Effects of drought on avian community structure

THOMAS P. ALBRIGHT*, ANNA M. PIDGEON*, CHADWICK D. RITTENHOUSE*,
MURRAY K. CLAYTON†, CURTIS H. FLATHER‡, PATRICK D. CULBERT*,
BRIAN D. WARDLOW§ and VOLKER C. RADELOFF*

**Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA,*
†*Department of Statistics, University of Wisconsin-Madison, Madison, WI 53706, USA,* ‡*Rocky Mountain Research Station,*
USDA Forest Service, Fort Collins, CO 80526, USA, §*National Drought Mitigation Center, University of Nebraska-Lincoln,*
Lincoln, NE 68583, USA

Abstract

Droughts are expected to become more frequent under global climate change. Avifauna depend on precipitation for hydration, cover, and food. While there are indications that avian communities respond negatively to drought, little is known about the response of birds with differing functional and behavioural traits, what time periods and indicators of drought are most relevant, or how response varies geographically at broad spatial scales. Our goals were thus to determine (1) how avian abundance and species richness are related to drought, (2) whether community variations are more related to vegetation vigour or precipitation deviations and at what time periods relationships were strongest, (3) how response varies among avian guilds, and (4) how response varies among ecoregions with different precipitation regimes. Using mixed effect models and 1989–2005 North American Breeding Bird Survey data over the central United States, we examined the response to 10 precipitation- and greenness-based metrics by abundance and species richness of the avian community overall, and of four behavioural guilds. Drought was associated with the most negative impacts on avifauna in the semiarid Great Plains, while positive responses were observed in montane areas. Our models predict that in the plains, Neotropical migrants respond the most negatively to extreme drought, decreasing by 13.2% and 6.0% in abundance and richness, while permanent resident abundance and richness increase by 11.5% and 3.6%, respectively in montane areas. In most cases, response of abundance was greater than richness and models based on precipitation metrics spanning 32-week time periods were more supported than those covering shorter time periods and those based on greenness. While drought is but one of myriad environmental variations birds encounter, our results indicate that drought is capable of imposing sizable shifts in abundance, richness, and composition on avian communities, an important implication of a more climatically variable future.

Keywords: abundance, birds, drought, Great Plains, greenness, mixed effects models, North American Breeding Bird Survey, precipitation, richness, United States

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Introduction

The consequences of rising temperature on biota have been the focus of many studies of global change (Parmesan & Yohe, 2003). While trends in mean conditions are clearly important, mounting evidence suggests that changes in the frequency distribution of extreme events may have equally far-reaching implications (e.g. Jentsch *et al.*, 2007). Globally, the area subject to drought is likely to increase in coming decades under climate change (IPCC, 2007). In the southwestern United States and

Correspondence: Thomas P. Albright, tel. + 1 608 265 2228,
fax + 1 608 262 9922, e-mail: talbrig1@wisc.edu

northern Mexico, substantial increases in precipitation variability are associated with the largest predicted North American climate change hot-spot (Diffenbaugh *et al.*, 2008). Extreme droughts can dramatically shift ecosystem structure by inducing widespread vegetation die-off (Breshears *et al.*, 2005). Both trends and increased variability in precipitation have important implications for avifauna and other biota (Parmesan & Yohe, 2003; Both *et al.*, 2006).

There are several mechanisms by which variation in precipitation, and specifically drought, may affect avifauna. First, some species simply require open water as habitat and many require free water for ingestion (Hilden, 1965). Precipitation is also a major driver of

vegetation productivity, flower, seed, and fruit production, and insect abundance, which are key resources for many birds. At local scales, drought may reduce species richness (Hicks, 1935; George *et al.*, 1992) and abundance of individual species and guilds (Marone, 1992; Verner & Purcell, 1999). During drought, birds can suffer increased adult mortality (Mooij *et al.*, 2002), select alternative habitat (Strong *et al.*, 1997; Mooij *et al.*, 2002), engage in fewer breeding attempts (Christman, 2002), be less successful in the attempts made (Li & Brown, 1999), or experience reduced postfledging survival (Adams *et al.*, 2006; Robinson *et al.*, 2007). However, a general broad scale response is not apparent – a perspective supported by a recent synoptic study encompassing central and eastern North America that was unable to detect an influence of interannual variations in precipitation on avian abundance (Valiela & Martinetto, 2007).

Sensitivity and response to drought may vary among avifauna with differing life histories and behavioural characteristics. Birds using habitats that are especially sensitive to varying moisture conditions might be expected to respond more adversely to drought than species that exploit human subsidies. Migratory habit might also influence response based on variations in flexibility in selecting optimum breeding habitat (Mettke-Hofmann & Gwinner, 2004).

The timing and duration of drought are important considerations, as some organisms and processes are sensitive to precipitation at a critical time of the year. It is unclear whether avifauna are more responsive to conditions prevailing during the establishment of territories or during peak nesting. It is also important to consider whether there are lags in observed community response to drought. For instance, drought in 1 year may cause low reproductive success or reduce adult survivorship, resulting in lower population size the subsequent year. Despite these potentially important considerations, neither the effects of drought timing nor the most relevant time periods are well understood for birds.

Adding another dimension to this already-complex picture, the most relevant ways of characterizing drought for avifauna are unknown. One way is based on standardized precipitation measurements for specified time periods (Hayes *et al.*, 1999; Keyantash & Dracup, 2002). Another set of measures is based on the vigour of vegetation, which is usually assessed by remotely sensed vegetation indices (Tucker *et al.*, 1985; Reed *et al.*, 1994; Jakubauskas *et al.*, 2002). Vegetation indices provide spatially detailed information regarding vegetation productivity from precipitation, but are also influenced by irrigation, soil characteristics, vegetation functional types, and other factors (Pennington & Collins, 2007).

In this study, our principal objective was to understand how drought and precipitation variability affect avian communities. We asked four questions pertaining to the avian community as measured by both abundance and species richness ('richness' hereafter). (1) How are overall abundance and richness affected by drought? (2) Are variations in avian communities more strongly related to greenness (i.e. vegetation vigour) or precipitation, and at what time periods are these relationships strongest? (3) How does response vary among behavioural and functional guilds? (4) Does the impact of drought on avian communities vary among ecoregions with different precipitation regimes?

