



Antagonistic, synergistic and direct effects of land use and climate on Prairie wetland ecosystems: Ghosts of the past or present?

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Abstract

Aim: Wetland loss and degradation threaten biodiversity to an extent greater than most ecosystems. Science-supported responses require understanding of interacting effects of land use and climate change on wetland biodiversity.

Location: Alberta, Canada.

Methods: We evaluated how current climate, climate change (as a ghost of the past), land use and wetland water quality relate to aquatic macroinvertebrates and birds.

Results: *Climatic relationships and climate-land use interactions were observed on chironomid abundance, but not macroinvertebrate taxa richness (MTR) or odonate abundance, which responded to land use and water chemistry.* Chironomid abundance was positively associated with cropland and negatively associated with total precipitation. Higher cropland cover and dissolved organic carbon synergistically interacted with total precipitation to affect chironomids. MTR was negatively related to salinity, yet greater area of non-woody riparian vegetation attenuated salinity effects on MTR. Odonate abundance was negatively related to total phosphorus. Higher grassland cover also increased the negative relationship of total phosphorus to odonate abundance. *Climatic relationships and climate-land use interactions were observed on bird species richness (BSR) and abundance of several bird functional groups.* Higher BSR and abundances of several bird groups were positively related to average rainfall and greater warming temperatures over time. Area of non-crop cover and wetlands was positively associated with most bird groups and BSR. Warming temperatures over time ameliorated the negative relationship of higher cropland or less shrubland on aerial insectivores and other bird groups.

Main conclusions: Climate patterns and climate change are as important as land use pressures with stronger impacts on birds. Climate change was more influential than current climate and provided novel empirical evidence that progressively warmer, wetter conditions is benefiting some bird groups, including aerial insectivores, a

group of conservation concern. Riparian vegetation ameliorated the negative impacts of climate and water quality gradients on MTR and could mitigate global change impacts in agricultural systems.

KEYWORDS

agriculture, antagonistic, aquatic macroinvertebrates, birds, climate change, functional group, interaction, synergistic, water quality, wetlands

1 | INTRODUCTION

Wetland ecosystems require immediate and sustained conservation attention as they are experiencing declines in biodiversity greater than those in the most affected terrestrial ecosystems (MEA, 2005). Concern has been mounting regarding how stressed freshwater systems will cope with rapid, ongoing global changes (Reid et al., 2018; Reis et al., 2017; Vörösmarty et al., 2010). Despite this, there remains a lack of integration of land use change and climate change in studies of species distributions and abundances (Sirami et al., 2017), especially in freshwater systems (Piggott, Townsend, & Matthaei, 2015; Taniwaki, Piggott, Ferraz, & Matthaei, 2017). Understanding the interacting effects of climate change and land use change is necessary to inform climate change adaptation and mitigation measures. Whether stressors act additively (i.e., the combined effect is the sum of their individual effects), synergistically (i.e., the combined effect is larger than the sum of their individual effects) or antagonistically (i.e., the combined effect is smaller than the sum of their individual effects) will have a critical bearing on outcomes for biodiversity and conservation decisions (Cochrane & Laurance, 2008; Oliver & Morecroft, 2014). If climate change and land use change have synergistic negative effects on biodiversity, then it is vital to anticipate these non-additive effects (Cochrane & Laurance, 2008; Zak, Cabido, Cáceres, & Díaz, 2008). If the interaction is antagonistic (e.g., increased precipitation buffers some land use change effects), then we may be able to allocate limited conservation resources more effectively (Didham, Tylianakis, Gemmill, Rand, & Ewers, 2007; Oliver & Morecroft, 2014). However, until we can identify and understand these interactions, our ability to recommend interventions with high likelihood of success in achieving broad biodiversity conservation goals is limited.

Multiple stressors in freshwater ecosystems have resulted in population declines and range reductions of freshwater species worldwide (Heino, Virkkala, & Toivonen, 2009; Reid et al., 2018). Yet, our understanding of the combined and interacting effects of climate change and land use change (e.g., habitat loss, nutrient enrichment) on wetland biodiversity is limited (Anteau, 2012; Porter et al., 2013; Schindler, 2001) and the implications of these interactions for wetland ecosystems have generally been based on broad assumptions rather than empirical data (Rashford et al., 2015; Schindler, 2001). For example, it is expected that climate change will interact with ecosystem conversion and degradation to alter turbidity and eutrophication of aquatic ecosystems (Häder, Kumar, Smith, & Worrest, 2007;

Schindler, 2001) and may be exacerbated by vegetation loss (Didham et al., 2007; Oliver & Morecroft, 2014). However, not all plant and animal species will be negatively affected; some will adapt and possibly benefit from changes (Davis, Lake, & Thompson, 2010), while other species are likely to suffer catastrophic declines (Didham et al., 2007; Oliver & Morecroft, 2014). Thus, to better adapt to climate change, we must improve our understanding of the processes generating climate and land use change interactions and assess the consequences of these interactions on wetland biodiversity. This will improve our ability to incorporate climate change predictions and interactions with land use change into the design of conservation strategies, which currently represents a major deficiency in wetland ecosystem management and policy (Abell, 2002; Munang et al., 2010).

Here, we examine whether interactions between current climate, climate change and agricultural land use drive patterns in avian and aquatic macroinvertebrate communities to gain insights about how climate change has affected biodiversity of prairie ecosystems. We differentiate between current climate and climate change because a warm and/or wetter year/period may benefit or disadvantage wetland biodiversity in the short term, for example, by improving foraging/growing conditions or starving young (Crick, 2004). However, greater rates of change in temperature and precipitation over time may act as a reoccurring "ghost" forcing species to adapt or perish depending on evolutionary processes and whether other species/stressor interactions are present (Brooker, Travis, Clark, & Dytham, 2007; Hoffmann & Sgrò, 2011).

We evaluate which guilds and functional feeding groups of birds and macroinvertebrates are influenced by climate and land use interactions by analysing a large spatially representative data set (617 sites across 156,318 km²) from south-central Alberta, Canada, within the North American Great Plains. The region has lost 60%–70% of its original wetlands and >70% of its native grasslands due to agricultural development (ABMI, 2015), and land conversion pressures continue. Climate change is causing profound shifts in the seasonal availability and distribution of water and aquatic vegetation (Johnson et al., 2005; Shook & Pomeroy, 2012). Climate change may dramatically affect the phenology (annual recurrence of phenomena) of vegetation, seed production and insect emergence (Skagen et al., 2011), the intensity of agriculture and the physiological suitability of the region for cold-limited plants and animals (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012). These stressors to wetland systems in south-central Alberta are similar to those faced across the Great Plains and throughout the world.

Thus, our broad goal was to clarify the impacts of climate variability and change on wetland-associated biota, factors that have received much less attention than land use or habitat-specific drivers. We predicted that (a) the abundance and richness of birds and aquatic macroinvertebrates would be positively related to area of natural, perennial upland cover (i.e., low cropland area) and high wetland abundance in sites with the highest precipitation and lowest temperatures because upland and wetland sites with lower precipitation and higher temperatures are more vulnerable to drought and eutrophication. We also predicted that (b) functional groups with less specialized diets, foraging habitats and greater adaptive capacity would be less influenced by climate and land use change (Brooker et al., 2007; Hoffmann & Sgrò, 2011). Aquatic macroinvertebrates, particularly midges and dragonfly and damselfly larvae would be most impacted by land use intensity and warmer/drier conditions due to their sensitivity to water quality (Hornung & Rice, 2003; McCormick, Shuford, & Rawlik, 2004). We also predicted that (c) sites with higher temperatures or that experienced larger long-term temperature increases would have lower overall bird species richness and macroinvertebrate taxa richness due to effects on physiological development (Cox, Thompson, Reidy, & Faaborg, 2013; Piggott et al., 2015) and (d) sites with higher precipitation or that experienced larger long-term precipitation increases would have higher species richness due to reduced predator activity or higher resource availability (Cox et al., 2013). However, excessive precipitation or long-term increases in precipitation could reduce invertebrate richness by increasing nutrient levels and the incidence of eutrophic water bodies as a result of higher agricultural run-off (McCormick et al., 2004). Furthermore, we predicted that (e) survey year and long-term temperature and precipitation effects on both avian and macroinvertebrate communities would be modest compared with the negative effects of low grassland cover and wetland abundance at sites with intensive agriculture (LeBrun, Thogmartin, Thompson, Dijak, & Millspaugh, 2016; Scrimgeour & Kendall, 2003; Stanton, Morrissey, & Clark, 2018).

