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RESEARCH ARTICLE

A life-history spectrum of population responses to simultaneous change in climate and land use

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Abstract

1. Climate and land use change are two of the primary threats to global biodiversity; however, each species within a community may respond differently to these facets of global change. Although it is typically assumed that species use the habitat that is advantageous for survival and reproduction, anthropogenic changes to the environment can create ecological traps, making it critical to assess both habitat selection (e.g. where species congregate on the landscape) and the influence of selected habitats on the demographic processes that govern population dynamics.
2. We used a long-term (1958–2011), large-scale, multi-species dataset for waterfowl that spans the United States and Canada to estimate species-specific responses to climate and land use variables in a landscape that has undergone significant environmental change across space and time. We first estimated the effects of change in climate and land use variables on habitat selection and population dynamics for nine species. We then hypothesized that species-specific responses to environmental change would scale with life-history traits, specifically: longevity, nesting phenology and female breeding site fidelity.
3. We observed species-level heterogeneity in the demographic and habitat selection responses to climate and land use change, which would complicate community-level habitat management. Our work highlights the importance of multi-species monitoring and community-level analysis, even among closely related species.
4. We detected several relationships between life-history traits, particularly nesting phenology, and species' responses to environmental change. One species, the early-nesting northern pintail (*Anas acuta*), was consistently at the extreme end of responses to land use and climate predictors and has been a species of conservation concern since their population began to decline in the 1980s. They, and the blue-winged teal, also demonstrated a positive habitat selection response to the proportion of cropland on the landscape that simultaneously reduced abundance the following year, indicative of susceptibility to ecological traps.

5. By distilling the diversity of species' responses to environmental change within a community, our methodological approach and findings will help improve predictions of community responses to global change and can inform multi-species management and conservation plans in dynamic landscapes that are based on simple tenets of life-history theory.

KEYWORDS
Bayesian hierarchical model, climate change, community ecology, demography, ecological trap, habitat selection, Prairie Pothole Region, waterfowl

1 | INTRODUCTION

Climate and land use change are two of the primary threats to global biodiversity (He et al., 2019; Newbold, 2018; Titeux et al., 2016, 2017). Understanding how species within a community are likely to respond to simultaneous changes in climate and land use is critical for developing anticipatory habitat protection and management plans (Cloern & Jassby, 2010). Studies examining how species within communities are affected by simultaneous changes in climate and land use have observed a variety of responses related to a changing environment. The findings of these studies have been equally diverse, ranging from synchronous responses to environmental variables among species in a community (Cloern & Jassby, 2010), asynchronous responses (Defriez et al., 2016; Northrup et al., 2019; Sirois-Delisle & Kerr, 2018) and both idiosyncratic Moritz et al. (2008) and consistent (Willis et al., 2008) responses among closely related species. However, there is growing evidence that species-level variation in response to climate and land use change may be related to life-history characteristics (Chevalier et al., 2014; Northrup et al., 2019; Pacifici et al., 2017; Perry et al., 2005), and these results suggest that some characteristics correspond to a greater ability to adapt to changing environmental conditions. Apart from situations of drastic anthropogenic change, this should not be surprising given that life-history traits have presumably evolved in response to historical environmental variability and species interactions (Stearns, 1992).

In the absence of information connecting environmental variables to specific demographic parameters across space and time, scientists often make inference on populations using the number of individuals present at a given location. However, 'where' individuals are on the landscape and 'how many there are' depend on a number of ecological processes that interact at various scales. For example, the relationship between ecological processes and landscape attributes can vary depending on the scale at which they are analysed (Levin, 1992). Mismatches between abundance or habitat selection and demographic parameters have also been observed in a number of systems (e.g. Bean et al., 2014; Best, 1986; Clark & Shutler, 1999; Gilroy et al., 2011; Mosser et al., 2009; Northrup et al., 2012). Focusing on one aspect of an ecological process to indicate optimal environmental conditions may present an incomplete picture of how species are affected by changes in climate and land use (Stephens et al., 2015; Van Horne, 1983). In particular, ecological traps can result from rapid environmental change when the environmental cue that an animal uses to select habitat stops being an indicator of habitat quality for demographic performance, resulting in individuals occupying unsuitable landscapes (Hale & Swearer, 2016; Martin & Forsyth, 2003). The susceptibility of a species to becoming trapped by the habitat cues they have evolved to respond to, and our ability to predict when ecological traps could develop, may be related to known behavioural and life-history characteristics of a species (Robertson & Chalfoun, 2016). Recognition of the existence of an ecological trap, and the underlying mechanism, could help guide multi-species management actions to remedy the resulting population declines (Schlaepfer et al., 2002).

Due to the unique composition of its landscape, the Prairie Pothole Region (PPR), which spans the northern Great Plains of Canada and the United States and contains a high density of shallow wetlands, is the most important breeding area for many duck species in North America (Doherty et al., 2018). The United States Fish and Wildlife Service (USFWS) and the Canadian Wildlife Service have monitored spring population abundances for North American waterfowl using the Waterfowl Breeding Population and Habitat Survey (WBPHS) since 1955 (Smith, 1995), producing one of the largest datasets on vertebrate populations in the world. While mallards (*Anas platyrhynchos*), American wigeon (*Mareca americana*) and canvasback (*Aythya valisineria*) abundances have hovered around the North American Waterfowl Management Plan population goals, with year-to-year variation generally proportional to abundance, other species, such as gadwall (*Mareca strepera*), blue- and green-winged teal (*Spatula discors* and *Anas carolinensis* respectively), northern shovelers (*Spatula clypeata*) and redheads (*Aythya americana*) have trended upward since 1955 (U.S. Fish and Wildlife Service, 2019). In contrast, northern pintail and scaup abundances did not recover following drought conditions in the 1980s and appear to have become decoupled from surveyed wetland abundance (i.e. they no longer track trends in wetland abundance Miller & Duncan, 1999; Podruzny et al., 2002; Ross et al., 2015; U.S. Fish and Wildlife Service, 2019). Moreover, previous evaluations of spatial variation in weather patterns, such as recently documented drier conditions in the western PPR and wetter conditions in the eastern PPR, have resulted in spatially asynchronous changes to wetland dynamics (fewer wetlands in the west, more in the east; Johnson et al., 2005; Millett et al., 2009). These altered dynamics have implications for shifting distributions and abundances of waterfowl within the PPR (Buderman et al., 2020; Podruzny et al., 2002).

Compounding climate change, a large proportion of wetlands have been drained or altered from their historical attributes (e.g. depth, vegetative characteristics; Dahl, 2014; Watmough et al., 2017). In certain areas of the PPR, drainage has focused on smaller wetlands, which often consolidates surface water into larger and deeper wetlands (Anteau, 2012; Watmough et al., 2017) that dry out less frequently, are less productive, and have more surface-water connections to other wetlands (McCauley et al., 2015). Coinciding with wetland drainage, the amount of land in the PPR that is seeded annually in the spring has increased by approximately 34% since 1959, with an increase of 6%–63% across PPR sub-regions (Agricultural Statistics Service, 2014; Statistics Canada, 2012). Technological advancements in irrigation and weed control practices, as well as concerns about soil erosion, have also resulted in a decline in summerfallow and a shift towards continuous cropping, in which most fields are seeded every spring (Carlyle, 1997). In addition, there has been a move towards conservation tillage, in which there is no, or minimal, tillage in the fall and spring seeding is performed in fields with standing stubble (i.e. seeds are drilled into soil Best, 1986). Earlier mechanical spring tilling and planting can also destroy a large percentage of initial waterfowl nests, and may have a stronger effect on species that nest earlier in the spring, have a low preponderance for renesting and prefer to nest in standing stubble (Cowan, 1982; Duncan & Devries, 2018; Miller & Duncan, 1999; Richkus, 2002), likely affecting reproductive success (Duncan & Devries, 2018). These landscape-level changes, which are occurring at a much faster rate than they have over evolutionary timescales, have the potential to induce ecological traps if species are unable to detect the change in habitat quality (Hale & Swearer, 2016; Robertson & Chalfoun, 2016).

