

PRECIPITATION AS A DRIVER OF
AVIAN COMMUNITY STRUCTURE
ACROSS TIME AND SPACE

By

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Abstract: Moisture variability can be a major driver of avian community structure across space by limiting species range edges, and over time by forcing individual movements or temporary species distributional shifts. This study examines (1) how temporal moisture variability changes patterns of species occurrence by assessing the impact of drought on birds in the Great Plains and (2) how spatial moisture variability structures avian communities across a longitudinal precipitation gradient in Oklahoma. Dickey et al. (2011) showed a greater within-range colonization probability during drought ($p < 0.001$) indicating that, in addition to a northward distribution shift already known of the species, Dickey et al. also seek out previously unoccupied areas within the southern/core portion of their range during drought conditions. Different bird species responded to drought assessed at different temporal extents, with most birds showing the strongest signal at an annual or near-annual scale. However, the direction of effect was the same across all drought-responsive species, such that an increased drought intensity at any scale was always associated with decreased bird occupancy. Because drought quantified at multiple temporal extents relates to different hydrologic attributes (for example, drought examined at an annual extent correlates with groundwater availability while drought quantified at a monthly extent relates to precipitation anomalies and soil moisture), considering temporal scale while analyzing drought impacts may begin to reveal the mechanisms behind those impacts. This may provide a broader understanding of the effects of global climate change on species and the landscapes they inhabit. In the Cross Timbers, avian communities had disproportionately higher species richness in riparian areas relative to the surrounding upland areas, a pattern which was not observed in the, comparatively more mesic, Ozark Plateau (i.e., richness was similar between riparian and surrounding upland areas in this region). This suggests high relative conservation importance of riparian areas in a more xeric environment, where riparian corridors represent ribbons of suitable habitat that highly contrast the surrounding landscape, which are crucial for supporting particular forest-dependent species and thus landscape-level biodiversity.

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CHAPTER I

BIRDS SHOW SPECIES-SPECIFIC RESPONSES TO DROUGHT

ASSESSED AT MULTIPLE TEMPORAL EXTENTS

ABSTRACT

A predicted effect of anthropogenic climate change is an increase in frequency and intensity of weather extremes, including increasingly frequent and severe drought conditions in many regions. Drought can negatively impact birds through a variety of mechanisms including inhibiting reproductive success, reducing bird abundance, and forcing range shifts or movement. Drought quantified at multiple temporal extents relates to different hydrologic attributes. For example, drought examined at an annual extent correlates with groundwater availability while drought quantified at a monthly extent relates to precipitation anomalies and soil moisture. Despite these differences, studies examining the impact of drought on birds often default to an arbitrary time scale without considering the largely variable life history requirements among bird species.

Additionally, it is well established that drought conditions can impact bird abundance or drive between-year range shifts overall, however drought may also cause within-range changes in species occupancy distribution. Research objectives were to (1) determine which temporal scale of drought (if any) is most related to Great Plains bird

presence/absence and whether this response is species-specific, and (2) assess whether drought causes within-range changes in local occupancy by quantifying the probability of local colonization and extinction within grassland songbird breeding ranges as a function of drought intensity. I leverage Breeding Bird Survey (BBS) data collected over 16 years, generalized linear mixed modeling coupled with AIC model ranking, and dynamic occupancy modeling to meet these objectives. Dickcissel showed a significantly greater within-range colonization probability during drought ($p < 0.001$) indicating that, in addition to a northward distribution shift already known of the species, dickcissel also seek out previously unoccupied areas within the southern/core portion of their range during drought conditions. Different bird species responded to drought at different temporal extents, with most birds showing the strongest signal at an annual or near-annual scale. The direction of effect was the same across all drought-responsive species, such that an increased drought intensity at any scale was always associated with decreased bird occupancy. Considering temporal scale while analyzing drought impacts may begin to reveal the mechanisms behind those impacts, which will provide a broader understanding of the effects of global climate change on species and the landscapes they inhabit.

INTRODUCTION

A predicted effect of anthropogenic climate change is an increase in frequency and intensity of weather extremes (Rahmstorf and Coumou 2011, IPCC 2013), including increasingly frequent and severe drought conditions in many regions (Seager et al. 2010, Seager et al. 2018). Drought relates to an imbalance between moisture supply

(precipitation) and demand (evapotranspiration; Palmer 1965). Although drought is a natural phenomenon, prolonged deviation from normal conditions can lead to significant agricultural, economic, and natural resource costs. Droughts affect a wide range of animal taxa including invertebrates (Yarnes and Boecklen 2005), fish (Matthews and Marsh-Matthews 2003), marsupials (Rhind and Bradley 2002), and birds (George et al. 1992). As some regions may become drier in the future, developing our knowledge of how species respond to drought conditions will be essential to their conservation and management.

Birds are well-suited to study the ecological effects of drought because they are mobile, they respond readily to changes in their environment, and they are easily observed. Drought affects birds a variety of ways, including driving between-year range shifts or interannual movement (George et al. 1992, Strong et al. 1997, Illán et al. 2014, Bateman et al. 2015) impairing breeding success (Yackel Adams et al. 2006, Skagen and Adams 2012), reducing population size (Albright et al. 2010a, Albright et al. 2010b, Selwood et al. 2015, Gorzo et al. 2016), and decreasing species richness (Albright et al. 2010a, Davey et al. 2011). Besides the impact prolonged drought may have on aquatic birds through direct alteration of foraging and roosting areas, drought may also affect terrestrial species by altering habitat structure or limiting food availability. For example, long term drought can reduce vegetation vigor (Ji and Peters 2003, Gu et al. 2007), cause plant mortality (Breshears et al. 2009), and restructure plant communities by facilitating exotic invasion (Manea et al. 2016). Such changes can directly affect nesting habitat for some species, as well as food availability for frugivores, and foraging efficiency for leaf-gleaning insectivores. Additionally, although the interplay between arthropod abundance

and precipitation is complex and probably taxa-specific (Barnett and Facey 2016), soil moisture can influence arthropod abundance (Carroll et al. 2011), which may restrict or change the availability of important bird food resources. Although there are documented exceptions showing positive bird responses to drought in some regions (Albright et al. 2010a, Albright et al 2010b), the overwhelming tendency is for drought to have a negative influence on birds.

Drought severity is generally determined by spatial extent, duration, and intensity (Wilhite and Glantz 1985). In addition, drought can be quantified at multiple temporal extents (averaging periods), each of which relates to different water resources (McKee et al. 1993). For example, drought quantified at a 12-month averaging period corresponds to groundwater availability (McKee et al. 1993) and reservoir storage (Lorenzo-Lacruz et al. 2010). Conversely, drought quantified at smaller timescales, such as a three-month averaging period, relates to precipitation anomalies that drive soil moisture (McKee et al. 1993) and reservoir input (Lorenzo-Lacruz et al. 2010). Short-term moisture variability can be overlooked when drought is assessed only at an annual or near-annual time scale (e.g., Hayes et al. 1999) and this short-term weather variability can be an important predictor of breeding bird distributions (Bateman et al. 2016).

Despite the differences in hydrologic and ecological attributes driven by varying drought timescales, little is known about which timescales are most important to individual bird species. Studies examining the impact of drought on birds frequently operate on the assumption that species are responsive to the same, dominant timescale and commonly default to a three-month scale aligned with the breeding season (Bateman et al. 2015, Gorzo et al. 2016), or identify a discrete year (or years) as a drought period

from which to compare to wetter period (Smith 1982, Smith 2015). These methods could overlook important species-specific variation due to dissimilarity in resource requirements among species and the variability in habitat attributes correlated with different drought timescales.

Most studies investigating effects of drought or precipitation variability on bird population dynamics have focused on detecting a change in abundance (e.g., George et al. 1992, Albright et al. 2010, Hinojosa-Huerta et al. 2013) or a shift in long-term species range boundary (e.g., Tingley et al. 2012, Illán et al. 2014). However, short-term distributional variability within the known range of a species may also be an important factor describing bird responses to drought stress. For example, Bateman et al. (2015) examined the impact of drought on the spatial pattern of abundance in Dickcissel (*Spiza americana*) and found an increased Dickcissel abundance at the northern edge of their range in response to drought. Aside from Bateman et al. (2015), relatively little is understood about which species might be vulnerable to drought effects that induce such within-range dispersal events or at what timescale they are likely to occur. Specifically I sought to identify whether deviation from normal precipitation patterns changes local colonization or extinction probabilities of grassland birds, a group known for its sensitivity to weather extremes (Gorzo et al. 2016, Zuckerburg et al. 2018) and which has experienced steep population declines in recent decades (Sauer and Link 2011, Sauer et al. 2013).

The objectives of this study are twofold. First, I assessed responses of multiple Great Plains bird species to drought based on which temporal scale (if any) was best

related to species occurrence. Next, I examined the probability of local colonization and extinction within grassland songbird breeding ranges as a function of drought intensity.

METHODS

Study Area

Because birds can have different responses to drought among different ecoregions (Albright et al. 2010a, Albright et al. 2010b), I reduced broad-scale variation by limiting the study area to a single USEPA Level II ecoregion, the South Central Semi-Arid Prairies (Figure 1.1), which includes portions of eight states in the US Great Plains. Land cover is dominated by grassland, cropland, grazing land, and woodland (Omernik 1987). The region has already experienced a recent increase in aridity and is expected to continue this drying trend in the future (Seager et al. 2018), making drought a regionally important facet of climate change in this area.

Data Sources and Pre-Processing

Because drought is difficult to predict (Seneviratne 2012), designing and executing a controlled field study is impractical, especially at large spatial extents. To study songbird responses to drought, repurposing long-term datasets is an attractive approach and the North American Breeding Bird Survey (BBS) is well-suited to meet our research objectives. Initiated in 1966, BBS is a continental-scale dataset of annually surveyed avian point counts across North America collected in May and June. Points are surveyed for three minutes, at approximately 800-meter intervals along established 41-kilometer, roadside transects in North America. All birds detected by sight or sound

within a 400-meter radius are recorded by a volunteer observer. A total of 50 point counts are conducted along each route, however, I included data from only the first five points to reduce the spatial scale of analysis from 41km to 4km, which more closely matches the spatial scale of the available climate data. Giving consideration to spatial scale is important because, although drought is spatially autocorrelated, it does not occur evenly across the landscape.

The study area and timeframe of interest (2000–2015) included 312 BBS route locations. Because I limited analysis to the first five point locations, I georeferenced each start point with a route path shapefile (USGS Patuxent Wildlife Research Center 1999) and selected the anticipated third point location (midpoint of the five point segment) from which to extract climate data. Additionally, I excluded the following data *a priori* to minimize unwanted variation and to strengthen the certainty of observations. First, I removed all data collected by first-year observers to minimize the novice effect (Kendall et al. 1996) and I removed data that did not pass the BBS quality standard (excludes incomplete routes, data collected under unsuitable weather conditions, or outside an ideal sampling time window). Additionally, to minimize effects driven by land cover changes at individual route locations, I removed all routes that had a detectable land cover change during the study period using the annual land cover product developed by the European Space Agency scaled to Level 1 land cover classifications (17 classifications; Defourny et al. 2017). A route with any classification change in one or more 300m-resolution pixels within a 400-m buffer around each 4-km route segment (route path encompassing the first five points, approximately a 3500-square-km area) between years 2000 and 2015 was considered a substantial change. In total, I excluded 32 routes because of a land

cover change and 55 routes due to route location uncertainty or insufficient data. After all data preprocessing steps, the total number of usable routes within the study area was reduced to 225 locations, surveyed by 278 unique observers.

Species included in analysis were only those that met *a priori* criteria including: (1) at least 80% overlap of the study area by the species' breeding range (estimated using Birds of North America species range maps); (2) enough occurrence data to apply the required statistical analyses (at least 600 species presences over 16-year study period); (3) species that sing predictably on their territories during breeding season (e.g. raptors and corvids were excluded); (4) species that are not nocturnal or strongly crepuscular (e.g. owls and nighthawks were excluded); (5) species without strong wetland or urban associations (e.g. European starling and red-winged blackbird were excluded); and (6) species that do not nest colonially (e.g. cliff swallow was excluded). Ten species qualified for analysis: American robin (*Turdus migratorius*), dickcissel (*Spiza americana*), grasshopper sparrow (*Ammodramus savannarum*), horned lark (*Eremophila alpestris*), lark sparrow (*Chondestes grammacus*), mourning dove (*Zenaida macroura*), northern bobwhite (*Colinus virginianus*), northern cardinal (*Cardinalis cardinalis*), scissor-tailed flycatcher (*Tyrannus forficatus*), and western kingbird (*Tyrannus verticalis*).