2 | METHODS

2.1 | Study region

South-central Alberta lies at the northern extent of the North American Great Plains, a region (156,318 km²) characterized by thousands of glacially formed wetlands in a landscape matrix of natural grassland and agriculture (Figure 1). It is renowned for biological diversity (ABMI, 2015), but is one of the most productive agricultural regions in the world (Campbell, Zentner, Gameda, Blomert, & Wall, 2002). The region is vulnerable to severe droughts due to low precipitation and high evapotranspiration in summer (Schindler & Donahue, 2006). The study region intersects the mixed grasslands and parkland ecoregions. The grassland ecoregions are typified by rolling terrain with dark-brown topsoil, subhumid to semi-arid moisture conditions, and a mix of native and tame grasses and shrubs in non-cropland areas. Parkland is classified by groves of aspen and patches of shrublands within a grass and cropland matrix; soils are

typically darker and the ecozone has a slightly cooler climate (Alberta Parks, 2015).

The Alberta Biodiversity Monitoring Institute (ABMI) has measured biodiversity, habitat and human footprint throughout Alberta (latitude: 49°–60°, longitude 110°–120°) since 2007. The ABMI database was chosen because it is one of the largest and longest-running systematic upland and wetland-specific monitoring programs in the North American prairies and was explicitly designed to allow assessments of biodiversity responses to environmental conditions over space and time. Upland survey sites were established on a 20 km systematic grid with a random distance and directional offset of up to 4 km from the 20 km systematic grid (ABMI, 2014). Wetland survey sites were determined by selecting the nearest wetland (>0.5 m deep and at least 1.0 ha of open water) to the upland site (ABMI, 2013). The ABMI surveys each site once every 5 years in June/July, within a 2-week window to reduce seasonal variation.

2.2 | Biodiversity, water chemistry and riparian habitat data

At each wetland site ($n = 280$; Figure 1), ABMI provided data (2007–2015) on aquatic macroinvertebrates (unique taxonomic counts taken from the International Taxonomic Information System [<http://www.itis.gov/>]) collected by standardized sweeps of the water column starting at the bottom of the wetland and sweeping the aquatic vegetation along a fixed transect line from the centre of the wetland (open water) moving across the emergent, fen and wetland margin zones using a modified D-ring dip net (mesh size: 500 μm); wetlands >3 m deep were removed from the database to exclude large lakes and reduce possible impacts of fish. The numbers of chironomids and odonates were calculated as the number of non-biting midge larvae from the family Chironomidae and the number of dragonfly and damselfly larvae from the infraorder Anisoptera + suborder Zygoptera, respectively. Chironomids and odonates are important dietary groups for many consumers, including waterbirds (larva) and passerine bird species (adults), and both insect taxa in particular serve as indicators of ecosystem quality (Hornung & Rice, 2003; McCormick et al., 2004). Macroinvertebrate taxa richness was calculated as the number of unique taxonomic ID numbers measured at the species, genus or family level to retain the diversity of macroinvertebrate lifecycles (ABMI, pers. comm.). At each ABMI upland site ($n = 337$; Figure 1), breeding bird species presence and abundance were determined using a standard 10-min point-count survey with audio recording units. Birds were classified into a species richness index and 21 functional groups according to Sundstrom, Allen, and Barichievsky (2012), Poole (2005) and co-author (RGC, EB) expertise on specific dietary and foraging strategies during the breeding season (see Appendix S1).

Water chemistry was measured at the deepest point of the wetland (dissolved oxygen and dissolved organic carbon [mg/L], specific conductance [mS cm^{-1}], salinity (ppt) and total nitrogen and phosphorous [$\mu\text{g/L}$]). Riparian habitat amount (riparian width = total width in metres for the emergent, fen and margin zones combined,

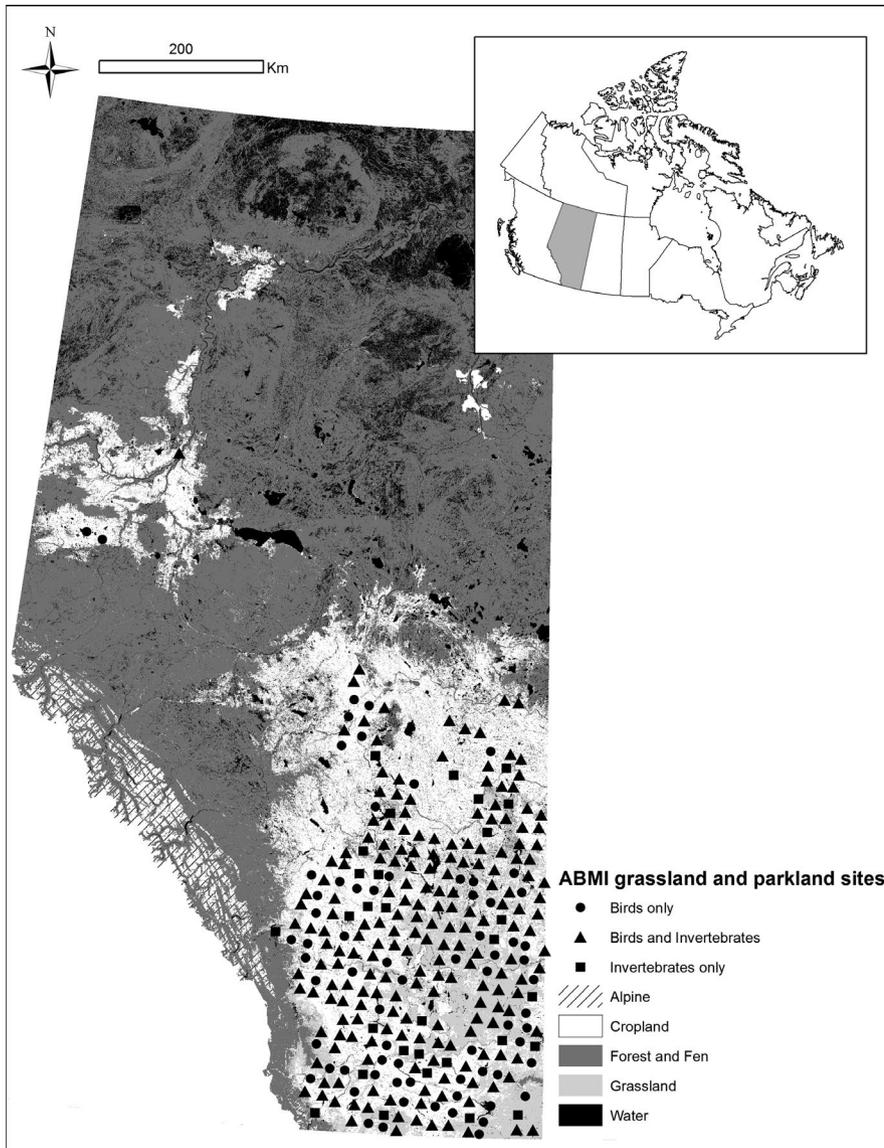


FIGURE 1 Map of Alberta, Canada (inset), showing the main land cover features as classified by the Government of Canada (AAFC, 2009) and the distribution of the Alberta Biodiversity Monitoring Institute survey sites (filled symbols) used in this study ($n = 337$ for birds and $n = 280$ for aquatic macroinvertebrates). Water represents lakes, rivers and wetlands

and the per cent cover of forbs, shrubs, grasses, sedges, rushes, and deciduous and coniferous trees) was recorded. The amount of 'non-woody vegetation' was then calculated as the total per cent cover of forbs, grasses, sedges and rushes averaged across all riparian quadrants (north, east, south, and west), whereas 'woody vegetation' was calculated as the total per cent cover of shrubs and all trees. Both variables are commonly used for incorporating different landscape attributes in grassland conservation studies (Cunningham & Johnson, 2006).

