



Heat waves measured with MODIS land surface temperature data predict changes in avian community structure

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ABSTRACT

Heat waves are expected to become more frequent and severe as climate changes, with unknown consequences for biodiversity. We sought to identify ecologically-relevant broad-scale indicators of heat waves based on MODIS land surface temperature (LST) and interpolated air temperature data and assess their associations with avian community structure. Specifically, we asked which data source, time periods, and heat wave indices best predicted changes in avian abundance and species richness. Using mixed effects models, we analyzed associations between these indices and data from the North American Breeding Bird Survey in the central United States between 2000 and 2007 in four ecoregions and five migratory and nesting species groups. We then quantified avian responses to scenarios of severe, but commonly-occurring early, late, and summer-long heat waves. Indices based on MODIS LST data, rather than interpolated air temperatures, were more predictive of avian community structure. Avian communities were more related to 8-day LST exceedances (positive anomalies only); and were generally more sensitive to summer-long heat waves. Across the region, abundance, and to a lesser extent, species richness, declined following heat waves. Among the ecoregions, relationships were most consistently negative in the southern and montane ecoregions, but were positive in a more humid northern ecoregion. Among migratory groups, permanent resident species were the most sensitive, declining in abundance following a summer-long heat wave by 19% and 13% in the montane and southern ecoregions, respectively. Ground-nesting species, which declined in the south by 12% following a late summer heat wave, were more sensitive than avifauna overall. These results demonstrate the value of MODIS LST data for measuring ecologically-relevant heat waves across large regions. Ecologically, these findings highlight the importance of extreme events for avian biodiversity and the considerable variation in response to environmental change associated with different functional groups and geographic regions. The magnitude of the relationships between avian abundance and heat waves reported here raises concerns about the impacts of more frequent and severe heat waves in a warming climate.

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1. Introduction

The loss of biodiversity is the least reversible form of global change, and has been observed recently in numerous taxonomic groups, including birds (Novacek & Cleland, 2001). Biodiversity decline results from numerous interacting factors, including habitat loss and fragmentation (Fahrig, 2003), invasive species (Courchamp et al., 2003), overexploitation (Hutchings, 2000), and climate change

(Parmesan & Yohe, 2003). A factor attracting increased attention, climate change encompasses changes in mean temperature and precipitation throughout the year and changes in variability among years. In some regions of North America, changes in interannual variability may be the most evident manifestation of climate change (Diffenbaugh et al., 2008) and more frequent extreme events such as heat waves are predicted (IPCC, 2007; Meehl & Tebaldi, 2004). Heat waves, which typically connote two or more consecutive days of hot and higher than average temperatures for a particular time period, have been linked to increased mortality among some wildlife species (Gordon et al., 1988; Jiguet et al., 2006).

However, relatively little is known about their effects among avian communities across diverse regions. Communities represent groups of species interacting at particular locations and may be subdivided according to taxonomic and functional characteristics. Responses by avian communities to heat waves are of particular interest for several

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reasons. Birds are near-ubiquitous, mobile, and responsive at fine temporal scales. Birds are of conservation interest because of a number of population declines in the United States (North American Bird Conservation Initiative – U.S. Committee, 2009) and worldwide, where one in eight species is threatened (BirdLife International, 2008). Birds also perform a broad array of ecosystem services including pollination, pest control, and recreation (Sekercioglu, 2006). In our study region, threats to already-diminished grassland habitats and associated grassland-specialist birds are of particular concern (Herkert, 1995). Finally, birds, being generally conspicuous, are among the most well monitored taxonomic groups.

Effectively relating heat waves to avian response requires spatially- and temporally-detailed data. Remote sensing plays an important role in informing biodiversity science (Turner et al., 2003), and Moderate Resolution Imaging Spectroradiometer (MODIS) data offer retrievals of biophysical parameters such as land surface temperature (LST, Wan et al., 2003) with an attractive balance of spatial and temporal resolution. Remote measurements of LST have been widely used in energy balance and agro-meteorology studies (e.g. Anderson et al., 2007; Dakhore et al., 2008), but much less in ecological and biogeographic studies (but see Mildrexler et al., 2007). Concurrently, advances in databases and interpolation algorithms have spurred the availability of gridded weather and climate summaries based on networks of ground measurements (e.g. Daly et al., 2002; Hijmans et al., 2005). The relative strengths of satellite and ground measurements for biodiversity and ecological studies are not clear. There are several key differences between these remotely-sensed and ground-based data sources. Meteorological stations measure air temperature, T_{air} , typically at 1.5–2.0 m in height. In contrast, remote sensors measure land surface temperature, which, though correlated, can differ greatly from T_{air} . Land surface temperature is heavily influenced by latent heat flux associated with evapotranspiration and is thus related to vegetation condition (Zaitchik et al., 2006). Because birds are often dependent on vegetation, this property of LST may render it an especially useful indicator of individual-scale weather conditions. For both T_{air} and LST, it is important to consider whether there are critical periods in the year when birds are more sensitive to extremes or whether entire seasons of above normal temperatures are most relevant. Lagged demographic responses (e.g. reduced recruitment) may influence whether population and community effects are more apparent during the year of a heat wave or in subsequent years.

Heat waves can elicit direct and indirect responses from birds and other animal taxa. Direct responses may include changes in behavior (Guthery et al., 2005), reduced recruitment (Guthery et al., 2001), or death (Finlayson, 1932). The same responses may occur indirectly, through effects of heat on resources (e.g. cover, forage, prey) that animals use (Becker et al., 1997). Responses to severe weather can also include dispersal to less-affected areas (Mooij et al., 2002). Responses are likely to depend on functional traits of species and groups of species. For instance, because air temperatures can differ drastically from surface temperatures, the vertical stratum (i.e. ground- vs. canopy-level) that birds occupy likely influences their sensitivity to heat waves. Migratory habit can affect both the amount of time spent in a locale and the way habitat is selected. Geographic location may also influence the severity of heat waves as well as the degree to which animals are adapted to thermal stressors (Yarbrough, 1971).