Analysis of Temporal Scale of Drought Response

To quantify drought, I calculated a total of 12 Standardized Precipitation Evapotranspiration Indices (SPEI) at each BBS point for each year from 2000 to 2015 at varying temporal scales (from averages based on 1 month to averages based on 12

months), timing of measurements (precipitation averaging periods ending in April or June), and time of drought (previous or current year) (SPEI; Vicente-Serrano et al. 2010) using Package SPEI Version 1.6 in Program R (Beguería and Vicente-Serrano 2013). SPEI uses long-term (at least 30-year timeframe) measurements of precipitation and evapotranspiration to determine standard deviations from normal conditions and has the added benefit of allowing temporal scale flexibility. I assessed precipitation and potential evapotranspiration relative to 45-year averages using climate data from 1970–2015. All climate data used for SPEI calculation were at a 4-kilometer resolution and were acquired from PRISM Climate Group (PRISM Climate Group 2004).

Drought scale selections were based off Albright (2010a). For current year drought conditions, I characterized drought at 1, 4, 8, and 12 month timescales using a rectangular kernel (all months weighted equally) and I calculated each scale ending in April (beginning of breeding season) and June (middle of breeding season). I also chose to include a time lag variable to determine whether the previous year's drought conditions impact the current year's bird presence. For these "lag year" drought conditions (dryness of the year preceding each bird survey), I characterized drought at 8 and 12 month timescales ending in April and June. For all metrics, the Hargreaves equation was used to compute potential evapotranspiration, an intermediate step for SPEI calculation (Beguería et al. 2014).

Bird species were assessed independently using presence/absence data from 2000 to 2015 as the response variable for each model. For each route location, I compiled all five points, such that detection at any point signified overall occurrence of the species at the route. I constructed generalized linear mixed models using R Package "lme4" (Bates

et al. 2015) with route location included as a random effect to mitigate the influence of differing land cover types at each sample location. For each species, a total of twelve models were built and each model contained one fixed effect representing a drought scale or lag scale of interest (Table 1). A null model containing only the random effect was also included in analysis. Models were ranked based on minimum Akaike's information criterion (AIC) using R package "bbmle" (Bolker and R Development Core Team 2017). Models with a delta AIC value less than or equal to 2.0 were considered substantially competitive (Burnham and Anderson 2002), but if the null model was also competitive, or if Wald confidence intervals overlapped zero, no drought models were considered competitive for that species, regardless of their delta AIC values.

Colonization and Extinction Rates

To determine whether drought conditions impact bird colonization and extinction rates I used single-species, multiple-season, dynamic occupancy modeling following the framework developed by Mackenzie et al. (2003) and R package "unmarked" (Fiske and Chandler 2011). The model is hierarchal in structure and incorporates a detection probability submodel, allowing for estimation of imperfect detection probabilities when a sampling area is visited more than once per season. Most importantly, the model does not assume consistent occupancy over sampling seasons (in this case, between years) and allows for the estimation of colonization and extinction probabilities and the integration of variables of interest into these estimations. I constructed the model using only one explanatory variable (SPEI) incorporated into both the colonization (γ) and the extinction

(ϵ) terms, initial occupancy (ψ) and detection probability (δ) were not modeled with covariates (Equation 1.1).

Equation 1.1 Dynamic Occupancy Model with drought index as explanatory variable for extinction and colonization probabilities: $\psi + \gamma * \text{SPEI} + \epsilon * \text{SPEI} + \delta$

To model detection probability (δ), I assumed each of the first five BBS points to be a subsample (secondary sampling period=5). I modeled each species separately using the scale of drought from the top model in the drought scale analysis. Only species with a competitive drought model were considered in the colonization/extinction analysis.

Results were considered significant at $p < 0.01$. I chose this higher significance threshold because applying the same statistical test to multiple species increases the probability of a Type I error (false positive), and setting a more conservative threshold mitigates this risk. For significant results, I used the predict command in program R to generate predicted occupancy probabilities using the dynamic occupancy model at 100 values of SPEI and plotted colonization and/or extinction probabilities against SPEI to illustrate the direction of effect.

RESULTS

Within the South Semi-Arid Central Prairies EPA Level II ecoregion in 2015, land cover classifications included grassland (47%), agriculture (34%), shrubland (14%), forest/woodland (4%), urban (1%), water/wetland (<1%), and bare ground/sparse vegetation (<1%). Across the 225 BBS survey locations used for analysis (within a 4km

circular buffer around the center of each route segment), land cover classifications included grassland (48%), agriculture (40%), shrubland (9%), forest/woodland (3%), urban (<1%), water/wetland (<1%), and bare ground/sparse vegetation (<1%). Within the 16-year study period, approximately 77% of BBS points experienced at least one multiyear drought (at least two annual-scale drought years in a row, where SPEI was less than -0.99). Additionally, approximately 35% of BBS points experienced at least one extremely wet year (12-month SPEI ending in June or April greater than 2.0) and approximately 88% BBS points experienced at least one extremely dry year (12-month SPEI ending in June or April less than -2.0). Annual scale (12 month, ending in June) drought conditions varied between -2.89 standard deviations (abnormally dry) and +2.59 standard deviations (abnormally wet) from a 45-year average. One-month scale drought conditions in June varied between -2.56 standard deviations (abnormally dry) and +2.47 standard deviations (abnormally wet) from a 45-year average. These results indicate a substantial variation in moisture across the temporal extent of the study.

Although all variables used in candidate models were a variation of a drought metric quantified using the same standardized precipitation evapotranspiration index, most were not highly correlated. Specifically, only 13 out of 66 total possible combinations of drought variable pairs had a Pearson's correlation coefficient that was greater than or equal to 0.7. Pearson's correlation coefficients ranged between -0.25 (4-month, April-ending current year drought and 8-month, June-ending lag year drought) and 0.91 (8-month, June-ending current year drought and 4-month, June-ending current year drought). Mean drought metric correlation (absolute value) was 0.39.

Temporal Drought Scale Analysis

Of the ten bird species included in analysis, the most frequently observed bird was mourning dove (2,120 occurrences) and the least frequently observed bird was American robin (666 occurrences). All substantially competitive models without zero-overlapping confidence intervals had positive fixed effect coefficients (Table 2). This indicates a negative association between drought conditions and bird presence across all drought-responsive species. The most common top models included an annual-scale, current year drought metric. Current year drought models performed best for American robin, dickcissel, grasshopper sparrow, horned lark, northern bobwhite, scissor-tailed flycatcher, and western kingbird. No species showed a strong response to any lag year drought metrics.

Five species showed the strongest signal at the annual or near-annual scale, including dickcissel (8-month, June-ending), grasshopper sparrow (12-month, June-ending), horned lark (12-month, April-ending), northern bobwhite (12-month, April-ending), and scissor-tailed flycatcher (12-month, April-ending). American robin (1-month, June-ending) and western kingbird (1-month, June-ending) both responded most strongly to fine drought scales. Northern cardinal, mourning dove and lark sparrow had no competitive drought models at any scale.

Colonization and Extinction Rates

Dickcissel colonization probability increased as conditions became more dry ($p < 0.001$, Figure 1.2) but showed no change in extinction probability. Dickcissel colonization probability decreased by about 11% across observed values of SPEI. No

colonization or extinction probability trends were significant for American robin, grasshopper sparrow, horned lark, northern bobwhite, scissor-tailed flycatcher, or western kingbird (Table 3).

DISCUSSION

Drought had a negative effect on all drought-responsive species. Western kingbird and American robin had the strongest response to drought assessed at a fine temporal scale. Specifically, presence of both species was negatively related to a fine temporal scale of 1-month droughts in June. Because fine temporal scale drought conditions are associated with short term precipitation anomalies and soil moisture levels (McKee et al. 1993), it is likely that habitat attributes driven by soil moisture or short term precipitation events during peak breeding season relate to some life history requirement for these species. American robin relies heavily on soft-bodied invertebrates for food during the breeding season (Vanderhoff et al. 2016), and decreased soil moisture likely makes it more difficult to extract earthworms from the soil. Less clear is the influence of soil moisture on western kingbird, a tyrant flycatcher that feeds primarily on flying insects during the breeding season, and the difference between its monthly-scale response and the annual-scale response displayed by its often sympatric congener, scissor-tailed flycatcher. Although both species have similar foraging habits and nutritional requirements, they differ in migration timing, with scissor-tailed flycatcher arriving to breed in the Great Plains several weeks earlier than western kingbird. It is possible that this difference in migration timing could stem from differences in preferred plant phenology and food resources at time of arrival, which may be tied to specific hydrologic

attributes. This could be an important area for future research into the mechanisms of species-specific responses to various temporal scales of drought.

Although the relationship between precipitation and northern bobwhite populations is not always a clear, linear trend (Guthery et al. 2002, see Parent 2016), it is understood that annual-scale drought is a major driver of northern bobwhite survival (Hernandez et al. 2005), reproduction (Guthery et al. 1988, Hernandez et al. 2005), and abundance (Bridges et al. 2001, Lusk et al. 2007). The results of my study supported this pattern: northern bobwhite responded strongly and negatively to annual-scale drought. Three of the five bird species that responded most strongly to annual or near-annual time scales, including northern bobwhite, dickcissel, and horned lark, depend heavily on plant material as an important food resource (Brennan et al 2014, Temple 2002, Beason 1995, respectively). Drought can dampen vegetation vigor (Ji and Peters 2003, Gu et al. 2007), delay seed germination (Dornbos et al. 1989), decrease aboveground net primary productivity (Hoover et al., 2014), decrease herbaceous plant species richness and cover (Copeland et al. 2016), and cause plant mortality (Breshears et al. 2009). Because drought causes damaging impacts to plants through a variety of mechanisms, food availability may be restricted for omnivores such as northern bobwhite, dickcissel, and horned lark during long-term, dry conditions.

Dickcissel showed a significant increase in colonization probability as drought conditions intensified. Dickcissel is an irruptive species with a polygynous mating strategy (Zimmerman 1966) and variable nest site fidelity (Temple 2002). The species is known for its erratic abundance shifts (Temple 2002), including an increase in abundance at the northern edge of its range during drought events (Prestby and Anich 2013,

Bateman et al. 2015). This northward dickcissel range shift has been recorded across multiple drought events, beginning with the 1930s' Dust Bowl drought and continuing through the droughts of 1964, 1988, 2006, and 2012 (Prestby and Anich 2013).

Although northern range abundance pulses have been well documented (e.g. Bateman et al. 2015), this study adds a new piece to the puzzle by assessing dynamic occurrence distribution within the southern/core portion of their range over multiple drought events. Given the known drought-sensitivity of the species, a significant response of dickcissel to drought was unsurprising, however the direction of effect was less expected. Because dickcissel are pushed north during drought conditions, I anticipated an increase in extinction events in the core/southern area of their range. However, this study detected a significant colonization probability increase without a concomitant increase in southerly extinctions. Results indicate that, in addition to a northward abundance pulse, dickcissel also seek out previously unoccupied territories within their range core during drought conditions. It is important to note that the dynamic occupancy model does not reflect abundance information, it simply assesses the species occurrence distribution in relation to the previous year's occupancy. Therefore, it is possible for dickcissel to show increased colonization probability, even if abundance is in decline. I caution against interpreting the lack of significant colonization or extinction probability changes for other species as a lack of effect because the dynamic occupancy model does not capture abundance change.

Although this study found a negative relationship between bird presence and drought conditions across all drought-responsive species, these results highlight the importance of assessing the impact of drought on birds using a species-by-species

approach due to the species-specific relative importance of different temporal scales. Taking temporal scale into consideration while assessing the impact of drought on birds is an approach that may begin to reveal the mechanisms behind drought impacts on birds species because each temporal scale is related to completely separate and often uncorrelated hydrologic attributes, each of which may drive different bird habitat features. Furthermore, this study indicates that birds may use novel areas during unfavorable weather conditions, which highlights the potential ecological importance of areas assumed to be marginal habitat simply because they are unoccupied under normal weather conditions.