2.3 | Land cover data

We calculated buffers for aquatic macroinvertebrates and birds separately because wetland survey locations were offset (247 m to 13.47 km) from upland survey points for birds. For indicators of land cover, we extracted 30–56 m resolution buffers (100 m radius for aquatic macroinvertebrates and 500 m radius for birds) around each survey point corresponding to the ABMI survey year (2007–2015)

using annual land cover data layers (2009–2015; (AAFC, 2009). For the two survey years preceding the annual crop inventory (2007–2008), we used the 2009 layer and assumed that the total cropland and land management/tillage system was representative. An additional tree cover indicator was calculated as the total % cover of mixed forest and broadleaf forest within each buffer. Coniferous forest was excluded because it was negligible in the study area. The two buffer sizes were chosen to characterize the surrounding landscape effects on aquatic macroinvertebrates within wetlands (100 m), and the habitat conditions where birds were detected (500 m) corresponding with field survey design (nine point-count stations in a grid pattern with 300 m between stations; ABMI, 2014).

2.4 | Climate data

We used the Canadian gridded estimates (50 km resolution) from the Second Generation of Daily Adjusted Precipitation and Temperature Data for Canada (<http://open.canada.ca/data/en/dataset/d6813>)

de6-b20a-46cc-8990-01862ae15c5f, accessed September 2017). Two long-term climate indices (mean maximum temperature and rainfall variability from the 40 years preceding the survey year), two climate change indices (precipitation change and temperature change between the 1901–1940 and 1976–2015 periods) representing the ghost of the past, and four recent weather and climate indices (spring temperature, spring precipitation, total fall/winter/spring precipitation and mean annual precipitation over the last 15 years) were calculated using values corresponding to the grid closest to each site (i.e., nearest neighbour) and survey year (see Appendices S2, S3 for details). All GIS processing was undertaken using ArcGIS 10.5 and R 3.4.0 (R Core Team, 2018).

2.5 | Statistical analyses

To test whether land use, water chemistry, current weather and climate, and climate change exert additive or interacting effects on biota, and whether specific functional groups of macroinvertebrates and birds are more vulnerable or resilient to land use, climate and climate change effects, we used mixed-effects linear regression models (Zuur, Ieno, Walker, Anatoly, & Smith, 2009). If only additive effects of climate and land use exist, then negative effects of cropland area and positive effects of wetland abundance (LeBrun et al., 2016; Scrimgeour & Kendall, 2003; Stanton et al., 2018) on (a) invertebrate and bird richness, and (b) functional groups with more specialized diets and/or foraging habitats, will be the same across sites regardless of precipitation or temperature. Conversely, temperature and precipitation effects on invertebrates and birds will be the same across sites regardless if nearby cropland and wetland area varies. If antagonistic interactive relationships exist, we predicted weaker negative effects of cropland area and weaker positive effects of wetland abundance on birds and invertebrates at sites with the lowest precipitation and highest temperatures, possibly due to negative effects of increased salinity and other aqueous chemicals in precipitation-related runoff (Hornung & Rice, 2003; McCormick et al., 2004). If synergistic interactive relationships exist, we predicted stronger negative effects of cropland area and stronger positive effects of wetland abundance on birds and invertebrates at sites with the lowest precipitation and highest temperatures (Cox et al., 2013; Piggott et al., 2015), because upland and wetland sites with lower precipitation and higher temperatures are more vulnerable to drought and eutrophication.

Prior to analysis, Pearson's correlation coefficient was used to test for correlations among predictor and response variables. No response variable was correlated with latitude or longitude ($r < 0.5$, $p < .05$). Breeding bird abundance was removed to reduce the number of analyses. We removed rainfall variability, mean maximum temperature, mean annual precipitation and specific conductance to reduce effects of collinearity (Graham, 2003), but climate variables were substituted and analyses rerun to confirm the importance of variables retained in the final models. We also retained precipitation change and temperature change because we predict that

greater rates of warming/rainfall will be linked to individual functional groups, and we tested whether total % cropland was a better predictor than grassland. The remaining weather, climate, land use, water quality and riparian habitat variables (Table 1) were standardized ($(x - \text{mean})/SD$) for effect size comparisons. Wetland sites were used for predictors in the macroinvertebrate surveys, but upland sites were used for predictors in the bird surveys.

Macroinvertebrate taxa richness and bird species richness were log-transformed and fit with a Gaussian error distribution (lme4 package, Bates, Maechler, Bolker, & Walker, 2014), while the number of chironomids, odonates and each of the 16 bird functional groups were fit with negative binomial error distributions (glmmADMB package) because of their skewed distributions (Fournier et al., 2012). Three bird functional groups (bark invertivore, bark omnivore and terrestrial pollinator) were too rare to model, and aerial carnivores were removed because their home-range size is greater than our 500 m radius land use buffer sizes (Leary, Mazaika, & Bechard, 1998).

Models were ranked based on AIC_c (Burnham & Anderson, 2002). We began with a small number of predictors as fixed effects (cropland, pasture and forages, spring temperature, temperature change and precipitation change) and potential random effects (survey year from 2007–2015, latitude [to account for a natural species richness-latitude patterns], latgroup [latitude grouped into six classes], longitude). We tested the relative fit of different random effects (intercept and slope) of year, latitude, latgroup and longitude, to determine which predictors to include in all subsequent linear mixed-effects models (Beale, Kendall, & Mann, 1967). Ultimately, we used only a random intercept effect of year with the five initial fixed effects predictors in all subsequent models, because only one random intercept for year was consistently significant ($p < .05$) across response variables (Table 1) to account for annual effects on biodiversity that were not explained by environmental covariates. We treated the initial model with five fixed effects and a random intercept for year as the initial null model, then sequentially added the remaining predictors, including interaction terms, one by one, and compared the AIC_c values of the models with and without the additional predictor. We fit models with interaction terms representing relationships depicted in Figure 2. The effects of multiple drivers were considered interactive if models including interaction terms had lower AIC_c values than their additive versions. To account for the probability that a given estimate came from the best model, parameter estimates were model-averaged from models that were within 2 AIC_c units ($\Delta AIC_c \leq 2$). We calculated R^2 statistics following Jaeger, Edwards, Das, and Sen (2017) as a measure of absolute model fit.

Some sites within the database were monitored twice (5-year rotation; $n = 48$ for birds and 41 for aquatic macroinvertebrates), but were considered independent due to the 4+ year interval relative to changing weather and land use rotations in this system. To confirm this, we re-analysed best approximating models by including random effects of year and siteID and obtained virtually identical results to a model with random effects of year alone.

3 | RESULTS

3.1 | Model selection

We looked at the relative ability of additive and interactive models to explain the data distribution of each dependent variable, with (a) better models having lower AIC_c statistics and (b) models with AIC_c within 2 AIC_c of the lowest AIC_c model having equivalent explanatory ability. Model selection yielded one to five plausible models within 2 AIC_c of the best approximating model for each biodiversity response (Appendix S4). In all cases, except aquatic and terrestrial invertebrates (where ΔAIC_c was 5.5), the ΔAIC_c of the null (intercept-only) model was >20.0 . All of the top-ranked models explained a relatively similar amount of the total variance in the data (R^2 mean = 0.2, range = 0.04–0.45), but the

model for terrestrial insectivores was highest, explaining 45%. Ten of twenty models with lowest AIC_c included an interaction term between two of the explanatory variables, suggesting that land use, weather and climate change exert interacting and additive influences on avian and aquatic invertebrate communities.

