



Landsat 8 TIRS-derived relative temperature and thermal heterogeneity predict winter bird species richness patterns across the conterminous United States

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ABSTRACT

The thermal environment limits species ranges through its influence on physiology and resource distributions and thus affects species richness patterns over broad spatial scales. Understanding how temperature drives species richness patterns is particularly important in the context of global change and for effective conservation planning. Landsat 8's Thermal Infrared Sensor (TIRS) allows direct mapping of temperature at moderate spatial resolutions (100 m, downscaled by the USGS to 30 m), overcoming limitations inherent in coarse interpolated weather station data that poorly capture fine-scale temperature patterns over broad areas. TIRS data thus offer the unique opportunity to understand how the thermal environment influences species richness patterns. Our aim was to develop and assess the ability of TIRS-based temperature metrics to predict patterns of winter bird richness across the conterminous United States during winter, a period of marked temperature stress for birds. We used TIRS data from 2013-2018 to derive metrics of relative temperature and intra-seasonal thermal heterogeneity. To quantify winter bird richness across the conterminous US, we tabulated the richness only for resident bird species, i.e., those species that do not move between the winter and breeding seasons, from the North American Breeding Bird Survey, the most extensive survey of birds in the US. We expected that relative temperature and thermal heterogeneity would have strong positive associations with winter bird richness because colder temperatures heighten temperature stress for birds, and thermal heterogeneity is a proxy for thermal niches and potential thermal refugia that can support more species. We further expected that both the strength of the effects and the relative importance of these variables would be greater for species with greater climate sensitivity, such as small-bodied species and climate-threatened species (i.e., those with large discrepancies between their current and future distributions following projected climate change). Consistent with our predictions, relative temperature and thermal heterogeneity strongly positively influenced winter bird richness patterns, with statistical models explaining 37.3% of the variance in resident bird richness. Thermal heterogeneity was the strongest predictor of small-bodied and climate-threatened species in our models, whereas relative temperature was the strongest predictor of large-bodied and climate-stable species. Our results demonstrate the important role that the thermal environment plays in governing winter bird richness patterns and highlight the previously underappreciated role that intra-seasonal thermal heterogeneity may have in supporting high winter bird species richness. Our findings thus illustrate the exciting potential for TIRS data to guide conservation planning in an era of global change.

1. Introduction

Understanding the determinants of species richness is a fundamental goal of ecology (Hawkins et al., 2003) and is essential to defining conservation priorities (Brooks et al., 2006) and predicting biodiversity responses to global change (Brook et al., 2008). Many factors govern

species distributions and give rise to biodiversity patterns at broad spatial scales (Brown et al., 1996). Climatic factors have particularly strong associations with species richness (Boucher-Lalonde et al., 2014), including that of endothermic species such as birds (Howard et al., 2018). Indeed, at continental to global scales, climatic factors outweigh land cover in explaining bird abundance (Howard et al.,

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2015) and richness (Davies et al., 2007).

Among climatic factors, temperature plays a dominant role in driving species richness. For example, warmer temperatures influence richness patterns by increasing the number of metabolic niches (Clarke and Gaston, 2006) and by reducing physiological burdens (Currie, 1991; Currie et al., 2004), thereby permitting more species to occur. Ample evidence showing that species' distributions can be limited by their physiological tolerances of temperature supports these hypotheses (Khaliq et al., 2014; Root, 1988).

The strong influence of the thermal environment has important consequences for endothermic species which must maintain body temperature well above ambient temperature for necessary physiologic function during winter, a period typically characterized by low temperatures and heightened climatic stress on physiology (Newton, 1998; Williams et al., 2014). A prominent example of this influence is the northward shift of wintering bird ranges in North America following recent warming trends (La Sorte and Thompson, 2007), suggesting a strong link between temperature and wintering bird distributions. While some species are able to cope with climatic stress by modifying foraging or roosting behaviors (Kwit et al., 2004), other species rely on fine-scale site occupancy decisions in regions with thermal heterogeneity to minimize exposure to extreme hot or cold temperatures (Scheffers et al., 2013). Thus, regions with high thermal heterogeneity would be expected to have higher species richness, and thermal heterogeneity may be a particularly important factor driving species richness at higher latitudes where species experience extreme cold conditions more frequently. This notion is supported by recent mechanistic models explaining richness patterns in hyper-diverse bird communities across South America (Rangel et al., 2018). However, while recent research has highlighted annual temperature seasonality as an important driver of bird species richness at broad scales (Howard et al., 2018), there has been no assessment of the importance of within-season thermal heterogeneity in explaining continental-scale species richness patterns.