Buderman et al. (2020) previously detected evidence for the development of an ecological trap in the PPR for northern pintail, an early-nesting species that has a low renesting probability and prefers to nest in standing stubble. Northern pintail often settled in areas with a high proportion of cropland for breeding, but the same landscape attribute reduced demographic performance (Buderman et al., 2020). The proposed mechanism for this trap is an apparent preference for cropland over other nesting habitats and early nesting that leaves nests susceptible to destruction from agricultural practices (Duncan & Devries, 2018). However, it is unknown how the entire community of waterfowl species is dealing with the same mismatch between habitat appearance and quality, or if ecologically similar species share similar responses. The waterfowl community of the PPR has shared a common environment, with the exception of micro-niche differences (Nudds, 1983; Nudds et al., 2000), and have therefore been exposed to the same simultaneous changes in climate and land use. In turn, the management and conservation of habitat in the PPR has the potential to affect multiple species simultaneously, but perhaps to differing magnitudes and even in opposing directions. The long-term WBPHS dataset provides a unique opportunity to compare species-level responses to environmental change without the confounding factors that can limit inference in macro-scale comparisons of species and populations that do not share common ranges. The novel method developed by Buderman et al. (2020) can moreover separate the cumulative processes that contribute to annual demographic changes in abundance from the habitat selection processes, allowing us to address hypotheses about relationships between both mechanisms and species life-history traits.

By fitting this model to the WBPHS data, we first quantified species-specific demographic and habitat selection responses to spatio-temporal changes in climate and land use variables. We then evaluated relationships among species-specific responses to environmental change and life-history traits. Although our detailed predictions are multifaceted and described in the subsequent section, our overarching hypothesis is that the response of any species to changes in climate and land use is, in part, determined by their position along the evolved slow–fast continuum of life histories within the Anatidae family (Koons et al., 2014). Generally, we would expect that species with similar life-history traits would be responding similarly to changes in habitat (Öckinger et al., 2010). More specifically, the demographic buffering hypothesis predicts that species should buffer the vital rates having the greatest impact on fitness against environmental change (Boyce et al., 2006; Gaillard & Yoccoz, 2003; Pfister, 1998). Empirical studies of age- and stage-structured populations have found that stochastic population growth rates for species with the greatest longevity are least responsive to environmental variability, or in other words they exhibit the strongest overall demographic buffering when evaluated across all vital rates (Compagnoni et al., 2021; Morris et al., 2008). Based on these comparative findings and substantial empirical support for the demographic buffering hypothesis in birds and mammals in general (Hilde et al., 2020), we predicted that longer-lived waterfowl with slow life histories would have the weakest demographic responses to changes in climate and land use variables. Our findings contribute to our understanding of how species cope with multiple dimensions of global change across a gradient of life-history strategies. In turn, these findings can be used by managers to identify areas on a landscape where multiple species are suffering simultaneously, thriving, or yet other areas where a few species are performing differently than the rest.

1.1 | Predicted relationships between life-history traits and responses to climate and land use

Anatidae are generally categorized as either diving (e.g. canvasback, redhead and ruddy duck [*Oxyura jamaicensis*]) or dabbling ducks (e.g. American wigeon, blue-winged teal, gadwall, mallard, northern pintail and northern shoveler) and we expect that responses to climate and land use will tend to systematically vary between the two groups due to their unique habitat requirements. Responses to climate and land use can also vary according to other, finer-scale, differences in life-history strategies across species. Therefore, we used three life-history traits that demonstrated considerable variation, and for which there was available information, across the prairie nesting duck species in question: longevity ($-1/\log(\text{annual survival})$; Caughley, 1977), mean nesting date relative to earliest nesting date (to capture interspecific differences in nesting phenology and exposure to early spring conditions and agricultural processes), and adult female breeding site fidelity (return rate, which should be inversely related to nomadism in habitat selection; Table 2).

1.2 | Habitat selection

Given that survival of offspring and adults can depend on nest-site selection, we assumed that habitat selection is an outcome of evolutionary processes (as reviewed in Clark & Shutler, 1999). In an environment that undergoes significant variation within the arrival period of migrants, we would expect that the habitat which maximizes fitness would be related to nesting phenology (Stearns, 1992; Verhulst & Nilsson, 2008), and therefore predicted strength of habitat selection to vary most strongly with a species' mean nesting date. Because the earliest upland nesters are likely arriving to the PPR prior to spring tillage, when crop stubble on the landscape is reminiscent of grassland prairie (Beauchamp et al., 1996; McLachlan et al., 2007; Richkus, 2002), we expected the earliest nesting species to apparently select areas with large amounts of cropland compared to later nesting species that can potentially use cues to avoid such habitat. We also expected later nesting species, compared to early nesting, to select areas within the PPR with a longer duration of snow cover, because areas with longer durations of snow cover would have fewer accessible wetlands when early-nesting species arrive in spring (although no relationship might also be reasonable since migration can coincide with the chronology of snow melt). Because we expect individuals to maximize fitness based on the availability of preferred habitat (Fretwell, 1969), the realized distribution of individuals should depend on their evolved ability to spatially track interannual changes in such habitat (Piper, 2011). As such, we expected species with generally low breeding site fidelity to be more capable of basing habitat selection decisions on current conditions as opposed to where they nested the prior year (Coulson, 2016). For example, we would expect that species with low breeding site fidelity would be more likely to select areas with more ponds (or other landscape variables) relative to other years and relative to other spatial areas. We did not expect relationships between longevity and habitat selection, because fitness benefits arising from habitat selection would be a function of conditions following breeding site selection.

1.3 | Demography

We expected species with the earliest nesting dates to suffer the most demographically from substantial amounts of cropland in their surrounding landscape, because mechanical tillage and planting, which occurs after the earliest ground-nesting waterfowl species have started nesting, can destroy nests. In addition, predators can easily find nests (and attendant females) in residual stubble from the prior year (Best, 1986; Duncan & Devries, 2018; Greenwood et al., 1995; Lokemoen & Beiser, 1997). Late-nesting species should experience relatively small demographic responses because they generally initiate nests after tillage and planting of croplands, and could even benefit by nesting in the cover eventually provided by the growth of annual crops as summer progresses (Skone et al., 2016). Conversely, when summerfallow replaces active cropland on the PPR landscape we might expect early-nesting species to demographically benefit most strongly from substantial amounts of this protective nesting cover, with later nesting species benefiting less strongly. Due to their early timing of arrival to the PPR in the spring, and energetic requirements to quickly acquire invertebrate foods for income allocation of protein and calcium into the production of eggs (Alisauskas & Davison, 1992; Krapu & Reinecke, 1992), we expected the demography of early-nesting species to be most sensitive to (and strongly affected by) spring temperature and precipitation (Messmer et al., 2021). Later nesting species have more time to acquire resources necessary for clutch production and their demography might be more weakly affected by spring climatic conditions (Messmer et al., 2021). We did not expect strong relationships between female site fidelity and the effects of land use and climate because the fitness benefits of site fidelity depend on the predictability of the environment (Andersson, 1980); however, the predictability of our system has likely changed over the duration of the study due to anthropogenic influences. Finally, empirical studies have found that species with the greatest longevity, and relatively low reproductive investment, are least responsive to environmental variability and exhibit the strongest overall demographic buffering when evaluated across all vital rates (Compagnoni et al., 2021; Morris et al., 2008). Based on these findings, we predicted that longer-lived species with slow life histories would have the weakest responses to changes in climate and land use variables. Finally, according to the theory of ecological traps, the temporal mismatch between cues used for habitat selection and subsequent demographic outcomes, such as survival and reproduction, could lead to strong negative demographic responses to environmental cues that have a strong positive influence on habitat selection, which is contrary to what we would expect for a species attempting to maximize its fitness (Delibes et al., 2001; Kristan, 2003).