Our goal was to identify relationships between heat waves and changes in the structure of avian communities. Our primary hypothesis was that both abundance and species richness decline due to heat waves, but that abundance would be more affected because the abundance of individual species has to decline to zero before producing a decline in species richness. We asked two sets of supporting questions. The first set aimed to identify the most relevant types of heat waves and indicators for avifauna. Specifically, we asked

whether avian communities 1a) are more related to remotely-sensed measurements of LST or T_{air} from interpolated ground measurements, with the expectation that they would be more related to LST than to T_{air} because of the influence of vegetation condition on the former; 1b) are more related to temperature anomalies (departures from means) or exceedances (above normal temperatures only), anticipating that that exceedances, by quantifying only above normal temperatures, would be better indicators; and 1c) respond differently to heat waves occurring during different same-season and previous-season time periods, hypothesizing that avian communities would respond more strongly to previous-season heat waves because of nest failure and that dispersal would be more common responses than outright adult mortality.

The second set of questions focused on identifying how avian response to heat waves varied with functional trait and geographic region. Specifically, we asked 2a) whether nest stratum and 2b) migratory habit influence avian response to heat waves with the expectation that birds nesting in the more thermally stressful ground level would respond most negatively and that responses would diminish with migratory distance as migration-related mortality would dominate the demography of migratory birds; and 2c) how responses vary among four ecoregions with different climatic regime, hypothesizing that responses would be greatest in warmer ecoregions where thermal stress would be greater.

2. Methods

2.1. Study region

Our study area is a large and diverse region, encompassing 15 states of the central United States (3.7 million km²; Fig. 1), and including both eastern and western US bird species. Largely temperate, the region is centered on the Great Plains, a gently sloping prairie landscape dominated by agriculture and rangelands. In the West are the Rocky Mountains and in the East are the Southern Mixed Forest, Ozark Highlands, and Eastern Broadleaf Forest. Excluding mountainous areas, there is a gradient of declining precipitation from east (80–140 cm yr⁻¹) to west (25–35 cm yr⁻¹). The mountainous west experiences more precipitation (e.g. 95 cm yr⁻¹), much of it in the form of snow. Mean maximum temperature in July generally exceeds 35 °C in the south, but declines to less than 25 °C in the north and often less than 15 °C in alpine areas.

2.2. Avian data

We obtained 2000–2007 data from the North American Breeding Bird Survey (BBS; (USGS, 2008)). Our study area includes 1233 BBS routes, each 39.4 km in length. Along each route, 50 3-minute point counts are conducted near-dawn annually during peak breeding season (most often during June) in which all birds seen or heard within 400 m are recorded. We removed data from first-year observers and those having inclement weather at the time of the survey (Link & Sauer, 1997; Sauer et al., 2004). For each suitable year within each route (“route-year”), we summed counts of individual birds for a) North American landbirds (“ALL”; (Rich et al., 2004), b) three different migratory groups (“RESIDENT”, “SHORTDIST”, and “NEOTROP”; (Rappole, 1995), and c) two guilds related to nest location (“GROUND” and “CANOPY”; (Pidgeon et al., 2007), for a total of 6 avian groups; (Table 1, complete membership lists in Table S1). We excluded rare species (<30 route-year occurrences over the history of BBS in the conterminous US) and marine or aquatic species, which are poorly sampled by BBS (Bystrak, 1981). In addition to abundance, we tabulated richness, i.e. the number of species identified in each group.

2.3. MODIS land surface temperature

From the MODIS sensor flown aboard the National Aeronautics and Space Administration's (NASA) Terra satellite, we obtained data from 2000 to 2008 MOD11C2 and MOD11C3 LST products composited for eight-day and one-month periods, respectively. MODIS LST data are based on the generalized split-window algorithm (Wan & Dozier, 1996) and day/night algorithm (Wan & Li, 1997) that resolve ambiguities arising from variable emissivity and are accurate to within 1 °C in most cases (Wan, 2008; Wan & Li, 2008; Wan et al., 2003). The summer seasonal windows from day-of-year 153 to 265 (June to mid-September) for MOD11C2 and June, July, and August for MOD11C3 were chosen based on examination of correlation coefficients and to capture leaf-on conditions for most vegetation types in the region. We excluded data with poor calibration, cloud contamination, or other quality issues based on the LST product quality assurance flags provided. For each pixel and time period, we subtracted 2000–2008 mean values to obtain temperature anomalies for each year. Images were projected into Albers equal-area projection with 5 km × 5 km cells, which is approximately equivalent to the 0.05° by 0.05° resolution of the MODIS products. The MODIS instrument aboard Terra collects images in the late morning, local time. While MODIS data from the Aqua platform, with its early afternoon overpass, would have provided measurements of LST closer to daily temperature maxima, those data were only available following 2002 and suffered from a large number of unacceptable quality flags over our study region.

In order to relate LST to BBS routes, we calculated mean LST within a 20-km buffer around BBS route centroids. In addition to encompassing the entire length of the route, this distance is comparable to the median maximum natal dispersal distance (31 km) of 76 avian species for which it has been observed (Sutherland et al., 2000), indicating that the buffer captures a biologically relevant area. To evaluate the influence of LST on avifauna in year t , we considered monthly anomalies for each summer month (June, July, and August) of the previous year ($t - 1$) as well as for June of the same year (t) as the BBS data (Table 2). We excluded July and August from year t analysis because it would involve temperature data collected after the BBS observations were made in a given year. While many other metrics could have been considered, we selected these as a balance between diverse formulations, use of readily-available data products, and a manageable number of metrics to analyze.

2.4. Air temperature

Monthly maximum air temperature (T_{air}) data (means of daily maxima for each month) for 2000–2005 (the last available year) were obtained from the 1-km resolution PRISM dataset (PRISM Climate Group, 2009) for the summer months. We calculated mean T_{air} for each summer month, subtracted these from monthly T_{air} values for each year, and resampled to 5-km cells to obtain monthly T_{air} anomalies. As with LST, we considered year $t - 1$ for each summer month as well as year t for June, the other months occurring after routes are surveyed (Table 2). We then intersected BBS route centroids with this grid to calculate monthly anomalies for each BBS route.

2.5. Seasonal summaries

From each year of the LST and T_{air} datasets, we calculated the average monthly anomaly and average exceedances over the summer (Table 2). We defined exceedances, T_E , as the deviation above the 2000–2008 mean temperature, \bar{T} , for a given period (8 days for MOD11C2 and 1 month for MOD11C3 and PRISM), such that:

$$T_E = T - \bar{T} \text{ for } T > \bar{T} \text{ and } T_E = 0 \text{ for } T \leq \bar{T} \quad (1)$$

Our rationale for using exceedances was that a cumulative index of high temperatures ignoring temperature variations below the mean would be a better proxy for heat wave conditions. A total of 14 monthly and seasonal heat wave metrics were considered, including same year (t) and previous year ($t - 1$) metrics (Table 2).