Because of the negative effects of drought on resources important to birds, we expected avian abundance to be negatively affected by drought. We expected a similar, but weaker response for avian richness, given that individual species must decline in abundance before local extirpation occurs. We predicted that synanthropic birds would be buffered from the effects of drought because of their ability to take advantage of food and water supplementation associated with humans. We expected that observed abundance and richness of migratory birds, with their ability to survey and select habitats, would be more likely to respond to drought than resident species. We did not expect any avian groups to respond positively to drought. Reasoning that avian communities are both directly and indirectly dependent on vegetation conditions, we expected greenness to be a stronger predictor of avian response than precipitation. We further expected that drought metrics culminating in June (the period of peak nesting, for most areas in this study), would be more strongly related to avian abundance and richness than April-culminating metrics. Finally, we expected to find geographic variation in response to drought, with stronger effects in arid and semiarid regions because vegetation in these regions may be more responsive to fluctuations in precipitation.

Methods

Our study area encompassed 15 states of the central United States (3.7 million km^2; Fig. 1). This largely temperate region is centred on the Great Plains, a gently sloping prairie landscape currently dominated by cropland and pasture. The region is bounded in the west by the Rocky Mountains and in the east by the Southern Mixed Forest, Ozark Highlands, and Eastern Broadleaf Forest. Excluding mountainous areas, the region is subject to an overall gradient of declining mean annual precipitation from east ($80–140$ cm yr^{-1}) to west ($25–35$ cm yr^{-1}), with central and western portions being the centre of the historic 'Dust Bowl' droughts of the
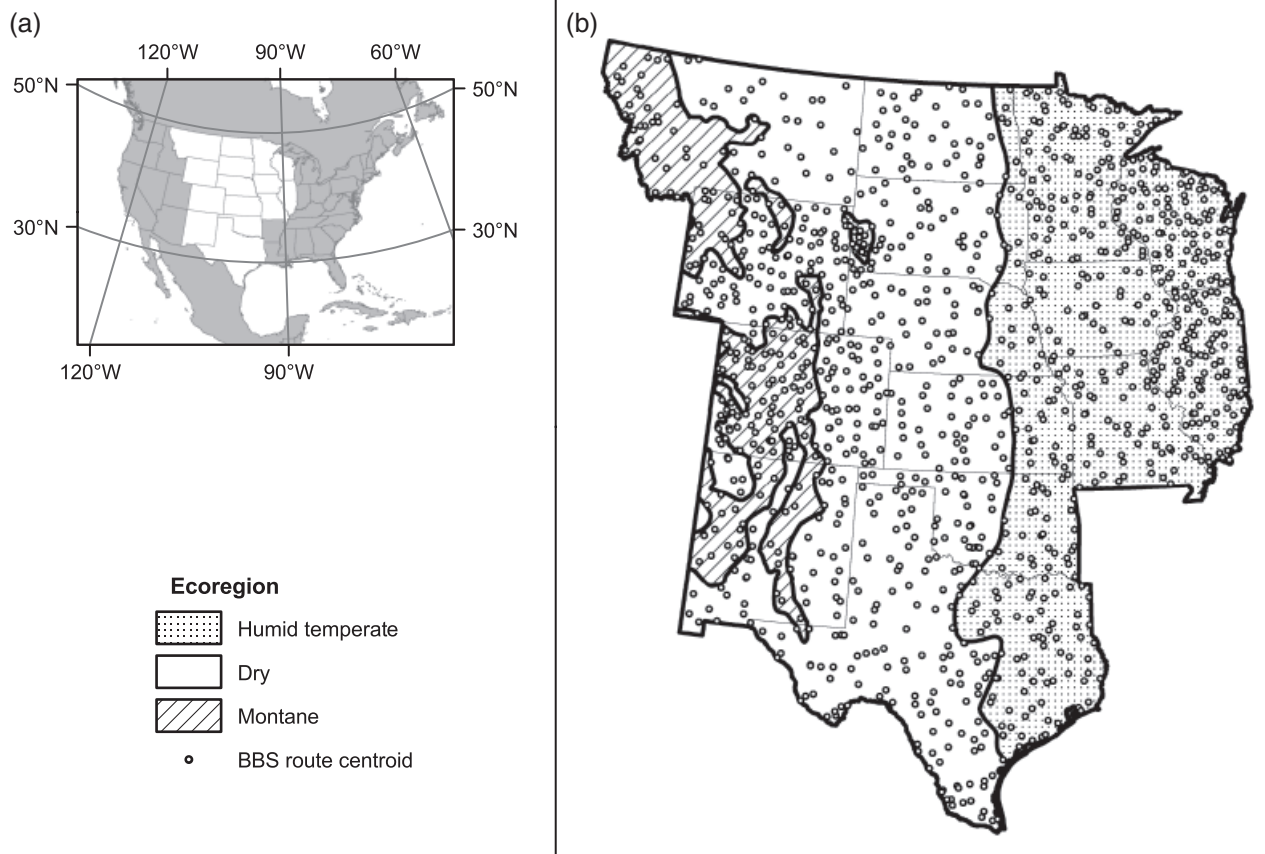
Fig. 1 The 15-state central United States study region (a) and North American Breeding Bird Survey route locations with the modified Bailey's Domains (1995) used in the study (b).

1920s and 1930s. Mountainous portions of the west depart from this gradient by experiencing more precipitation (e.g. $95 \, cm \, yr^{-1}$), much of it as snow. This diverse region, with its wide range of temperature, precipitation, and elevation, includes both eastern and western United States bird species.

Avian response measures

We used counts of breeding birds obtained from the North American Breeding Bird Survey (BBS) (Sauer *et al.*, 2008). Our study area includes 1,287 39.4 km BBS routes (Fig. 1b). Along each route, fifty 3-min point counts are conducted annually during peak breeding season in which all birds seen or heard within 400 m are recorded. The conditions under which data are obtained in any given route and year can vary due to differences in the observer, weather, and other factors (Link & Sauer, 1997; Sauer *et al.*, 2004). Because of this, we retained observer identification codes and removed route-year data collected by first-year observers and those conducted during inclement weather. For each suitable

route-year between 1989 and 2005, we tabulated counts of individual birds for (a) the overall avian community, (b) three migratory guilds (Rappole, 1995), and (c) one guild composed of full and partial synanthropic birds (Johnston, 2001) (Table 1). We used data from this period to correspond to the availability of drought metric data (below). We excluded rare species, which occurred in fewer than 30 route-years over the history of BBS in the conterminous United States, as these species may be transient or poorly sampled by the BBS. We omitted unidentified species that could not be reliably assigned to a species based on geographic location. For each guild, we additionally generated a 'common species-removed' abundance dataset by removing from the abundance tallies the 12 most common bird species, which constituted 49% of all individuals tabulated from the BBS during the period of our study over the 15-state region. Lists of guild membership and proportions of shared membership among guilds are provided in supporting information (Tables S1 and S2, respectively).