2 | METHODS

2.1 | Data collection

The traditional survey area of the WBPHS covers central Canada, the north-central United States, and Alaska, and is delineated into strata reflective of habitat differences and political boundaries. Waterfowl are counted in May and June by two-person aerial crews flying fixed-wing aircraft along established transect lines, which are 400 m wide and divided into segments that are approximately 29 km in length, at low altitude (Figure 1). The WBPHS counts pairs (i.e. one pair equals two ducks) and lone drakes and the sum of these is considered here as a measure of total indicated pairs; lone drakes are

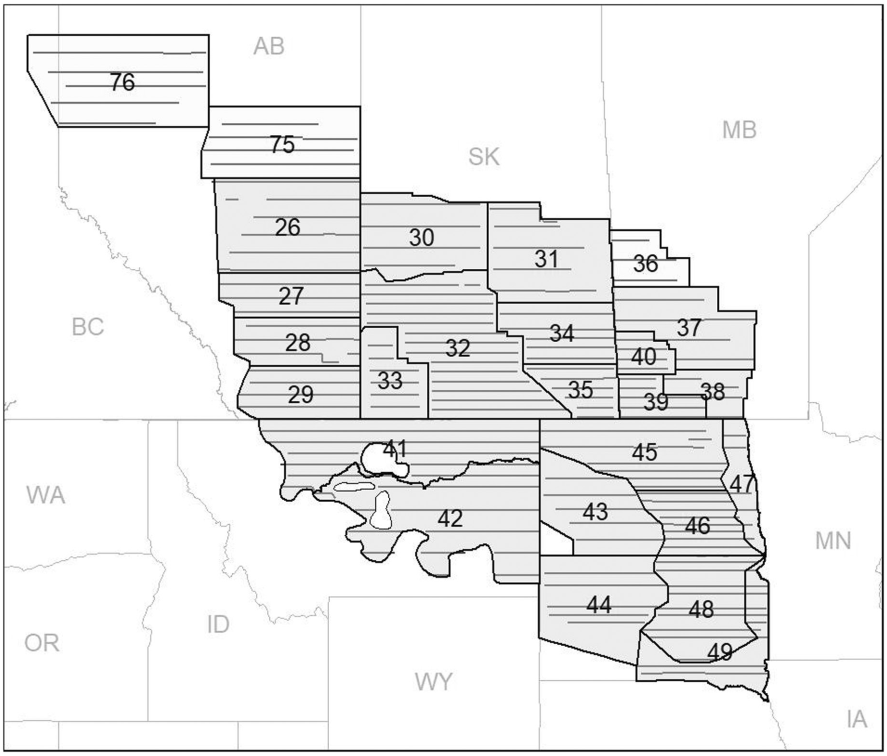

FIGURE 1 Map of the Waterfowl Breeding Population and Habitat Survey strata in the Prairie Pothole Region, which spans Canada (strata 26–40 and 75–76) and the United States. Strata 36, 75 and 76 were removed from this analysis due to missing covariate information. The numbers within each stratum represent the stratum number. Within each stratum are transects consisting of variable numbers of 29-km segments which are surveyed via fixed-wing aircraft.

counted because they are assumed to be paired with an unobserved female (U.S. Fish and Wildlife Service, 2015). Mixed-sex flocks are excluded because these represent individuals that may still be migrating. For the segment-level count, we doubled the numbers of observed pairs and single drakes for each species, which simply scales the total indicated pairs up to the number of individuals. The number of seasonal and permanent wetlands, both artificial and natural, expected to persist for at least 3 weeks beyond the survey date are also counted simultaneously (hereafter referred to as ponds). We used data from 1958 to 2011 and analysed nine species that have traditionally used the PPR as their breeding grounds: American wigeon (AMWI), blue-winged teal (BWTE), canvasback (CANV), gadwall (GADW), mallard (MALL), northern pintail (NOPI), northern shoveler (NSHO), redhead (REDH) and ruddy duck (RUDU). Cinnamon teal (*Anas cyanoptera*, CITE) are conflated with blue-winged teal in the aerial survey; however blue-winged teal outnumber cinnamon teal across the PPR as cinnamon teal are restricted to the western portion. We focused our analysis on the strata that fall within the PPR (26–49, 75 and 76), but removed 36, 75 and 76 due to unavailable covariate data. No ethical approval was needed for this study.

2.2 | Habitat selection and demographic responses to climate and land use change

We used the hierarchical model developed by Buderman et al. (2020) to model annual observed counts as a function of two ecological processes, habitat selection and demography (e.g. the balance of survival and reproduction), which can both vary as a function of environmental variables. This model allows us to simultaneously estimate the effect of a variable on habitat selection and demography and produces two abundances: one is the stratum-level model which describes the expected number of individuals in a stratum based on habitat conditions in year $t-1$ (demographic processes) and one is the segment-level model that describes the realized number of individuals that settled in segments within a stratum based on habitat conditions in year t (habitat selection). We summarize the model below, and full details can be found in Buderman et al. (2020).

The observed counts of the number of individuals for a given species on a segment in a year arise from a zero-inflated negative binomial model with a segment-level intensity parameter. Zero-inflated models account for excess zeros in the observations, which can arise through the sampling process or the ecological process. Sampling zeros represent when individuals are present and unobserved or present but temporarily absent during the survey; actual zeros represent survey units that individuals do not occupy. The additional parameter in the negative binomial model, compared to the Poisson, models over-dispersion. The segment-level intensity parameter represents the realized number of individuals in a segment. The realized number of individuals in a segment, using the log-link, is a function of the average number of individuals that are available to settle in a given segment (the stratum-level intensity parameter divided by the number of segments in a stratum), and spatially referenced segment-level habitat covariates that we hypothesized would be related to an individual's decision to settle in a particular segment. In other words, the segment-level model scales the stratum-level model down to the scale of observation and then allows for adjustments based on nonrandom settling dynamics due to habitat selection. Positive effect sizes represent more individuals on the segment compared to what would be expected given an even distribution across landscape, whereas a negative effect size represents fewer individuals compared to the expected number. We are therefore using the log intensity of individuals at a segment as an indicator of habitat selection (Jędrzejewski et al., 2008; Sawyer et al., 2006).

The stratum-level model is based on an inhomogeneous Poisson process and describes how many individuals, on the log scale, one would expect in a stratum given the number that were there in year $t-1$ and the effects of conditions that may contribute to demographic changes in abundance (e.g. reproduction and survival [which were not directly observed in this study], and how they collectively affect population growth rate) between annual survey periods. We based the stratum-level model on a Gompertz model, which incorporates an intrinsic growth rate and density dependence as a function of the realized population size the previous year (the sum of the segment-level counts) with covariates that can contribute to changes in abundance between years. The Gompertz model has been used in many studies of population growth, including waterfowl (e.g. Sæther et al., 2008), to account for density dependence; it also has the property of being linear on the log scale, which facilitates fitting the model in a generalized linear modelling framework (Eberhardt et al., 2008; Tjørve & Tjørve, 2017). Due to identifiability issues with the Gompertz model (and other state-space models with density dependence), we used an informative prior on the intrinsic growth rate for each species (Dennis et al., 2006; Lebreton & Gimenez, 2013). We also note that models imposing strong constraints on the demographic process can result in counter-intuitive inference when a small number of uninformative predictor variables are used.

By summing the segment-level intensities on the real scale we can describe a realized intensity of individuals in a stratum, whereas the latent stratum-level intensities on the real scale describe the expected intensity of individuals based on demographic processes. Predictors for the segment-level habitat selection process included the proportion cropland and summerfallow for the county in which the segment was located (Agricultural Statistics Service, 2014; Statistics Canada, 2012), number of ponds relative to other segments available for selection in a given stratum and year (referred to as the spatial effect of ponds on habitat selection) and relative to that segment across years (referred to as the temporal effect of ponds on habitat selection), and the duration of snow cover (Kalnay et al., 1996). Predictors for the stratum-level demographic process included the average proportion cropland and summerfallow across segments in a stratum (Agricultural Statistics Service, 2014; Statistics Canada, 2012), counts of ponds, average temperature (Fan & Van den Dool, 2008) and precipitation for May–June (Chen et al., 2002), and the multivariate ENSO index (MEI, where positive values indicate El Niño, or warm phase, and negative indicate La Niña, or cool phase Wolter & Timlin, 1998, 2011). The latter was consistent for all strata within a year. Stratum-level predictors were based on conditions the year prior to the abundance being modelled. We also included a version of the latitude bias correction, which is provided by the USFWS and accounts for drought years in which individuals may overfly the PPR and settle in the boreal forest (U.S. Fish and Wildlife Service, 2018). These predictors were selected based on previously observed relationships among variables and waterfowl habitat use and reproduction across the PPR region (e.g. Buderman et al., 2020; Devries et al., 2018; Drever et al., 2012; Podruzny et al., 2002; Raquel et al., 2016). In addition, we chose predictors that were consistently collected for the duration of the study (1958–2011) across both the United States and Canada. See Supporting Information S1 for additional details on the source and calculation for each variable.