REFERENCES

- Albright, T. P., A. M. Pidgeon, C. D. Rittenhouse, M. K. Clayton, C. H. Flather, P. D. Culbert, B. D. Wardlow, and V. C. Radeloff. 2010a. Effects of drought on avian community structure. *Global Change Biology* **16**: 2158–2170.
- Albright, T. P., A. M. Pidgeon, C. D. Rittenhouse, M. K. Clayton, B. D. Wardlow, C. H. Flather, P. D. Culbert, and V. C. Radeloff. 2010b. Combined effects of heat waves and droughts on avian communities across the conterminous United States. *Ecosphere* **1**: 1–22.
- Barnett, K. L., and S. L. Facey. 2016. Grasslands, invertebrates, and precipitation: a review of the effects of climate change. *Frontiers in Plant Science* **7**: 1196.
- Bateman, B. L., A. M. Pidgeon, V. C. Radeloff, A. J. Allstadt, H. R. Akçakaya, W. E. Thogmartin, S. J. Vavrus, and P. J. Heglund. 2015. The importance of range edges for an irruptive species during extreme weather events. *Landscape Ecology* **30**: 1095–1110.
- Bateman, B. L., A. M. Pidgeon, V. C. Radeloff, C. H. Flather, J. VanDerWal, H. R. Akçakaya, W. E. Thogmartin, T. P. Albright, S. J. Vavrus, and P. J. Heglund. 2016. Potential breeding distributions of US birds predicted with both short-term

- variability and long-term average climate data. *Ecological Applications* **26**: 2720–2731.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software* **67**: 1–48.
- Beason, R. C. 1995. *The birds of North America online*. Cornell Laboratory of Ornithology, Ithaca, New York, USA. <http://bna.birds.cornell.edu/BNA/>
- Begueraía, S. and Vicente-Serrano, S. M. 2013. SPEI: Calculation of the Standardised Precipitation-Evapotranspiration Index. R package version 1.6. <https://CRAN.R-project.org/package=SPEI>
- Begueraía, S., S. M. Vicente-Serrano, F. Reig, and B. Latorre. 2014. Standardized precipitation evapotranspiration index (SPEI) revisited: parameter fitting, evapotranspiration models, tools, datasets and drought monitoring. *International Journal of Climatology* **34**: 3001–3023.
- Bolker, B. and R Development Core Team. 2017. Bbmle:Tools for General Maximum Likelihood Estimation. R package version 1.0.19. <https://CRAN.R-project.org/package=bbmle>.
- Brennan, L. A., F. Hernandez and D. Williford. 2014. *The birds of North America online*. Cornell Laboratory of Ornithology, Ithaca, New York, USA. <http://bna.birds.cornell.edu/BNA/>
- Breshears, D. D., O. B Myers, C. W. Meyer, F. J. Barnes, C. B. Zou, C. D, Allen, N. G. McDowell, and W. T. Pockman. 2009. Tree die-off in response to global change-

type drought: Mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment* **7**: 185–189.

Bridges, A. S., M. J. Peterson, N. J. Silvy, F. E. Smeins, and X. Ben Wu. 2001.

Differential influence of weather on regional quail abundance in Texas. *The Journal of Wildlife Management* **65**: 10–18.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer, New York, New York, USA.

Carroll, M. J., P. Dennis, J. W. Pearce-Higgins, C. D. and Thomas. 2011. Maintaining northern peatland ecosystems in a changing climate: effects of soil moisture, drainage and drain blocking on craneflies. *Global Change Biology* **17**: 2991–3001.

Copeland, S. M., S. P. Harrison, A. M. Latimer, E. I. Damschen, A. M. Eskelinen, B. Fernandez-Going, M. J. Spasojevic, B. L. Anacker, and J. H. Thorne. 2016. Ecological effects of extreme drought on Californian herbaceous plant communities. *Ecological Monographs* **86**: 295–311.

Davey, C. M., D. E Chamberlain, S. E. Newson, D. G. Noble, and A. Johnston. 2012. Rise of the generalists: evidence for climate driven homogenization in avian communities. *Global Ecology and Biogeography* **21**: 568–578.

Defourny, P., C. Brockmann, S. Bontemps, C. Lamarche, M. Santoro, M. Boettcher, and J. Wevers. 2017. CCI-LC PUGv2 Phase II. Land Cover Climate Change

Initiative—Product User Guide v2. Issue 2.0.

http://maps.elie.ucl.ac.be/CCI/viewer/download/ESACCI-LC-Ph2-PUGv2_2.0.pdf

Dornbos, D. L., R. E. Mullen, and R. E. Shibles. 1989. Drought stress effects during seed fill on soybean seed germination and vigor. *Crop Science* **29**: 476–480.

Fiske, I. J. and R. B. Chandler. 2011. unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. *Journal of Statistical Software* **43**: 1–23.

Hernández, F., F. Hernández, J. A. Arredondo, F. C. Bryant, L. A. Brennan, and R. L. Bingham. 2005. Influence of precipitation on demographics of northern bobwhites in southern Texas. *Wildlife Society Bulletin* **33**: 1071–1079.

Hinojosa-Huerta, O., P. L. Nagler, Y. K. Carrillo-Guererro, and E. P. Glenn. 2013. Effects of drought on birds and riparian vegetation in the Colorado River Delta, Mexico. *Ecological Engineering* **51**: 275–281.

Hoover, D. L., A. K. Knapp, and M. D. Smith. 2014. Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology* **95**: 2646–2656.

George, T. L., A. C. Fowler, R. L. Knight, and L. C. McEwen. 1992. Impacts of a severe drought on grassland birds in western North Dakota. *Ecological Applications* **2**: 275–284.

Gorzo, J. M., A. M. Pidgeon, W. E. Thogmartin, A. J. Allstadt, V. C. Radeloff, P. J. Heglund, and S. J. Vavrus. 2016. Using the North American Breeding Bird

- Survey to assess broad-scale response of the continent's most imperiled avian community, grassland birds, to weather variability. *The Condor* **118**: 502–512.
- Gu, Y., J. F. Brown, J. P. Verdin, and B. Wardlow. 2007. A five-year analysis of MODIS NDVI and NDWI for grassland drought assessment over the central Great Plains of the United States. *Geophysical Research Letters* **34**: 1–6.
- Guthery, F. S., N. E. Koerth, and D. S. Smith. 1988. Reproduction of northern bobwhites in semiarid environments. *The Journal of Wildlife Management* **52**: 144–149.
- Guthery, F. S., J. J. Lusk, D. R. Synatzske, J. Gallagher, and S. J. DeMaso. 2002. Weather and age ratios of northern bobwhites in south Texas. *National Quail Symposium Proceedings* **5**: 99–105.
- Hayes, M. J., M. D. Svoboda, D. A. Wilhite, and O. V. Vanyarkho. 1999. Monitoring the 1996 drought using the standardized precipitation index. *Bulletin of the American Meteorological Society* **80**: 429–438.
- Illán, J. G., C. D. Thomas, J. A. Jones, W. K. Wong, S. M. Shirley, and M. G. Betts. 2014. Precipitation and winter temperature predict long-term range-scale abundance changes in Western North American birds. *Global Change Biology* **20**: 3351–3364.
- IPCC. 2013. Climate Change 2013: The Physical Science Basis. Intergovernmental Panel on Climate Change, Geneva, Switzerland.

- Ji, L., and A. J. Peters. 2003. Assessing vegetation response to drought in the northern Great Plains using vegetation and drought indices. *Remote Sensing of Environment* **87**: 85–98.
- Kendall, W. L., B. G. Peterjohn, and J. R. Sauer. 1996. First-time observer effects in the North American breeding bird survey. *The Auk* **4**: 823–829.
- Lorenzo-Lacruz, J., S. M. Vicente-Serrano, J. I. López-Moreno, S. Beguería, J. M. García-Ruiz, and J. M. Cuadrat. 2010. The impact of droughts and water management on various hydrological systems in the headwaters of the Tagus River (central Spain). *Journal of Hydrology* **386**: 13–26.
- Lusk, J. J., F. S. Guthery, M. J. Peterson, and S. J. Demaso. 2007. Evidence for regionally synchronized cycles in Texas quail population dynamics. *Journal of Wildlife Management* **71**: 837–843.
- MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* **84**: 2200–2207.
- Omernik, J. M. 1987. Ecoregions of the conterminous United States. *Annals of the Association of American Geographers* **77**: 118–125.
- Manea, A., D. R. Sloane, and M. R. Leishman. 2016. Reductions in native grass biomass associated with drought facilitates the invasion of an exotic grass into a model grassland system. *Oecologia* **181**: 175–183.

- Matthews, W. J., and E. Marsh-Matthews. 2003. Effects of drought on fish across axes of space, time and ecological complexity. *Freshwater Biology* **48**: 1232–1253.
- McKee, T. B., N. J. Doesken, and J. Kleist. 1993. The relationship of drought frequency and duration to time scales. In Proceedings of the 8th Conference on Applied Climatology **17**: 179–183.
- Palmer, W. C. 1965. Meteorological drought. Washington, DC: US Department of Commerce, Weather Bureau.
- Parent, C. J., F. Hernández, L. A. Brennan, D. B. Wester, F. C. Bryant, and M. J. Schnupp. 2016. Northern bobwhite abundance in relation to precipitation and landscape structure. *The Journal of Wildlife Management* **80**: 7–18.
- Prestby, T. G., and N. M. Anich. 2013. The summer of the Dickcissel: 2012. *Passenger Pigeon* **75**: 155–168.
- PRISM Climate Group. 2004. Oregon State University. <http://prism.oregonstate.edu>
- Rahmstorf, S., and D. Coumou. 2011. Increase of extreme events in a warming world. *Proceedings of the National Academy of Sciences*. **108**: 17905–17909.
- Rhind, S. G. and J. S. Bradley. 2002. The effect of drought on body size, growth and abundance of wild brush-tailed phascogales (*Phascogale tapoatafa*) in southwestern Australia. *Wildlife Research* **29**: 235–245.
- Sauer, J. R., and W. A. Link. 2011. Analysis of the North American breeding bird survey using hierarchical models. *The Auk* **128**: 87–98.

- Sauer, J. R., W. A. Link, J. E. Fallon, K. L. Pardieck, and D. J. Ziolkowski Jr. 2013. The North American breeding bird survey 1966–2011: summary analysis and species accounts. *North American Fauna* **79**: 1–32.
- Seager, R., J. Feldman, N. Lis, M. Ting, A. P. Williams, J. Nakamura, H. Liu, and N. Henderson. 2018. Whither the 100th Meridian? The Once and Future Physical and Human Geography of America’s Arid–Humid Divide. Part II: The Meridian Moves East. *Earth Interactions* **22**: 1–24.
- Seager, R., N. Naik, and G. A. Vecchi. 2010. Thermodynamic and dynamic mechanisms for large-scale changes in the hydrological cycle in response to global warming. *Journal of Climate* **23**: 4651–4668.
- Selwood, K. E., J. R. Thomson, R. H. Clarke, M. A. McGeoch, and R. Mac Nally. 2015. Resistance and resilience of terrestrial birds in drying climates: do floodplains provide drought refugia? *Global ecology and Biogeography* **24**: 838–848.
- Seneviratne, S. I. 2012. Climate science: Historical drought trends revisited. *Nature* **491**: 338–339.
- Skagen, S. K., and A. A. Y. Adams. 2012. Weather effects on avian breeding performance and implications of climate change. *Ecological Applications* **22**: 1131–1145.
- Smith, J. E. 2015. Effects of environmental variation on the composition and dynamics of an arid-adapted Australian bird community. *Pacific Conservation Biology* **21**: 74–86.

- Smith, K. G. 1982. Drought-induced changes in avian community structure along a montane sere. *Ecology* **63**: 952–961.
- Strong, A. M., G. T. Bancroft, and S. D. Jewell. 1997. Hydrological constraints on Tricolored Heron and Snowy Egret resource use. *The Condor* **99**: 894–905.
- Temple, Stanley A. 2002. *The birds of North America online*. Cornell Laboratory of Ornithology, Ithaca, New York, USA. <http://bna.birds.cornell.edu/BNA/>
- Tingley, M. W., M. S. Koo, C. Moritz, A. C. Rush, and S. R. Beissinger. 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. *Global Change Biology* **18**: 3279–3290.
- USGS Patuxent Wildlife Research Center. 1999. 1999 Breeding Bird Survey Route Paths for the Lower 48 States. Publisher: National Atlas of the United States.
- Vanderhoff N., P. Pyle, M. A. Patten, R. Sallabanks and F. C. James. 2016. *The birds of North America online*. Cornell Laboratory of Ornithology, Ithaca, New York, USA. <http://bna.birds.cornell.edu/BNA>
- Vicente-Serrano, S. M., S. Beguería, and J. I. López-Moreno. 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *Journal of Climate* **23**: 1696–1718.
- Wilhite, D. A., and M. H. Glantz. 1985. Understanding the drought phenomenon: the role of definitions. *Water International* **10**: 111–120.

Yackel Adams, A. A., S. K. Skagen, and J. A. Savidge. 2006. Modeling post-fledging survival of Lark Buntings in response to ecological and biological factors.

Ecology **87**: 178–188.

Yarnes, C. T., and W. J. Boecklen. 2005. Abiotic factors promote plant heterogeneity and influence herbivore performance and mortality in Gambel's oak (*Quercus*

gambelii). *Entomologia Experimentalis et Applicata* **114**: 87–95.

Zimmerman, J. L. 1966. Polygyny in the Dickcissel. *The Auk* **83**: 534–546.

Zuckerberg, B., C. A. Ribic, and L. A. McCauley. 2018. Effects of temperature and precipitation on grassland bird nesting success as mediated by patch size.

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Table 1.1 Candidate models used in drought scale analysis and a description of the fixed effect represented by each. “Bird” represents annual presence/absence data for each species from 2000–2015; “SPEI” represents the current year drought index (i.e. drought measurements are aligned temporally with presence/absence data); “Lag” represents a drought index from the year prior to bird survey years (i.e., drought measurements are offset from bird surveys by one year to test potential drought lag effects); “RouteID” is a factor assigned to each BBS route location and is included as a random effect in all models.