It has become common to estimate species richness derived from BBS data using the program COMDYN

Table 1 Avian guilds used in the study

Guild theme	Guild	Species pool	Description
Avifauna	Overall	406	Sum of the three migratory guilds
Synanthropy	Synanthropes	30	Full and partial synanthropes
Migratory habit	Permanent residents	82	Do not migrate away from breeding range
	Short distance migrants	88	Winter north of Tropic of Cancer
	Neotropical migrants	236	Winter south of Tropic of Cancer

'Species pool' refers to the number of species in the guild observed and included in the routes in the study area over the period 1989–2005.

(http://www.mbr-pwrc.usgs.gov/software/estimation_of_bird_community_dyn.hrm), which accounts for non-uniform detectability in point counts and associated downward-biased richness estimates (Boulinier *et al.*, 1998; Hines *et al.*, 1999). Although we also analysed COMDYN-adjusted richness estimates (see supporting information), we present results using 'raw' BBS richness counts because the jackknife-based adjustments used by COMDYN have been shown to reduce precision of richness estimates relative to raw counts (Kéry & Royle, 2008). As our interest lies in interannual comparisons within routes, poor precision is a greater concern than downward biases in absolute richness estimates.

Indicators of drought

To characterize drought and precipitation variability, we used the standardized precipitation index (SPI) (Hayes *et al.*, 1999). This index provides the temporal flexibility to assess drought conditions across multiple time intervals ranging from a few weeks to a year or longer. The SPI scales precipitation in units of standard deviations (SDs) from mean precipitation for each location and time period. For SPI calculation, the long-term precipitation record (ideally >60 years) over a specific time interval in a specific geographic location is used to fit a gamma distribution that places the long-term mean SPI for that time interval and location to zero. A negative SPI value indicates that precipitation is less than the historical mean precipitation and a positive SPI value reflects greater precipitation than the historical average. Using the Applied Climate Information System (http://rcc-acis.org) (Hubbard *et al.*, 2004), we obtained the entire available record of SPI data (1989–2005) from the High Plains Regional Climate Center based on precipitation data from a network of 1639 weather stations. We included eight SPIs from 4-, 16-, 32-, and 52-week windows ending on the 18th (April) and 26th (June) weeks of the year, corresponding roughly to territory establishment and peak nesting activity, respectively. We produced a map of each SPI by interpolating values from the weather stations using inverse distance weighting (Fig. 2a). All geoprocessing operations were performed in ArcGIS (ESRI, Redlands, CA, USA) and the add-on Hawth's Tools (Spatial Ecology, Alberta, Canada). Finally, we intersected each of the interpolated SPI maps with locations of BBS route centres.

Interannual variation in greenness was characterized by measurements of standardized seasonal greenness (SSG). For each year in the same 1989–2005 period, greenness during each 10-day period of the year was measured from normalized difference vegetation index (NDVI) values obtained from the conterminous United States and Alaska 1 km Advanced Very High-Resolution Radiometer (AVHRR) dataset (Eidenshink, 2006). Greenness measurements were integrated up to the 18th and 26th weeks of the year, corresponding to the SPI time periods. The annual deviations from normal greenness were measured in units of SD from mean values to produce the SSG metric (Fig. 2b), similar to the SPI. Thus, SSG was calculated using the following equation:

$$SSG = (SG_{current} - xSG_{historical})/\sigma_{historical},$$

where $SG_{current}$ is the SG value for a specific 10-day period, $xSG_{historical}$ is the historical SG value for that same period, and $\sigma_{historical}$ is the SD of the observed SG for the entire 17-year period. Values of SSG measured in 1-km pixels were linked to BBS routes by calculating the mean SSG value within 20-km buffers around each of the BBS route centres. In addition to encapsulating the entire length of the route, this buffer size is comparable to the median maximum natal dispersal distance (31.0 km) of 76 avian species for which natal dispersal distance has been observed (Sutherland *et al.*, 2000). This dispersal distance and buffer size thus represent an area that integrates the effects of landscapes surrounding BBS routes, which is important for understanding the effects of changes on biota (Turchin, 1998).
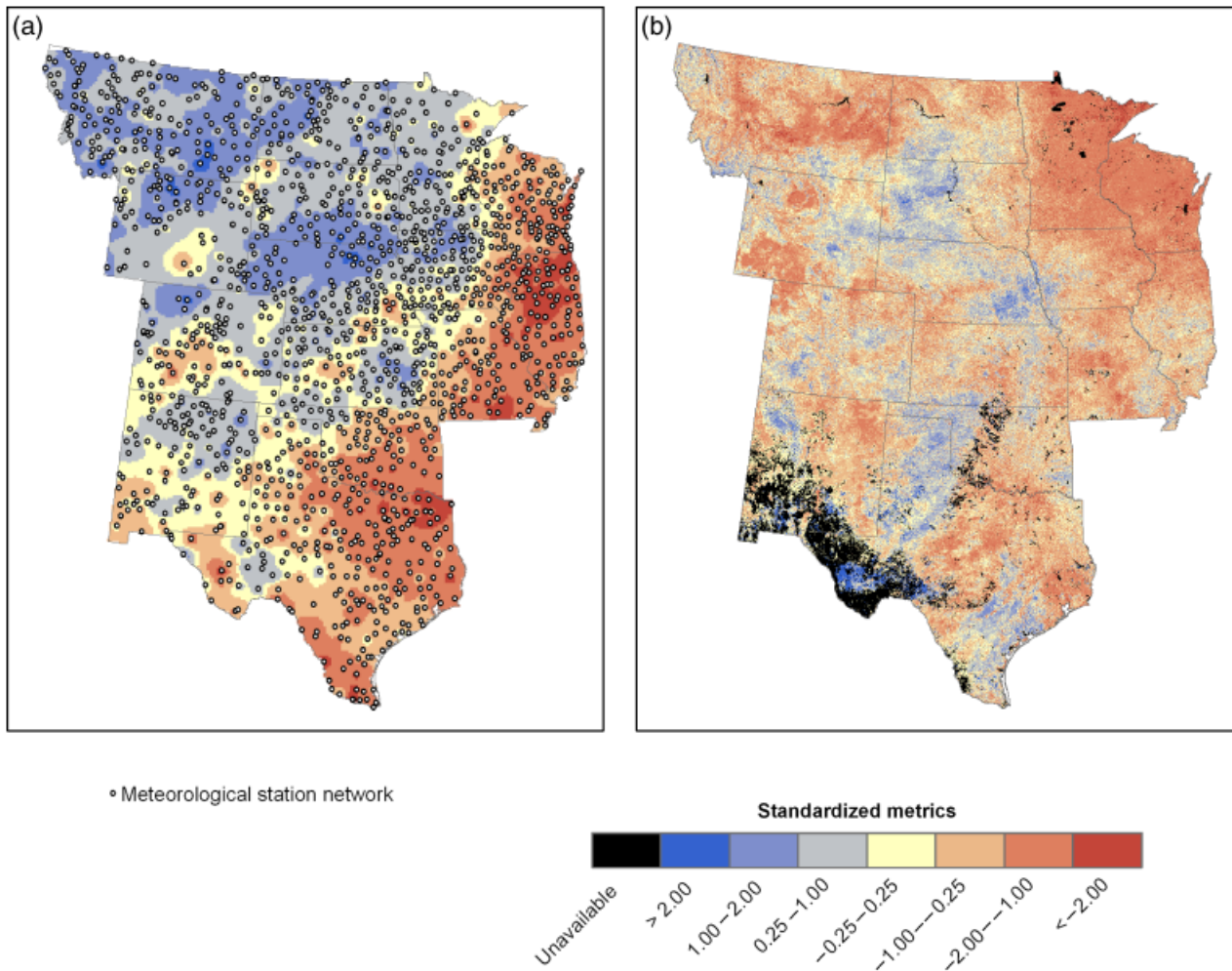
Standardized metrics