3.2 | The influence of land use and climatic factors on aquatic macroinvertebrates

We tested for positive effects of grassland and woody plant cover, wetland abundance and precipitation, and negative effects of increased cropland cover, temperature, salinity, TP and/or DOC on different aquatic invertebrates. We found that numbers of chironomids and odonates, and overall macroinvertebrate taxa richness, were

Type of variable	Parameter	Description
Temporal variation	Year	The survey year (2007–2015) in which ABMI ^a measured biodiversity, habitat and water quality
Current weather	Spring temperature	Mean maximum monthly temperature during the spring (March to May) prior to the year of the survey
Current weather	Spring precipitation	Rainfall + snowfall during the spring (March to May) prior to the year of the survey
Current weather	Total precipitation	Rainfall + snowfall during the fall/winter/spring (Sept to May) prior to the year of the survey
Climate change	Precipitation change	Difference in mean annual precipitation [(1976–2015)–(1901–1940)]
Climate change	Temperature change	Difference in mean monthly spring (March–May) temperatures [(1976–2015)–(1901–1940)]
Land cover	Pasture and forages	The % of pastures and forages in the landscape
Land cover	Trees	The % of mixed forest and broadleaf forest in the landscape
Land cover	Cropland	The % of all cropland in the landscape
Land cover	Shrubland	The % of shrubland in the landscape
Land cover	Wetlands	The % of wetlands in the landscape
Land cover	Grassland	The % of native grasses and other non-woody vegetation (e.g., forbs) in the landscape
Water chemistry	TP ^b	Total phosphorous ($\mu\text{g/L}$)
Water chemistry	Salinity ^b	Salinity (ppt)
Water chemistry	DO ^b	Dissolved oxygen (mg/L)
Water chemistry	DOC ^b	Dissolved organic carbon (mg/L)
Water chemistry	TN ^b	Total nitrogen ($\mu\text{g/L}$)
Riparian habitat	Riparian width ^b	Total width (m) of the emergent, fen and margin zones combined
Riparian habitat	Non-woody veg ^b	Total % cover of forbs, grasses, sedges and rushes in the riparian zone
Riparian habitat	Woody veg ^b	Total % cover of shrubs and deciduous and coniferous trees in the riparian zone

TABLE 1 Descriptions of parameters included in the linear mixed-effects regression analyses to test whether land use, weather, climate and climate change exert an additive or interacting effect on bird species richness, aquatic macroinvertebrate taxa richness, and numbers of odonates, chironomids and 16 different wetland or upland-associated bird functional groups

Note: The mixed-effects model structure included 'Year' as a random intercept and all other variables as fixed effects.

^aABMI = Alberta Biodiversity Monitoring Institute (<http://www.abmi.ca>).

^bIncluded as fixed effects for aquatic macroinvertebrate taxa richness and the number of odonates and chironomids only.

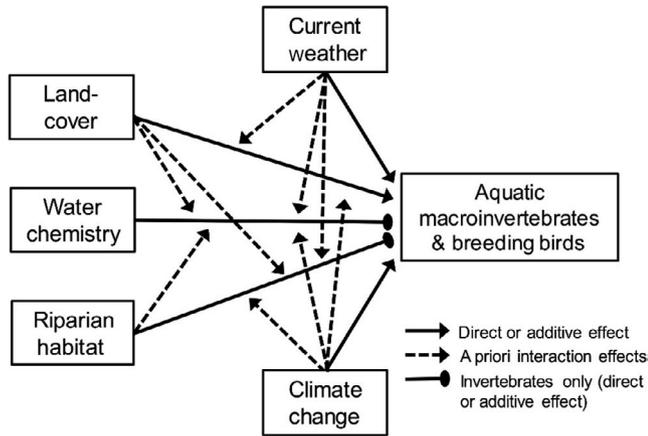


FIGURE 2 A conceptual model of the direct and a priori interaction effects between land use, current weather and climate change that were tested. All indirect links (i.e., dashed lines) are bidirectional interactions in terms of their effects on invertebrates and birds, but with only one arrow shown for each link. For a description of each type of variable (e.g., current weather, climate change), see Table 1 and main text. The direct and interacting effects of riparian habitat and water chemistry were only tested with aquatic macroinvertebrates in this study because this wetland information could not be directly related to the breeding bird data (>200 m between wetlands and bird survey sites)

negatively related to salinity, TP and/or DOC (model-averaged coefficients, Figure 3). Salinity had the strongest negative relationship on macroinvertebrate taxa richness, whereas total precipitation, DOC and TP had the strongest negative relationship on chironomids. Odonates responded most negatively to TP. Abundances of chironomids were positively related to amount of cropland surrounding the wetland basins.

We tested whether negative effects of aqueous chemistry and climate variables were reduced (antagonistic interactions) or intensified (synergistic interactions) by increases in specific land cover types around aquatic survey sites. We found that an antagonistic relationship occurred between non-woody vegetation and salinity on macroinvertebrate taxa richness; a relatively high (>75% = 50th data percentile) % cover of non-woody riparian vegetation reduced the negative relationship of salinity (Figure 4a). A weak synergistic relationship between cropland and total precipitation on chironomids was detected; under higher total precipitation, sites with more cropland cover (>55% = 80th data percentile) were associated with fewer chironomids than sites with less cropland cover, but the trend reversed under dryer conditions (chironomids were more abundant at sites with higher cropland cover (>45% = 75th data percentile); Figure 4b). Another weak synergistic relationship was detected between total precipitation and DOC on chironomids; lower precipitation (188 mm = 20th data percentile) and high DOC were associated with lower chironomid abundance, whereas low precipitation and low DOC were associated with higher abundance (Figure 4c). Finally, a synergistic relationship was found between grassland and TP on odonates; more grassland cover (50% = 75th data percentile) increased the negative impact of higher TP on

odonate abundance (Figure 4d), but when TP was lowest and high grassland cover was present, odonates were most abundant. All other interactions and coefficients were small in magnitude and/or had large error estimates.

3.3 | The influence of land use and climatic factors on birds

We tested for positive effects of grassland and woody plant cover, wetland abundance and precipitation, and negative effects of increased cropland cover and temperature on bird richness and abundance of different functional groups. There were many similarities in the land use and climatic effects among bird functional groups and overall bird species richness (Figure 3). Bird species richness and abundances of aquatic and terrestrial insectivores, aquatic invertivores, terrestrial herbivores and terrestrial insectivores all showed a negative response to cropland. However, for aquatic and terrestrial omnivores, terrestrial carnivores and terrestrial invertivores, the coefficient for cropland was positive. The coefficients for pasture and forages, shrubland, grassland and trees were also positive for bird species richness, aerial insectivores, aquatic and terrestrial insectivores, arboreal herbivores, arboreal omnivores, arboreal insectivores, terrestrial herbivores and terrestrial insectivores. In contrast, aquatic and terrestrial carnivores, terrestrial omnivores, terrestrial carnivores, aquatic omnivores and terrestrial invertivores displayed a negative coefficient for trees. Area of wetlands had a positive relationship on aquatic and terrestrial invertivores, aquatic and terrestrial omnivores, aquatic carnivores, aquatic and terrestrial carnivores, aquatic invertivores and aquatic omnivores. On average, precipitation change and temperature change coefficients were the largest climatic effects and positive, except for aquatic carnivores, aquatic omnivores, terrestrial carnivores and terrestrial omnivores which showed negative relationships with temperature change. Aquatic invertivores, aquatic omnivores and terrestrial invertivores displayed larger negative coefficients for spring temperature or total precipitation.

