biodiversity. Agric. Ecosyst. Environ. 200, 219–234. https://doi.org/10.1016/j.agee.2014.11.018.

Feldman, M.J., Imbeau, L., Marchand, P., Mazerolle, M.J., Darveau, M., Fenton, N.J., 2021. Trends and gaps in the use of citizen science derived data as input for species distribution models: a quantitative review. PLoS One 16, e0234587. https://doi.org/10.1371/journal.pone.0234587.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315. https://doi.org/10.1002/joc.5086.

Fitzpatrick, M.C., Lachmuth, S., Haydt, N.T., 2021. The ODMAP protocol: a new tool for standardized reporting that could revolutionize species distribution modeling. Ecography 44, 1067–1070. https://doi.org/10.1111/ecog.05700.

Florkowski, C.M., 2008. Sensitivity, specificity, receiver-operating characteristic (ROC) curves and likelihood ratios: communicating the performance of diagnostic tests. Clin. Biochem. Rev. 29, S83–S87.

Foley, J.A., 2005. Global consequences of land use. Science 309, 570–574. https://doi.org/10.1126/science.1111772.

Fournier, R.A., Grenier, M., Lavoie, A., Hélie, R., 2007. Towards a strategy to implement the Canadian Wetland Inventory using satellite remote sensing. Can. J. Remote. Sens. 33, S1–S16. https://doi.org/10.5589/m07-051.

Gage, A.M., Olimb, S.K., Nelson, J., 2016. Plowprint: tracking cumulative cropland expansion to target grassland conservation. Great Plains Res. 26, 107–116. https://doi.org/10.1353/gpr.2016.0019.

Garibaldi, L.A., Oddi, F.J., Miguez, F.E., Bartomeus, I., Orr, M.C., Jobbágy, E.G., Kremen, C., Schulte, L.A., Hughes, A.C., Bagnato, C., Abramson, G., Bridgewater, P., Carella, D.G., Díaz, S., Dicks, L.V., Ellis, E.C., Goldenberg, M., Huaylla, C.A., Kuperman, M., Locke, H., Mehrabi, Z., Santibañez, F., Zhu, C., 2021. Working landscapes need at least 20% native habitat. Conserv. Lett. 14 https://doi.org/10.1111/conl.12773.

Government of Canada, 2013. Canadian Digital Elevation Model.

Government of Canada, 2021. Census of Agriculture. URL. https://www.statcan.gc.ca/en/census-agriculture. (Accessed 23 August 2023) (WWW Document).

Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T.G., Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H.P., Buckley, Y.M., 2013. Predicting species distributions for conservation decisions. Ecol. Lett. 16, 1424–1435. https://doi.org/10.1111/ele.12189.

Hanson, J.O., Schuster, R., Morrell, N., Strimas-Mackey, M., Watts, M., Arcese, P., Bennett, J., Possingham, H.P., 2019a. prioritizr: Systematic Conservation Prioritization in R (R Package Version 4.1. 4.3) (Computer software).

Hanson, J.O., Schuster, R., Strimas-Mackey, M., Bennett, J.R., 2019b. Optimality in prioritizing conservation projects. Methods Ecol. Evol. 10, 1655–1663. https://doi.org/10.1111/2041-210X.13264.

Hijmans, R.J., Phillips, S.J., Leathwick, J., Elith, J., 2022. dismo: Species Distribution Modeling.

Hoskins, A.J., Harwood, T.D., Ware, C., Williams, K.J., Perry, J.J., Ota, N., Croft, J.R., Yeates, D.K., Jetz, W., Golebiewski, M., Purvis, A., Robertson, T., Ferrier, S., 2020. BILBI: supporting global biodiversity assessment through high-resolution macroecological modelling. Environ. Model Softw. 132, 104806 https://doi.org/10.1016/j.envsoft.2020.104806.

Jari Oksanen, F., Blanchet, Guillaume, Friendly, Michael, Kindt, Roeland, Legendre, Pierre, McGlinn, Dan, Minchin, Peter R., O’Hara, R.B., Simpson, Gavin L., Solymos, Peter, Stevens, M. Henry H., Szoecs, Eduard, Wagner, Helene, 2020. vegan: Community Ecology Package.

Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D.E., Coscieme, L., Golden, A.S., Guerra, C.A., Jacob, U., Takahashi, Y., Settele, J., Díaz, S., Molnár, Z., Purvis, A., 2022. The direct drivers of recent global anthropogenic biodiversity loss. Sci. Adv. 8, eabm9982 https://doi.org/10.1126/sciadv.abm9982.

Jenkins, C.N., Pimm, S.L., Joppa, L.N., 2013. Global patterns of terrestrial vertebrate diversity and conservation. Proc. Natl. Acad. Sci. USA 110. https://doi.org/10.1073/pnas.1302251110.

Kahl, S., Wood, C.M., Eibl, M., Klinck, H., 2021. BirdNET: a deep learning solution for avian diversity monitoring. Eco. Inform. 61, 101236 https://doi.org/10.1016/j.ecoinf.2021.101236.

Knight, M.L., Overbeck, G.E., 2021. How much does is cost to restore a grassland? Restor. Ecol. 29, e13463 https://doi.org/10.1111/rec.13463.

Kraus, D., Hebb, A., 2020. Southern Canada's crisis ecoregions: identifying the most significant and threatened places for biodiversity conservation. Biodivers. Conserv. 29, 3573–3590. https://doi.org/10.1007/s10531-020-02038-x.

Lafuite, A.-S., Denise, G., Loreau, M., 2018. Sustainable land-use management under biodiversity lag effects. Ecol. Econ. 154, 272–281. https://doi.org/10.1016/j.ecolecon.2018.08.003.

Lambin, E.F., Turner, B.L., Geist, H.J., Agbola, S.B., Angelsen, A., Bruce, J.W., Coomes, O.T., Dirzo, R., Fischer, G., Folke, C., George, P.S., Homewood, K., Imbernon, J., Leemans, R., Li, X., Moran, E.F., Mortimore, M., Ramakrishnan, P.S., Richards, J.F., Skånes, H., Steffen, W., Stone, G.D., Svedin, U., Veldkamp, T.A., Vogel, C., Xu, J., 2001. The causes of land-use and land-cover change: moving beyond the myths. Glob. Environ. Chang. 11, 261–269. https://doi.org/10.1016/S0959-3780(01)00007-3.

Landis, D.A., 2017. Designing agricultural landscapes for biodiversity-based ecosystem services. Basic and Applied Ecology 18, 1–12. https://doi.org/10.1016/j.baae.2016.07.005.

Mahony, N.A., Dale, B.C., Miller, D.A.W., 2022. Grassland bird population declines at three Breeding Bird Survey spatial scales in contrast to a large native prairie. Ecosphere 13, e4309. https://doi.org/10.1002/ecs2.4309.

Mantyka-Pringle, C., Leston, L., Messmer, D., Asong, E., Bayne, E.M., Bortolotti, L.E., Sekulic, G., Wheater, H., Howerter, D.W., Clark, R.G., 2019. Antagonistic, synergistic and direct effects of land use and climate on prairie wetland ecosystems: ghosts of the past or present? Divers. Distrib. 25, 1924–1940.

McKercher, R.B., Bertram, W., 1986. Understanding Western Canada's Dominion Land Survey System. University of Saskatchewan, Division of Extension and Community Relations, Saskatoon, Canada.

Naidoo, R., Balmford, A., Ferraro, P., Polasky, S., Ricketts, T., Rouget, M., 2006. Integrating economic costs into conservation planning. Trends Ecol. Evol. 21, 681–687. https://doi.org/10.1016/j.tree.2006.10.003.

Newbold, T., Hudson, L.N., Hill, S.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520, 45–50.

Newbold, T., Hudson, L.N., Arnell, A.P., Contu, S., De Palma, A., Ferrier, S., Hill, S.L., Hoskins, A.J., Lysenko, I., Phillips, H.R., 2016. Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. Science 353, 288–291.

Olimb, S.K., Robinson, B., 2019. Grass to grain: probabilistic modeling of agricultural conversion in the North American Great Plains. Ecol. Indic. 102, 237–245. https://doi.org/10.1016/j.ecolind.2019.02.042.