Unavailable | >2.00 | 1.00–2.00 | 0.25–1.00 | −0.25–0.25 | −1.00−−0.25 | −2.00−−1.00 | <−2.00

° Meteorological station network

Fig. 2 Examples of precipitation and greenness data used in the study: (a) 2000 16-week June standardized precipitation index (SPI) interpolated from meteorological stations shown and (b) 2000 June-ending standardized seasonal greenness (SSG). Both maps are scaled in standard deviations from normal values.

Testing for a drought effect

To characterize the relationship between drought metrics and avian abundance and richness, we developed a series of linear mixed effect models using the nlme package within the R language and environment for statistical analysis (Pinheiro & Bates, 2000, R Core Development Team, 2006). We considered abundance [natural log-transformed as: ln(abundance + 1)] and raw species richness as response variables. We included a fixed-effect term for ecoregion in order to account for broad scale variation in baseline abundance and richness among three broad regions having differing precipitation regimes (modified from Bailey, 1995): the humid temperate ecoregion occupying the eastern portion of the study region, the dry ecoregion in the centre, and the mountainous west, which is intermediate in precipitation, with most falling as snow (Fig. 1b).

Because exploratory data analysis made it clear that the relationship between drought and avian response varied among these regions, we included a drought metric by ecoregion interaction term, which allowed fixed effects of drought to be estimated for each. We evaluated the use of finer ecoregion delineations (i.e. Divisions), but these resulted in less parsimonious models. While our objective was not to understand variations in baseline abundance and richness among the routes in our study, it was nonetheless an important source of variability in our dataset. Thus, we include a random effect for BBS route. Similarly, different BBS observers possess different skill levels in detecting birds, which may result in biased estimates of abundance and richness (Sauer *et al.*, 1994), prompting us to treat observers as random effects nested within BBS routes. Finally, we added a continuous time autoregressive component to account for correlations over time. The resulting model

for predicting the richness or ln(abundance + 1), y, is given as

$$y = \beta_{0i} + \beta_{1i}X_{jk} + b_j + b_k + e(t),$$

where the β_{0i} and β_{1i} are the intercept and slope for the specified metric at ecoregion i, X_{jk} is the value of a metric at route j observed by observer k, b_j, and b_k are random effects for route j and observer k, and $e(t)$ is a continuous time autoregressive process of order 1. All models were fit using restricted maximum likelihood estimation.

Our first task was to identify the environmental metrics most related to avian community structure. We specified models based on the above framework for overall avifaunal abundance and richness using each of the 10 environmental metrics. For this step, we used the subset of the full dataset with complete observations for each of the metrics ($n = 11\,080$, an average of 9.56 observations along 1159 routes) to facilitate model comparison. Because of temporal overlap and correlation among precipitation-based metrics, we sought to identify one best metric in this class. We also wished to identify the better of our two greenness-based metrics. As such, we selected the best single precipitation-based and greenness-based environmental metrics from the candidates based on minimum Akaike's information criterion (AIC) (Burnham & Anderson, 2002).

We fit the models based on the best precipitation- and greenness-based metrics identified above for abundance and richness of each avian guild and avifauna overall. To identify lags in avian response, we also examined the relationship between metrics and BBS observations from subsequent years by comparing metrics at year $y-1$ with BBS data at year y. Using the GeoR module (Ribeiro Jr & Diggle, 2001), we examined semivariograms of model residuals and generated confidence envelopes using Monte Carlo permutations ($n = 99$) in order to identify any signs of residual spatial autocorrelation.

Finally, in order to better understand the influence of drought on avian communities, we used values for coefficients and confidences intervals estimated using the complete dataset ($n = 11\,654$) to predict the relative change in abundance and richness of avian communities in each of the ecoregions under conditions of extreme drought. In order to evaluate whether responses inferred from our analyses were driven by only a few common species, we generated a second set of abundance predictions using the common species-removed dataset. For each region, we identified mean abundance and richness of each of the guilds. We then predicted the per cent change in abundance and richness for each of these communities under an extreme drought, which was defined as a June 32-week SPI of -3.