When fitting a model to multiple species, one would ideally model the species jointly, which would provide species-level deviations from an overall among-species mean. However, fitting the model to species jointly was computationally infeasible for our analysis. To approximate the among-species mean that would have been obtained from a joint model, we fit an intercept-only Bayesian hierarchical model to the species-level responses to climate and land use change. This is the same type of model used in the analysis of life-history patterns, in which species were represented by samples drawn from the posterior distribution of the effect size of a given variable (see Life-History Patterns in Responses to Climate and Land Use Change). The model accounted for these repeated measures, as well as phylogenetic relationships. However, given there are no additional explanatory variables, the estimate of the intercept would be interpreted as the among-species response to a climate or land use variable (i.e. the inference that would have been obtained in a joint model as a measure of overall response).

Species-specific models were fit using the R package Nimble (NIMBLE Development Team, 2018) and convergence was assessed using the Gelman–Rubin statistic (<1.2, as well as visual inspection of the MCMC chains). Inference was made using three chains of 200,000 iterations, including 20,000 iterations discarded for burn-in, each thinned to 6000 samples for a total of 18,000 samples used for inference on each species (the exception was canvasback which required 300,000 iterations, with 30,000 discarded for burn-in, each thinned to 6000 samples). See Table 1 for a summary of all environmental variables and the scale at which they were incorporated. We made inference using the proportion of the posterior distribution of the effect size that was greater or less than zero (the probability of direction Makowski et al., 2019). In a Bayesian framework, this is interpreted as the probability that the effect is greater (or less) than zero (Hobbs & Hooten, 2015).

2.3 | Life-history patterns in responses to climate and land use change

We described life-history strategies using three variables: longevity ($-1/\log(\text{annual survival})$), mean nesting date relative to earliest nesting date (to capture interspecific differences in nesting phenology and exposure to early spring conditions and agricultural processes), and adult female breeding site fidelity (return rate,

TABLE 1 Predictor variables used to model each response variable in year t; habitat selection variables were summarized at the segment level and demographic variables were summarized at the stratum level. The visibility correction factor was also used as a predictor variable for segment-level counts. SPEI is the Standardized Precipitation-Evapotranspiration Index, an indicator of drought.

Response (year t)	Climatic	Hydrologic	Land use
Habitat selection (segment counts)	November–April snow duration t	Pond count (spatial) t Pond count (temporal) t	% Crop acreage t % Summerfallow acreage t
Demography (stratum abundance)	ENSO intensity $t - 1$ May–June temp. $t - 1$ May–June precip. $t - 1$	Adjusted latitude bias correction pond count $t - 1$	% Crop acreage $t - 1$ % Summerfallow acreage $t - 1$

TABLE 2 Predictors used to determine effects of life-history attributes on correlations between habitat selection and demography and landscape and climate variables. Values for life-history traits were obtained from and/or summarized from Batt (1992), Arnold and Clark (1996), Anderson et al. (1997), Arnold et al. (2002), Baldassarre (2014) and Bartzen and Dufour (2017). Strong priors were used for the intrinsic growth rates and were based on values reported by Murray et al. (2010).

Species	Intrinsic growth rate	Female survival[a]	Nesting date	Site fidelity
American wigeon	0.494	0.635	18	44.40
Blue-winged teal	0.413	0.488	14	6.07
Gadwall	0.1925	0.568	19	40.08
Mallard	0.240	0.563	4	40.74
Northern shoveler	0.42	0.514	9	28.10
Northern pintail	0.435	0.64	0	32.80
Canvasback	0.657	0.666	9	74.50
Redhead	0.3	0.640	8	45.63
Ruddy duck	0.405[a]	0.694[b]	31	1[c]

[a] Given data deficiencies, intrinsic growth rate for ruddy duck was based on the average of other species.

[b] Given data deficiencies, female survival for ruddy duck was based on the average of the other two diving duck species.

[c] According to Batt (1992), sample sizes were too small to calculate return rate although some birds did return; we approximated this by using a return rate of 1%.

which should be inversely related to nomadism in habitat selection; Table 2). We obtained values for the life-history traits from Batt (1992) and Baldassarre (2014); where appropriate we averaged values across studies. All life-history variables were standardized to have a mean of zero and standard deviation of one. We note that a strong assumption of our measured life-history traits is that the studies in the literature are good representations of the mean life-history characteristic across space and time of the PPR for our study species.

We used a multiple imputation approach to determine the relationship between life-history traits and species-specific responses to land use and climatic variables. We selected 100 random samples from the posterior distribution of each climatic and land use effect size for each species (i.e. from the analyses described above), and used each set of sub-samples for an effect size as the response variable in a Bayesian mixed-effects model with life-history traits as predictors. The random effect for species allowed us to account for unexplained variation in the multiple samples drawn from each posterior distribution. In addition, given that phylogenetic relatedness among species is a form of nonindependence and may account for similarities between species, we incorporated relatedness through an additional random effect for species with a specified covariance matrix (Villemereuil & Nakagawa, 2014). The covariance matrix was calculated by obtaining a phylogenetic tree for Anatinae from BirdTree (http://www.birdtree.org; Jetz et al., 2012, 2014) and calculating the variance–covariance matrix for the nine species of interest. Phylogenetic analyses to obtain the covariance matrix were performed using the R packages ape (Paradis & Schliep, 2019) and caper (Orme et al., 2018). We fit the hierarchical life-history comparison model using the R package brms (Bürkner, 2017), which is a wrapper for the Stan programming language (Stan Development Team, 2022). We made inference about the importance of the life-history traits in predicting the relationships described above, while accounting for phylogenetic relatedness, using the proportion of the posterior distribution of the life-history effect that was greater or less than zero (Makowski et al., 2019). Figure 2 provides a schematic diagram demonstrating the connection between the models for habitat selection, demography and life-history traits across species.

2.4 | Community-level patterns in susceptibility to ecological traps

Lastly, we calculated stratum-level realized abundance by summing the segment-level intensities across a stratum; this represents the latent number of individuals that ultimately settled on segments within the stratum. The stratum-level expected abundance represents the number of individuals that would have been expected in a stratum given demographic processes alone. We used the expected and realized annual abundances to calculate expected and realized geometric mean growth rates (the geometric mean of annual growth rates; hereafter referred to as expected growth rate and realized growth rate) for each stratum over the time series. A realized growth rate that is larger than the expected growth rate would indicate that more individuals on average are settling in the stratum each year than would be predicted by demographic performance, and indicate

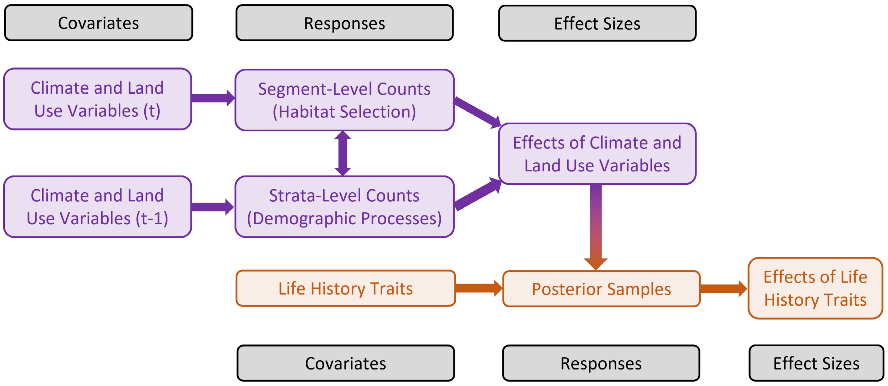

FIGURE 2 A schematic diagram demonstrating the analytical process for connecting the models for habitat selection and demography to the models for the life-history trait analysis.