Model Structure	Fixed Effect Description
Bird~SPEI1A+(1 RouteID)	Current year drought index, 1mo scale, ending in April
Bird~SPEI1J+(1 RouteID)	Current year drought index, 1mo scale, ending in June
Bird~SPEI4A+(1 RouteID)	Current year drought index, 4mo scale, ending in April
Bird~SPEI4J+(1 RouteID)	Current year drought index, 4mo scale, ending in June
Bird~SPEI8A+(1 RouteID)	Current year drought index, 8mo scale, ending in April
Bird~SPEI8J+(1 RouteID)	Current year drought index, 8mo scale, ending in June
Bird~SPEI12A+(1 RouteID)	Current year drought index, 12mo scale, ending in April
Bird~SPEI12J+(1 RouteID)	Current year drought index, 12mo scale, ending in June
Bird~Lag8A+(1 RouteID)	Previous year drought index, 8mo scale, ending in April
Bird~Lag8J+(1 RouteID)	Previous year drought index, 8mo scale, ending in June
Bird~Lag12A+(1 RouteID)	Previous year drought index, 12mo scale, ending in April
Bird~Lag12J+(1 RouteID)	Previous year drought index, 12mo scale, ending in June
Bird~1+(1 RouteID)	Null model

Table 1.2 Response (occurrence) of 10 bird species to temporal scale of drought from generalized linear mixed models ranked by AIC. Only models with $\Delta\text{AIC} \leq 4.0$ and the null model are displayed. Coefficient of the fixed effect (β) and Wald confidence intervals (95%) are provided for models where $\Delta\text{AIC} \leq 2.0$. Each model included route ID as a random effect and one drought scale as the only fixed effect. Models with confidence intervals that did not overlap zero are denoted with “*”.

	Drought Scale	ΔAIC	Weight	β	95% CI
American Robin	Jun-ending 1mo*	0.0	0.46	+0.19	+0.03, +0.35
<i>Turdus migratorius</i>	Null Model	3.5	0.08		
Dickcissel	Jun-ending 8mo*	0.0	0.94	+0.72	+0.57, +0.86
<i>Spiza americana</i>	Null Model	106.7	<0.01		
Grasshopper Sparrow	Jun-ending 12mo*	0.0	0.72	+0.25	+0.13, +0.36
<i>Ammodramus savannarum</i>	Apr-ending 12mo	3.3	0.13		
	Null Model	17.0	<0.01		
Horned Lark	Apr-ending 12mo*	0.0	0.24	+0.16	+0.01, +0.31
<i>Eremophila alpestris</i>	Apr-ending 4mo	0.7	0.16	-0.14	-0.29, +0.01
	Jun-ending 1mo	2.0	0.09	+0.11	-0.03, +0.26
	Jun-ending 8mo	2.1	0.08		
	lag				
	Null Model	2.1	0.08		
Lark Sparrow	Apr-ending 12mo	0.0	0.15	-0.09	-0.19, +0.02
	lag				
<i>Chondestes grammacus</i>	Null Model	0.6	0.12		
Mourning Dove	Null Model	0.0	0.13		
<i>Zenaida macroura</i>					
Northern Bobwhite	Apr-ending 12mo*	0.0	0.88	+0.26	+0.13, +0.38
<i>Colinus virginianus</i>	Null Model	13.5	<0.01		
Northern Cardinal	Null Model	0.0	0.16		
<i>Cardinalis cardinalis</i>					
Scissor-tailed Flycatcher	Apr-ending 12mo*	0.0	0.30	+0.17	+0.02, +0.33
	Jun-ending 12mo	1.3	0.16	+0.14	-0.01, +0.30
<i>Tyrannus forficatus</i>	Apr-ending 8mo	1.7	0.13	+0.14	-0.01, +0.30
	Apr-ending 12mo	2.6	0.08		
	lag				
	Null Model	2.7	0.08		
Western Kingbird	Jun-ending 1mo*	0.0	0.41	+0.13	+0.02, +0.24
<i>Tyrannus verticalis</i>	Null Model	3.1	0.09		

Table 1.3 Summaries of extinction (Ext) and colonization (Col) parameters from dynamic occupancy models. Significant result ($p < .01$) denoted with “*”.

	Drought Scale	Model Parameter	P value	β	95% CI
American Robin	Jun-ending 1mo	Col	0.10	-0.27	-0.60, +0.06
<i>Turdus migratorius</i>	Jun-ending 1mo	Ext	0.62	-0.08	-0.40, +0.24
Dickcissel	Jun-ending 8mo	Col*	<0.001	-0.32	-0.50, -0.14
<i>Spiza americana</i>	Jun-ending 8mo	Ext	0.33	+0.12	-0.12, +0.36
Grasshopper Sparrow	Jun-ending 12mo	Col	0.61	+0.06	-0.16, +0.27
<i>Ammodramus savannarum</i>	Jun-ending 12mo	Ext	0.67	+0.21	-0.01, +0.43
Horned Lark	Apr-ending 12mo	Col	0.70	+0.05	-0.27, +0.17
<i>Eremophila alpestris</i>	Apr-ending 12mo	Ext	0.06	+0.20	-0.01, +0.42
Northern Bobwhite	Apr-ending 12mo	Col	0.50	-0.07	-0.27, +0.12
<i>Colinus virginianus</i>	Apr-ending 12mo	Ext	0.80	+0.04	-0.21, +0.27
Scissor-tailed Flycatcher	Apr-ending 12mo	Col	0.56	-0.10	-0.45, +0.24
<i>Tyrannus forficatus</i>	Apr-ending 12mo	Ext	0.60	+0.09	-0.25, +0.43
Western Kingbird	Jun-ending 1mo	Col	0.75	+0.04	-0.19, +0.27
<i>Tyrannus verticalis</i>	Jun-ending 1mo	Ext	0.99	-0.00	-0.24, +0.23

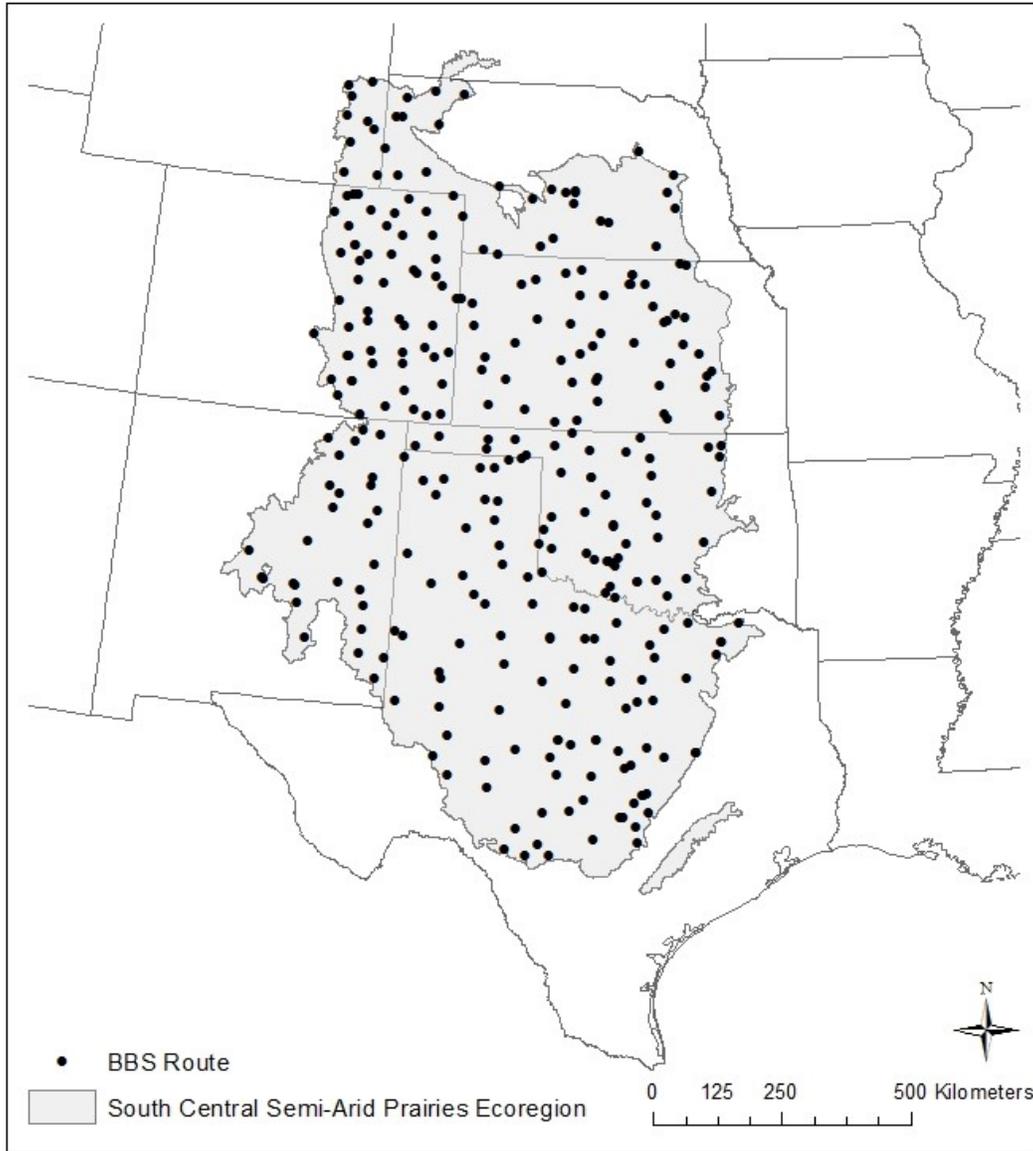


Figure 1.1 South Central Semi-Arid Prairies with starting point location for Breeding Bird Survey routes.

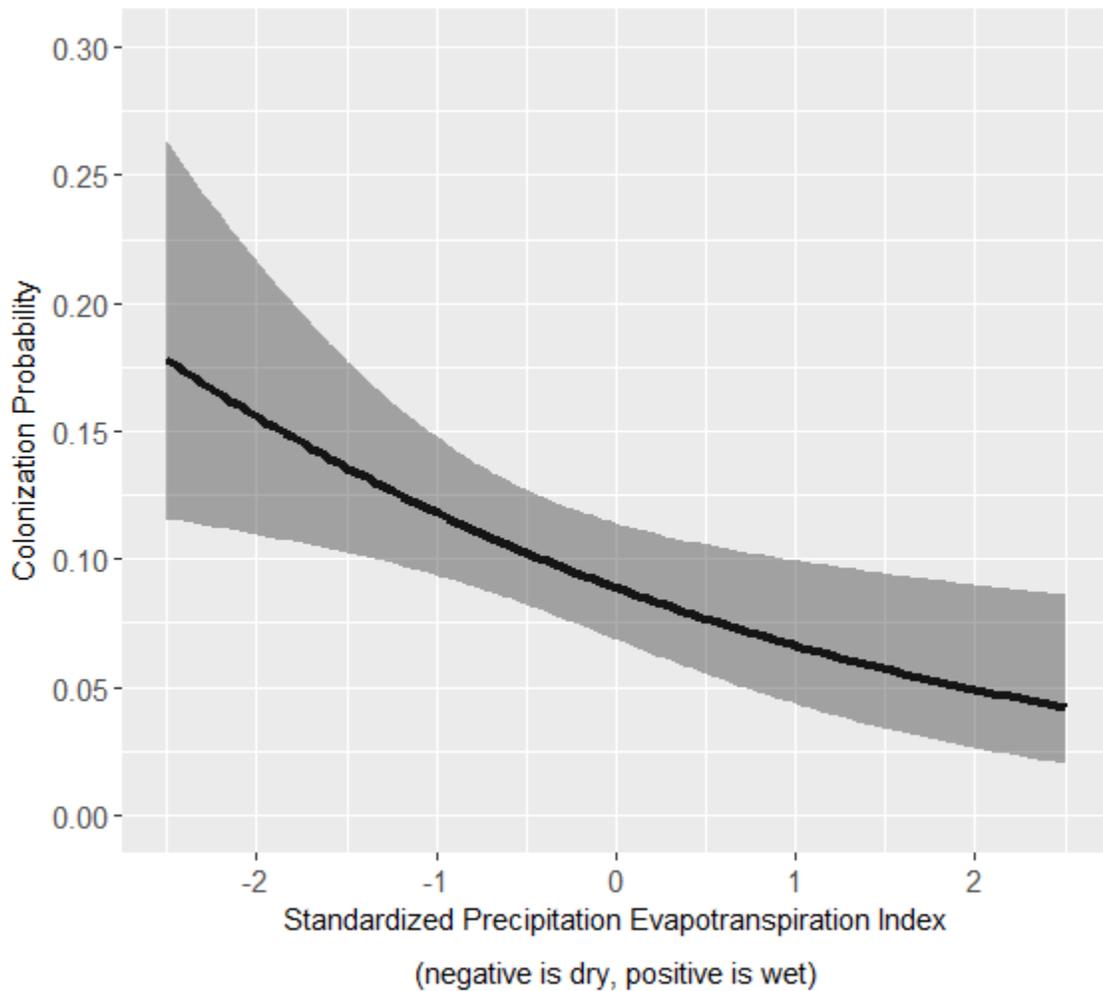


Figure 1.2 Dickcissel colonization probability as a function of 8-month, June-ending standardized precipitation evapotranspiration index with 99% confidence intervals, predicted using dynamic occupancy model.