Data from the Thermal Infrared Sensor (TIRS) onboard Landsat 8 now enables mapping of temperature at 100 m resolution (Jimenez-Munoz et al., 2014). This is exciting when assessing thermal heterogeneity, because remotely-sensed thermal data avoid the pitfalls associated with interpolated temperature surfaces from weather stations (Behnke et al., 2016), and provide more ecologically-relevant information for modeling abundance (Pianalto and Yool, 2017) and predicting species distributions and richness patterns (Albright et al., 2011; Deblauwe et al., 2016). In particular, the spatial resolution of the TIRS data (100 m downscaled to 30 m by the USGS) offers substantial advantages for capturing spatial variability of the thermal environment compared to coarser resolution sensors, such as MODIS (1 km), to more accurately predict biodiversity patterns at broad spatial scales (Tuanmu and Jetz, 2015). Furthermore, utilizing thermal data directly in investigations of biodiversity patterns overcomes the limitations of often-used proxy measures for temperature, such as elevation or topographic complexity, that may poorly reflect true temperature gradients and that are correlated with other abiotic factors, thereby limiting robust inference (Minder et al., 2010).

Our goal was to develop new metrics of relative temperature and thermal heterogeneity during winter from Landsat 8 TIRS data for biodiversity studies, and to assess their performance in predicting patterns of winter bird richness across the conterminous US. We chose the conterminous US as our spatial extent because it contains (1) a large range of both relative temperature and thermal heterogeneity, (2) environmental data necessary to isolate the unique contribution of thermal factors (i.e., control data) at consistent spatial resolutions, and (3) a rich and extensive set of biodiversity data originating from standardized, decades-long monitoring programs. We chose to focus on winter bird communities because temperature plays a particularly strong role in regulating bird populations during this season (Newton, 1998). To determine winter bird richness patterns across the

conterminous US, we analyzed only resident bird species, i.e., those that are present at a given location throughout the year, from the North American Breeding Bird Survey (BBS), the most extensive survey of birds in the US.

We predicted that winter bird species richness would be positively associated with warmer relative temperatures and greater thermal heterogeneity because colder temperatures challenge birds' ability to maintain their body temperature in an optimal range (Root, 1988), and greater thermal heterogeneity can provide more niches potentially supporting more species (Letten et al., 2013). We further predicted that relative temperature and thermal heterogeneity would in particular affect richness patterns of bird species with greater sensitivities to thermal environments, i.e., small- versus large-bodied species, and species under greater threat from climate change. Specifically, we predicted that small-bodied species, which generally have lower thermoregulatory abilities than large-bodied species (Porter and Kearney, 2009), would be more sensitive to colder conditions and thus that both relative temperature and thermal heterogeneity would more strongly predict their species richness patterns. We also predicted that climate-threatened species—those with large discrepancies between their current and future distributions following projected climate change (Langham et al., 2015)—would be more associated with areas of high thermal heterogeneity because these species tend to occur in mountainous areas that exert strong temperature gradients and are characterized by pronounced thermal heterogeneity (La Sorte and Jetz, 2010; Sekercioglu et al., 2008).

2. Methods

2.1. Remotely sensed data

2.1.1. Landsat 8 Thermal Infrared Sensor (TIRS) data

To develop metrics of relative temperature and thermal heterogeneity with which to predict winter bird richness patterns across the conterminous US, we analyzed data from the Thermal Infrared Sensor (TIRS) of Landsat 8. Launched in February 2013, the thermal imaging by the TIRS consists of two bands (Bands 10 and 11) centered on 10.9 and 12 μm , respectively, that collect thermal data at 100 m resolution (Jimenez-Munoz et al., 2014). The data are resampled to 30 m using cubic convolution to match the native resolution of imagery provided by the Operational Land Imager (Roy et al., 2014). The resampled TIRS imagery thus represents the highest-resolution source of remotely-sensed thermal data available for the conterminous US. Out-of-field stray light has led to some bias in both thermal bands, and has particularly affected Band 11 (Barsi et al., 2014). We therefore used data only from Band 10 in our analysis.