TABLE 3 We calculated the proportion of the posterior distribution that was greater or less than zero for the climate and land use effect sizes. Variables used for habitat selection are denoted with an H and demography with a D. Similar variables across the two scales have been grouped together to facilitate comparison. The numbers describe the probability of direction, or the proportion of the posterior on the same side of zero as the median; positive values indicate that the median was positive and negative values indicate the median was negative.

	Species								
Variable	**AMWI**	**BWTE**	**GADW**	**MALL**	**NOPI**	**NSHO**	**CANV**	**REDH**	**RUDU**
H: Prop. Cropland	**−0.95**	**+0.90**	−0.73	**+0.98**	**+0.96**	**+0.88**	**+0.95**	**+0.98**	**+0.85**
D. Prop. Cropland	**−0.85**	**−1.00**	**−0.94**	**−0.80**	**−0.99**	−0.74	**−0.85**	+0.59	**+0.92**
H: Prop. Fallow	**+0.97**	+0.79	**+0.93**	+0.71	**+0.99**	**+0.96**	+0.58	−0.62	**−0.92**
D: Prop. Fallow	**+0.90**	**−1.00**	**−1.00**	+0.67	**+1.00**	**−1.00**	**−0.98**	**−1.00**	**−1.00**
H: Ponds (Temporal)	**+1.00**	**+1.00**	**+1.00**	**+1.00**	**+1.00**	**+1.00**	**+1.00**	**+0.99**	**+1.00**
H: Ponds (Spatial)	**+1.00**	**+1.00**	**+1.00**	**+1.00**	**+1.00**	**+1.00**	**+1.00**	**+1.00**	**+1.00**
D: Ponds	+0.69	**+0.97**	+0.66	−0.78	**−0.88**	+0.77	**+0.96**	**+1.00**	−0.78
H: Snow Cover	**−0.92**	**−0.90**	**−0.93**	−0.50	**−0.97**	−0.56	**+0.93**	**+0.83**	**+0.97**
D: MEI	**+0.95**	−0.57	+0.71	+0.76	**−0.94**	+0.51	**+0.87**	**+0.86**	**+0.96**
D: Temp.	**+0.98**	**+1.00**	**+1.00**	**+1.00**	**+1.00**	**+1.00**	**+1.00**	**+1.00**	**+0.93**
D: Precip.	**+1.00**	**+1.00**	**+1.00**	**+1.00**	**+1.00**	**+1.00**	**+1.00**	**+1.00**	**+0.85**

Note: Bold font indicates that $\geq 80\%$ of the posterior was positive or negative.

Abbreviations: AMWI, American wigeon; BWTE, blue-winged teal; CANV, canvasback; GADW, gadwall; MALL, mallard; MEI, multivariate ENSO index; NOPI, northern pintail; NSHO, northern shoveler; REDH, redhead; RUDU, ruddy duck.

where these two processes have become disconnected from one another, which would be indicative of a potential ecological trap. To quantify this mismatch, we used the posterior mean of realized and expected growth rate to calculate when the realized growth rate was more than 0.01 greater (to account for uncertainty) than the expected growth rate for each species and stratum.

3 | RESULTS

In the following sections we highlight which predictors had a positive, negative or no observed relationship with the response variables based on a probability of direction of 80% (Makowski et al., 2019). To facilitate interpretation, we report the probability with respect to the sign of the median (e.g. −0.80 would mean that 80% of the posterior distribution was negative, +0.80 would indicate that it was positive). (Values in parenthesis represent the proportion of the posterior greater than 0, such that lower values indicate a more negative posterior distribution.)

3.1 | Habitat selection and demographic responses to climate and land use change

Effect sizes for the habitat selection portion of the model represent correlation between the intensity of segment-level counts and predictors in the current year (e.g. positive values suggest selection for a variable). Effect sizes for the demographic portion of the model represent correlation between the intensity of stratum-level counts and the predictors during the previous year (e.g. positive values indicate that larger values of the variable correlate with more individuals the following year). Posterior probabilities of direction are summarized in Table 3.

The majority of waterfowl species selected for segments with a high proportion of cropland in the surrounding landscape, with

American wigeon being the only species that avoided segments with a high proportion of cropland (Figure 3a). We observed no response to cropland for gadwall (Figure 3a). Northern pintail demonstrated the strongest selection for summerfallow, but American wigeon, gadwall and northern shoveler also demonstrated a positive relationship. Only ruddy duck responded negatively to summerfallow, and no discernible relationship was observed for blue-winged teal, mallard, canvasback and redhead (Figure 3b). All species selected for habitat with a large number of ponds on a segment relative to other years (Figure 3c) and other segments within a year, although to varying degrees (Figure 3d). Diving duck species selected for segments with long snow cover duration (e.g. areas that thaw later in spring) between November and April (canvasback, ruddy duck, with redhead following the same direction of response but not meeting our threshold for discussion), whereas the majority of dabbling duck species demonstrated avoidance (American wigeon, blue-winged teal, gadwall, northern pintail; Figure 3e). Mallard and northern shoveler habitat selection was not correlated with snow cover duration (Figure 3e).

At the demographic level, the response to proportion cropland was negative for American wigeon, blue-winged teal, gadwall, mallard, northern pintail and canvasback, and positive for ruddy duck; northern shovelers and redheads showed no correlation (Figure 4a). The response to summerfallow was highly variable; given a high proportion of summerfallow in year $t-1$, there were fewer blue-winged