2.6. Analysis

To explore the relationship between LST and T_{air} , we calculated a series of linear regression models. To characterize the relationship between heat wave 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 et al., 2007; R Development Core Team, 2010). We used abundance (transformed as $\ln(\text{abundance} + 1)$ to normalize the distributions) and species richness (untransformed) as response variables. We included a fixed-effect for ecoregion to account for broad-scale variation in abundance and richness among four broad regions with differing climatic regimes (modified from Bailey, 1995): the Humid North occupying the northeastern portion of the study region, the Dry North in the north central, the Montane West, which is intermediate in precipitation, with most falling as snow, and the South, which experiences the highest temperatures (Fig. 1b). We included a heat wave metric by ecoregion interaction term, which allowed fixed effects of temperature variation to be estimated for each ecoregion. While our objective was not to understand finer-scale spatial variations in abundance and richness among the routes, it was nonetheless an important source of variability in our dataset. Thus, we included 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 temporal autocorrelation. The resulting model for predicting the richness or $\ln(\text{abundance} + 1)$ was:

$$y = \beta_{0i} + \beta_{1i}X_{jk} + b_j + b_k + e(t) \quad (2)$$

where the β_{0i} and β_{1i} are the intercept and slope for the specified heat wave metric at ecoregion i , X_{jk} is the value of a heat wave 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, which accommodates irregularly spaced samples in time. All models were fit using restricted maximum likelihood estimation.

We compared models using the LST and T_{air} metrics for each of the groups. In this step, we used a subset of the 2000–2005 dataset having complete observations in a year for each metric ($n = 3796$, an average of 3.6 years of observation along 1048 routes) so that sample size was constant. Comparisons were based on the Akaike Information Criterion (AIC, Akaike, 1974), which is a likelihood-based indicator of relative fit, penalized for model complexity. Values of AIC for various models based on the same dataset may be directly compared and ranked using Δ_i , the difference in AIC between the best model and a particular model in question. As a rule of thumb, $\Delta_i < 2.0$ indicates a similar level of support as the “best” model (Burnham & Anderson, 2002). Because of the short time series of PRISM-based T_{air} estimates, we generated a second set of model comparisons based exclusively on complete MOD11C2 and MOD11C3 datasets, which additionally allowed inclusion of 2006–2007 data ($n = 5297$, an average of 5.1 years of observation). We then refit the most supported abundance and richness models for each group using all data available for each heat wave metric (up to $n = 6060$) to obtain coefficient estimates. We examined variograms and corresponding confidence envelopes of residuals from the best models in search of residual spatial autocorrelation but found none.

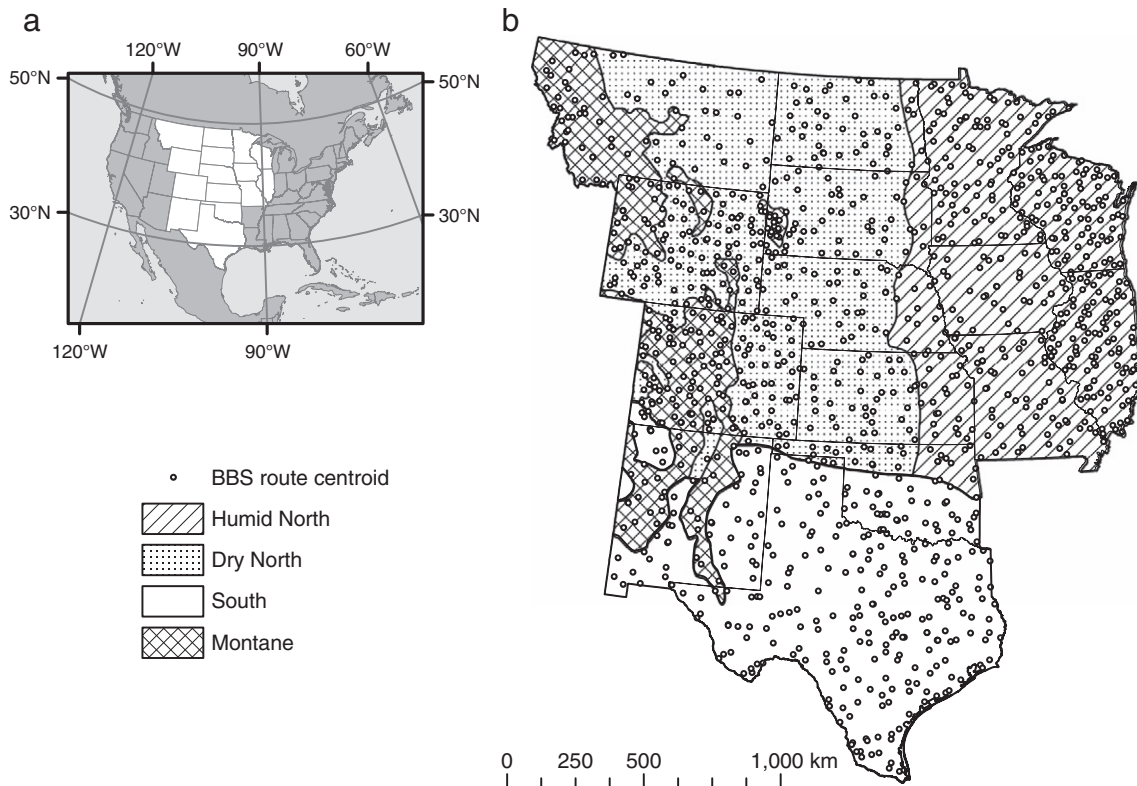


Fig. 1. The 15-state study region (a), four ecoregions (modified from Bailey, 1995) and network of North American Breeding Bird Survey routes (b). Projection: Albers Conic Equal-Area.