CHAPTER II

A COMPARISON OF RIPARIAN FOREST BIRD COMMUNITIES ACROSS A CLIMATE GRADIENT IN OKLAHOMA

ABSTRACT

Riparian areas, which encompass the interface between a stream and adjacent terrestrial environment, are dynamic systems with high habitat heterogeneity and sharp environmental gradients. Riparian zones are often biodiversity hotspots that support a disproportionately high representation of some taxa, however this pattern is not always present in bird communities. Although regionally high bird richness in riparian zones has been revealed in arid and semi-arid regions of the globe, this pattern is less consistently observed in more mesic areas. To investigate these bird community patterns, I completed a snapshot study that assessed the degree to which forest bird use of riparian zones was influenced by location on a longitudinal precipitation gradient in Oklahoma. Field crews collected avian community data and vegetation attribute measurements at 192 points in the mesic Ozark Plateau ecoregion and the comparatively xeric Cross Timbers ecoregion in Oklahoma, USA. I qualitatively compared shared species scores and species richness patterns along environmental gradients between these two regions using partial canonical

correspondence analysis. In the Cross Timbers, avian communities had disproportionately higher species richness in riparian areas relative to the surrounding upland areas, a pattern which was not observed in the Ozark Plateau (i.e., richness was similar between riparian and surrounding upland areas in this region). Additionally, some facultative riparian songbirds such as northern parula, Acadian flycatcher, Kentucky warbler, and yellow-throated vireo displayed a weakening in the strength of selection for some vegetation attributes in the Ozark Plateau when compared to the Cross Timbers. This study suggests a pattern of high relative conservation importance of riparian areas in a more xeric environment, where riparian corridors represent ribbons of suitable habitat that highly contrast the surrounding landscape, which are crucial for supporting particular forest-dependent species and thus landscape-level biodiversity.

INTRODUCTION

Riparian zones are dynamic transitional areas that encompass the interface between a stream and its adjacent terrestrial environment, and are recognized as hotspots of habitat heterogeneity (Naiman et al. 2005a) that can exhibit sharp microclimatic and vegetation gradients (Gregory et al. 1991). Specifically, riparian zones are strongly influenced by their stream system and often encompass a steep, localized change in temperature (Naiman et al. 2005b), increase in soil moisture/humidity, and change in canopy and understory vegetation (Moore et al. 2005). Riparian zones provide a wealth of ecosystem services, including nutrient uptake and filtering (Lowrance et al. 1984), high rates of productivity (Naiman and Decamps 1997), provision of refugia during

climatic stress (Selwood et al. 2015, Ninmo et al. 2016), and support for terrestrial, semiaquatic, and aquatic species obligate to these areas (Kelsey and West 1998).

A riparian zone is often a nexus of heterogeneous conditions supporting locally high biodiversity (Naiman et al. 1993, Woinarski et al. 2000, Bub et al. 2004). However, this gradient of diversity defined by local upland and riparian conditions is dependent on both the taxa and the region of interest (Sabo et al. 2005). For example, the relative significance of riparian corridors is at least partially determined by the surrounding landscape matrix (Saab 1999, Rodewald and Bakermans 2006, Lee and Rotenberry 2015) and altitude (Knopf 1985). In arid regions, riparian areas are often structured as ribbons of mesic conditions that strongly contrast the surrounding landscape whereas in more mesic regions, riparian areas may contrast less with the surrounding landscape matrix, which may include a higher percentage cover of upland forests.

Riparian zones support obligate aquatic plants and animals that contribute to their biodiversity, but there is more to be learned about the contribution of riparian zones to regional diversity from species that use them facultatively. Birds are the most frequently studied taxa for analyses of riparian/upland diversity gradients because there are many species of varying riparian affinity (Naiman et al. 2005b) and avian survey methods are well established. Regionally high bird richness in riparian zones has been revealed in arid and semi-arid regions of North America (Szaro and Jakle 1985, Knopf and Samson 1994) and Australia (Shelly 2000, Palmer and Bennett 2006, Woinarski et al. 2008). The contrast between bird communities of riparian zones and associated uplands is often more subtle in more mesic regions (Naiman et al, 2005b) but such differences have still been illustrated in, for example, Newfoundland, Canada (Whitaker and Montevecchi 1999)

and the central Appalachians region of the United States (Murray and Stauffer 1995, O'Connell et al. 2000). The gradient between upland and riparian microclimate and vegetation is not as sharp in mesic regions as it is in arid regions (Naiman et al. 2005b), and the impact of this difference concomitant faunal diversity gradients is not well understood. It is possible, for example, that some species could be obligate riparian-associates in xeric regions but only facultatively riparian in mesic areas (Cavalieri et al. 2009, Sinnott 2014). Riparian zones could also be important in expanding the realized niche of mesic-associated birds into more xeric regions than they could otherwise occupy (Sinnott 2014, Selwood et al 2017).

With its unique position at the transition between temperate broadleaf forest and grassland biomes in central North America, Oklahoma provides a natural laboratory to examine upland/riparian diversity gradients in both mesic and xeric environments. The longitudinal precipitation gradient defines boundaries for ecoregions and distributions of individual species of plants and animals. For example, multiple species of breeding passerine birds with population centers in the forests of eastern North America reach a western distribution limit in eastern or central Oklahoma, and reliance on riparian zones could have a profound effect on how far various species can extend within an otherwise unsuitable matrix (Cavalieri et al. 2009).

My objectives in this study were to first determine whether riparian areas in the Cross Timbers of Oklahoma support a disproportionately higher avian species richness compared to the surrounding upland ecosystems than those located in the more mesic, eastern Oklahoma Ozark Plateau. Next, I studied the degree to which individual songbird

species reliance on riparian zones within forests was influenced by climatic matrix in the mesic Ozark Plateau and the comparatively xeric Cross Timbers ecoregions.

METHODS

Study Area and Site Selection

I sampled public and private land in the Ozark Plateau (which includes sampling within the Ozark Highland and Boston Mountains EPA Level III ecoregions) and Cross Timbers (Cross Timbers EPA Level III ecoregion) in Oklahoma (Figure 2.1). The Ozark Plateau of northeastern Oklahoma, defined here as the area contained by the Arkansas border, the Neosho River, and the Arkansas River, represents eastern hardwood forest habitat conditions typically used by forest birds native to eastern temperate North America. The Ozark Plateau is characterized by deeply dissected limestone and flint formations punctuated with seeps, springs, and caves (Blair and Hubbell, 1938). The region receives approximately 111–132 cm of annual rainfall (PRISM, 2012) and supports oak-hickory forest over most of its area. Dominant upland tree species include blackjack oak (*Quercus marilandica*), post oak (*Q. stellata*), black hickory (*Carya texana*), and winged elm (*Ulmus alata*). In riparian areas, sugar maple (*Acer saccharum*), eastern hop hornbeam (*Ostrya virginiana*), white oak (*Q. alba*) and Chinquapin oak (*Q. muehlenbergii*) can also be common (Blair and Hubbell, 1938).

The Cross Timbers is an ecotone that forms the transition between North America's eastern forest and Great Plains biomes in the south-central US. In undeveloped areas, land cover is a patchwork of grassland, savanna, and oak forest (Johnson and Risser, 1975) with prevailing structure and species composition largely determined by

soil structure and disturbance regime. The Cross Timbers is mostly rolling plains but also contains tablelands and open hills (Omernik, 1987). Post and blackjack oak dominate the canopy of forested areas with eastern redcedar (*Juniperus virginiana*), black hickory, and black oak (*Q. velutina*) also present in high concentrations (Hoagland et al., 1999). The Cross timbers is more xeric than the Ozark Highlands; precipitation averages approximately 80–118 cm annually (PRISM, 2012).

Site Selection and Field Techniques

I targeted survey sites within forested patches with an estimated 50% or greater canopy cover and sampled a total of 192 points (96 paired upland/riparian points, with half of point pairs in the cross timbers and half in the Ozarks). Points were considered riparian if they (1) were located along a first or second order stream bed and (2) supported at least one key woody species often associated with riparian/mesic areas including common spicebush (*Lindera benzoin*), slippery elm (*Ulmus rubra*), American sycamore (*Platanus occidentalis*), bitternut hickory (*Carya cordiformis*), black walnut (*Juglans nigra*), red mulberry (*Morus rubra*), box elder (*Acer negundo*), willow (*Salix* spp.), bur oak (*Quercus macrocarpa*), flowering dogwood (*Cornus florida*), or cottonwood (*Populus deltoides*) (Hoagland 2000). Upland points were sited at least 200m uphill (measured in horizontal distance) from riparian points. Avian point counts were conducted twice during peak breeding season (May and June) in 2017, using an estimated 50-meter fixed radius. All adult birds detected by sight or sound were recorded but potential migrants were not included in analysis.

A suite of vegetation community and structure data were also collected at each sample point and two subpoints. One subpoint was located 30 meters downstream from the original point location, (or 30 meters uphill, if upland) and the second subpoint was located 30 meters southwest from the original sample point. The point/subpoint layout was designed to capture typical vegetation attributes throughout the 50m point count radius, rather than at the observer's location alone. At all bird sampling points and their corresponding subpoints (576 total vegetation sampling points) I: (1) used a clinometer to estimate canopy height of a co-dominant tree, (2) took a spherical densiometer reading in each cardinal direction to determine canopy cover, and (3) took a cover board reading in each cardinal direction and five meters from the observer to estimate understory density (Nudds, 1977). At each sample point and one of its subpoints (randomly selected *a priori*), all trees (dbh > 6cm) in a 10 X 10m plot were identified to species. Finally, we used a diameter tape to estimate dbh for all tree stems identified to species.

Statistical Analysis

To examine the differences between riparian and vegetation attributes in the Cross Timbers and Ozark Plateau, I ran a series of univariate statistical tests. Differences between upland and riparian canopy height, canopy cover, understory density, and basal area were calculated using ANOVA. Differences in tree species richness were calculated using generalized linear mixed models with Poisson distributions. Vegetation attribute differences were considered significant at $p < 0.05$.

I analyzed community-level species scores along environmental gradients using unimodal constrained ordination in Canoco version 5 (Ter Braak and Šmilauer, 2012).

Because study points were clustered due to limited land accessibility, I used partial canonical correspondence analysis (pCCA) with covariate “area” to factor out variation explained by each of the six property areas sampled (Figure 2.1). Response variables included songbird species presence/absence with rare species downweighted (an option selected in Canoco 5 that reduces the effect of species with few occurrences).

Environmental variables included basal area, canopy height, understory density, mature tree species richness, canopy cover, and riparian/upland point location (binary variable).

Species richness diagrams were derived using a loess smoother and count of species present at each point as the response variable. Cross Timbers and Ozark data were analyzed as separate ordinations to allow for comparison among the two regions. I qualitatively compared species richness diagrams and shared species scores between the Cross Timbers and Ozark Plateau regions.

RESULTS

We observed 59 species during point count surveys, 39 of which were used for analysis (Table 2.1). For analysis, I excluded species detected outside their breeding range (cedar waxwing, orange-crowned warbler, and Swainson’s thrush) and birds unreliably detected by point counts (American crow, belted kingfisher, chimney swift, chuck-will’s-widow, Cooper’s hawk, fish crow, great blue heron, Mississippi kite, red-shouldered hawk, ruby-throated hummingbird, turkey vulture, and wild turkey). Of the 39 bird species included in analysis, the most frequently observed species was blue-gray gnatcatcher (260 occurrences over 384 surveys). One survey point was discarded as an outlier because no birds were detected on either of two survey attempts.

Across all sites, ranges of vegetation variables were 35–99% (canopy cover), 4–30m canopy height, 5–116 m²/ha, and 1–62% understory density (horizontal cover < 2m). We encountered 56 species of overstory trees across all 200m² areas sampled at the 96 point locations for birds. Richness averaged 6 tree species/200m² area; post oak was the most abundant species across all sites.

Although basal area estimates were similar across Ozark and Cross Timbers sites, understory density was higher in the Cross Timbers and mean tree richness, canopy height, and canopy cover all tended to be higher in the Ozark Plateau (Table 2.2). Within ecoregions there was no difference in basal area, but canopy height, canopy cover, tree richness, and understory density were higher in riparian than in upland plots. Estimates for canopy height, canopy cover, tree richness, and basal area were similar between Cross Timbers riparian sites and Ozark Plateau upland sites.