We tested whether negative effects of temperature and positive effects of precipitation were reduced (antagonistic interactions) or intensified (synergistic interactions) by increases in specific land cover types around bird survey sites, for instance, to unveil whether negative effects of cropland could be offset by extent of natural habitat or warmer, wetter climatic conditions. A negative interaction effect (cf. synergistic relationship) was found between temperature change and cropland on aquatic and terrestrial insectivores, these being less abundant at sites where temperature has increased the most over time (1.32°C = 80th data percentile) and where the % cover of cropland was high (100%); at sites where % cropland was low (0%) and temperature has increased the most over time (1.32°C), abundances of aquatic and terrestrial insectivores were highest (Figure 4e). We also found an interaction (cf. antagonistic relationship) between cropland and temperature change on terrestrial insectivores (Figure 4f); in areas where temperature has increased the most over time, the negative relationship of

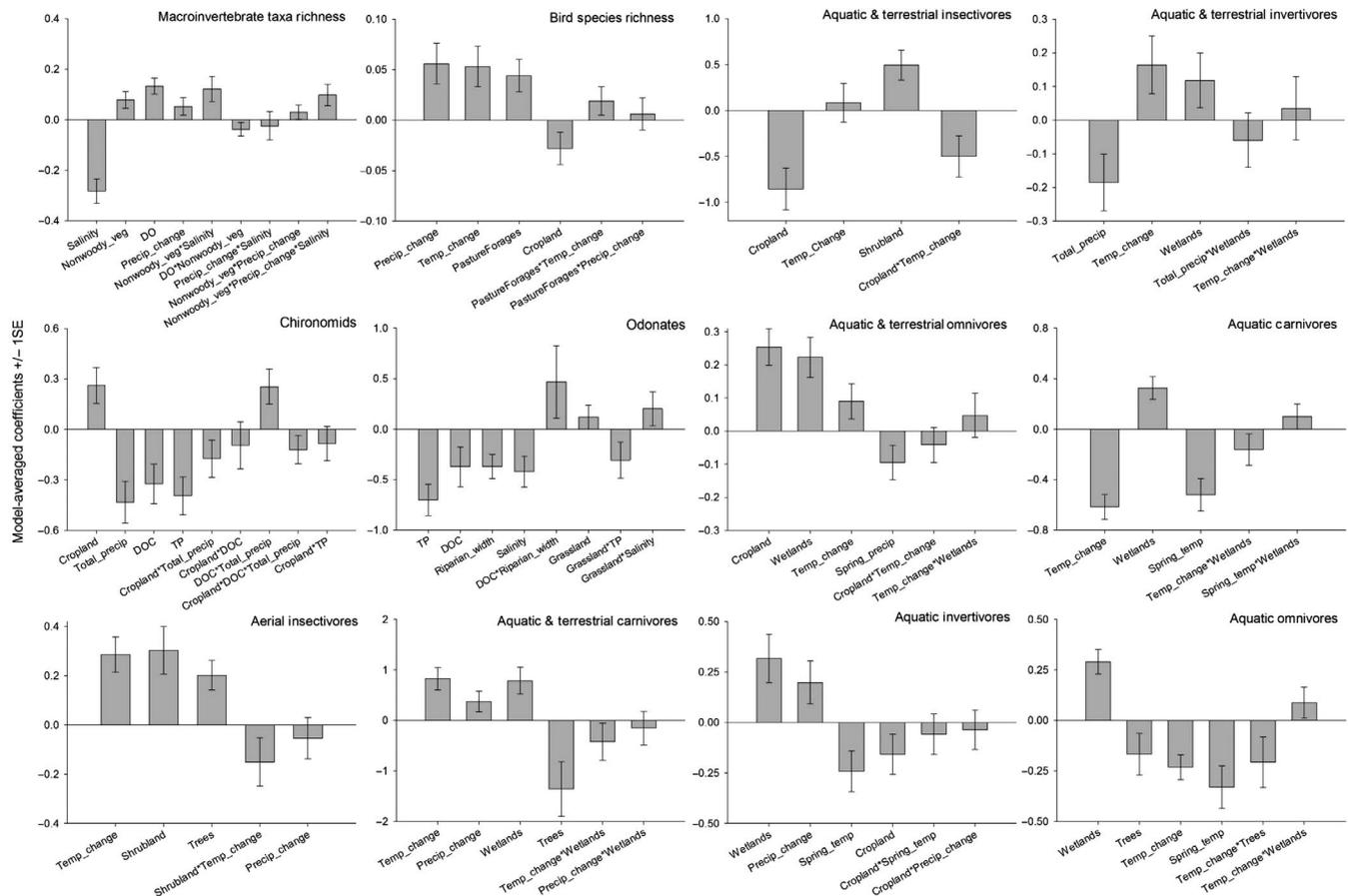


FIGURE 3 Model-averaged (\pm unconditional SE) coefficients from the linear regression models in Appendix S4. All variables are scaled to enable direct comparisons among coefficients in both direction and magnitude. See Table 1 for a description of all variables

cropland on terrestrial insectivores was less in comparison with sites where temperature has increased the least. We identified an antagonistic relationship between shrubland and temperature change on aerial insectivores (Figure 4g); in areas where shrubland was low, higher temperature change ameliorated the negative relationship of less shrubland on aerial insectivores. This antagonistic interaction between shrubland and temperature change was also evident for terrestrial herbivores, arboreal herbivores and arboreal insectivores, but at sites with relatively high shrubland cover (>50%), the abundances of these functional groups were highest where temperature has increased the least (<0.97°C = 20th data percentile; Appendix S5). We identified two opposing interactions between trees and temperature change on terrestrial omnivores and aquatic omnivores: higher temperature change antagonistically reduced the negative relationship of trees on terrestrial omnivore abundance (Figure 4h), whereas higher temperature change synergistically increased the negative impact of higher tree cover on the abundance of aquatic omnivores (Appendix S5). Similarly, higher total precipitation also synergistically increased the negative relationship of higher tree cover on the abundance of terrestrial invertivores (Appendix S5). Finally, a synergistic relationship between shrubland and precipitation change was detected on arboreal omnivores that was not shared with any other functional

group (Appendix S5). All other interactions and coefficients were small or error estimates were large.

4 | DISCUSSION

Climatic and land use variables are related to the responses of avian populations and aquatic macroinvertebrates, but most responses were taxon-specific. Most relationships were direct and several were strong, including some antagonistic and synergistic interactions.

4.1 | Aquatic macroinvertebrates

Macroinvertebrate abundance and taxa richness appear largely driven by water quality, specifically salinity levels, TP and DOC, with some modulation by the surrounding upland and climate. Prairie ponds vary naturally in salinity depending on soil composition and diverse hydrological processes (Euliss & Mushet, 1999). Salinity alters macroinvertebrate community structure and increasing salinity reduces richness in prairie wetlands (Bortolotti, Vinebrooke, & St Louis, 2016; Euliss & Mushet, 1999) and other wetland types (James, Cant, & Ryan, 2003). Likewise, large DOC gradients are common in prairie wetlands and are likely driven more by in-pond processes (e.g.,