Because of the log-scaling of response variables and differences in mean abundance and richness among ecoregions and assemblages in this study, estimated model coefficients did not provide a practical gauge of the apparent effects of heat waves on avian communities. In order to better understand these, we quantified in percentage the magnitude of avian community changes associated with a series of scenarios based on fitted models. We focused on scenarios representing severe heat waves occurring with an approximate 50-year return interval (98th percentile) based on the record of climate conditions contained in our datasets. First, we considered a prolonged heat wave in which previous year ($t-1$) 8-day LST exceedances during summer ($M2LSTex_{t-1}$) averaged $3\text{ }^{\circ}\text{C}$ above normal. We also considered two acute within-month heat waves in which mean LST for August of year $t-1$ ($M3LST08_{t-1}$) and June of year t ($M3LST06_t$) were $5\text{ }^{\circ}\text{C}$ above normal temperatures for each BBS route. In quantifying changes, we multiplied model coefficients by the metric values identified as the 50-year events to predict the percent change in abundance and richness of average routes in each ecoregion under a neutral (neither positively nor negatively biased) observer.

3. Results

We found highly significant regression slopes ($P < 0.0001$ in all cases) between MODIS LST and PRISM-based T_{air} measurements used in this study (Fig. 2). The strength of correlation between these temperature measurements varied considerably among regions and among time periods, with stronger correlations occurring later in the summer. Total bird abundance on routes ranged from 83 to 4764 individuals and richness varied from 8 to 85 species. Abundance and richness were correlated over time within routes, with a median Spearman rank correlation of 0.43 (Wilcoxon signed-rank test, $P < 0.0001$). Richness and abundance were highest in the northeastern and lowest in the southwestern portions of the study area. SHORTDIST were the most abundant group (median = 293 individuals per route) and RESIDENT were the least (median = 39). Richness was highest among NEOTROP (median = 22 species per route) and lowest among RESIDENT (median = 6). While mostly within $1.5\text{ }^{\circ}\text{C}$, monthly temperature anomalies exceeded $+6\text{ }^{\circ}\text{C}$ in approximately 1% of cases, but were never greater than $+10\text{ }^{\circ}\text{C}$.

Table 1

Avifauna groups used in the study. "Species pool" refers to the number of species in the group observed and included in the routes in the study area over the period 2000–2007. Groups within themes are mutually exclusive but not exhaustive, as some birds not assigned a group may nest across strata or have multiple or unknown migratory habits.

Group theme	Group	Short name	Species pool	Description
Avifauna	All	ALL	327	North American landbirds
Nest location	Ground-nesting	GROUND	98	Nest within 1 m of ground
	Midstory-/canopy-nesting	CANOPY	117	Nest more than 1 m above ground
Migratory habit	Permanent residents	RESIDENT	79	Do not migrate away from breeding range
	Short distance migrants	SHORTDIST	84	Winter north of Tropic of Cancer
	Neotropical migrants	NEOTROP	158	Winter south of Tropic of Cancer

Table 2
Heat wave metrics used.

Variable	Measurement	Source	Temporal grain	Time period
T_{air06_t}	June mean T_{air} anomaly	PRISM	Month	June
$M3LST06_t$	June LST anomaly	MOD11C3	Month	June
$T_{air06_{t-1}}$	Lagged June mean T_{air} anomaly	PRISM	Month	June _{t-1}
$M3LST06_{t-1}$	Lagged June LST anomaly	MOD11C3	Month	June _{t-1}
$T_{air07_{t-1}}$	Lagged July mean T_{air} anomaly	PRISM	Month	July _{t-1}
$M3LST07_{t-1}$	Lagged July LST anomaly	MOD11C3	Month	July _{t-1}
$T_{air08_{t-1}}$	Lagged August mean T_{air} anomaly	PRISM	Month	Aug _{t-1}
$M3LST08_{t-1}$	Lagged August LST anomaly	MOD11C3	Month	Aug _{t-1}
$T_{air}mean_{t-1}$	Summer average max. T_{air}	PRISM	Month/3-month	JJA _{t-1} ^a
$M3LSTmean_{t-1}$	Summer average land surface temperature	MOD11C3	Month/3-month	JJA _{t-1}
$M2LSTmean_{t-1}$	Summer average land surface temperature	MOD11C2	8-day/112-day	d153–d264 _{t-1} (1 Jun–20 Sep)
$T_{air}ex_{t-1}$	Mean summer maximum T_{air} exceedance	PRISM	Month/3-month	JJA _{t-1}
$M3LSTex_{t-1}$	Mean summer land surface temperature exceedance	MOD11C3	Month/3-month	JJA _{t-1}
$M2LSTex_{t-1}$	Mean summer land surface temperature exceedance	MOD11C2	8-day/112-day	d153–d264 _{t-1} (1 Jun–20 Sep)

^a June, July, August.

Comparison of the models based on the complete-observations dataset (2000–2005 heat wave metrics) revealed that models of abundance and richness based on monthly or season-long metrics from MODIS LST were clearly superior to their corresponding PRISM-based T_{air} alternatives. In all cases, AIC differences between the best MODIS- and PRISM-based models were greater than 25, indicating that PRISM-based metrics had considerably lower explanatory power (Table S2). Thus, subsequent results presented are based on 2000–2007 MOD11C2 and MOD11C3 datasets. In this MODIS-only comparison set, models also varied widely in support, as gauged by Δ_i (Table 3). August MOD11C3 LST anomalies from the previous year ($M3LST08_{t-1}$) resulted in the most supported models of abundance of ALL, GROUND, and SHORTDIST birds. Season-long 8-day LST exceedance from the previous year ($M2LSTex_{t-1}$) was the best predictor of the abundance of CANOPY and RESIDENT birds. Same-year June MOD11C3 LST anomalies ($M3LST06_t$) formed the basis of the most supported model for NEOTROP abundance. Models based on July measurements were generally less supported than those based on other months. In each group, the best abundance model was clearly better than all competing models, indicated by $\Delta_i > 4.0$. Season-long exceedances using 8-day MOD11C2 ($M2LSTex_{t-1}$) were consistently better than models based on mean anomalies.

Comparisons of support among richness models also indicated the utility of 8-day LST exceedance from the previous year ($M2LSTex_{t-1}$), which was the best predictor of richness for all groups except GROUND (Table 3). For this group, using monthly exceedances ($M3LSTex_{t-1}$) resulted in the best model.