We used imagery from Landsat 8 Surface Reflectance Tier 1, which is atmospherically corrected and contains the TIRS Band 10 data processed to orthorectified brightness temperature. As our focus was on relative rather than absolute temperature measurements, we did not require any further processing. Relative temperature can adequately capture thermal heterogeneity and may not suffer from biases introduced by further processing (Young et al., 2017). We first selected all images collected in the conterminous US between December–February of each year from 2013 to 2018 to bound the winter period. We then used the included QA flags to mask out clouds (including cirrus clouds), cloud shadows, and water based on the CFMASK algorithm, and used a static water mask derived from Landsat imagery (Hansen et al., 2013) to limit potential artifacts from ice. All imagery was obtained and processed in Google Earth Engine (GEE; ImageCollection ID LANDSAT/LC08/C01/T1_SR).

We calculated two metrics related to the thermal environment that we hypothesized would influence winter bird richness patterns. The first variable is a metric of *relative temperature* (Fig. 1a), which we derived by first calculating the mean value within a 11 \times 11 pixel moving window from each image and assigning it to the central pixel of the

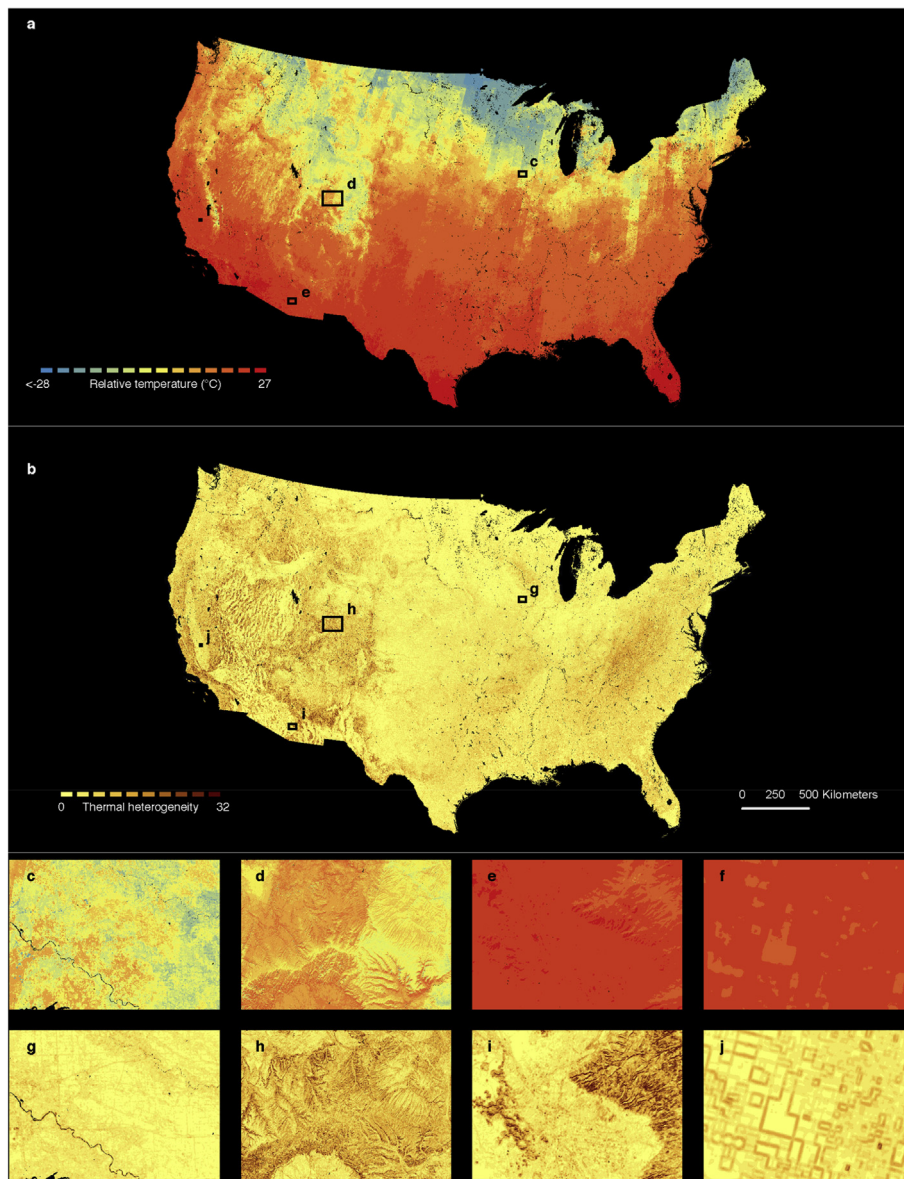


Fig. 1. Maps of relative temperature (a) and thermal heterogeneity (b) for the conterminous US based on thermal satellite imagery from Landsat 8 (TIRS band 10). (c–j) Detailed relative temperature and thermal heterogeneity maps for regions of the Great Plains in Iowa (c, g); the southern Rocky Mountains (d, h); Tucson, Arizona and the surrounding Santa Catalina Mountains (e, i); and fields in the Central Valley near Fresno, California (f, j). Letters and boxes in (a) and (b) denote inset locations in (c–j).