Partners in Flight, 2021. Avian Conservation Assessment Database, version 2021. Available at. http://pif.birdconservancy.org/ACAD (Accessed on <date>).

Paterson, J.E., Bortolotti, L.E., Boychuk, L., 2023. A wetland permanence classification tool to support prairie wetland conservation and policy implementation. Conservation Science and Practice 5, e12954.

Pereira, H.M., Ferrier, S., Walters, M., Geller, G.N., Jongman, R.H.G., Scholes, R.J., Bruford, M.W., Brummitt, N., Butchart, S.H.M., Cardoso, A.C., Coops, N.C., Dulloo, E., Faith, D.P., Freyhof, J., Gregory, R.D., Heip, C., Höft, R., Hurtt, G., Jetz, W., Karp, D.S., McGeoch, M.A., Obura, D., Onoda, Y., Pettorelli, N., Reyers, B., Sayre, R., Scharlemann, J.P.W., Stuart, S.N., Turak, E., Walpole, M., Wegmann, M., 2013. Essential biodiversity variables. Science 339, 277–278. https://doi.org/10.1126/science.1229931.

Phalan, B., Hayes, G., Brooks, S., Marsh, D., Howard, P., Costelloe, B., Vira, B., Kowalska, A., Whitaker, S., 2018. Avoiding impacts on biodiversity through strengthening the first stage of the mitigation hierarchy. Oryx 52, 316–324. https://doi.org/10.1017/S0030605316001034.

Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31, 161–175. https://doi.org/10.1111/j.0906-7590.2008.5203.x.

Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., Blair, M.E., 2017. Opening the black box: an open-source release of Maxent. Ecography 40, 887–893. https://doi.org/10.1111/ecog.03049.

R Core Team, 2021. R: A Language and Environment for Statistical Computing.

Rashford, B.S., Adams, R.M., 2007. Improving the cost-effectiveness of ecosystem management: an application to waterfowl production. American J Agri Economics 89, 755–768. https://doi.org/10.1111/j.1467-8276.2007.00984.x.

Raven, P.H., Wagner, D.L., 2021. Agricultural intensification and climate change are rapidly decreasing insect biodiversity. Proc. Natl. Acad. Sci. 118, e2002548117.

Rissman, A.R., Lozier, L., Comendant, T., Kareiva, P., Kiesecker, J.M., Shaw, M.R., Merenlender, A.M., 2007. Conservation easements: biodiversity protection and private use. Conserv. Biol. 21, 709–718. https://doi.org/10.1111/j.1523-1739.2007.00660.x.

Rosenberg, K.V., Dokter, A.M., Blancher, P.J., Sauer, J.R., Smith, A.C., Smith, P.A., Stanton, J.C., Panjabi, A., Helft, L., Parr, M., Marra, P.P., 2019. Decline of the North American avifauna. Science 366, 120–124. https://doi.org/10.1126/science.aaw1313.

Sarkar, S., Pressey, R.L., Faith, D.P., Margules, C.R., Fuller, T., Stoms, D.M., Moffett, A., Wilson, K.A., Williams, K.J., Williams, P.H., Andelman, S., 2006. Biodiversity conservation planning tools: present status and challenges for the future. Annu. Rev. Environ. Resour. 31, 123–159. https://doi.org/10.1146/annurev.energy.31.042606.085844.

Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J.C., Linsenmair, K.E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E.-D., Vogt, J., Wöllauer, S., Weisser, W.W., 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature 574, 671–674. https://doi.org/10.1038/s41586-019-1684-3.

Shutler, D., Mullie, A., Clark, R.G., 2000. Bird communities of prairie uplands and wetlands in relation to farming practices in Saskatchewan. Conserv. Biol. 14, 1441–1451. https://doi.org/10.1046/j.1523-1739.2000.98246.x.

Silvestro, D., Goria, S., Sterner, T., Antonelli, A., 2022. Improving biodiversity protection through artificial intelligence. Nat Sustain 5, 415–424. https://doi.org/10.1038/s41893-022-00851-6.