Avian abundance and richness usually, but not always, declined during or after heat waves (Table 4, complete information in Table S3). This was particularly true in the South ecoregion, where nine of twelve models indicated significant negative avian responses to increased temperatures. However, in the Humid North ecoregion, the abundance and richness of RESIDENT (significantly) and most other groups (non-significantly) increased with elevated temperatures.

Fig. 3 depicts the impacts of the three heat wave scenarios on avian communities in our study region. A season-long heat wave with mean $M2LSTex_{t-1}$ of +3 °C, resulted in particularly large changes in abundance and richness. Most groups saw declines in both abundance and richness in the Montane and South ecoregions, with the largest declines in RESIDENT bird abundance, which declined 19.4% and 12.8%, respectively. In contrast, RESIDENT birds in the Humid North and NEOTROP birds in the Dry North increased by 15.0% and 11.6%, respectively. Here, and in other scenarios unless otherwise noted, similar but more modest patterns of change occurred for avian richness. For instance, in the Montane ecoregion, RESIDENT richness declined by 6.3%.

Under an acute heat wave with $M3LST08_{t-1}$ 5 °C above normal, modeled changes were smaller, but mostly negative, with the largest declines in the South, where the abundance of ALL and GROUND

declined by 8.3% and 11.6%, respectively, by the following year. Declines in abundance also occurred among several avian groups in the Dry North and Montane regions. Declines in abundance and richness during years with $M3LST06_t$ 5 °C above normal were generally more modest and, in some cases, increases occurred. In particular, NEOTROP and GROUND abundance declined by 9.8% and 7.8% in the Dry North, and RESIDENT abundance increased by 8.7% and 5.2% in models in the Humid and Dry North respectively.

4. Discussion

4.1. Metrics and timing of heat waves

As expected, anomalies of remotely-sensed land surface temperature and interpolated air temperature derived from meteorological station networks were correlated in all ecoregions and time periods examined. However, MODIS LST provided more ecologically-relevant information as models based on LST were clearly superior to those based on T_{air} (Table S2). From a practical standpoint, this is encouraging, as meteorological networks suffer from poor coverage in many parts of the world and deriving high quality interpolated surfaces is challenging, meaning that spatial and temporal data continuity is not assured. Furthermore, satellite measures of temperature at the land surface, as opposed to the air, may also be advantageous. Specifically, measurements of LST are related to vegetation conditions with, for example, sharp rises associated with disturbance events (Mildrexler et al., 2007). Because we use mean LST over larger areas, the effect of small-scale disturbances is moderated, but likely still contributes to LST values. At broader scales, drought can be associated with heat waves (Trenberth & Shea, 2005) and likely entails elevated LST. Thus, MODIS LST may act as a synthetic indicator of both temperature and vegetation condition enhancing predictive utility over measurement of these aspects individually and producing a greater dynamic range than T_{air} (e.g. the interquartile ranges of temperature anomalies in July are 3.16 °C and 2.48 °C for LST and T_{air} , respectively; Fig. 2). Indeed, comparison with previous results examining the influence of drought on avian communities (Albright et al., 2010) reveals stronger associations with LST than with drought.

Both long-lasting as well as short but intense heat waves late in the breeding season influenced avian communities in our study. Avian community structure was most related to 1-year lagged metrics corresponding to either season-long or late-season heat waves. In most locations, temperature maxima in August are higher than in June, so heat waves are likely more intense during this time as well. On the other hand, responses of birds to July metrics were less strong despite the occurrence of the year's highest temperature maxima in this month at most locations. For many species, August corresponds to a time of high vulnerability for juvenile birds, as they have generally