Explanatory variables described 13.6% of the total avian community variation in the Cross Timbers and 10.9% of total variation in the Ozark Plateau. Bird species richness was associated with different forest attributes in the two ecoregions (Figure 2.2). In the Cross Timbers, bird species richness was positively associated with tree species richness, canopy height, basal area, canopy cover, and understory density. Conversely, in the Ozark Plateau, bird species richness was highest at intermediate levels of understory density, canopy cover, tree species richness and canopy height. Although upland or riparian point location did not seem to be the primary environmental driver of bird species richness variation at either location, the effect of this factor was slightly higher in the Cross Timbers than in the Ozark Plateau, where species richness was higher in riparian areas compared to surrounding upland areas.

Based on interpretation of ordination results, some bird species selected similar habitat attributes in both the Ozarks and Cross Timbers ecoregions (Figure 2.3 and Figure 2.4). For example, generalist species including tufted titmouse and red-bellied woodpecker, did not show a strong association with any environmental variable in the Cross Timbers or the Ozark Plateau. Black-and-white warbler was associated with moderately open canopy in both study areas. Similarly, eastern wood-pewee was associated with upland sites with open canopy and low understory density, though they tolerated moderately (relatively) higher understory density at Ozark Plateau sites. Louisiana waterthrush, a riparian obligate, selected riparian sites in both study areas.

Other species showed different preferences between the Cross Timbers and the Ozark Plateau (Figure 2.3 and Figure 2.4). For example, some species generally considered to be riparian facultative species, including Acadian flycatcher and northern parula, were more strongly associated with increasing tree species richness in the Cross Timbers, but showed more generalist selection in the Ozark Plateau. Kentucky warbler selected dense understory density in the Cross Timbers, but was closely associated with riparian areas in the Ozark Plateau. Yellow-throated vireo selected for increasing canopy height in the Cross Timbers but selected more intermediate canopy height in the Ozark Plateau.

DISCUSSION

Assemblages of breeding birds in Ozark Highlands and Cross Timbers forests of Oklahoma sorted along gradients of structural vegetation attributes at our scale of inquiry. Regardless of riparian or upland setting, canopy height and canopy cover

explained significant variation in all models, as did the compositional effect of tree species richness and vegetation density in the understory. Basal area of stands was generally not informative to Ozark Plateau models, but did add information to Cross Timbers models. Thus, even within oak-hickory systems, as opposed to broader habitat-selection gradients (such as forested to non-forested matrix), I detected community-level responses of breeding birds to basic information about overstory trees and understory cover.

My study area included two ecoregions that characterize a transition between biomes of broadleaf forest to the east and grassland to the west. Multiple species of birds in this study were encountered at or near a western edge of their global breeding distribution (Cavaliere et al. 2009). These included forest generalists such as tufted titmouse and red-bellied woodpecker that responded similarly to specific habitat attributes in the Cross Timbers or the Ozark Plateau. Additionally, the riparian obligate Louisiana waterthrush (Prosser and Brooks 1998) selected strongly for riparian zones in both ecoregions. Most eastern forest generalists and the Louisiana waterthrush reach their western breeding terminus in Oklahoma at least 150 km west of my study area (Reinking et al. 2004); the conditions they used in my study were similar to conditions occupied by these species across most of their range in the temperate United States.

Other species, especially some closer to their western distribution limit in my study area, revealed variability in their response to vegetation structure in my study area compared to elsewhere in their range. Black-and-white warbler and Eastern wood pewee used moderately open canopy and were more closely associated with upland than riparian points in both the Ozark Plateau and Cross Timbers. This pattern shows a marginal

departure from some documented black-and-white warbler life history descriptions. For example, in eastern Texas, black-and-white warbler was generally associated with tall, dense canopy (Conner et al. 1983). In addition to open canopy, eastern wood-pewee were associated with points with clear understory in the Cross Timbers, though this selection appears to loosen in the Ozark Plateau, possibly because the understory in the Ozark Plateau was significantly less dense than in the Cross Timbers (Table 2.1). This difference continues further east into the Missouri Ozarks, where eastern wood-pewee had no relationship with understory shrub density (Reidy et al 2014).

Some facultative riparian songbirds such as northern parula, Acadian flycatcher, Kentucky warbler, and yellow-throated vireo displayed different habitat affinities in the Ozark Plateau than they did in the Cross Timbers. These are species that reach a western terminus of their distribution in my study area (Reinking 2004). For these species, strength of selection for vegetation attributes in the Ozark Plateau was generally weaker than in the Cross Timbers. For example, Acadian flycatcher and northern parula were associated with high tree species richness and high forest canopy cover in the Cross Timbers, but displayed more generalist patterns in the Ozark Plateau. Similarly, yellow-throated vireo selected for tall canopy in the Cross Timbers but selected more intermediate canopy height in the Ozark Plateau. Kentucky warbler selected dense understory with heavy canopy cover in the Cross Timbers, but was associated with intermediate understory densities and canopy cover in the Ozark Plateau. In the Cross Timbers, Acadian flycatcher, Kentucky warbler, northern parula, and yellow-throated vireo were almost exclusively found in riparian sites. The pattern of facultative riparian birds displaying stronger habitat attribute association in the Cross Timbers could be due

to the overall higher average canopy height, canopy cover, and tree species richness in the Ozark Plateau. Given that a species has an optimal level of a certain habitat attribute, that level may only be reached at the most extreme side of the gradient in the Cross Timbers, but may be found in relatively more intermediate levels in the Ozark Plateau.

Avian diversity gradients were driven by different habitat attributes in the Ozark Plateau and the Cross Timbers. Although the upland/riparian binary variable did not appear to be the strongest driver of bird diversity in the Cross Timbers or the Ozark Plateau, high bird diversity was closely associated with an increase in habitat characteristics that generally describe riparian zones in the Cross Timbers. In general, riparian areas are associated with relatively high basal area (Naiman and Decamps 1997), tall canopy (Palmer and Bennett 2006), dense understory (Palmer and Bennett 2006) and diverse vegetation (Gregory et al 1991). My results indicate that bird diversity in the Cross Timbers was higher where vegetation attributes more closely match this description. The fact that the upland/riparian distinction did not explain a wide range of bird diversity could be a function of lost variability when describing a forest as a simple binary system (upland or riparian), especially because riparian areas are extraordinarily diverse across sites (Minore and Weatherly 1994, Ross et al. 2004). For example, riparian vegetation composition and structure are largely dependent on factors such as flow regime and disturbance frequency (e.g. Nilsson and Svedmark 2002, Lite et al. 2005), water availability (e.g. Lite et al. 2005), geology and fluvial landforms (e.g. Bendix and Hupp 2000, Ross et al. 2004), buffer width (e.g. Elliott and Vose 2016), and surrounding landscape composition (Saab 1999, Rodewald and Bakermans 2006, Lee and

Rotenberry 2015), including anthropogenic disturbances (Nilsson and Berggren 2000, Patten 1998, Pennington et al. 2010).

The same bird diversity pattern was not observed in the Ozark Plateau, where intermediate levels of most environmental variables were associated with the highest bird diversity. Although there were significant differences between vegetation structure and tree diversity between riparian and upland sites in the Ozark Plateau (Table 2.3), bird species richness did not trace those gradients in any single direction. One potential factor driving this difference between Cross Timbers and Ozark Plateau bird diversity patterns is that the Ozark Plateau forests (riparian and upland variables consolidated) have overall significantly higher canopies, more canopy cover, and higher tree diversity than forests in the Cross Timbers (Table 2.2), and therefore the minimum levels of these variables required for some species may be met in upland adjacent to riparian areas as well as the riparian areas themselves. For example, although Ozark Plateau forests had overall significantly higher canopy, more canopy cover, and higher tree diversity than Cross Timbers forests (Table 2.2), there were no significant departures between canopy height, canopy cover, tree species richness, and basal area among Cross Timbers riparian sites and Ozark Plateau upland sites (Table 2.4). It is important to note that species richness does not include information about bird abundance, and it is possible that riparian areas in the Ozark Plateau support a higher abundance of birds without showing a change in species richness. Further research is necessary to refine these patterns using higher resolution bird data such as abundance or population vital rates.

Because avian species richness was disproportionately higher in Cross Timbers riparian areas than their surrounding upland areas, and because this trend was not

observed in the Ozark Plateau, this study supports the pattern that riparian forests in a xeric landscape contribute more to regional diversity than those in a more mesic region. Therefore, these results emphasize the importance of focusing conservation efforts on riparian areas in the Cross Timbers with tall, closed canopy and high tree species richness for maximum avian diversity protection. Furthermore, although there is considerable uncertainty regarding projected global drought trends (IPCC 2013), the Cross Timbers region has already experienced a recent increase in aridity and is expected to continue this drying trend in the future (Selwood et al. 2018). This underlines the importance of future riparian management because riparian areas provide climate refugia for some bird species during times of drought stress (Selwood et al. 2015). It is important to note that this study is structured as a snapshot of a dynamic region and future long-term studies should test whether these patterns hold over time, especially in an increasingly variable climate (IPCC 2013).

REFERENCES

- Bendix, J. and C. R. Hupp. Hydrological and geomorphological impacts on riparian plant communities. *Hydrological Processes* **14**: 2977–2990.
- Blair, W. F., and T. H. Hubbell. 1938. The biotic districts of Oklahoma. *American Midland Naturalist* **20**: 425–454.
- Bub, B. R., D. J. Flaspohler, and C. J. Huckins. 2004. Riparian and upland breeding-bird assemblages along headwater streams in Michigan's Upper Peninsula. *Journal of Wildlife Management* **68**: 383–392.
- Cavalieri, V. S., T. J. O'Connell, and D. M. Leslie, Jr. 2009. A bird community on the edge: Habitat use of forest songbirds in eastern Oklahoma. *Proceedings of the Fourth International Partners in Flight Conference: Tundra to Tropics*: 118–127.
- Conner, R. N., J. G. Dickson, B. A. Locke, and C. A. Segelquist. 1983. Vegetation characteristics important to common songbirds in east Texas. *The Wilson Bulletin* **95**: 349–361.
- Elliott, K. J. and J. M. Vose. 2016. Effects of riparian zone buffer widths on vegetation diversity in southern Appalachian headwater catchments. *Forest Ecology and Management* **376**: 9–23.
- Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. *BioScience* **41**: 540–551.

- Hoagland, B. 2000. The vegetation of Oklahoma: A classification for landscape mapping and conservation planning. *The Southwestern Naturalist* **45**: 385–420.
- Hoagland, B. W., I. H. Butler, F. L. Johnson, and S. Glenn. 1999. The Cross Timbers. Pages 231–246 in R. C. Anderson, J.S. Fralish, and J. M. Baskin, editors. Savannas, barrens, and rock outcrop plant communities of North America. Cambridge University Press, New York, New York, USA.
- IPCC. 2013. Climate Change 2013: The Physical Science Basis. Intergovernmental Panel on Climate Change, Geneva, Switzerland.
- Johnson, F. L., and P. G. Risser. 1975. A quantitative comparison between an oak forest and an oak savannah in central Oklahoma. *The Southwestern Naturalist* **20**: 75–84.
- Kelsey, K. A. and S. D. West. 1998. Riparian wildlife. Pages 235–258 in R. J. Naiman and R. E. Bilby, editors. River ecology and management: lessons from the Pacific coastal ecoregion. Springer-Verlag, New York, New York, USA.
- Knopf, F. L. 1985. Significance of riparian vegetation to breeding birds across an altitudinal cline. Pages 105–111 in R. R. Johnson, C. D. Zeibell, D. R. Patton, P. F. Ffolliott, R. H. Hamre, technical coordinators. Riparian Ecosystems and their Management: Reconciling Conflicting uses. First North American Riparian Conference, Rocky Mountain Forest and Range Experimental Station. Tucson, Arizona, USA.
- Knopf, F. L. and F. B. Samson. 1994. Scale perspectives on avian diversity in western riparian ecosystems. *Conservation Biology* **8**: 669–676.

- Lee, M. B. and J. T. Rotenberry. 2015. Effects of land use on riparian birds in a semiarid region. *Journal of Arid Environments* **119**: 61–69.
- Lite, S. J., K. J. Bagstad, and J. C. Stromberg. 2005. Riparian plant species richness along lateral and longitudinal gradients of water stress and flood disturbance, San Pedro River, Arizona, USA. *Journal of Arid Environments* **63**: 785–813.
- Lowrance, R., R. Todd, J. Fail Jr, O. Hendrickson Jr, R. Leonard, and L. Asmussen. 1984. Riparian forests as nutrient filters in agricultural watersheds. *BioScience* **34**: 374–377.
- Minore, D. and H. G. Weatherly. 1994. Riparian trees, shrubs, and forest regeneration in the coastal mountains of Oregon. *New Forests* **8**: 249–263.
- Moore, R., D. L. Spittlehouse, and A. Story. 2005. Riparian microclimate and stream temperature response to forest harvesting: a review. *Journal of the American Water Resources Association* **41**: 813–834.
- Naiman, R. J., J. S. Bechtold, D. C. Drake, J. J. Latterell, T. C. O'Keefe, and E. V. Balian. 2005a. Origins, patterns, and importance of heterogeneity in riparian systems. Pages 279–309 in G. M. Lovett, M. G. Turner, C. G. Jones, and K. C. Weathers, editors. *Ecosystem function in heterogeneous landscapes*. Springer, New York, New York, USA.
- Naiman, R. J. and H. Decamps. 1997. The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics* **28**: 621–658.
- Naiman, R. J., H. Decamps, and M. E. McClain. 2005b. Riparia: ecology, conservation, and management of streamside communities. Pages 1–418. Elsevier, Amsterdam, Netherlands.