Sirami, C., Gross, N., Baillod, A.B., Bertrand, C., Carrié, R., Hass, A., Henckel, L., Miguet, P., Vuillot, C., Alignier, A., Girard, J., Batáry, P., Clough, Y., Violle, C., Giralt, D., Bota, G., Badenhausser, I., Lefebvre, G., Gauffre, B., Vialatte, A., Calatayud, F., Gil-Tena, A., Tischendorf, L., Mitchell, S., Lindsay, K., Georges, R., Hilaire, S., Recasens, J., Solé-Senan, X.O., Robleño, I., Bosch, J., Barrientos, J.A., Ricarte, A., Marcos-Garcia, M.Á., Miñano, J., Mathevet, R., Gibon, A., Baudry, J., Balent, G., Poulin, B., Burel, F., Tscharntke, T., Bretagnolle, V., Siriwardena, G., Ouin, A., Brotons, L., Martin, J.-L., Fahrig, L., 2019. Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. Proc. Natl. Acad. Sci. 116, 16442–16447. https://doi.org/10.1073/pnas.1906419116.

Soil Landscapes of Canada Working Group, 2010. Soil Landscapes of Canada Version 3.2. Agriculture and Agri-Food Canada (digital map and database at 1:1 million scale).

Valavi, R., Elith, J., Lahoz-Monfort, J.J., Guillera-Arroita, G., 2018. blockCV: An R Package for Generating Spatially or Environmentally Separated Folds for k-Fold Cross-Validation of Species Distribution Models. https://doi.org/10.1101/357798.

Vargas Soto, J.S., Beirne, C., Whitworth, A., Cruz Diaz, J.C., Flatt, E., Pillco-Huarcaya, R., Olson, E.R., Azofeifa, A., Saborío-R, G., Salom-Pérez, R., Espinoza-Muñoz, D., Hay, L., Whittaker, L., Roldán, C., Bedoya-Arrieta, R., Broadbent, E.N., Molnár, P.K., 2022. Human disturbance and shifts in vertebrate community composition in a biodiversity hotspot. Conserv. Biol. 36, e13813 https://doi.org/10.1111/cobi.13813.

Wagner, D.L., Grames, E.M., Forister, M.L., Berenbaum, M.R., Stopak, D., 2021. Insect decline in the Anthropocene: death by a thousand cuts. Proc. Natl. Acad. Sci. 118, e2023989118.

Watmough, M.D., Li, Z., Beck, E.M., 2017. Prairie Habitat Monitoring Program: Canadian Prairie Wetland and Upland Status and Trends 2001–2011. Canadian Wildlife Service, Edmonton, Alberta, Canada. URL. https://www.phjv.ca/wp-content/uploads/2020/11/ECCC_PHJV_HabitatMonitoringReport_LowRes.pdf (WWW Document).

Watts, M.E., Ball, I.R., Stewart, R.S., Klein, C.J., Wilson, K., Steinback, C., Lourival, R., Kircher, L., Possingham, H.P., 2009. Marxan with Zones: software for optimal conservation based land- and sea-use zoning. Environmental Modelling & Software, Special issue on simulation and modelling in the Asia-Pacific region 24, 1513–1521. https://doi.org/10.1016/j.envsoft.2009.06.005.

Wood, S.N., 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. J. Am. Stat. Assoc. 99, 673–686. https://doi.org/10.1198/016214504000000980.

Wood, S., 2023. mgcv: Mixed GAM Computation Vehicle With Automatic Smoothness Estimation.

Ziolkowski Jr., D., Lutmerding, M., Aponte, V., Hudson, M.-A., 2022. 2022 Release - North American Breeding Bird Survey Dataset (1966–2021). https://doi.org/10.5066/P97WAZE5.

Zurell, D., Franklin, J., König, C., Bouchet, P.J., Dormann, C.F., Elith, J., Fandos, G., Feng, X., Guillera-Arroita, G., Guisan, A., Lahoz-Monfort, J.J., Leitão, P.J., Park, D.S., Peterson, A.T., Rapacciuolo, G., Schmatz, D.R., Schröder, B., Serra-Diaz, J.M., Thuiller, W., Yates, K.L., Zimmermann, N.E., Merow, C., 2020. A standard protocol for reporting species distribution models. Ecography 43, 1261–1277. https://doi.org/10.1111/ecog.04960.