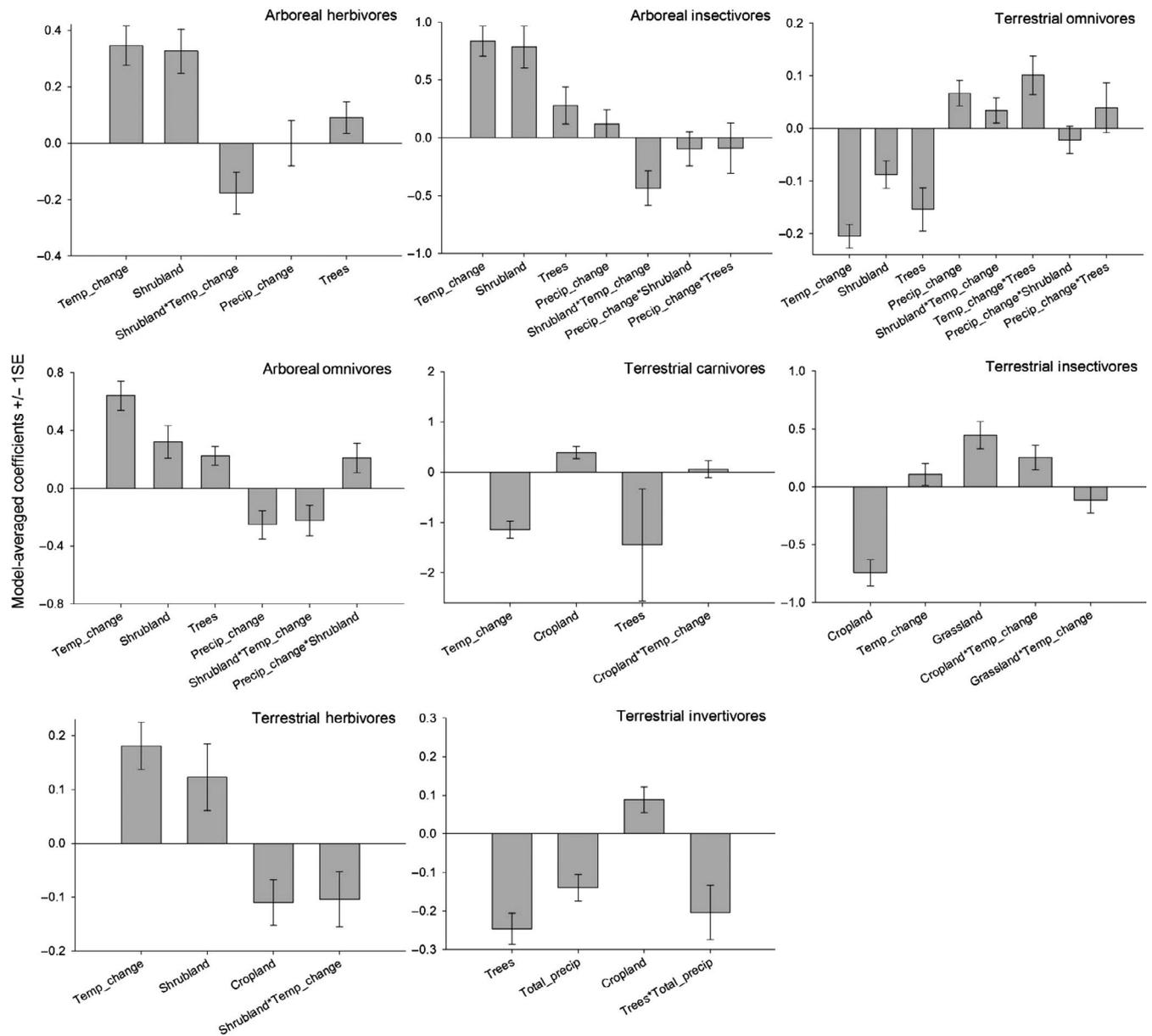


FIGURE 3 (Continued)

production, respiration) than surrounding land use (Waiser, 2006). Chironomids and odonates could respond to factors that may covary with a DOC gradient such as whole-system productivity, vegetation community composition or sediment characteristics (Bortolotti et al., 2016; Euliss & Mushet, 1999). The negative associations between TP and chironomid and odonate abundances coupled with positive associations with the amount of surrounding cropland were surprising, although wetland invertebrate abundance was positively associated with cropland cover in a recent study (Janke, Anteau, & Stafford, 2019). Positive associations between cropland and invertebrates could be driven by the association that more productive land tends to have higher agricultural intensity. TP concentrations tended to increase with surrounding cropland, but multiple ponds had high (>3 mg/L) TP and no cropland within 100 m of wetland survey points, suggesting that macroinvertebrates may respond to anthropogenic and livestock inputs and impacts that occur at larger

scales. Riparian buffer strips can greatly improve the quality of agricultural wetlands by reducing nutrient loading, erosion and other contaminants entering the water due to surface run-off (Schulte et al., 2017; Vought, Pinay, Fuglsang, & Ruffinoni, 1995). Our finding of an antagonistic relationship between non-woody vegetation and salinity on macroinvertebrate taxa richness is important, and consistent with the theory that riparian cover and less intense land use surrounding wetland basins can ameliorate impacts of water quality and potentially future climate change on aquatic macroinvertebrate communities (Mantyka-Pringle, Martin, Moffatt, Linke, & Rhodes, 2014). Protecting and/or restoring riparian zones could also prevent shifts in higher trophic levels from specialized to generalized insectivores due to changes in relative abundances of primary producers (Blann, Anderson, Sands, & Vondracek, 2009). However, our finding of a synergistic relationship between grassland and TP on odonates is inconsistent with this theory. Despite the interaction being weak,

higher grassland cover did not ameliorate the impact of higher TP on odonate abundance. Odonates may be responding to factors that we did not measure (e.g., grazing cattle entering wetlands or per cent cover of bare ground).

We also found a negative relationship of precipitation and synergistic relationships between cropland and total precipitation and between DOC and total precipitation on chironomids. Precipitation and climate play critical roles in the ecology of wetlands (Brooks,

2000; Eimers, Buttle, & Watmough, 2008), with heavy precipitation events known to depress or delay chironomid production at certain times of year (Euliss & Mushet, 1999) or to affect invertebrates via flushing out nutrients from exposed soils (Steinman, Conklin, Bohlen, & Uzarski, 2003), causing higher sedimentation (Gleason, Euliss, Hubbard, & Duffy, 2003) or diluting water chemistry (Eimers et al., 2008). It is possible that fewer chironomids found at sites with higher precipitation and higher cropland could represent a “flushing