- Naiman, R. J., H. Decamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* **3**: 209–212.
- Nimmo, D. G., A. Haslem, J. Q. Radford, M. Hall, and A. F. Bennett. 2016. Riparian tree cover enhances the resistance and stability of woodland bird communities during an extreme climatic event. *Journal of Applied Ecology* **53**: 449–458.
- Nilsson, C. and K. Berggren. 2000. Alterations of riparian ecosystems caused by river regulation: Dam operations have caused global-scale ecological changes in riparian ecosystems. How to protect river environments and human needs of rivers remains one of the most important questions of our time. *AIBS Bulletin* **50**: 783–792.
- Nilsson, C. and M. Svedmark. 2002. Basic principles and ecological consequences of changing water regimes: riparian plant communities. *Environmental Management* **30**: 468–480.
- Nudds, T. D. 1977. Quantifying the vegetative structure of wildlife cover. *Wildlife Society Bulletin* **5**: 113–117.
- O’Connell, T. J., L. E. Jackson, and R. P. Brooks. 2000. Bird guilds as indicators of ecological condition in the central Appalachians. *Ecological Applications* **10**: 1706–1721.
- Omernik, J. M. 1987. Ecoregions of the conterminous United States. *Annals of the Association of American Geographers* **77**: 118–125.
- Palmer, G.C. and A. F. Bennett. 2006. Riparian zones provide for distinct bird assemblages in forest mosaics of south-east Australia. *Biological Conservation* **130**: 447–457.

- Patten, D.T. 1998. Riparian ecosystems of semi-arid North America: Diversity and human impacts. *Wetlands* **18**: 498–512.
- Pennington, D.N., J. R. Hansel, and D. L. Gorchov. 2010. Urbanization and riparian forest woody communities: diversity, composition, and structure within a metropolitan landscape. *Biological Conservation* **143**:182–194.
- PRISM Climate Group. 2004. Oregon State University. <http://prism.oregonstate.edu>.
- Prosser, D. J. and R. P. Brooks. 1998. A verified habitat suitability index for the Louisiana Waterthrush. *Journal of Field Ornithology* **69**: 288–298.
- Reidy, J. L., F. R. Thompson III, and S. W. Kendrick. 2014. Breeding bird response to habitat and landscape factors across a gradient of savanna, woodland, and forest in the Missouri Ozarks. *Forest Ecology and Management* **313**: 34–46.
- Rodewald, A. D. and M. H. Bakermans 2006. What is the appropriate paradigm for riparian forest conservation? *Biological Conservation* **128**: 193–200.
- Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. *Ecological Applications* **9**:135–151.
- Sabo, J. L., R. Sponseller, M. Dixon, K. Gade, T. Harms, J. Heffernan, A. Jani, G. Katz, C. Soykan, J. Watts, and J. Welter. 2005. Riparian zones increase regional species richness by harboring different, not more, species. *Ecology* **86**: 56–62.
- Selwood, K.E., R. H. Clarke, M. A. McGeoch, and R. MacNally. 2017. Green tongues into the arid zone: river floodplains extend the distribution of terrestrial bird species. *Ecosystems* **20**: 745–756.

- Selwood, K. E., J. R. Thomson, R. H. Clarke, M. A. McGeoch, and R. MacNally. 2015. Resistance and resilience of terrestrial birds in drying climates: do floodplains provide drought refugia? *Global Ecology and Biogeography* **24**: 838–848.
- Shelly, D. 2000. Comparative vertebrate fauna survey of the Paroo, Cobham and Gumbalara landsystems in the Western Division of New South Wales. *Australian Zoologist* **31**: 470–481.
- Sinnott, E. 2014. Riparian influence on eastern songbirds in semi-arid transitional forest. MS thesis, Oklahoma State University, Stillwater, OK.
- Szaro, R. C. and M. D. Jakle, M.D. 1985. Avian use of a desert riparian island and its adjacent scrub habitat. *Condor*: **87**: 511–519.
- Ter Braak, C. J. F. and P. Šmilauer. 2012. Canoco reference manual and user's guide: software for ordination, version 5.0. Microcomputer Power, Ithaca, New York, USA.
- Whitaker, D. M. and W. A. Montevecchi. 1999. Breeding bird assemblages inhabiting riparian buffer strips in Newfoundland, Canada. *The Journal of Wildlife Management* **63**: 167–179.
- Woinarski, J. C. Z., C. Brock, M. Armstrong, C. Hempel, D. Cheal, and K. Brennan. 2000. Bird distribution in riparian vegetation in the extensive natural landscape of Australia's tropical savanna: a broad-scale survey and analysis of a distributional data base. *Journal of Biogeography* **27**: 843–868.

Table 2.1 Thirty-nine bird species detected during 2017 point counts that were included in analysis of riparian and upland communities in the Oklahoma Cross Timbers and Ozark Highlands.

Common Name	Scientific Name	Alpha Code	Common Name	Scientific Name	Alpha Code
Acadian Flycatcher	<i>Empidonax vireescens</i>	ACFL	Northern Cardinal	<i>Cardinalis cardinalis</i>	NOCA
Baltimore Oriole	<i>Icterus galbula</i>	BAOR	Northern Parula	<i>Setophaga americana</i>	NOPA
Black-and-white Warbler	<i>Mniotilta varia</i>	BAWW	Orchard Oriole	<i>Icterus spurius</i>	OROR
Bewick's Wren	<i>Thyromanes bewickii</i>	BEWR	Painted Bunting	<i>Passerina ciris</i>	PABU
Blue-gray Gnatcatcher	<i>Poliophtila caerulea</i>	BGGN	Pine Warbler	<i>Setophaga pinus</i>	PIWA
Brown-headed Cowbird	<i>Molothrus ater</i>	BHCO	Pileated Woodpecker	<i>Dryocopus pileatus</i>	PIWO
Blue Grosbeak	<i>Passerina caerulea</i>	BLGR	Prothonotary Warbler	<i>Protonotaria citrea</i>	PRWA
Blue Jay	<i>Cyanocitta cristata</i>	BLJA	Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	RBWO
Carolina Chickadee	<i>Poecile carolinensis</i>	CACH	Red-eyed vireo	<i>Vireo olivaceus</i>	REVI
Chipping Sparrow	<i>Spizella passerine</i>	CHSP	Scarlet Tanager	<i>Piranga olivacea</i>	SCTA
Downy Woodpecker	<i>Picoides pubescens</i>	DOWO	Summer Tanager	<i>Piranga rubra</i>	SUTA
Eastern Bluebird	<i>Sialia sialis</i>	EABL	Swainson's Warbler	<i>Limnithlypis swainsonii</i>	SWWA
Eastern Phoebe	<i>Sayornis phoebe</i>	EAPH	Tufted Titmouse	<i>Baeolophus bicolor</i>	TUTI
Eastern Wood-peewee	<i>Contopus virens</i>	EAWP	Warbling Vireo	<i>Vireo gilvus</i>	WAVI
Field Sparrow	<i>Spizella pusilla</i>	FISP	White-breasted nuthatch	<i>Sitta carolinensis</i>	WBNU
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	GCFL	White-eyed vireo	<i>Vireo griseus</i>	WEVI
Hairy Woodpecker	<i>Picoides villosus</i>	HAWO	Worm-eating warbler	<i>Helmitheros vermivorum</i>	WEWA
Indigo Bunting	<i>Passerina cyanea</i>	INBU	Yellow-breasted chat	<i>Icteria virens</i>	YBCH
Kentucky Warbler	<i>Geothlypis formosa</i>	KEWA	Yellow-throated vireo	<i>Vireo flavifrons</i>	YTVI
Louisiana Waterthrush	<i>Parkesia motacilla</i>	LOWA	Yellow-throated warbler	<i>Setophaga dominica</i>	YTWA
Mourning Dove	<i>Zenaida macroura</i>	MODO			

Table 2.2 Vegetation structure in Oklahoma Cross Timbers and Ozark Plateau plots. Difference between vegetation structure attributes are significant between Cross Timbers and Ozark Plateau at $p < 0.05$.

	Cross Timbers (n=87)				Ozark Plateau (n=104)				
	Min	Max	Mean	SE	Min	Max	Mean	SE	p
canopy height (m)	4	25	11	0.47	6	30	15	0.54	<0.001
canopy cover (%)	35	99	86	1.55	51	99	92	0.70	<0.001
tree species richness	1	11	5	0.23	2	15	7	0.27	<0.001
understory density (%)	5	53	23	2.25	1	62	19	2.73	0.030
basal area (m ² /ha)	5	78	29	8.00	8	116	26	6.10	0.200

Table 2.3 Vegetation structure of upland and riparian plots in the Oklahoma Cross Timbers and Ozark Plateau. Difference between vegetation structure attributes are significant between riparian and upland areas at $p < 0.05$.

OZARK PLATEAU									
	Riparian (n=52)				Upland (n=52)				p
	Min	Max	Mean	SE	Min	Max	Mean	SE	
canopy height (m)	8	30	18	0.78	6	23	13	0.52	<0.001
canopy cover (%)	75	99	94	0.74	51	99	91	1.16	0.030
tree species richness	3	15	9	0.37	2	11	6	0.29	<0.001
understory density (%)	6	61	22	3.77	1	62	16	3.84	0.050
basal area (m ² /ha)	8	302	35	6.90	11	444	41	10.1	0.600

CROSS TIMBERS									
	Riparian (n=44)				Upland (n=43)				p
	Min	Max	Mean	SE	Min	Max	Mean	SE	
canopy height (m)	7	25	14	0.67	4	15	9	0.38	<0.001
canopy cover (%)	70	99	92	1.05	35	98	79	2.57	<0.001
tree species richness	2	11	6	0.34	1	10	4	0.27	<0.001
understory density (%)	7	53	25	3.23	5	51	20	3.00	0.030
basal area (m ² /ha)	10	344	56	12.0	5	334	47	10.56	0.600

Table 2.4 Vegetation structure from plots in riparian Cross Timbers and upland Ozark Plateau in Oklahoma.

	Cross Timbers Riparian (n=44)				Ozark Plateau Uplands (n=52)				p
	Min	Max	Mean	SE	Min	Max	Mean	SE	
canopy height (m)	7	25	14	0.67	6	23	13	0.52	0.300
canopy cover (%)	70	99	92	1.05	51	99	91	1.16	0.210
tree species richness	2	11	6	0.34	1	10	4	0.29	0.900
understory density (%)	7	53	25	3.23	1	62	16	3.84	<0.001
basal area (m ² /ha)	10	344	56	12.0	11	444	41	10.1	0.400