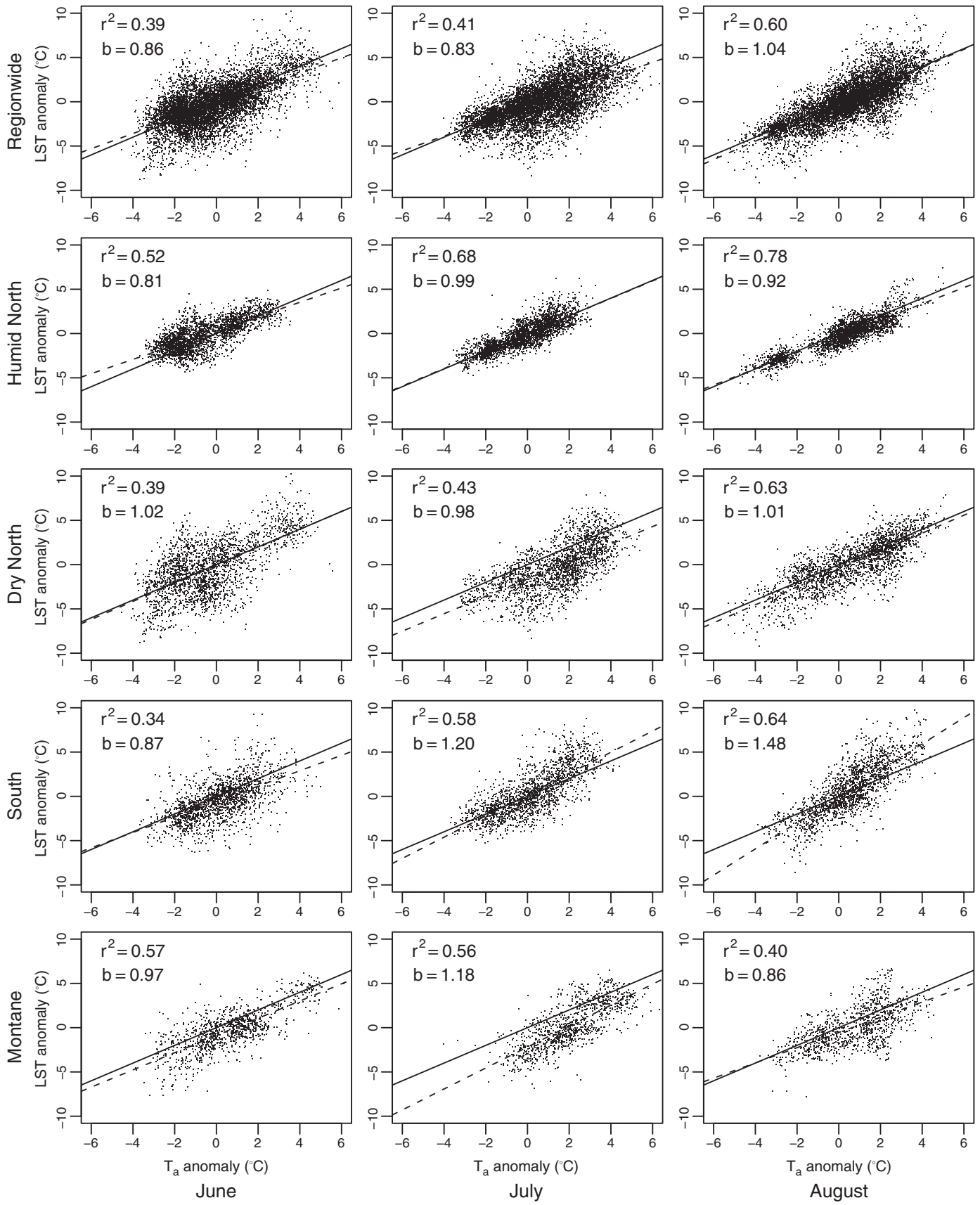


Fig. 2. Relationships between T_{air} and LST observed at the BBS routes. Plots are arranged with columns representing months and rows representing different ecoregions used in the study. Coefficient of determination (R^2), slope (b), a 1:1 line (solid line), and linear regression fit (dashed line) are shown for each plot.

Table 3
Model comparisons for overall and group-level avian abundance and richness based on the 2000–2007 dataset. Relative support for each individual heat wave metric within each avian group is shown by Δ_i , on which model ranking is based. Best identified models are highlighted in **bold**.

Heat wave metric	ALL						GROUND						CANOPY						RESIDENT						SHORTDIST						NEOTROP					
	Abundance			Richness			Abundance			Richness			Abundance			Richness			Abundance			Richness			Abundance			Richness			Abundance			Richness		
	Δ_i	Rank		Δ_i	Rank		Δ_i	Rank		Δ_i	Rank		Δ_i	Rank		Δ_i	Rank		Δ_i	Rank		Δ_i	Rank		Δ_i	Rank		Δ_i	Rank							
M3LST06 _t	65.1	6	40.3	8	58.1	4	10.5	5	35.1	8	27.1	7	26.4	8	98.1	7	26.2	8	0	1	16	6														
M3LST06 _{t-1}	84.4	7	38.4	7	109.7	8	16.1	7	34.9	7	27.4	8	21.1	7	101.8	8	24.9	7	42.9	2	21.5	8														
M3LST07 _{t-1}	88.5	8	27.3	6	103.1	7	17.7	8	16.7	4	20	4	13.7	6	82.9	6	20.4	6	91.2	8	16.6	7														
M3LST08 _{t-1}	0	1	9.1	3	0	1	9.8	4	34.2	6	20.3	5	4.8	3	0	1	14.2	4	76.6	7	6.2	4														
M3LST _t mean _{t-1}	65	5	21	5	63.8	5	11.7	6	21.7	5	21.7	6	11.4	5	52	5	14.9	5	68.3	6	13	5														
M2LST _t mean _{t-1}	36.4	2	7.6	2	54.2	2	9.1	3	16.6	3	12.5	2	3.3	2	29.3	2	8.6	3	62.7	4	5.5	2														
M3LST _t ex _{t-1}	58.8	4	17.5	4	57.4	3	0	1	12.8	2	12.9	3	6.6	4	43.2	3	7.7	2	65.6	5	5.6	3														
M2LST _t ex _{t-1}	41.5	3	0	1	75.8	6	3.2	2	0	1	0	1	0	1	45.3	4	0	1	50.4	3	0	1														

fledged and are largely independent of parental care (Anders et al., 1997). It is also possible that birds are more sensitive to end-of season conditions when confronting dispersal decisions than to conditions earlier in the season. For example, post-breeding song can be an important social cue for dispersing individuals, influencing habitat selection the following year (Betts et al., 2008). For season-long metrics, exceedances based on MOD11C2 8-day composites, rather than mean temperatures or measurements at monthly intervals, were more predictive of avian community changes. This suggests that 1) it is positive temperature anomalies specifically (e.g. associated with heat waves) that drive avian response and 2) finer temporal resolution (8-day vs. month) is beneficial for detecting ecologically-relevant heat waves.

4.2. Relationships between heat wave metrics and avian community change

Avifauna diversity is highly variable in time (Bengtsson et al., 1997; Rittenhouse et al., 2010). Our results suggest that a substantial portion of this variability can be explained by the occurrence of heat waves (Table S3). For a majority of avian groups and ecoregions, the most supported models indicated negative relationships between heat waves and avian abundance (Table 4), which is consistent with observations of avian populations following the 2003 European heat wave (Jiguet et al., 2006). A weaker, but similarly negative relationship between avian richness and heat wave metrics was observed for most ecoregions and avian groups. These relationships suggest that heat waves tend to reduce avian abundance, and to a lesser extent, richness, both during the same year and the subsequent year. Several mechanisms may underlie this relationship. Avian declines concurrent with heat waves may be caused by movements away from the breeding grounds and, in extreme cases, mortality (Finlayson, 1932). Because many of the heat waves observed during this study were mild, movement away from heat wave-affected areas, rather than mortality, appears a more likely cause. Reductions in abundance in the breeding season following a heat wave may additionally be due to reduced reproduction (Lusk et al., 2001), as individuals may choose to invest fewer resources in reproduction during heat wave conditions, or reduced young of the year survival. Furthermore, operating as informed dispersers (Clobert et al., 2009), individuals experiencing poor outcomes in one location may select different breeding ranges in following years, sometimes prospecting for locations occupied by successful conspecifics prior to migration to their wintering range (Doligez et al., 2004; Reed et al., 1999). It is also possible that during heat waves, birds may be present but be less likely to be detected. While the cooler temperatures associated with the near-dawn timing of the survey free birds from the need to seek shade (becoming harder to detect), it is possible that even early-morning vocalizations could be reduced if breeding has already been forgone. However, such detectability issues would only apply to same-year relationships and not to those observed during the year following a heat wave. Because of these reasons, we do not think that variable detectability influenced our findings.

Species richness was considerably less related to heat waves than abundance. Only in rare cases (e.g. GROUND and SHORTDIST in the Dry North following season-long heat waves, Fig. 3), was the response by richness significant when abundance was not. Certainly, at a species level, declines in abundance precede extirpation. Our results show that this relationship tends to hold at the community level, as individual species must first decline in abundance before extirpation from the community reduces species richness, suggesting a longer time scale for richness response than examined in this study.