window, and subsequently taking the median value of those means across the image stack. We chose 11×11 pixel window sizes (equivalent to $108,900 \text{ m}^2$) in our analysis to maintain a relatively high spatial resolution that could then be summarized within each BBS route buffer (see below), noting that the predictive performance of first-order texture measures on bird richness patterns are relatively robust to the choice of window size (St-Louis et al., 2006).

The second variable is a metric of *thermal heterogeneity* (Fig. 1b), which we derived by first calculating the standard deviation value within a 11×11 pixel moving window from each image and assigning it to the central pixel of the window, and subsequently taking the median value of those standard deviations across the image stack. For both metrics, we tested alternative algorithms, such as calculating the mean value of the coldest winter image, but those efforts sometimes resulted in stark temperature contrasts between adjacent Landsat paths, or resulted in large data gaps due to clouds and their shadows in the coldest scene. Our approach as outlined above minimized these issues and produced almost seamless composites with few data gaps (Figs. 1a,

b, S1).

Our analysis thus resulted in two continuous layers of thermal metrics across the conterminous US at a spatial resolution of 30 m (Fig. 1a and b). We then took the mean value of each variable within a 19.7 km radius buffer of each BBS route's centroid for further analysis, following established methodologies utilizing BBS data (Pidgeon et al., 2007; Rittenhouse et al., 2012). We chose a 19.7 km radius as it is equivalent to half the distance of a BBS route and thus encompasses an entire route. We calculated each BBS route centroid from the minimum bounding rectangle encompassing the georeferenced route.

Altogether, our data processing workflow included three important steps to minimize potential spatial and temporal biases in calculations of relative temperature and thermal heterogeneity arising from variability in the number of TIRS observations that were unobstructed by clouds and snow. First, by using an 11×11 pixel window in our analysis to calculate mean values to assign to the central pixel, we incorporated information from the entire $108,900 \text{ m}^2$ window neighborhood, reducing the influence of no-data pixels. Second, by taking the

median pixel value across the image stack of six years of winter data (a total of 18 months) in calculations, we minimized temporal patterns of bias by deriving representative winter temperatures. Finally, by summarizing each metric by taking the mean value within BBS route buffers of 19.7 km radius (a total area of 1219 km²), we significantly reduced spatial patterns of bias by averaging temperatures derived from potentially different numbers of thermal observations per pixel.

2.1.2. Ancillary remotely-sensed environmental variables

We included five additional ancillary environmental variables related to elevation, topography, and land cover that are known to influence bird richness patterns at regional to continental scales as control variables in our analysis (Davies et al., 2007; McCain, 2009; Rahbek and Graves, 2001; Tuanmu and Jetz, 2015; van Rensburg et al., 2002). We used a void-filled version of the NASA Shuttle Radar Topography Mission (SRTM) digital elevation model at 1 arc-second (30 m) resolution (GEE Image ID USGS/SRTMGL_003), which matches the resolution of our thermal data. Using these data, we derived a metric of topographic heterogeneity known as the terrain ruggedness index (TRI; Riley et al., 1999), which is calculated as the square root of the sum of squared differences between a focal pixel and its eight neighbors (e.g., within a 3 × 3 pixel moving window). To summarize the data for each BBS route, we first calculated the TRI across the conterminous US and then took the mean TRI value within each BBS route buffer as above. We further calculated the mean elevation within each BBS route buffer using the SRTM data. Topographic heterogeneity and elevation are often considered as proxies for thermal heterogeneity and relative temperature in studies predicting species richness patterns (Davies et al., 2007; Rahbek and Graves, 2001). By including these variables in our analysis, our objective was to isolate the true effects of relative temperature and thermal heterogeneity on bird richness, independent of temperature gradients and heterogeneity arising from topographic complexity and temperature change over elevation.