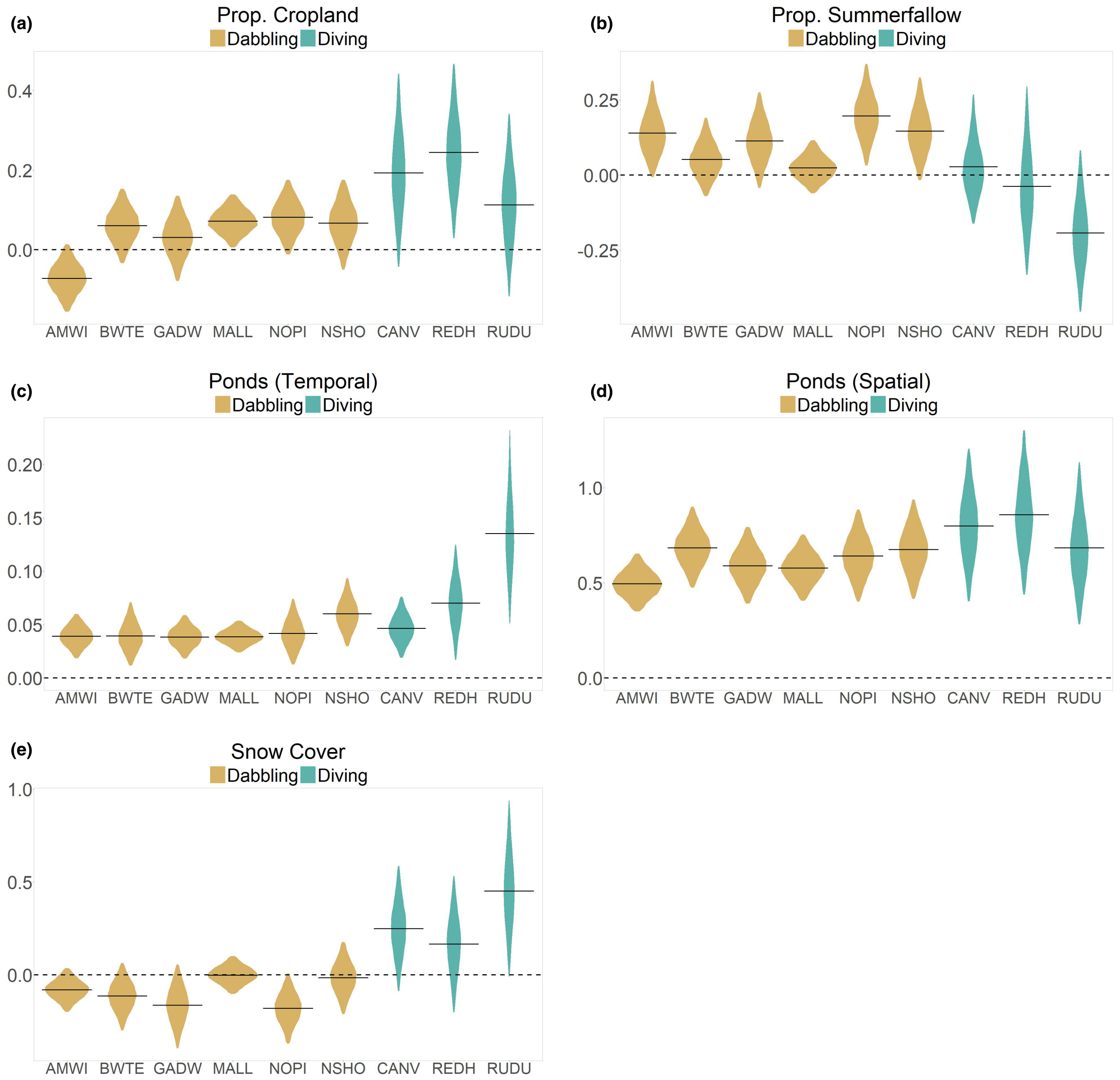

FIGURE 3 Posterior 95% distributions of population-level coefficients (log scale) contributing to habitat selection (i.e. within-stratum settling dynamics) of nine species in the Prairie Pothole Region from 1958 to 2011 (a–e).

teal, gadwall, northern shoveler, canvasback, redhead and ruddy duck in year *t* but more American wigeon and northern pintail (Figure 4b). Northern pintail were the only species to decrease in year *t* given large numbers of ponds in year *t* – 1, and three (blue-winged teal, canvasback, redhead) increased (Figure 4c).

Blue-winged teal, gadwall, mallard and northern shoveler were unaffected by increases in MEI, while American wigeon and all three diving duck species increased (Figure 4d), which indicates that population abundance increased following winters in El Niño years. Northern pintail were the only species to have a negative response to El Niño years (Figure 4d). All species positively responded to increases in average May–June temperature (Figure 4e) and precipitation (Figure 4f). Posterior probabilities of direction are summarized in Table 3 and results describing the among-species mean response to climate and land use variables are available in Supporting Information S3.

3.2 | Life-history patterns in responses to climate and land use change

A positive relationship between a life-history trait and the effect size does not mean that the effect itself was positive. For example, all species could demonstrate a negative response to a land use predictor, but if low values of the life-history predictor

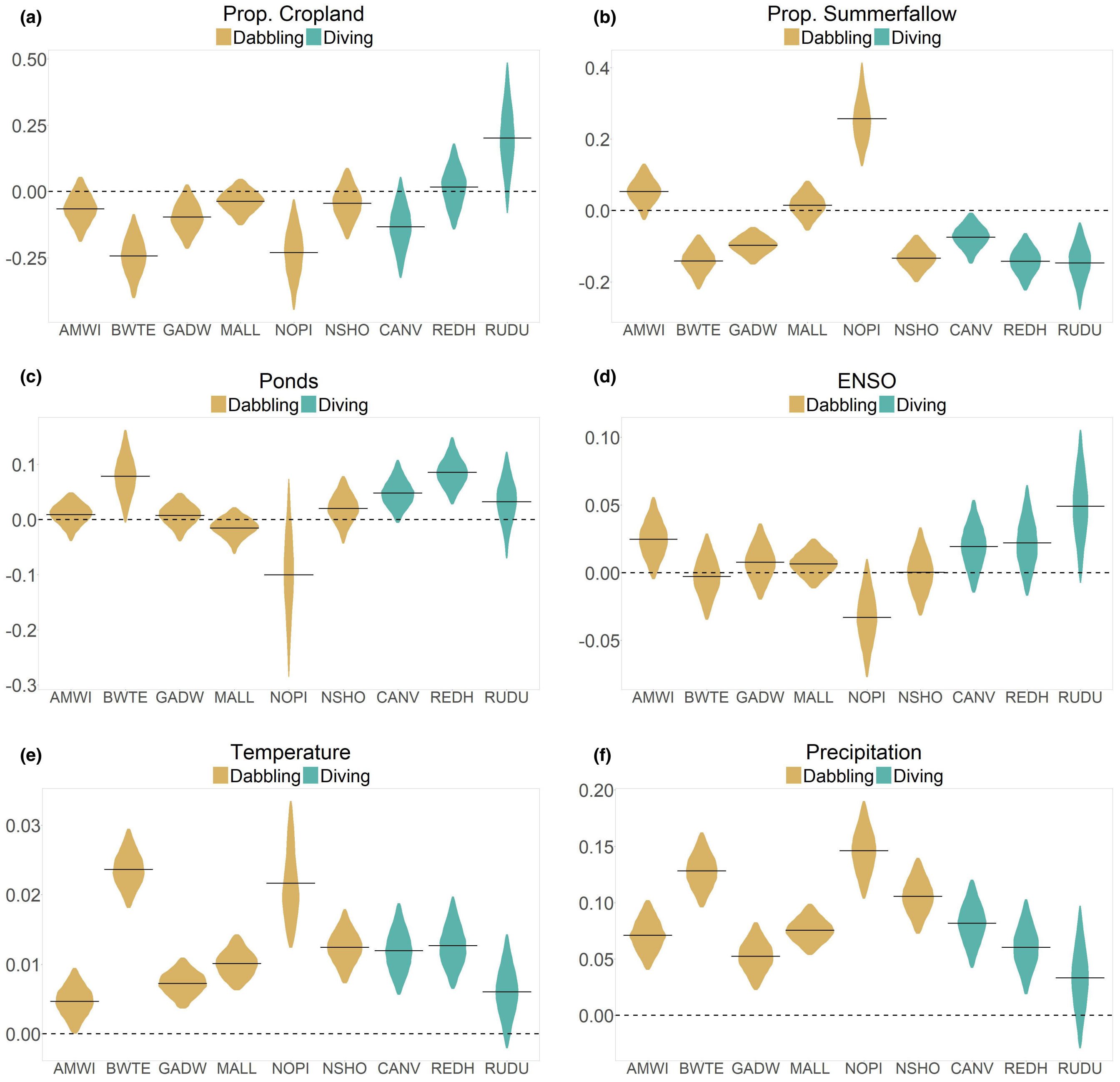

FIGURE 4 Posterior 95% distributions of population-level coefficients (log scale) contributing to demographic processes (i.e. the number of individuals available the following year) of nine species in the Prairie Pothole Region from 1958 to 2011 (a–f).

corresponded to more negative effect sizes (as predictor increases, response moves towards zero) then there will be a positive relationship between the effect and the life-history predictor. We also note that we carried forward uncertainty about the effect sizes to the second-stage analysis, which is atypical but better represents our uncertainty about the system, given the data. We also present the proportion of the distribution that is greater than zero for each effect, such that these values can be directly interpreted by other researchers and their own threshold implemented (Table 3). The values in parentheses following each variable refer to the probability of direction.

There was one relationship between life-history traits and habitat selection that met our threshold for inference. The phenology of nesting date among species was positively related to the habitat selection effect of the number of ponds on a segment relative to other years (0.88; Table 4), which means that later nesting birds demonstrate higher selection for pockets of high-density ponds. Nesting date was also the trait most consistently related to the relationship between demography and land use and climate variables. Nesting date was negatively related to species demographic responses to proportion fallow (−0.81), summer temperature (−0.88) and summer precipitation (−0.90) the prior year (Table 4). A negative relationship with nesting date indicates that earlier nesting species had greater, or more positive, demographic responses to the predictor variable than later nesting species. Nesting date was also positively related to the demographic effect sizes of the number of ponds the prior year (0.83) and the intensity of El Niño conditions (0.94; Table 4). Here, the positive relationship with nesting date indicates that earlier nesting species had lower, or more negative, demographic responses to the given predictor variable compared to later nesting species. Female breeding site fidelity was also negatively related to the effect of temperature (−0.88), meaning less fidelitous species had more, or less negative, demographic responses in years with higher precipitation compared to species with high site fidelity species (Table 4).