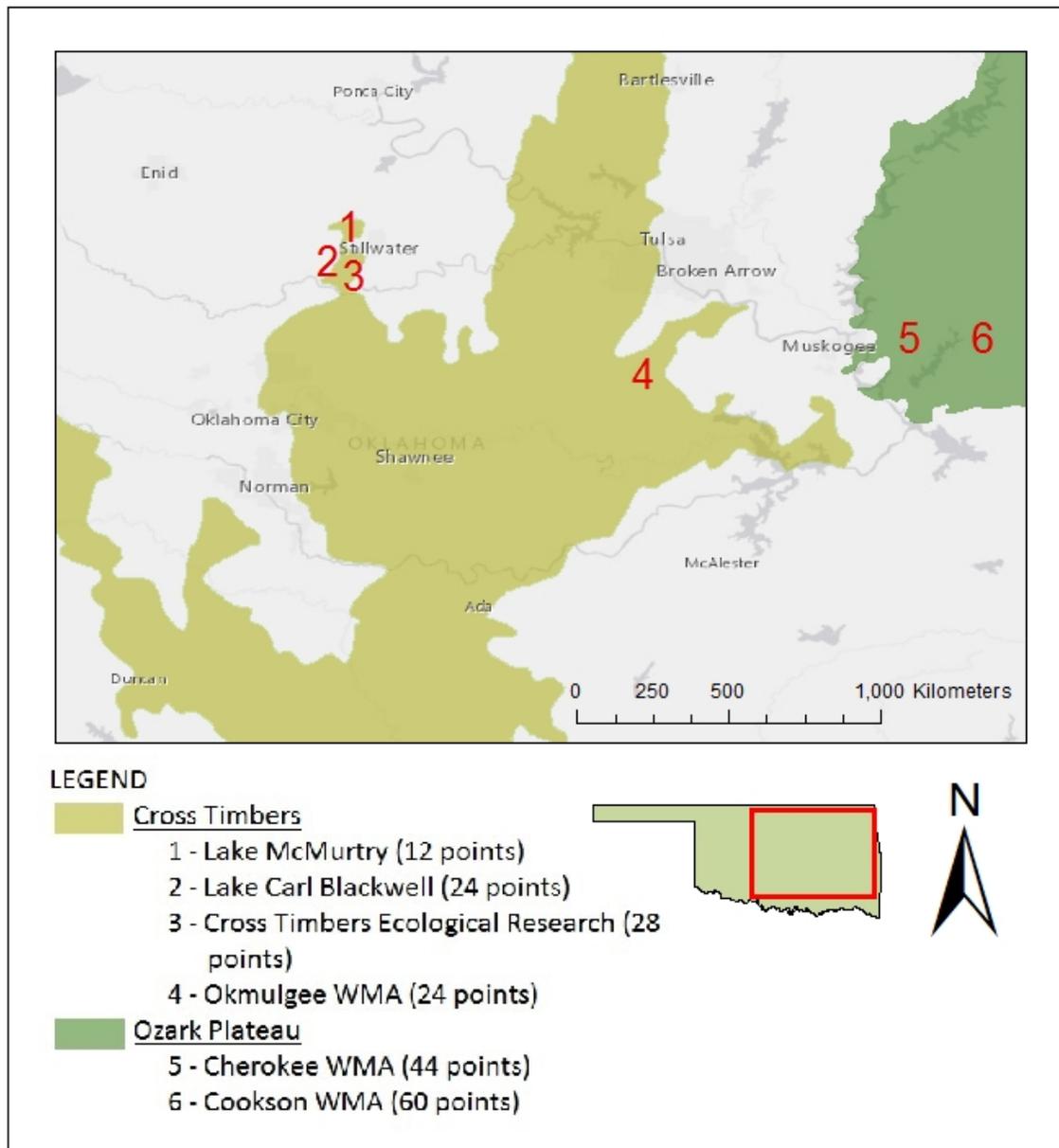


Figure 2.1 Study area with point locations and ecoregion delineations.

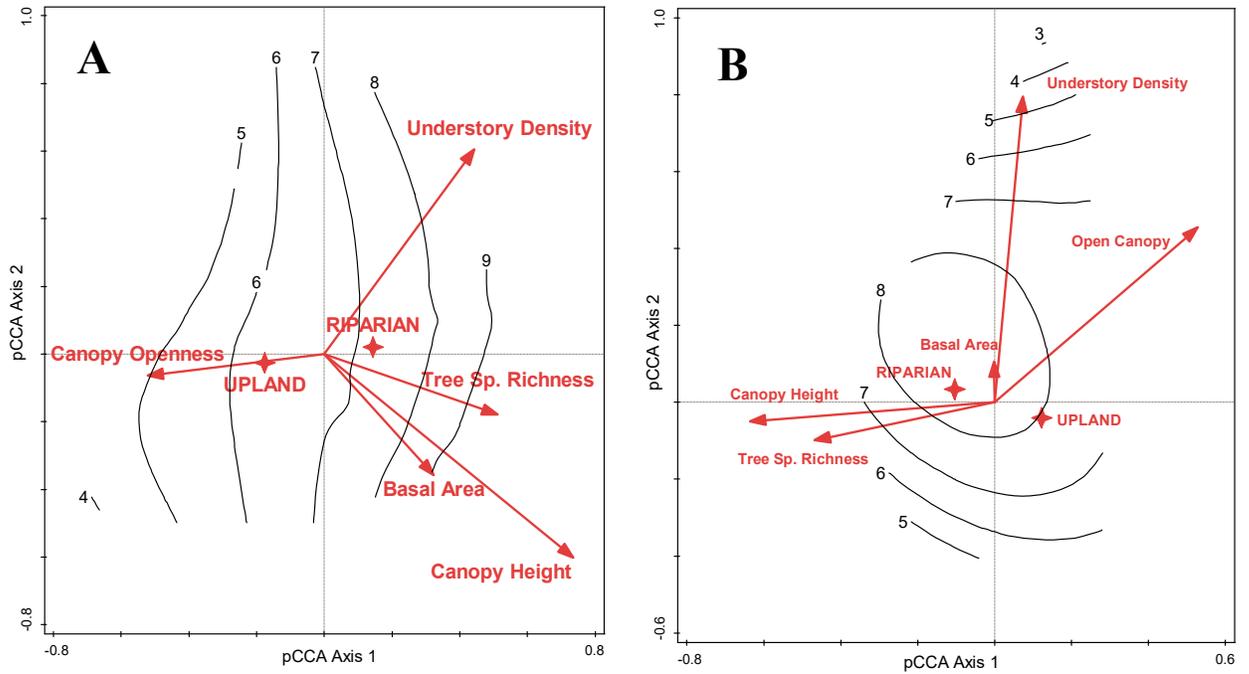


Figure 2.2 Biplots of environmental gradients for upland and riparian forest in the (A) Cross Timbers and (B) Ozark Plateau ecoregions of Oklahoma, USA. Isolines indicate bird species richness at the sampling locations from which the environmental data were obtained.

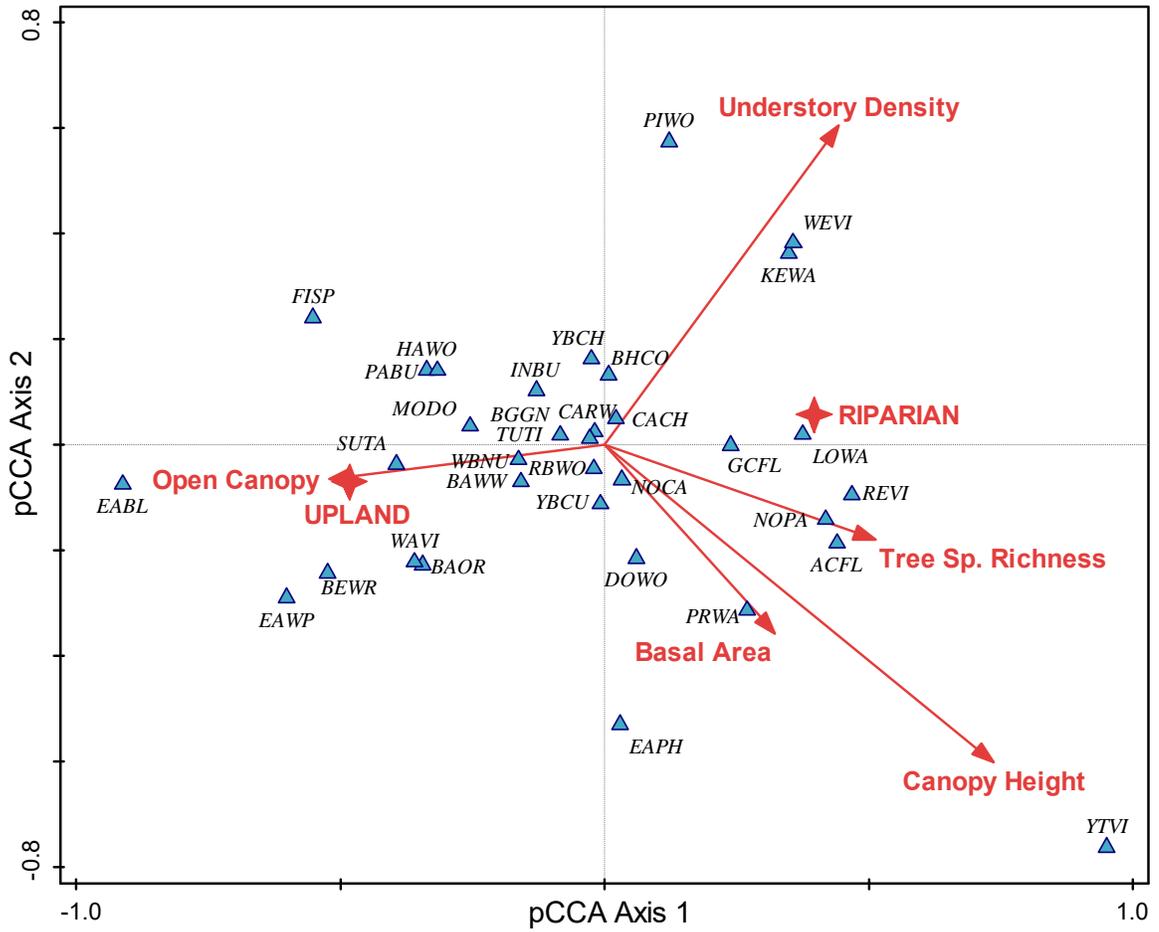


Figure 2.3 Biplot and associated environmental axes of bird species assemblages in upland and riparian forests of the Cross Timbers ecoregion in Oklahoma, USA. Alpha codes for bird species names are listed in Table 2.1.

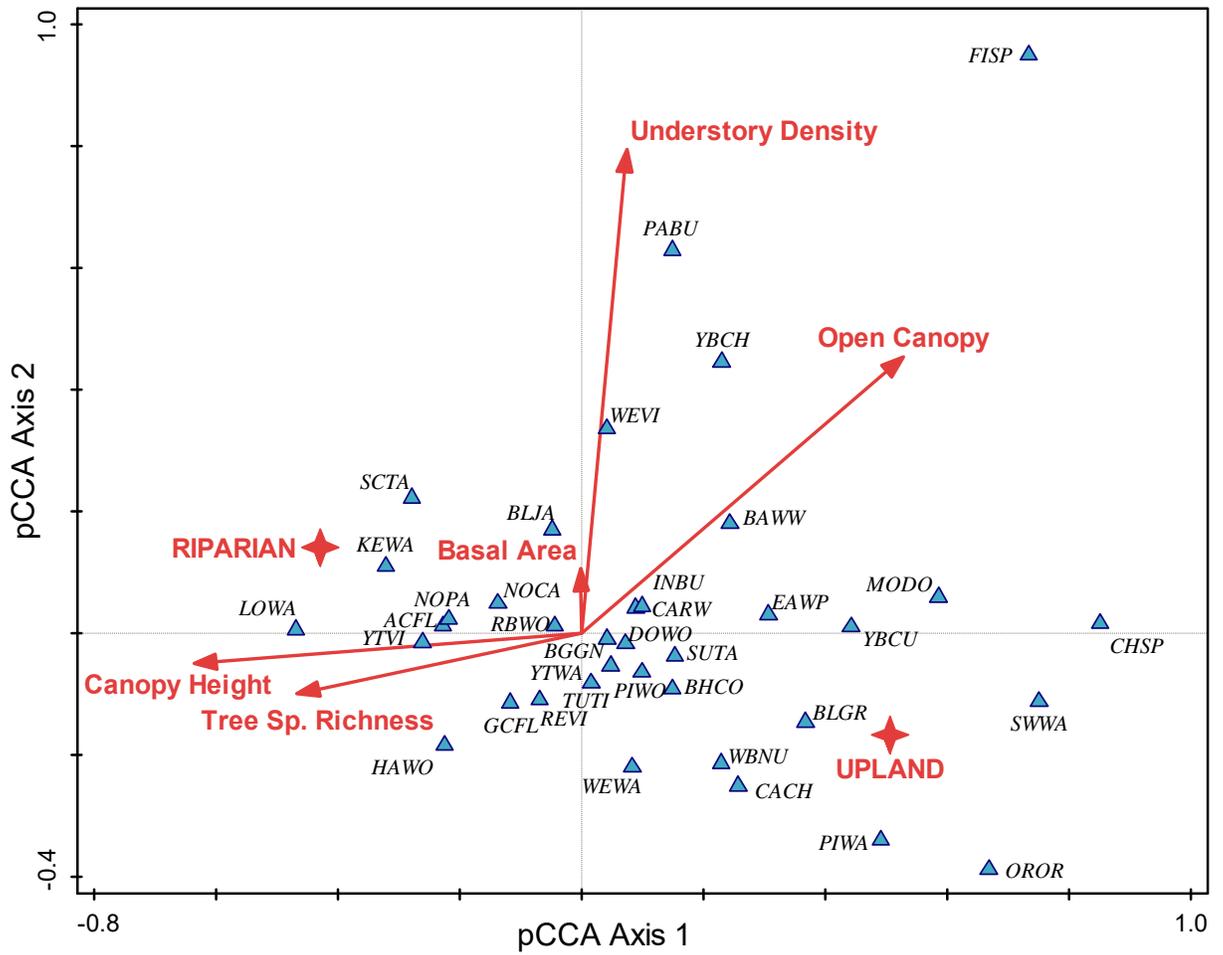


Figure 2.4 Biplot and associated environmental axes of bird species assemblages in upland and riparian forests of the Ozark Plateau ecoregion in Oklahoma, USA. Alpha codes for bird species names are listed in Table 2.1.

VITA

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