Many species also have distinct habitat affinities, such that the spatial distribution of land cover across the US can also influence bird richness patterns. To control for this source of environmental variability, we used the USGS National Land Cover Database (NLCD), a Landsat-based land cover classification for the continental US at a spatial resolution of 30 m, again matching the spatial resolution of our other environmental variables. We used the 2011 version of the NLCD (GEE ImageCollection ID USGS/NLCD), the most recent version available, and that which most closely matched the time period of the TIRS data (Homer et al., 2015). We focused on three natural vegetation types that represent broad-scale habitat types for birds: forest (combining deciduous, evergreen, and mixed forest classes), shrubland, and grassland. To summarize the data for each BBS route buffer, we calculated three variables representing the proportion of all pixels that were classified as forest, as shrubland, or as grassland.

2.2. Bird survey data

We used data from both the North American Breeding Bird Survey (BBS, <http://www.mbr-pwrc.usgs.gov/bbs>) and the Christmas Bird Count (CBC, <http://www.audubon.org/conservation/science/christmas-bird-count>) to calculate winter bird richness patterns across the conterminous US. The BBS is the most extensive standardized survey of birds in the US (Sauer et al., 2017), consisting of an annual survey of breeding birds by volunteer observers along 39.4 km routes (4027 total routes). The primary limitation of the BBS for the purposes of our analysis is that bird distribution data are not collected during winter, which is a temporal mismatch with our predictor variables. Therefore, in order to adequately quantify bird richness patterns during winter, we restricted our analysis to include only those species with stable year-round distributions (i.e., resident species) and excluded short- and long-distance migratory species. We reviewed the known movement patterns of each resident species included in our analysis

based on data in the Birds of North America (Rodewald, 2015). We classified species as 'sedentary residents' (i.e., species reported to not move from the breeding grounds during winter), 'residents exhibiting localized movement' (i.e., species reported to remain close to the breeding grounds year-round, with some localized movements), and 'residents exhibiting longer-distance movement' (i.e., species reported to show more extensive movement during the non-breeding season; Tables S1 and S2). The categories are not mutually exclusive, and a given species could be assigned to multiple categories if, for example, individuals or populations of a species remain sedentary while others are known to move (i.e., the species exhibits partial migration). However, 95% of resident species included in our analysis were classified solely as either 'sedentary resident' or 'resident with localized movement', or both, which suggests that richness patterns based on data collected during the breeding season for these species should closely reflect richness patterns during the winter.

We also considered an alternative, US-wide survey of winter birds, the Christmas Bird Count (CBC, <http://www.audubon.org/conservation/science/christmas-bird-count>), because it aligns more closely with the seasonal timing of our predictors, and we conducted all our analyses with both datasets. However, there are a number of biases in the CBC data, and several advantages of the BBS that make the BBS more suitable for our research questions, and that is why we show BBS results in the main manuscript and CBC results in the Supplementary Material. These include: (1) there are more BBS survey locations than CBC survey locations (2743 BBS routes versus 1944 CBC circles from 2013-2018; Fig. S7a; Fig. S8), resulting in 40% more richness observations in our BBS-based analysis; (2) the survey extent of BBS routes is 3.75 times greater than that of CBC circles (buffered BBS routes cover an area of 3.34 million km² in our analysis versus an area of 0.89 million km² for CBC circles), which captures more variation in our predictors and helps improve inferences on how they may influence richness patterns; (3) BBS survey locations are more evenly distributed throughout the conterminous US, with much more adequate coverage between California and Mississippi (Butcher et al., 1990), whereas CBC circles are biased towards the Northeast and West Coast (Fig. S7a; Fig. S8); (4) land cover near BBS survey routes is more representative of the conterminous US, whereas the CBC circles are biased towards urban areas: on average, the proportion of developed land within CBC circles is 2.8 times higher than the conterminous US as a whole (<https://www.mrlc.gov/data/statistics/national-land-cover-database-2016-nlcd2016-statistics-2016>), and 2.3 times greater than the proportion of developed land within BBS route buffers based on summarized NLCD data within respective survey extents (BBS routes: mean = 0.063, SD = 0.07; CBC circles: mean = 0.15, SD = 0.17; Fig. S7b); and (5) BBS surveys are standardized and survey effort is equal among routes whereas CBC surveys differ in terms of survey effort by four orders of magnitude and can include any number of observers who are allowed to cover as much or as little of the CBC circle and use any method to count birds, including recording observations from bird feeders (Link et al., 2008; Figs. S7c and S7d). Unfortunately, there is no way to correct for the biases listed under 3) and 4) above, and while we corrected for survey effort in our CBC-based analyses (see Supplementary Material), those corrections are imperfect. Therefore, we deemed the BBS data for resident species only, i.e., those species whose breeding distributions closely reflect winter distributions, to be more suitable for our study and present our BBS-based findings in the main manuscript, and the qualitatively similar CBC-based findings in the Supplementary Material (Figs. S9–10).