Results

During the 17-year study period, individual routes were observed by up to five different observers for an average of 1.78 observers per route. Avifaunal abundance on BBS routes ranged from 84 to 6075 individuals and richness varied from 10 to 100 species. Abundance and richness were correlated over time within the routes, with median Spearman's rank correlation $r_s = 0.43$ (Wilcoxon's signed-rank test, $P < 0.0001$). Richness and abundance were generally highest in the northeastern and lowest in the southwestern portions of the study area. Short distance migrants were the most abundant guild (median = 337 individuals per route) and residents the least (median = 23). Richness was highest in the Neotropical migrants (median = 26 species per route) and lowest in synanthropes (median = 6).

Model comparison revealed that relationships between both avian abundance and richness were strongest with a 32-week SPI ending in June and, among greenness-based indices, April SSG (Table 2). Note that we use the difference in AIC between the best model considered and other models (Δ_i) as an indicator of the strength of support. As a rule of thumb, $\Delta_i < 2.0$ indicates a similar level of support as the 'best' model. Therefore, for subsequent analysis, we considered these two metrics ('SPI' and 'SSG') and their 1-year lagged versions ('SPI$_{y-1}$' and 'SSG$_{y-1}$'). Models based on COM-DYN-estimated richness were generally less predictive and are provided together with *ad hoc* goodness-of-fit indicators in supporting information (Table S3). In no case did we observe evidence of spatial autocorrelation in model residuals.

Table 2 Linear mixed effect model AIC ranking for overall avian abundance and richness

Environmental metric	Avian abundance		Avian richness	
	Δ_i	Ranking	Δ_i	Ranking
April-ending standardized precipitation index				
4-week	165.9	10	34.9	9
16-week	108	6	21.2	6
32-week	90.9	4	5.8	2
52-week	109.8	7	6.1	3
June-ending standardized precipitation index				
4-week	146	8	34.5	8
16-week	90.8	3	19.6	5
32-week	0	1	0	1
52-week	32.6	2	6.6	4
Standardized seasonal greenness				
April	101.7	5	27.1	7
June	152.2	9	35.1	10

AIC, Akaike's information criterion.

Overall and synanthropy

Avifauna overall was clearly most related to SPI, based on the considerably higher Δ_i of other models considered (Table 3). Values of SPI were positively related to overall abundance and richness in the dry region, where coefficients were the largest, and negatively related to abundance in the montane ecoregion. Similar relationships were observed with SSG although these were weaker in magnitude for the dry ecoregion and stronger for the montane ecoregion, where a negative relationship with richness was also observed. In

Table 3 Linear mixed model summaries for response of avifauna to different drought metrics

Guild	Response	Metric (SD)	Δ_i	Ecoregion slope terms for metric		
				Humid	Dry	Montane
All	Ln (abundance + 1)	SPI	0	+	0.0387 ± 0.0057	-0.0105 ± 0.0100
		SSG	129.4	−	0.0275 ± 0.0069	-0.0244 ± 0.0124
		SPI_{y-1}	153.1	−	-0.0095 ± 0.0058	0.0198 ± 0.0100
		SSG_{y-1}	179.9	0.0075 ± 0.0057	-0.0109 ± 0.0068	0.0209 ± 0.0124
	Richness	SPI	0	+	0.4196 ± 0.1384	−
		SSG	54.8	+	0.1752 ± 0.1685	-0.3937 ± 0.2999
		SPI_{y-1}	20.6	-0.2031 ± 0.1218	+	0.2919 ± 0.2400
		SSG_{y-1}	62.7	+	+	+
Synanthropes	Ln (abundance + 1)	SPI	0	+	0.0189 ± 0.0121	−
		SSG	33.9	−	+	−
		SPI_{y-1}	2.5	−	+	0.0251 ± 0.0210
		SSG_{y-1}	31.9	+	0.0158 ± 0.0143	+
	Richness	SPI	0.7	+	0.0419 ± 0.0357	−
		SSG	32.3	+	−	−
		SPI_{y-1}	0	−	+	+
		SSG_{y-1}	32.1	−	+	+
Permanent residents	Ln (abundance + 1)	SPI	20.8	−	−	-0.0342 ± 0.0230
		SSG	0	-0.0229 ± 0.0137	-0.0346 ± 0.0161	-0.0828 ± 0.0287
		SPI_{y-1}	29.1	−	+	+
		SSG_{y-1}	50.9	+	0.0173 ± 0.0158	0.0302 ± 0.0288
	Richness	SPI	1.6	-0.046 ± 0.0428	−	−
		SSG	22.9	−	-0.0894 ± 0.0558	-0.1002 ± 0.0997
		SPI_{y-1}	0	−	+	0.1046 ± 0.0784
		SSG_{y-1}	27.1	−	−	0.1566 ± 0.0998
Short distance migrants	Ln (abundance + 1)	SPI	0	+	0.0384 ± 0.0068	−
		SSG	105.3	-0.0118 ± 0.0070	0.0171 ± 0.0083	-0.0305 ± 0.0147
		SPI_{y-1}	69.6	−	−	0.0438 ± 0.0119
		SSG_{y-1}	127.6	0.008 ± 0.0068	−	0.0299 ± 0.0147
	Richness	SPI	22.2	−	+	+
		SSG	46.3	−	−	−
		SPI_{y-1}	0	-0.0833 ± 0.0508	0.0775 ± 0.0582	0.143 ± 0.0983
		SSG_{y-1}	48.1	+	+	+
Neotropical migrants	Ln (abundance + 1)	SPI	0	0.0126 ± 0.0076	0.0488 ± 0.0082	−
		SSG	69.6	+	0.0508 ± 0.0100	−
		SPI_{y-1}	119.6	−	-0.0214 ± 0.0084	+
		SSG_{y-1}	147.6	+	-0.0232 ± 0.0098	+
	Richness	SPI	0	0.1398 ± 0.0957	0.4216 ± 0.1028	−
		SSG	72.5	+	0.3176 ± 0.1254	−
		SPI_{y-1}	70.2	-0.1021 ± 0.0909	−	+
		SSG_{y-1}	97.8	+	−	−

In the table, 'SPI' refers to 32-week June standardized precipitation index and 'SSG' refers to April-ending standardized seasonal greenness. Delta AIC (Δ_i) is reported within each guild response; '0' indicates the most supported model. Significant ($P<0.05$) coefficients ($\pm$ 95% confidence intervals) and signs of nonsignificant estimates are shown for slopes of the specified metric in each ecoregion. Intercepts and *ad hoc* goodness-of-fit indicators are reported in supporting information (Table S3).