TABLE 4 We calculated the proportion of the posterior distribution that was greater or less than zero for the life-history effects on responses to climate and land use (Table 3). Effect sizes were estimated using a mixed-effects model, with species as a phylogenetic random effect, in which life-history variables were used as predictors for random samples from the posterior distribution of the effect sizes between climate and land use predictors and habitat selection. Variables used for habitat selection are denoted with an H and demography with a D. Similar variables across the two scales have been grouped together to facilitate comparison. The numbers describe the probability of direction, or the proportion of the posterior on the same side of zero as the median; positive values indicate that the median was positive and negative values indicate the median was negative.

	Life-history variable		
Variable	Longevity	Nesting date	Site fidelity
H: Prop. Cropland	+0.70	−0.79	−0.59
D. Prop. Cropland	+0.79	+0.73	+0.50
H: Prop. Fallow	−0.61	−0.74	+0.69
D: Prop. Fallow	0.66	**−0.81**	+0.54
H: Ponds (Temporal)	**+0.88**	+0.65	−0.74
H: Ponds (Spatial)	+0.72	−0.76	0.64
D: Ponds	−0.53	**+0.83**	−0.64
H: Snow Cover	+0.75	+0.67	+0.69
D: MEI	+0.74	**+0.94**	+0.77
D: Temp.	−0.61	**−0.88**	**−0.88**
D: Precip.	−0.73	**−0.90**	−0.79

Note: Bold font indicates that ≥ 80% of the posterior was positive or negative.

Abbreviation: MEI, multivariate ENSO index.

3.3 | Community-level patterns in susceptibility to ecological traps

We detected both species-level differences and spatial variation in population growth rates. For example, species ranged from having greater realized than expected growth rates in 1 to 14 strata. Strata also ranged from having zero to nine species with realized growth rates greater than expected (Figure 5). All nine species had realized growth rates greater than demographically expected growth rates in stratum 29. More species had realized growth rates greater than expected in Canada, and a larger proportion of strata in Canada had species with larger realized growth rates compared to expected. The diving ducks (canvasback, redhead and ruddy duck), blue-winged teal and gadwall also had realized growth rates that were greater than expected in a number of strata in which other species did not. Species-specific realized and expected growth rates by stratum can be found in the Supporting Information S2, which may be of particular interest to managers.

4 | DISCUSSION

4.1 | Habitat selection and demographic responses to climate and land use change

Most North American bird species are experiencing perilous declines in abundance, but wetland-dependent species, including waterfowl, have increased as a whole since 1970 (Rosenberg et al., 2019). That said, not all waterfowl species are experiencing identical trends in abundance, and it would be expected that some species are responding differently to simultaneous global change processes. Indeed, we found species-level variation in responses to climate and land use variables; in some cases, we found opposing responses among species. Conflicting directional relationships among species indicate that an increase in a given predictor can have a negative effect on some species and a positive effect on others, complicating community-level conservation and management (e.g. Elphick, 2004; Gallo &

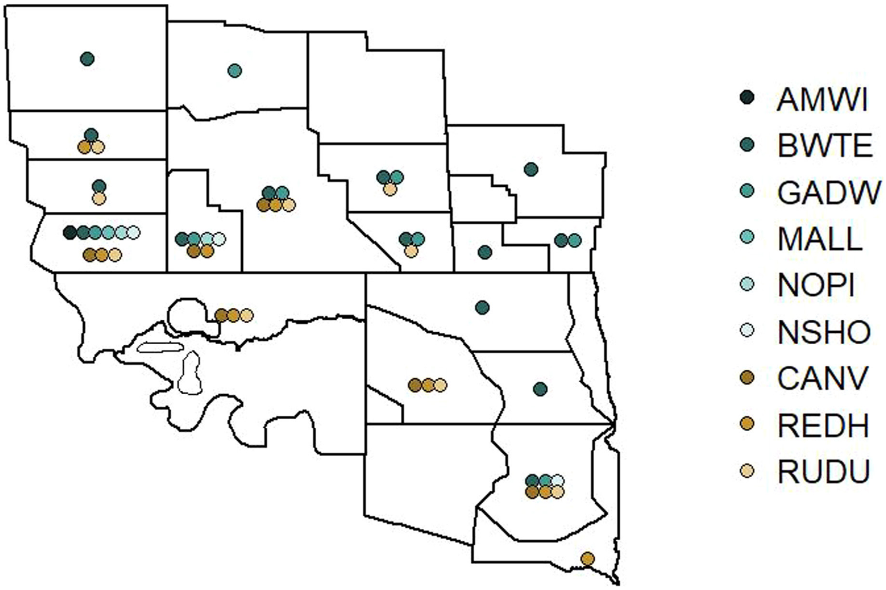

FIGURE 5 Map of the Prairie Pothole Region showing the stratum and species for which the posterior mean of the realized geometric mean growth rate (based on the selection model) was more than 0.01 larger than the posterior mean of the expected geometric mean growth rate (based on the demographic model).

Pejchar, 2016; Suarez-Rubio & Thomlinson, 2009). For example, diving duck species, such as the canvasback, selected for areas with a longer duration of snow cover on the landscape, whereas most of the dabbling duck species selected against such conditions. We interpret this more so as diving duck preference for the more northern parkland region within the PPR where there are a greater number of permanent and semipermanent wetlands that provide nesting habitat for these over-water nesting species (Maxson & Riggs, 1996; Nudds, 1983). In contrast, gadwall, pintail and other dabblers prefer, to varying degrees, the true prairie landscapes that provide a mix of upland and productive (less permanent) wetlands, which are conducive to dabbling ducks that invest heavily in reproduction (Nudds, 1983). At the level of demographic processes, species either responded very positively (American wigeon, northern pintail) or very negatively (blue-winged teal, gadwall, northern shoveler and the diving ducks) to the proportion of summerfallow. Although we know that single-species management can cause species management conflicts (as reviewed in Simberloff, 1998), our analysis was able to identify which species are predisposed to conflict and which variables are likely related to conflict (e.g. summerfallow), providing managers with predictable avenues based on species biology to navigate such conflicts when managing habitat for an entire community of waterfowl.

Within a species, the relationship between an environmental variable and several ecological processes, such as habitat selection and demography, may be quite different. Previous work on northern pintail found that habitat selection and demography were related to proportion cropland in opposing ways, with pintail selecting for areas with a high proportion of cropland, but cropland negatively affecting the number of individuals the following year (Buderman et al., 2020). This pattern may be indicative of an ecological trap (Buderman et al., 2020), potentially due to reduced nest success or mortality (Richkus, 2002). We detected a similar pattern for blue-winged teal, mallard and canvasbacks, however, their negative demographic response to cropland was not as extreme. The less negative response of canvasbacks may be due to the fact that they nest over water, meaning their nests are not exposed to agricultural tilling practices; however, intensely farmed landscapes can still alter the predator community in a manner that is deleterious for nest success, as it does for upland nesting ducks such as northern pintail and blue-winged teal (Crimmins et al., 2016; Duncan & Devries, 2018).

Pintail were at the extreme end of the response curve for many of the demographic-level predictors, which may explain why their population trajectories have been in the largest decline during a period when most other waterfowl species in the PPR are stable or increasing in abundance (U.S. Fish and Wildlife Service, 2019). For example, they were one of only two species that demonstrated a positive demographic correlation with summerfallow, and the effect size was three times that of the other species, the American wigeon. They also had some of the strongest positive demographic relationships to temperature and precipitation and the strongest negative response to ponds the prior year. However, we note that the ponds being counted by the WBPHS, which have generally been increasing through time (Podruzny et al., 2002), are not the ponds that pintail typically use, which are the temporary, ephemeral ponds (not counted in the WBPHS) that form in early spring (Drever, 2006; Krapu, 1974; Naugle et al., 2001). These ponds form as a result of snow melt and precipitation and may explain the pintail's the strong positive response to spring temperature and precipitation. Because our findings are correlative and not causal, there may be unmodelled or unobserved variables that are confounded with changes in climate and land use that are mechanistically related to population growth over time for some species but not accounted for in our model (Hefley et al., 2016). The combination of inverse relationships between habitat selection and demography and their strong correlations with some of the landscape and climate variables may make northern pintail populations especially sensitive to changes occurring in the PPR, such as the decline in summerfallow acreage due to the adoption of minimum tillage practices, in parallel with increased crop acreage, as well as changes in climate, which together affect available ephemeral wetland habitat (Awada et al., 2014; Carlyle, 1997; Greenwood et al., 1995; Mattsson et al., 2020; Podruzny et al., 2002; Zhao et al., 2019).