During BBS surveys, the occurrence and abundance of all birds along a route are recorded during 3-min counts at 50 stops each spaced 0.8 km apart along with ancillary data describing observer, observation date and time, and weather conditions. Each route is surveyed once per year between May and July, when species are typically breeding and detectability is maximized. Observations are checked for validity and potentially erroneous or questionable entries are flagged. To ensure

high data quality, we excluded all observations made by an observer in their first year on a given route, which can lead to biased observations (Kendall et al., 1996), or where data quality flags indicated routes that a) were not randomly located; b) were not surveyed using the official BBS sampling protocol; or c) did not meet the BBS weather, date, time, and route completion criteria. Such records are flagged with a RunType Code of '0' in the BBS metadata, so we selected all records with a RunType Code of '1', which indicates that the observation meets official BBS criteria.

BBS routes are distributed throughout North America, but we restricted observations to the 48 conterminous states of the US (7.8 million km²) to match the spatial extent of our predictor variables. In addition to excluding short- and long-distance migratory birds, as previously noted, we further excluded species associated with habitats that are underrepresented by BBS route locations (Bart et al., 2005), including those with freshwater, coastal, or marine distributions (including waterbirds and waders), as well as those which are not adequately surveyed using diurnal line transect methods, such as raptors, crepuscular species, and rare species (those with < 30 total observations). These species also are closely tied to particular habitats, such as water bodies, or can disperse beyond the extent of a BBS buffer, thus we would not expect temperature to strongly drive their distributions at the spatial scale of our analysis. Finally, we excluded all hybrid species and observations that were not identified to species-level by observers. We adopted the BBS classifications of migration habit and breeding habitat groups (available at <https://www.mbr-pwrc.usgs.gov/bbs/guild/guildst.html>), in some cases supplemented by information from Audubon's online Guide to North American Birds (available at <https://www.audubon.org/bird-guide>), to inform these exclusions.

BBS routes have been surveyed since 1966, but to match the temporal resolution of our remotely sensed data, we further restricted bird observations to those collected between 2013-2017 (BBS data for 2018 were not yet available). We used BBS routes as our unit of analysis and tabulated resident species richness at each route as the total number of unique species observed on the route during this time period. In total, we analyzed 91,582 observations of 108 resident species along 2743 BBS routes.

We assigned each of the 108 resident species to a size class, distinguishing 'small-' and 'large-bodied' birds by following the approach of distinguishing 'small-' and 'large-ranged' bird species in the ecological trait database EltonTraits (Wilman et al., 2014). We first used body mass information from Dunning (2008) for all 332 breeding species in the BBS (after excluding freshwater, marine, coastal, raptor, crepuscular, and hybrid species) to calculate an overall median body mass (23.45 g; range = 2.64–5791.37 g; SD = 362.98 g). All species below and above the median body mass were assigned as small-bodied and large-bodied, respectively, resulting in 166 small-bodied species and 166 large-bodied species. We removed from further consideration any species that was not among our focal set of 108 resident species, resulting in 34 small-bodied resident species and 74 large-bodied resident species (Table S1). We then calculated small-bodied and large-bodied species richness at each BBS route by tabulating the number of small-bodied and large-bodied resident species.

We also assigned each of the 108 resident species to a climate sensitivity class, distinguishing 'climate-stable' and 'climate-threatened' species according to the classification provided by Langham et al. (2015). The climate sensitivity classification is based on the degree to which a species' current geographic distribution matches its projected geographic distribution under climate change. Those species that are predicted to have at least 50% or more of their current and future ranges overlapping are assigned climate-stable, while species with < 50% predicted overlap are considered climate-threatened. This resulted in 65 climate-stable resident species and 43 climate-threatened resident species (Table S1).