AIC, Akaike's information criterion; SPI, standardized precipitation index; SSG, standardized seasonal greenness.

general, relationships were weaker and inverted for metrics measured during the previous year, although a positive relationship between SSG_{y-1} and abundance and a negative relationship between richness and SPI_{y-1} were observed in the humid ecoregion.

Synanthrope abundance and richness were less strongly related to the precipitation and greenness metrics than was avifauna overall, based on the smaller magnitude and significance of coefficients. While relationships with SPI were clearly stronger than with SSG, models based on SPI and SPI_{y-1} were approximately equal in strength (Δ_i generally <2.0). Although relationships between environmental metrics and synanthropes were generally weaker than for avifauna overall, they were uniformly positive when significant, with synanthrope abundance related to SPI and SSG_{y-1} in the dry ecoregion and with SPI_{y-1} in the montane region and richness related to SPI_{y-1} in the dry region. Among richness models, the model based on SPI_{y-1} was strongest, although none of the ecoregion-level coefficients attained significance.

Predictions of the effect of extreme drought on overall abundance and richness (Fig. 3) indicate the largest changes occur in the dry ecoregion, where a 10.7% reduction in overall abundance and a 3.2% drop in species richness were predicted during a year of extreme drought. Synanthrope abundance and richness were predicted to drop by 5.3% and 2.6%, respectively. We found weaker or nonsignificant results in other regions. Removal of the 12 most abundant species from avifauna overall and synanthropes resulted in greater and more significant predicted declines of 2.6% and 7.0%, respectively in the humid region and a much greater 20.5% predicted increase in synanthropes in the montane region. Note that, because of the log-scaled response, predictions of per cent change in abundance hold for any 3 SD interval in SPI (e.g. from +1.5 to −1.5 SPI) on any route in its respective ecoregion, regardless of baseline abundance.

Migratory habit

There was wide variation in the relationship between precipitation and greenness metrics and the response of different migratory guilds. The abundance of permanent resident birds was most strongly related to SSG, while richness within this guild was related slightly more strongly with both SPI and SPI_{y-1} than with SSG. Unlike other guilds examined, residents responded negatively to both SPI and SSG irrespective of ecoregion, with the strongest declines in the montane region (Table 3). In contrast, they were positively related to SSG_{y-1} and SPI_{y-1}.

Short distance migrant abundance and richness responded most to SPI and SPI_{y-1}, respectively. Specifically, short distance migrant abundance was positively related to both SPI and SSG in the dry ecoregion. However, abundance was negatively related to SSG in the montane and humid-temperate ecoregions. As with residents, the response of short distance migrant abundance to previous-year SPI and SSG metrics was inverted relative to same-year metrics. Richness in this guild was only related to SPI_{y-1}, with positive relationships observed in the dry and montane regions and a negative relationship in the humid region.

Models of Neotropical migrant abundance and richness based on the SPI were the strongest among the environmental metrics examined. Abundance and richness in this guild were positively related to SPI in both the humid-temperate and dry ecoregions. They were also positively related to SSG in the dry ecoregion. A weaker, but negative, relationship was observed between Neotropical migrant abundance and previous-year metrics in the dry region. A negative relationship was also observed between richness and SPI_{y-1} in the humid region.

Predictions of abundance and richness during years of extreme drought exhibited similar variation among the migratory guilds (Fig. 3). The largest changes were found in Neotropical migrants in the dry region, which were predicted to experience 13.2% and 6.0% reductions in abundance and richness, respectively. Sizable increases in abundance and richness (11.5% and 3.6%) were predicted for residents in the montane ecoregion. Changes in short distance migrant abundance and richness were more modest and intermediate between Neotropical migrants and residents. Removal of the 12 most abundant species from the migratory guilds did not greatly alter the predicted abundance changes during drought years in most cases, although the predicted increase in permanent resident abundance in the humid region lost significance.