4.3. Functional and geographic variation in response

Sensitivity to the timing and duration of heat waves varied among migratory groups (Tables 3 and 4). RESIDENT birds were most strongly

Table 4
Regional heat wave effect coefficients derived from best models for each group response. Significant ($P < 0.05$) coefficients ($\pm 95\%$ confidence intervals) and signs of non-significant estimates are shown for slopes of the specified heat wave metric in each ecoregion. Intercepts are reported in Supporting Information (Table S3). Note that abundance response is scaled as: $\ln(\text{abundance} + 1)$.

Group	Response	Metric	Humid North	Dry North	Montane	South
ALL	Abund	M3LST08 _{t-1}	+	-0.0098 ± 0.0034	–	-0.0173 ± 0.0036
	Rich	M2LSTex _{t-1}	+	–	-0.5905 ± 0.2929	-0.3434 ± 0.1900
GROUND	Abund	M3LST08 _{t-1}	–	-0.0126 ± 0.0045	-0.0087 ± 0.0059	-0.0244 ± 0.0046
	Rich	M3LSTex _{t-1}	+	–	–	+
CANOPY	Abund	M2LSTex _{t-1}	+	+	-0.0242 ± 0.0204	-0.0325 ± 0.0132
	Rich	M2LSTex _{t-1}	–	+	-0.3271 ± 0.1750	-0.1407 ± 0.1121
RESIDENT	Abund	M2LSTex _{t-1}	$+0.0452 \pm 0.0293$	+	-0.0697 ± 0.0359	-0.0455 ± 0.0230
	Rich	M2LSTex _{t-1}	$+0.1229 \pm 0.0904$	+	-0.1324 ± 0.1108	-0.0816 ± 0.0693
SHORTDIST	Abund	M3LST08 _{t-1}	–	-0.0115 ± 0.0042	-0.0124 ± 0.0056	-0.0191 ± 0.0044
	Rich	M2LSTex _{t-1}	+	-0.1098 ± 0.0949	-0.2183 ± 0.1424	-0.1412 ± 0.0882
NEOTROP	Abund	M3LST06 _t	+	-0.0206 ± 0.0038	–	–
	Rich	M2LSTex _{t-1}	–	–	-0.2926 ± 0.1992	–

related to season-long heat waves, based on the magnitude of their response irrespective of sign. The availability of resources over the breeding season may influence the ability of RESIDENT birds to produce optimum fat reserves, which in turn influences winter survival (Rogers & Smith, 1993). In contrast, NEOTROP birds were most influenced by elevated June temperatures (in the Dry North), which in some cases corresponds to the timing of their arrival in their breeding range. Relative to other migratory groups NEOTROP birds are less-affected by previous-year conditions, particularly during August. For some members of this group (e.g. the Common Nighthawk, *Chordeiles minor*, Western Tanager (*Piranga ludoviciana*) Black-headed Grosbeak (*Pheucticus melanocephalus*), Northern Waterthrush (*Seiurus noveboracensis*), Black-and-white Warbler (*Miniotilta varia*)) migration is already underway before in August. While not widespread among the species in this study (Carlisle et al., 2005; Murray, 1966), such early fall migration would tend to obscure any relationships between late summer heat waves and avian abundance and richness. Furthermore, the long migrations undertaken by Neotropical migrants increase their mortality risk, minimizing the relative contribution of the breeding season to total annual mortality. For instance, mortality rates of a population of Black-throated Blue Warblers (*Dendroica caerulescens*) during migration are approximately 15 times those experienced during stationary periods, constituting 85% of annual mortality (Silllett & Holmes, 2002). However, mortality during and even following migration may be elevated following heat waves if body condition has been impaired because of lower food resources (Merila & Svensson, 1997). Finally, we note as a caveat that some BBS routes in the South may be surveyed before June, obviously limiting the value of June temperature metrics in this region.

The sign of the relationship between avian community measures and heat wave metrics was strongly dependent on avian functional traits. We expected that the GROUND group would be most negatively affected by heat waves, and our results generally supported this. In response to the acute heat wave scenarios, GROUND abundance declined in all but the Humid North ecoregion, whereas for CANOPY abundance, declines were only predicted in the South during an acute August heat wave (Fig. 3). However, both GROUND and CANOPY abundance declined similarly following a season-long heat wave. Considerable variation associated with heat waves was observed for birds with different migratory habits. SHORTDIST birds were the most likely to decline in association with heat waves. Several factors may explain this. Among them, SHORTDIST birds stay in their breeding range for a longer duration than NEOTROP birds and because they do not travel as far as NEOTROP birds, they may have more time to scout suitable habitat at the beginning of the breeding season. Compared to RESIDENT birds, post-natal dispersal of SHORTDIST birds is greater (Paradis et al., 1998), which may grant them more flexibility in their selection of habitat to avoid areas impacted by heat waves during the previous year. In some cases, RESIDENT birds increased in association

with heatwaves, even when other migratory guilds showed declines. We speculate that this may be a consequence of these species being adapted to highly variable conditions and possibly even exploiting reduced abundance of migrants during heat waves.

Our models indicated substantial ecoregional variation in the strength, and even sign, of avifauna–temperature relationships (Table 4, Fig. 3). In most cases, associations of heat waves were strongest in the South, where decreases in abundance and richness were most consistently negative and of the largest magnitude. Birds have a variety of adaptations to cope with extreme heat, but these have limits, particularly for small passerines (McNab, 1970; Weathers, 1997). In the South, birds may approach these limits and suffer thermal stress (McKechnie & Wolf, 2010). The effect of season-long heat waves on montane avian communities was surprisingly large and warrants further study. Less strong, but also generally negative was the relationship between temperature and avian response in the Dry North. In the Humid North, however, abundance and richness of avifauna were generally positively related (significantly for RESIDENT) to heat waves. It may be that even considerably above normal temperatures, such as the $+5\text{ }^\circ\text{C}$ anomalies we use in our June heat wave scenario, are not sufficient to exert substantial thermal stress on birds and the resources they use in this region. In fact, elevated temperatures associated with heat waves may increase vegetative and arthropod production where it is limited by temperature.