2.3. Statistical analysis

To quantify the relationship between each of our environmental predictors and winter bird richness, we fit a series of linear models containing all combinations of our environmental variables as predictors and winter bird richness as the response variable. We also included squared terms for relative temperature and elevation because bird species richness sometimes shows non-linear relationships with these variables, with richness peaking at intermediate temperatures and at mid-elevations (McCain, 2009). We separately fit models for each of our five groups of species: all resident species, small-bodied resident species, large-bodied resident species, climate-stable resident species, and climate-threatened resident species. This resulted in a total of 512 models considered for each group (2560 models total). Prior to fitting models, we assessed collinearity of our predictors by calculating Spearman's correlation coefficients between all pairwise predictors (Fig. S2). The highest correlation between any two predictors was 0.78 (between terrain ruggedness and thermal heterogeneity). All other pairwise correlations were generally low (mean |correlation| = 0.23), so we retained all predictors in our model set. Furthermore, as a secondary measure to ensure that predictors in models were not collinear, we calculated variance inflation factors for each predictor in fitted models.

The full model for each species group therefore included a total of nine predictor variables along with an intercept (Table 1). For each species group, we ranked models based on the Bayesian Information Criterion (BIC), which penalizes over-parameterized models (Table 2), and centered and standardized all predictors to enable unbiased comparisons of coefficients. We assessed the total explanatory power of the models by calculating their adjusted R^2 , and assessed the contribution of each predictor in predicting bird richness for each group by plotting their effect sizes with standard errors. To further assess relative variable importance of our predictors, we used hierarchical partitioning to evaluate the independent, joint, and total contributions of each predictor to overall explained deviance (Chevan and Sutherland, 1991). We assessed potential biases arising from spatial autocorrelation of the BBS routes by calculating Moran's I and analyzing model residuals in correlograms using 500 permutations. We performed all statistical analyses in R version 3.5.1, using the 'hier.part' (Walsh and Mac Nally, 2013) and 'ncf' (Bjornstad, 2019) packages to perform hierarchical partitioning and calculate Moran's I , respectively.

3. Results

3.1. TIRS-derived relative temperature and thermal heterogeneity

Our TIRS-derived map of relative temperature showed strong gradients across the conterminous US (Fig. 1a). As expected, regions at higher latitudes and elevations were generally colder, yet we were also

Table 1
Variables used in linear models to predict winter bird species richness.

Environmental variable	Data source	Temporal resolution	Spatial resolution
Relative temperature	Landsat 8 TIRS Band 10	16-day	100 m, downscaled to 30 m
Relative temperature ²	Landsat 8 TIRS Band 10	16-day	100 m, downscaled to 30 m
Thermal heterogeneity	Landsat 8 TIRS Band 10	16-day	100 m, downscaled to 30 m
Terrain ruggedness	SRTMGL1 V003	Static	30 m
Mean elevation	SRTMGL1 V003	Static	30 m
Mean elevation ²	SRTMGL1 V003	Static	30 m
Proportion forest	NLCD 2011	Static	30 m
Proportion shrubland	NLCD 2011	Static	30 m
Proportion grassland	NLCD 2011	Static	30 m

Table 2
 Summary of similarly-ranked models ($\Delta BIC < 4$) predicting winter bird richness for five different species groups, including coefficient values for all environmental variables and model fit and weight statistics (abbreviations: Int = Intercept; df = degrees of freedom; logLik = log likelihood; Wt = weight).

Species group	Model rank	Int	Mean elev	Mean elev ²	Terrain rugged.	Rel. temp	Rel. temp ²	Therm. heter.	Prop forest	Prop grass	Prop shrub	df	logLik	BIC	Delta	Wt	R _{adj} ²
Resident	1	11.08	-1.52	-	-	1.33	0.32	1.37	0.55	-	-	7	-7112.8	14281.0	0.00	0.47	0.38
	2	11.09	-1.44	-	-	1.36	0.31	1.33	0.49	-0.20	-	8	-7109.1	14281.4	0.46	0.37	0.38
	3	11.09	-1.49	-	0.27	1.39	0.31	1.18	0.39	-0.20	-	9	-7106.6	14284.4	3.41	0.08	0.38
	4	11.08	-1.57	-	0.25	1.36	0.32	1.24	0.46	-	-	8	-7110.6	14284.6	3.60	0.08	0.38
Small-bodied	1	2.98	-1.12	0.17	0.23	0.32	-0.13	0.71	0.39	-0.12	-	10	-4692.5	9464.1	0.00	1.00	0.50
Large-bodied	1	7.94	-0.66	-	-	1.02	0.43	0.53	-	-	-	6	-6285.9	12619.3	0.00	0.88	0.28
	2	8.03	-0.54	-0.09	-	1.03	0.44	0.53	-	-	-	7	-6283.9	12623.2	3.93	0.12	0.28
Climate-stable	1	8.47	-2.07	-	-	1.63	-	0.82	-	-	-	5	-6365.2	12769.9	0.00	0.64	0.58
	2	8.37	-2.06	-	-	1.64	0.10	0.83	-	-	-	6	-6362.2	12771.9	2.05	0.23	0.58
	3	8.47	-2.10	-	0.17	1.67	-	0.69	-	-	-	6	-6362.7	12773.0	3.08	0.14	0.58
Climate-threatened	1	2.71	0.60	-	-	-0.28	0.22	0.50	0.54	-0.11	-	8	-5047.3	10157.9	0.00	0.58	0.40
	2	2.72	0.50	-	-	-0.32	0.21	0.50	0.61	-	0.12	8	-5048.1	10159.5	1.60	0.26	0.40
	3	2.70	0.56	-	-	-0.29	0.22	0.52	0.58	-	-	7	-5052.5	10160.4	2.49	0.17	0.39