Discussion

Community-wide species richness and abundance

Avian communities exhibit considerable interannual variability and our results indicated that some of this variability can be explained by variations in precipitation and greenness. Our expectations and previous local-scale studies (Hicks, 1935; George et al., 1992) suggested that drought conditions associated with low SPI and SSG values would reduce both avian abundance and richness. While we discovered a surprising diversity of responses by avifauna overall to same-year or $y-1$ drought metrics across regions (Table 3) the
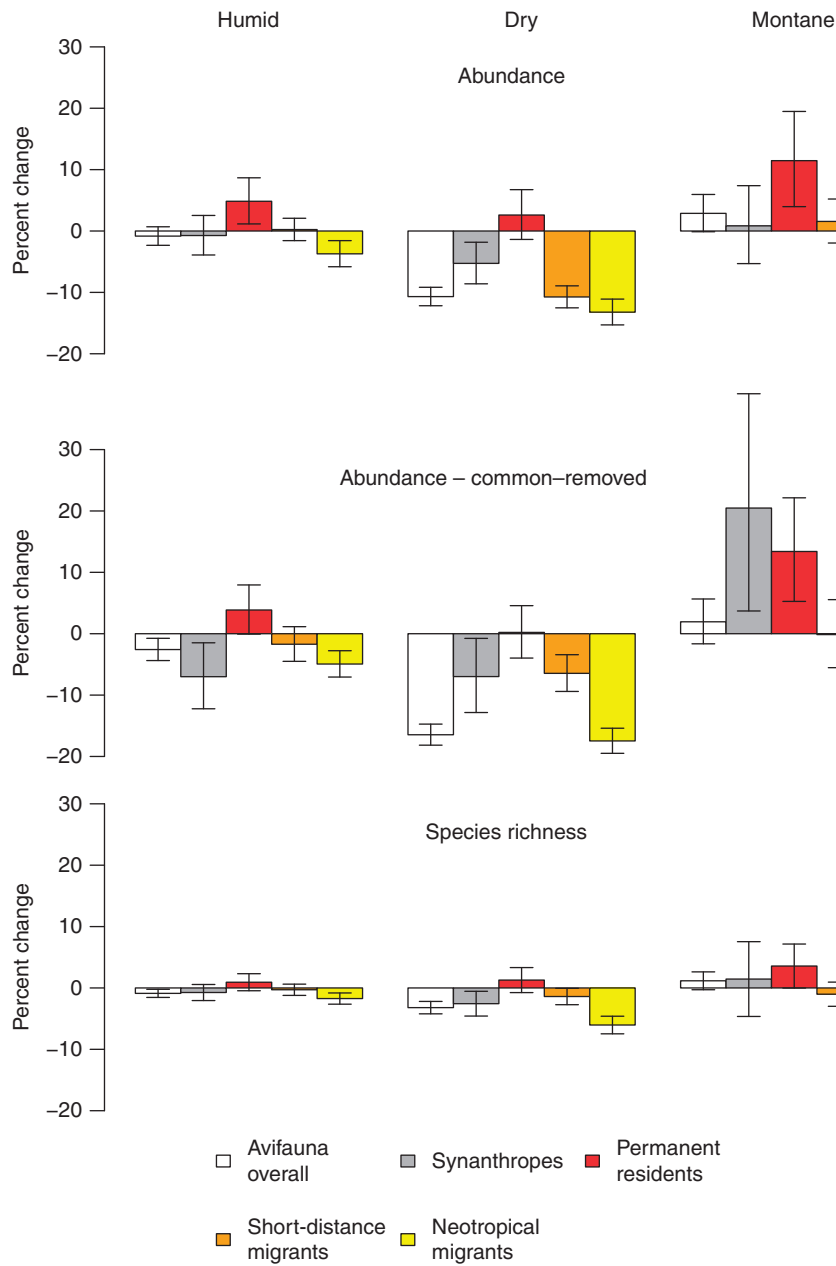
Fig. 3 Predicted changes in abundance (complete guilds and with the 12 most common species removed) and richness under an extreme drought (32-week June standardized precipitation deficit of 3, equivalent to 3 SD less than mean precipitation for that period). Shown are predictions (± 95% confidence intervals) of per cent change within each avian guild in the three ecoregions considered in this study.

strongest responses by avifauna overall were indeed negative. The influence of drought was stronger on abundance than on richness in most cases. Certainly at a species level, abundance must decline before extirpation can be observed. In a study of an avian community in Puerto Rico, Faaborg (1982) found that, despite declines in abundance among many species following a 3-year drought, none was extirpated. There is reason to expect this relationship to hold at the

community level; the greater the number of species in a community that decline in abundance, the more likely extirpations become.

Variable guild responses

The behavioural and functional guilds we considered responded in diverse ways to interannual variability in precipitation and greenness, although most declined

during drought. Synanthropes appear less negatively affected by droughts, as expected. Such birds may be able to maintain high abundance and richness in times of environmental stress thanks to resource subsidies afforded by humans, including feeding (Lepczyk *et al.*, 2004; Fuller *et al.*, 2008), provision of habitat, and irrigation (Brotons *et al.*, 2004).

The three migratory guilds represent three points on a continuum of migratory strategy ranging from Neotropical migrants to permanent residents, with short distance migrants being an intermediate case. Following this continuum, Neotropical migrant abundance and richness were most negatively affected by drought, permanent residents responded positively, and short distance migrants, though exhibiting a negative response, held the middle position (Table 3, Fig. 3). It is not clear why residents were both more abundant and species-rich in dryer years, although there are several possible explanations. One involves reduced snow cover in drought years and conforms to several previous findings. The abundance of Carolina Wren (*Thyrothorus ludovicianus*), a permanent resident of eastern North America, was negatively correlated with the duration of snow cover (Link & Sauer, 2007). Similarly, in Kansas (USA), declines in the richness of wintering birds were associated with days with deep snow cover (Stapanian *et al.*, 1999). However, this explanation does not apply to many of the routes in the region that do not regularly experience snow. Another possible explanation for the lack of a negative response by residents to drought is that they lack flexibility in selecting habitat according to prevailing conditions at the onset of breeding season; while migratory birds may simply pass over areas with unfavourable conditions, residents may be required to (and, by extension, be adapted to) endure drought conditions – an hypothesis that is consistent with theory on the origin of migration in New World avifauna (Cox, 1985). Indeed, the opposite response of residents and Neotropical migrants and the inversions in the sign of these relationships between metrics at year y and at year $y-1$ (Table 3) suggest that complex interactions among guilds and time periods may be operating. One scenario is that (a) residents in year y suffer the consequences of reduced reproductive success and survival under drought conditions during year $y-1$ and (b) Neotropical migrants reoccupy the same postdrought areas in year y as in year $y-1$, but have fewer resident competitors to contend with. Furthermore, to the extent that breeding abundance of Neotropical migrants is limited by conditions in their wintering range (Rappole & McDonald, 1994), the conditions in the breeding range in year $y-1$ may have only limited impact on the population in year y. This raises the question for future studies of how habitat selection, reproductive

success, and survival of Neotropical migrants compare with residents in drought conditions. The mechanism underlying the stronger response by Neotropical migrants relative to short-distance migrants is unclear and worthy of further study.

Responses of most guilds were robust to the removal of the 12 species that constitute half of all birds tallied by BBS in this study. In fact, responses, whether positive or negative, were generally stronger among guilds with these most common species removed (Fig. 3). Changes were greatest among synanthropes, notably a guild for which removal of the most common species reduced total abundance across years and routes from 6 015 273 to 1 813 421 individuals. The tendency of responses to be amplified among less common species not only points to functional differences related to commonness (Gaston, 2008), but indicates that common species may be more robust to drought and perhaps other perturbations.

Precipitation and greenness metrics

With the exception of permanent resident abundance, variation in precipitation, rather than in greenness, had greater effects on avian communities. While it is intuitive that the avian community should respond to vegetation conditions, there are reasons why greenness, as measured here, may be an imperfect indicator of drought relevant to avifauna. With much of the study region intensively farmed, greenness measurements may be heavily influenced by both irrigation and the phenology of various crops rather than the condition of natural vegetation. For example, a shift from winter wheat (peak greenness in May) to corn (peak greenness in July/August) would result in major seasonal greenness changes from year-to-year that are unrelated to drought. Furthermore, greenness measurement in areas having bare soil may be problematic (Bannari *et al.*, 1996) and greenness has been found to recover rapidly in grassland systems (Pennington & Collins, 2007), potentially masking important moisture deficits. Nonetheless, as greenness measurements are collected globally on a far more consistent basis than precipitation measurements, there is considerable value in continued exploration of their relationships with avifauna and other biota. The strong negative relationship between permanent resident abundance and greenness is perplexing and invites further investigation of land cover, irrigation, and other factors.