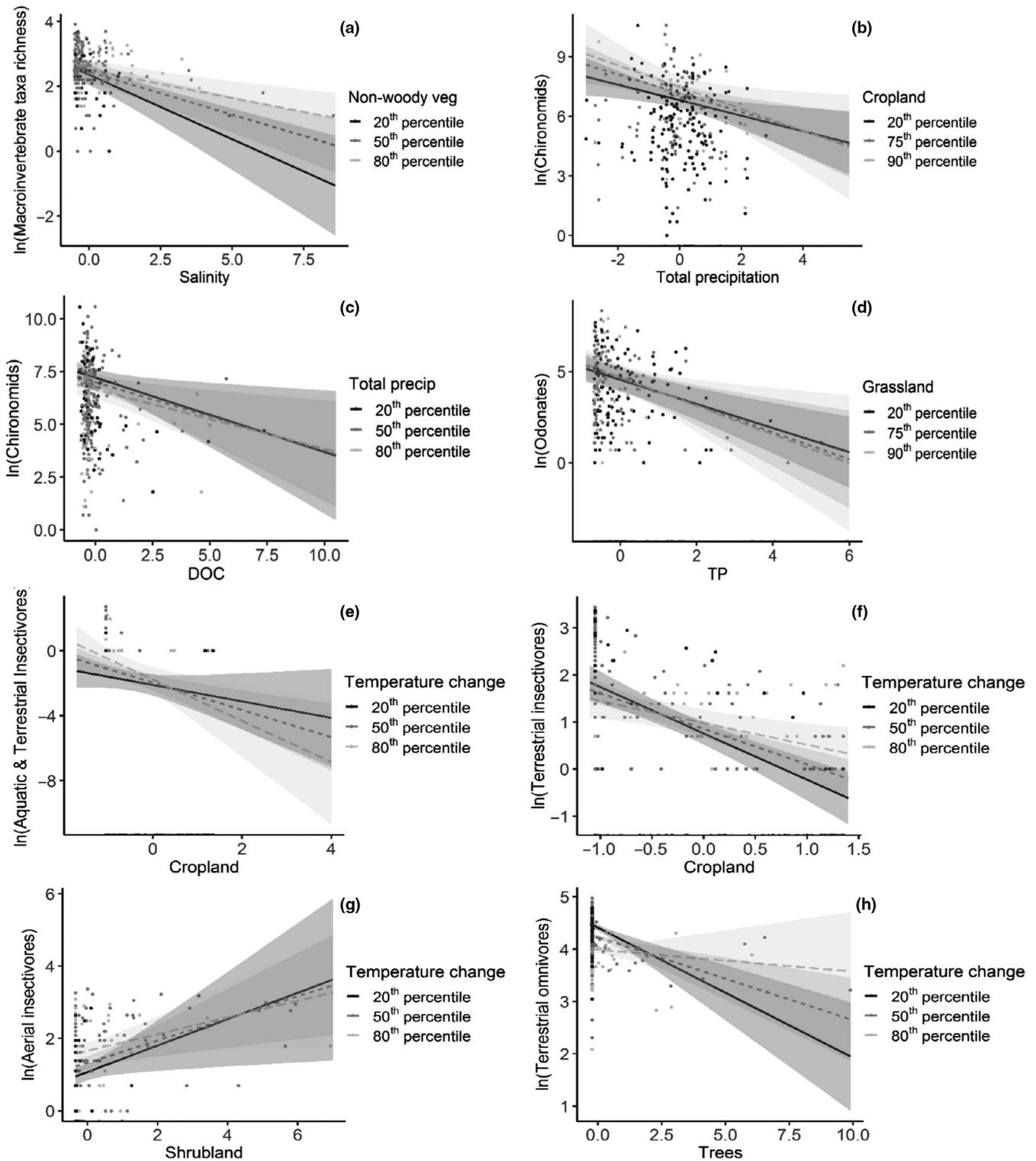


FIGURE 4 Interactions between land use, weather and climate change for aquatic macroinvertebrates ($n = 280$ sites) and bird functional groups ($n = 337$ sites). (a) Antagonistic relationship between salinity and non-woody vegetation on macroinvertebrate taxa richness. (b) Synergistic relationship between cropland and total precipitation on chironomids. (c) Synergistic relationship between total precipitation and DOC on chironomids. (d) Synergistic relationship between TP and grassland on odonates. (e) Synergistic relationship between cropland and temperature change on aquatic and terrestrial insectivores. (f) Antagonistic relationship between cropland and temperature change on terrestrial insectivores. (g) Antagonistic relationship between shrubland and temperature change on aerial insectivores. (h) Antagonistic relationship between trees and temperature change on terrestrial omnivores. Each of the three shaded regression lines represents the 20th, 50th and 80th data percentile or the 20th, 75th and 90th percentiles (if data are highly skewed) in the moderator with 95% confidence intervals. Confidence intervals for these predictions do not incorporate uncertainty in the estimate of variance for the random intercept 'Year', so may be slightly narrower than they should be. Response variables were plotted in log scale and the covariates were standardized ($(x - \text{mean})/SD$) to better display the relationships between variables. Note that other covariates in these models (cf. Appendix S4) were set to their mean values

effect"—supported by the weaker three-way interaction with DOC that we found (Figure 3). Yet, under drier conditions (i.e., less precipitation), chironomids were more abundant at sites with higher cropland cover and lower DOC. This might be due to environmental factors that we did not measure, such as the composition of underlying sediments or the abundance of predators (Schindler, 2006). For instance, the depth of organic sediment may benefit certain taxa, including chironomids, and agricultural activities such as tillage and seeding operations may increase organic sedimentation rates (Cooper, Uzarski, & Burton, 2007). Given that >100 species of chironomids occur in Alberta, it is also possible that these patterns reflect abundance–species trade-offs associated with varying land use and climate conditions, or to species-specific responses to wetland chemistry (Saether, 1979). Odonates use different habitats within wetlands and may be less susceptible to sedimentation effects. In comparison with other freshwater systems such as streams and rivers, prairie wetlands support relatively low macroinvertebrate diversity and communities composed of ecological generalists that are relatively resilient to extreme environmental conditions as a result of a long history of agriculture, strong natural environmental gradients, including drought–deluge cycles in the region (Euliss & Mushet, 1999; Tangen, Butler, & Ell, 2003). In other regions less heavily impacted by climatic extremes and agriculture or other intensive land use, we may anticipate stronger relationships.

In the best model(s) for each response variable, the proportion of variance in our response variables explained by model predictors varied from 0.04 to 0.45 at most, suggesting that there were important variables missing from our models. Differences in prairie wetland hydrology, including variation in water depth and levels over time, may have influenced some of our results, at least for the invertebrate samples. For example, chironomids, odonates and birds in some feeding guilds may have been more abundant at sites with higher cropland cover and lower precipitation, because wetlands surrounded by more cropland may be more likely to be replenished by run-off than wetlands surrounded by more grassland. Grass roots have been shown to facilitate greater soil infiltration of water and reduce the time that water is on the surface to contribute to run-off (Van der Kamp, Hayashi, & Gallen, 2003). At the same time, wetlands surrounded by more cropland may experience greater fluctuations in water levels (Euliss & Mushet, 1996), with fluctuations declining with wetland permanence

and water depth (Johnson, Boettcher, Poiani, & Guntenspergen, 2004). Upland wetlands are more likely to be temporary and to lose solutes to groundwater over time, while lowland wetlands are more likely to be permanent and accumulate water and solutes (McKenna, Mushet, Rosenberry, & LaBaugh, 2017). Wetland water levels are also influenced by water drainage from surrounding lands, and changes in land use may affect drainage patterns (Anteau, Wiltermuth, Burg, & Pearse, 2016); for example, crop ditches can facilitate consolidated drainage into larger, more permanent wetlands (McCauley, Anteau, Burg, & Wiltermuth, 2015). While we lack drainage and water level fluctuation data for the wetlands in our study, we probably reduced some hydrological effects on our results by limiting our analyses to test the effects of fish-free wetlands <3 m deep.

4.2 | Avian species richness and functional groups

Positive associations of pasture and forages, grassland and wooded lands, and negative associations of cropland with most bird groups and overall bird species richness were consistent with previous avian studies in grassland communities globally (Azpiroz et al., 2012; Fuller et al., 1995; Stanton et al., 2018). As natural grasslands are converted to farmland, bird specialists decline and some generalist species benefit (Julliard, Clavel, Devictor, Jiguet, & Couvet, 2006; Kampichler, Turnhout, Devictor, & Jeugd, 2012). In Alberta, aquatic and terrestrial omnivores, terrestrial invertivores and terrestrial carnivores showed a positive association with cropland, and breeding birds such as some duck species, Red-winged Blackbird, and Ring-billed Gull (aquatic and terrestrial omnivores) and Long-billed Curlew (terrestrial carnivore) can increase in response to increases in hayfields and croplands (Clark & Weatherhead, 1986; Janke et al., 2019; Jobin, DesGranges, & Boutin, 1996). Patterns could also be associated with higher soil fertility in cropland. Area of wetlands also had a positive relationship on almost all of the aquatic associated bird functional groups, which typically breed or forage in wetland-rich areas (Steen & Powell, 2012).

Our findings suggest that climate change and recent climate may have a stronger influence than current land use on birds and while climate relationships are well documented, the additional effects of changes since the early 1900s constitute novel findings that merit further investigation as explained below. We initially predicted stronger

land use effects (LeBrun et al., 2016; Scrimgeour & Kendall, 2003). This unexpected result could reflect the relatively low number of studies that have evaluated simultaneously climate change effects relative to those of land use. Precipitation and/or temperature changes over time were consistently key determinants of bird species richness and abundances of specific functional groups, showing three times more positive relationships than negative. Richness and abundance of birds were highest at sites where precipitation and temperature increased the most since the early-mid-1900s, consistent with previous studies (Skagen & Adams, 2012). Other studies indicate that climate plays an important role in determining abundance, but effects tend to be habitat- and species-specific and may differ over a species' annual cycle and range (LeBrun et al., 2016; Lemoine, Bauer, Peintinger, & Böhning-gaese, 2007; Stephens et al., 2016). As the earth is warming, some migratory birds are arriving from the south and nesting earlier in North America and Europe (Butler, 2003). Many species are also moving to areas that have become progressively warmer and possibly wetter (Hitch & Leberg, 2007; Thomas & Lennon, 1999). Thus, if climate trends continue as projected, it is likely that the influence of local climate and climate change will overtake land use as the principal driver of bird populations (Forcey, Linz, Thogmartin, & Bleier, 2007; Lemoine et al., 2007), with evidence here that the shift has already begun in the Canadian prairies. Some species might also shift ranges to escape extreme temperature conditions, and the areas that have become progressively warmer and wetter in Alberta over the past century, may now be more attractive or suitable to birds. Another possible mechanism for this response is that there may be a long-term lag effect of precipitation or temperature change over time (since 1901)—where systems that experience progressively warmer, wetter conditions become more productive, diverse and take longer to develop more abundant biological populations (Pearson & Dawson, 2003).