4.2 | Life-history patterns in responses to climate and land use change

Differences among species in their responses to changing land use and climate were somewhat predictable based on basic life-history attributes, particularly in terms of nesting date for both habitat selection and demographic relationships. As expected, earlier nesting species (e.g. northern pintail) had a stronger habitat selection coefficient for cropland, although the effect size did not meet our predefined threshold. This relationship likely occurs because cropland, prior to spring tillage, has a somewhat similar appearance and dominance on the landscape as the senescent grasses that historically dominated the prairie landscape in early spring (Beauchamp et al., 1996; McLachlan et al., 2007; Richkus, 2002). However, we did not predict the negative relationship with summerfallow, as summerfallow would appear the same to waterfowl regardless of when they arrive in the spring, which indicates that some early-nesting species either show more selection for summerfallow-type habitat, or association with the prairie where summerfallow was a more common practice to improve soil moisture (Carlyle, 1997) compared to late nesters. We found weak support that less fidelitous species showed greater selection for segments with more ponds relative to other years, given that the less fidelitous species are more likely to make decisions based on current conditions and not where they nested the prior year (Coulson, 2016). However, contrary to our prediction, we did not find support for the less fidelitous species selecting areas with more ponds relative to other areas within a year.

Supporting our predictions, earlier nesting species had greater (or more positive) relationships between demography and proportion fallow and lower (or more negative) relationships between demography and proportion cropland, although the relationship with proportion fallow did not meet our predefined threshold. These results are likely mechanistically related and were expected given previous fine-scale research on the overlap between nesting dates and mechanical tillage, especially for pintail, and predation in cropland (Best, 1986; Duncan & Devries, 2018; Greenwood et al., 1995; Lokemoen & Beiser, 1997). As expected, earlier nesting species also had greater (or more positive) demographic relationships with average May–June temperature and precipitation compared to later nesters, which may reflect a more sensitive response to productivity and resource availability for allocation into clutch formation and later duckling development during the May–June period.

Based on the demographic buffering hypothesis, we predicted weaker demographic responses to pond counts, El Niño conditions, temperature and precipitation for species with the greatest longevity. We did detect a negative relationship between demographic responses to temperature and longevity, and a weak negative relationship between precipitation and longevity. Given all species responded positively to temperature and precipitation, this would indicate that longer-lived species had weaker, but still positive, responses to increases in precipitation. Contrary to our prediction, we detected a weak positive relationship between longevity and the demographic response to El Niño conditions (i.e. longer-lived species had stronger, or more positive, responses to El Niño conditions the previous year). Despite the positive relationship, four of the five longest-lived species (American wigeon and the three diving duck species) were the only ones to have a positive response to El Niño conditions, with the remaining species either not responding or responding negatively (northern pintail). Additional relationships between longevity and environmental variables were unsupported by the second-stage model for life-history relationships.

We also found some unexpected relationships for which we did not have a priori hypotheses. We had expected that later nesting species, compared to early nesting, would select areas within the PPR with a longer duration of snow cover; we did not find strong evidence for this, however, we found weak evidence that earlier nesting species had stronger selection for the number of ponds relative to other segments within a stratum. This could be attributed to two fairly early nesters, canvasbacks and redheads, having the strongest positive selection for segments with relatively large numbers of ponds (reminiscent of the wetland permanence in the Parkland landscape they prefer). Earlier nesting species also showed lower demographic response to pond counts, which may reflect the use by early-nesting pintail of early, temporary wetlands that are formed from snow melt (which are not counted by the aerial flight surveys given traditional protocol), as opposed to seasonal and semipermanent wetlands (Kantrud & Stewart, 1977). Finally, later nesting species had more positive responses to El Niño conditions. Later nesting species are also more likely to migrate later in the spring; later migration and nesting may buffer them against any adverse effects from extreme weather events that occur in El Niño years. For example, previous research found that birds arrived earlier to the breeding grounds following years with high North American Oscillation indices (El Niño years), and this effect was greater for birds arriving in the earlier phase of migration (Rainio et al., 2006). We saw in the life-history and demographic modelling that northern pintail, which are an early-nesting species, often had extreme responses to climate and land use, and in the subsequent life-history trait analysis we observed that these responses most correlated with nesting date. Although we did not expect relationships between demographic responses and breeding site fidelity, we detected a negative relationship between fidelity and the response to precipitation and temperature (a weaker response given that all species had positive demographic responses). This result is likely related to the fact that two of the three diving duck species had very high rates of female breeding site fidelity and the seasonal, semipermanent and permanent ponds that diving ducks prefer are less sensitive to variations in precipitation and temperature. We also unexpectedly found strong, positive relationships between female longevity and the strength of habitat selection for various climate and land use variables, such as proportion cropland, ponds relative to other years and relative to other segments, and snow cover duration. However, we note that the three longest-lived species were the three diving ducks, which typically had the largest, most positive responses to cropland and pond count metrics. In addition, they were the only three species that responded positively to snow cover duration, all of which may be associated with the northern Parklands landscape in the PPR that they prefer.

4.3 | Community-level patterns in performance

Given the spatially heterogeneous changes in climate and agricultural land use across the PPR over time (Anteau, 2012; Dahl, 2014; Niemuth et al., 2014; Watmough et al., 2017), and differential life-history responses to these changes, species are generally prospering in some strata, suffering in a few and responding idiosyncratically in yet other strata (Figure 5). These results highlight that waterfowl conservation in the PPR should be species and context dependent, because species will respond differently to conservation actions given their life history and the environmental conditions of their local habitat. In fact, averaging across species would typically lead one to think that climate and anthropogenic land use are not related to waterfowl habitat selection and demographic processes, because species are responding divergently (Supporting Information S2 and S3).

Our work represents not only a community-level analysis of waterfowl responses to climate and land use variables, but also one of the first analyses of how life-history characteristics are related to the environmental mechanisms governing both habitat selection and demography among species in a community. By separating the habitat selection and demographic processes for nine species of waterfowl using data from 1958 to 2011 and a unique hierarchical model, we were able to identify species-specific habitat selection and demographic relationships with ever-changing land use and climate variables. Basic life-history traits moreover explained species-level differences in these estimated relationships, some of which were consistent with our predictions and others not. Our results will be useful for anticipating future responses of species to changes in land use and climate and for predicting breeding-pair abundance within the flight survey path as waterfowl managers in the PPR develop multi-species conservation programs alongside targeted efforts for species of concern and areas of conservation priority (Doherty et al., 2013, 2015; Reynolds et al., 2006; Schlaepfer et al., 2002).

AUTHOR CONTRIBUTIONS

Frances E. Buderman and David N. Koons conceived the idea for the manuscript; Frances E. Buderman designed the modelling framework with ecological insights from David N. Koons and James H. Devries; Frances E. Buderman analysed the data and led the writing of the manuscript with input from David N. Koons and James H. Devries on waterfowl ecology and management. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

All data are published and publicly available, with those publications properly cited in this submission. Waterfowl and pond counts are available from The U.S. Fish and Wildlife Service and can be found at https://migbirdapps.fws.gov/mbdc/databases/mas/maydb.asp. Climate data, including the GHCN Gridded V2 data, PRECL Precipitation data, NOAA/NCEP Reanalysis 1 data and MEI data, were provided by NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, and are available from their website at https://www.esrl.noaa.gov/psd/. Agricultural census data are available via https://www.nass.usda.gov/AgCensus/ and https://www.statcan.gc.ca/en/census-agriculture for the United States and Canada respectively. Code and data are available on GitHub: https://github.com/fbuderman/PublicationSupplement_JAE2023. It has also been versioned and archived via a Zenodo Repository: https://doi.org/10.5281/zenodo.7750471 (Buderman et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Land cover and climatic covariates.

Appendix S2. Species-level results for expected and realized abundances.

Appendix S3. Population-level effect sizes.

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