4.4. Implications and conclusions

We have developed and demonstrated the utility of a simple index of MODIS LST exceedance that could be modified to suit a variety of applications. While our study used a temperature threshold based on mean LST for each time period, other values based on relevant biophysical thresholds could be chosen, for example from physiological studies of thermal ecology. We have shown that heat waves may have strong and geographically- and functionally-dependent effects on avian communities in temperate North America. This supports the importance of considering the effect of extremes in studies of historic, contemporary, and future climate change (Parmesan et al., 2000). Yet, we consider our study to be conservative in a number of regards. Responses may be considerably more dramatic among individual species, at specific locations, and over longer time periods than our examination revealed over a broad spatial scale, for broad species groups, and over a short time period. For example, we included both common and uncommon species in our guilds and there is some evidence that less common species may be more responsive to extreme weather events (Albright et al., 2010).

It is also important to consider avian community response to heat waves in light of predictions of higher frequency and severity of heat waves due to climate change. The 2003 European heat wave was an extreme event with 8-day LST anomalies of about $15\text{ }^\circ\text{C}$ in some areas

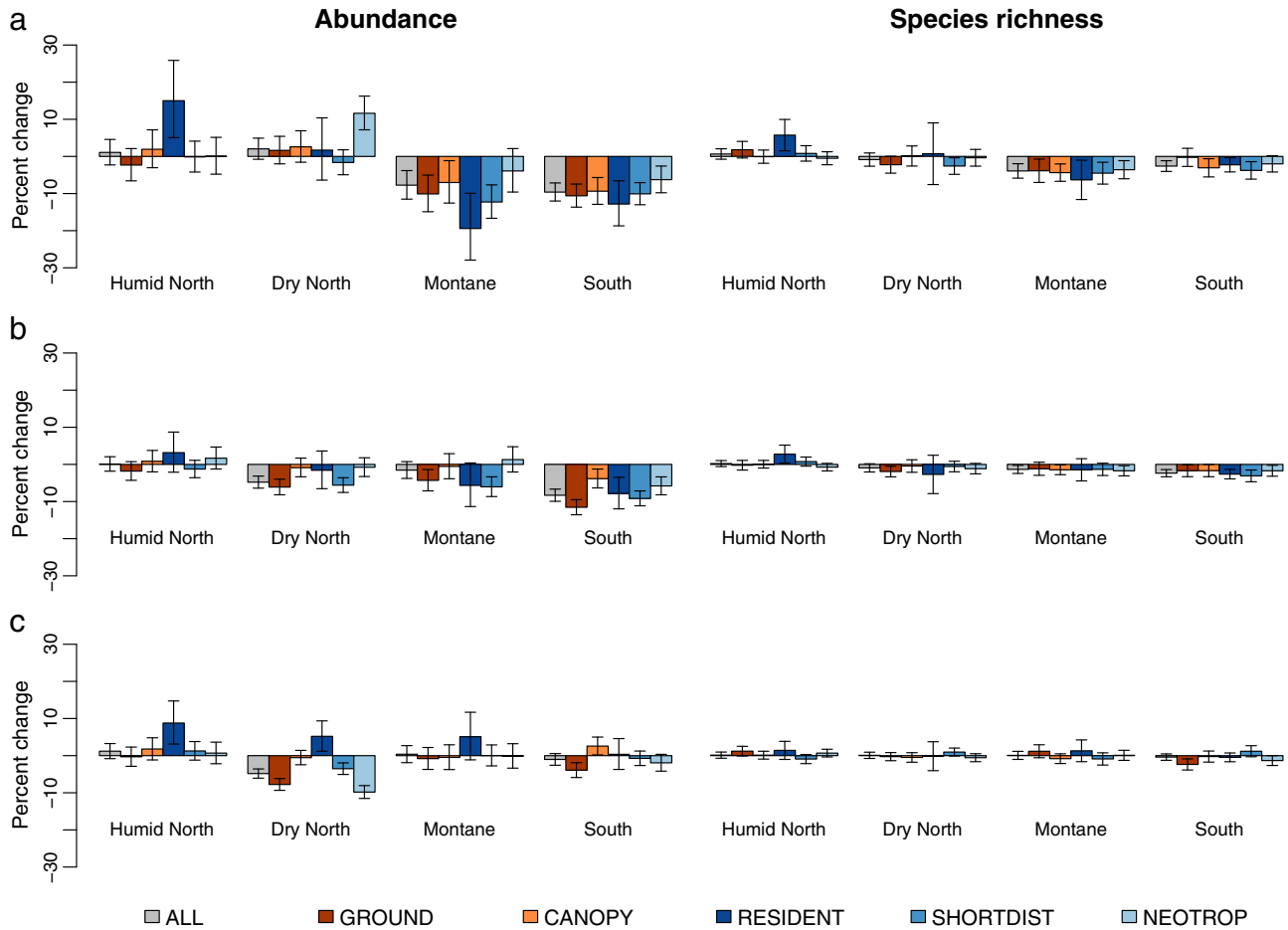


Fig. 3. Predicted changes in abundance and richness in a) the year following a prolonged season-long heat wave (mean 8-day LST exceedances during Summer were +3 °C), b) the year following an acute late-season heat wave (mean August LST 5 °C above normal), and c) the year of an acute early-season heat wave (mean June LST 5 °C above normal). Shown are predictions (\pm 95% confidence intervals) of percent change within each avian group in the four ecoregions considered in this study. Note that the order of groups in the figure is maintained to facilitate identification and comparison.

(Zaitchik et al., 2006). A comparable event occurring in North America could presage even larger declines in abundance and richness than predicted in our much more modest (50-year) heat wave scenarios, particularly if response is not linear at such extremes, as it appears in cases of human mortality (Filleul et al., 2006). Should such a dramatic heat wave occur, conservation managers may wish to consider targeted interventions, such as irrigation of critical habitat for the most threatened species. Heat waves may interact with other forms of environmental change to affect avifauna. In particular, a reduction in shrub cover stemming from the invasion of exotic grass and overgrazing may reduce the availability of fine-scale microclimatic refugia (D’Antonio & Vitousek, 1992). Maintenance of these aspects of bird habitat may be important tools of land management. Finally, considerable uncertainty remains regarding the specific mechanisms by which heat waves reduce avian abundance and richness and long-term effects of increased heat wave occurrence, which we hope will be addressed in future studies.

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