In contrast, aquatic carnivores, aquatic omnivores, terrestrial carnivores and terrestrial omnivores were less abundant where temperature has increased the most. Likewise, in Europe, increasing temperatures associated with climate change led to both increasing agricultural intensification and reduced terrestrial invertebrate food sources and foraging habitat available to grassland and aquatic birds (Kleijn et al., 2010). Alternatively, these functional groups along with terrestrial carnivores and omnivores (like sparrows and blackbirds) usually nest on the ground or in low vegetation where intensified agricultural practices expose nests to more predators or destruction by farm machinery (Wilson, Whittingham, & Bradbury, 2005), or patterns could potentially be correlated with other factors. For instance, sites that experienced the greatest change in temperature and precipitation since 1901 are also the wettest in recent years and have fluctuated the least in rainfall. Aquatic invertebrates, aquatic omnivores and terrestrial invertebrates, on the other hand, were more sensitive to spring temperature or total precipitation; their abundances decreased with increasing spring temperatures and higher rainfall. Rather than affecting these bird groups physiologically, negative temperature relationships might be associated with changes in the distribution of other species (competitors, predators, parasites) or reduce habitat quality for the affected bird groups (Pearson & Dawson, 2003).

To date, few studies have examined the response of avian communities to interactions between habitat and climatic changes, and these generally focused on species range shifts in forests (Benning, LaPointe, Atkinson, & Vitousek, 2002; Guo, Lenoir, & Bonebrake, 2018; Melles, Fortin, Lindsay, & Badzinski, 2011), global predictions of species richness (Jetz, Wilcove, & Dobson, 2007; Storch et al., 2006) or the widely recognized synergistic effects between temperature, precipitation and habitat loss (Cox et al., 2013; Mantyka-Pringle, Martin, & Rhodes, 2012). We observed several land use–climate interactions on aquatic and terrestrial birds (combined) in agricultural landscapes. First, we detected that greater cropland cover at sites where temperature has increased the most over time resulted in lower abundance of aquatic and terrestrial insectivores. Higher temperatures over time have exacerbated the negative effects of cropland and habitat loss on bird abundances in other studies (Kleijn et al., 2010; Mantyka-Pringle et al., 2012). However, we detected an antagonistic relationship between cropland and temperature change on terrestrial insectivores alone (which includes a variety of ground, shrub, tree, and cavity-nesting birds, mostly passerines). Higher temperature change ameliorated negative relationships of cropland on terrestrial insectivore abundance, a group that could have responded negatively to lower food supplies due to agricultural intensification (Benton, Bryant, Cole, & Crick, 2002; Wilson et al., 2005). We also found that shrubland cover and temperature change had positive relationships on aerial insectivores, terrestrial herbivores, arboreal herbivores and arboreal insectivores. Adverse impacts of shrub cover losses weakened where temperatures had increased the most over time. Finally, we identified opposing relationships between temperature change or total precipitation and tree cover. Temperature change and tree cover had negative relationships on aquatic omnivores and terrestrial omnivores like sparrows, blackbirds and shorebirds, which tend to be less abundant as woodland dominates the landscape (Bakker, Naugle, & Higgins, 2002). However, higher temperature change reduced the negative relationship of trees on the abundance of terrestrial omnivores possibly by enhancing terrestrial food sources, whereas higher temperature change and higher total precipitation synergistically increased the negative relationship of trees on aquatic omnivores and terrestrial invertebrates, respectively. It is possible that higher temperatures provide some birds with greater food availability in cropland sites or sites with less species-specific natural habitat (Skagen & Adams, 2012). Evidence suggests that stressful conditions appear to drive local population dynamics (Parmesan, 2006), and the different responses observed by the avian functional groups probably relate to how their life history traits and physiology influence the ability of species to adapt to changes (Jiguet, Gadot, Julliard, Newson, & Couvet, 2007).

Despite our large sample size (i.e., sites), caution is required when interpreting correlative information because manipulative research is necessary to verify our findings. We also cannot rule out the possibility that the temperature and precipitation relationships are the result of other confounding spatial variables, even though we considered critical land use and weather variables (and spatial location—latitude and longitude) in our analyses. Further work is needed on soils, hydrology, topography, agricultural pesticides and other potential predictors (Kennedy, 1999; Main et al., 2014) before we can generalize conclusions about

specific mechanisms. Likewise, it is difficult to distinguish whether responses to climate change variables represent climate changes alone, recent climatic conditions or some combination; regardless, climate change variables were consistently more informative and retained in best approximating models, suggesting incremental relationships associated with long-term temperature and precipitation changes.

4.3 | Conservation implications

There is an urgent need to address multiple drivers of environmental change, given that interacting threats intensify biodiversity loss (Mazor et al., 2018). A better understanding of interactions can result in improved mitigation strategies, for example, by reducing the impact of local stressors that synergistically interact with global stressors such as climate change and affect biodiversity loss (Didham et al., 2007; Oliver & Morecroft, 2014; Zak et al., 2008). There will always be relative winners and losers with global change. Consequently, species with low adaptability and/or dispersal capacity are generally disproportionately negatively impacted (Heino et al., 2009; Walther et al., 2002). We therefore hypothesize that smaller-sized and/or more specialized organisms tend to respond more strongly to environmental and climate variation than larger and more generalist organisms because of their smaller-scale dependencies on water chemistry, climate and habitat heterogeneity. That we found several interactions between climate and land cover variables on birds also illustrates that each group responds according to specific habitat needs. Generalizing across taxa or even guilds and functional feeding groups can be problematic as we may miss important species-specific responses. One avian group of high conservation concern comprises aerial insectivores because recent population declines may be linked to changes in populations of flying insects (Michel, Smith, Clark, Morrissey, & Hobson, 2016; Nebel, Mills, McCracken, & Taylor, 2010). Now that we have highlighted an important antagonistic response between temperature change and shrubland on aerial insectivores, further work is needed to evaluate how aquatic and terrestrial insects are linked and how these insects respond to on-farm manipulations of natural habitats such as vegetation buffers along field margins and within wetland basins. Some of the patterns presented contrast with our predictions that higher temperatures would be associated with a decrease in overall richness of birds and aquatic macroinvertebrates, and higher rainfall would be associated with increased richness (Cox et al., 2013; Piggott et al., 2015), and these signal that region-specific climate patterns and climatic change may be just as important as local land use pressures and global trends.

Landscapes with a higher proportion of riparian vegetation provide more refugia for species already vulnerable to habitat loss and will only become more important as climate and land use effects intensify. Therefore, our discovery that riparian vegetation ameliorates the negative impacts of climate and water quality gradients on a variety of aquatic macroinvertebrates is key for mitigation. Increasing or maintaining riparian vegetation should be considered in future studies using land management experiments in agricultural environments. Government policies, however, should retain wetlands, areas of natural habitat and riparian

buffers to reduce disturbances and the negative consequences from increasingly intensive agriculture.

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DATA ACCESSIBILITY

All data sources are either cited in text or available from other sources. (e.g., ABMI website).

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BIOSKETCH

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SUPPORTING INFORMATION

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

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