SPIs encompassing intermediate- with longer time periods were more strongly related to avian abundance and richness than were indices based on shorter time periods (Table 2), demonstrating that drought duration is an important factor. It appears that greenness measurements coincident with early-season establishment

of territories (April) are superior to later-season greenness measurements, while precipitation metrics culminating during midseason peak nesting (June) were superior to earlier precipitation indices (Table 2).

Avian communities were generally more related to same-year drought metrics. With the exception of short distance migrant richness, coefficients estimated for year $y-1$ metrics were generally smaller in magnitude or lost significance compared with their year y counterparts (Table 3). More surprising was the tendency for relationships with year $y-1$ metrics to change sign relative to their year y counterparts. As described above, this tendency was strongest among permanent residents and Neotropical migrants and may reflect competitive dynamics and population rebounds. It may also be that long-term droughts (lasting >1 year) are important in determining resource availability for birds. In fact, long-term droughts have been implicated in declines in avian populations (George *et al.*, 1992; Bock & Bock, 1999).

Geographic variation in avian response

Patterns of avian community response to drought differed among the three ecoregions considered (Table 3, Fig. 3). Avian communities in the dry ecoregion were most responsive to drought, as predicted. Vegetation in this region is limited by precipitation and may respond more immediately to precipitation (Rich *et al.*, 2008). Avian communities in areas with vegetation having a strong seasonal phenology (e.g. deciduous trees, grasslands) appear to be more affected by drought (Rich *et al.*, 2008). In contrast, much of the landscape of the montane ecoregion, where avian community response was generally weakest, is covered by coniferous evergreen trees, which vary less in response to drought (Smith, 1982). One exception to this is the resident guild, which was most negatively related to precipitation and greenness in the mountains. As previously discussed, this may be due to the negative effects of deep and persistent snow cover in years having above average precipitation. Permanent residents were negatively related to precipitation in the east, but these associations were even stronger in the mountainous west. In these two regions, average abundance of permanent residents was generally higher than in the dry region, which may make their response to drought more apparent. Finally, we note that the number of BBS routes is considerably smaller in the montane ecoregion, which limited our power to detect drought effects there.

Implications and conclusions

Our results indicate that avian communities respond to drought in diverse ways, adding new dimensions to the understanding of avian responses to environmental change (Julliard *et al.*, 2004). We described two chief drivers of this diversity in response. From a regional perspective, drought may have the strongest effects on avifauna in semiarid ecoregions. Also, avifauna in areas having predominantly snow-driven precipitation regimes, such as the montane region we examined, may tend to respond positively to reduced precipitation (snowfall), at least on the time scale considered here. From a biological perspective, avifaunal response was strongly influenced by migratory habit, with more distant migration being associated with a more negative same-year response to drought. It will be important to determine the specific processes responsible for changes in local community structure: adult mortality, reduced recruitment, or habitat selection.

While our results revealed sizeable negative responses to drought, especially among migratory birds and in semiarid areas, the effect of drought on avifauna was often modest among resident birds and in other ecoregions. Avifauna are subject to numerous sources of interannual variability, including long term population trajectories (Valiela & Martinetto, 2007), density dependence, predator–prey dynamics (Oro *et al.*, 2006), harvest (Keane *et al.*, 2005), demographic stochasticity (Saether *et al.*, 2004), conditions in wintering range (Robbins *et al.*, 1989), and disturbances such as severe storms, fire, and forest harvest (Hobson & Schieck, 1999). That the magnitude of drought effects was often modest suggests that many bird species are well adapted to moisture-related variability in their range. Previous studies have found that avian communities are often *resilient* to, i.e. quick to recover from, drought effects (George *et al.*, 1992; Verner & Purcell, 1999). The present study further emphasizes the ability of some avian communities to be *resistant* to drought-induced changes.

However, some ecological effects of droughts may be larger than what is apparent in this study. This may be particularly true for the responses of individual species or guilds of species that are defined more narrowly than the guilds in the present study. Several of the drought metrics found to be significantly associated with avian response are only weakly correlated among themselves, suggesting that they may exert a considerably stronger cumulative affect, such as the case of multiyear droughts. The time period of our SPI dataset was confined to 52 weeks. Although SPIs calculated for longer periods encounter limitations in characterizing the distribution of precipitation amounts (Wu *et al.*, 2005), it may be fruitful to examine droughts at longer time scales. Most of the SPI values used in this study can be placed within the range of variability to which the avian community is adapted. However, if extremes

beyond the 'normal' range of variability are experienced, as been suggested in the case in Europe in 2003 (Schar et al., 2004), avian communities may respond with considerably larger shifts in abundance and richness. Because such an increase in frequency of extreme weather conditions is predicted in general (IPCC, 2007) and especially for the southwestern United States (Diffenbaugh et al., 2008), we must caution that drought may be a more important factor in determining the future structure of avian communities than our observed relationships would suggest.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Classification of species by guilds and whether they are in the most common group constituting 49% of all individuals tallied by the BBS during the study period. Due to intraspecific variation, not all species were assigned a migratory habit.

Table S2. Proportions of shared memberships among guilds. Values represent the fraction of the guild indicated on the column that is also a member of the guild indicated on the row.

Table S3. Linear mixed effect model summaries for response of avian guilds to different drought metrics. In the table, 'SPI' refers to 32-week June standardized precipitation index and 'SSG' refers to April-ending standardized seasonal greenness. An indicator of goodness-of-fit, R_{LR}^2 (Magee, 1990), is based on a comparison of the specified model with a null (intercept-only) model (R_{LR}^2 full) and a comparison of the specified model with a model that omits fixed effects (R_{LR}^2 fixed). Delta AIC (Δ_i) is reported within each guild response; a '0' indicates the model most supported by the data. Coefficient estimates ($\pm$ 95% confidence intervals) are shown for intercept and slope of the specified metric in each ecoregion.

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