able to capture fine-scale and localized thermal dynamics. For example, warmer and cooler areas of the Great Plains were apparent in Iowa (Fig. 1c), temperature gradients were well-captured along the slopes of the Rocky mountains (Fig. 1d) and in the Santa Catalina Mountains near Tucson (Fig. 1e), and individual crop fields with varying thermal environments were delineated in the Central Valley of California (Fig. 1f).

Thermal heterogeneity derived from TIRS also showed strong patterns across the conterminous US (Fig. 1b). Thermal heterogeneity was generally lower in less topographically complex regions, such as the Great Plains (Fig. 1g), and highest in mountainous regions, such as the Rocky Mountains (Fig. 1h). In addition to these broad-scale patterns, our approach captured thermal heterogeneity around city blocks in urban areas (e.g., in Tucson, Arizona; Fig. 1i) and at the edges of fields (e.g., in croplands in the Central Valley outside Fresno, California; Fig. 1j).

We found a moderate positive correlation ($r = 0.34$) between relative temperature and thermal heterogeneity across the study region (Fig. S2), with strongest deviations at mid-high relative temperatures. For example, both relative temperature and thermal heterogeneity were high throughout much of Arizona and New Mexico (Fig. 1a and b), but in the adjacent state of Texas, thermal heterogeneity was fairly low while relative temperature remained high (Fig. 1b). For both temperature variables, the presence of clouds in winter generally affected the midwestern and northeastern regions most (indicated by small data gaps in black in Fig. 1a and b), as well as areas on select mountain peaks, but utilizing six years of data enabled the robust calculation of our metrics for the vast majority of the conterminous US (Fig. S1).

3.2. Predicting winter bird species richness

The top-ranked model predicting overall winter bird richness included five predictors (relative temperature, relative temperature², thermal heterogeneity, mean elevation, and proportion forest cover) and explained 37.3% of the variance (Table 2). Thermal heterogeneity had the strongest positive influence on winter bird richness according to its effect size, followed by relative temperature (Fig. 2). A significant positive relationship between winter bird richness and the squared term of relative temperature indicated that richness increases exponentially with relative temperature. Among our control predictors, proportion of forest cover surrounding BBS routes had a weak but significant positive influence on winter bird richness. Mean elevation had a strong negative influence on winter bird richness. Terrain ruggedness and proportion of grassland were not included in the top-ranked model, but had a significant weak-positive and weak-negative influence on winter bird richness in similarly ranked models, respectively (Fig. S3).

Hierarchical partitioning analysis, which we used to determine relative variable importance and the independent versus joint contributions of each predictor towards the variance explained by the model, indicated that relative temperature had the greatest independent effect on predicted winter bird richness patterns, followed by mean elevation and thermal heterogeneity, though thermal heterogeneity had a larger total contribution than mean elevation (Fig. 3). In general, most of the contributions were independent of the other predictors considered (Fig. 3).

Relative temperature, thermal heterogeneity, and mean elevation were also always included in the top-ranked models for small-bodied, large-bodied, climate-stable, and climate-threatened species (Fig. 2). The top-ranked models for small-bodied and large-bodied species richness explained 49.2% and 27.3% of the variance in richness patterns, respectively, while the top-ranked models for climate-stable and climate-threatened species explained 57.3% and 38.9%, respectively (Table 2). For small-bodied and climate-threatened species, thermal heterogeneity had a stronger positive effect on richness than relative temperature, consistent with our predictions. The opposite was true for large-bodied and climate-threatened richness patterns, such that

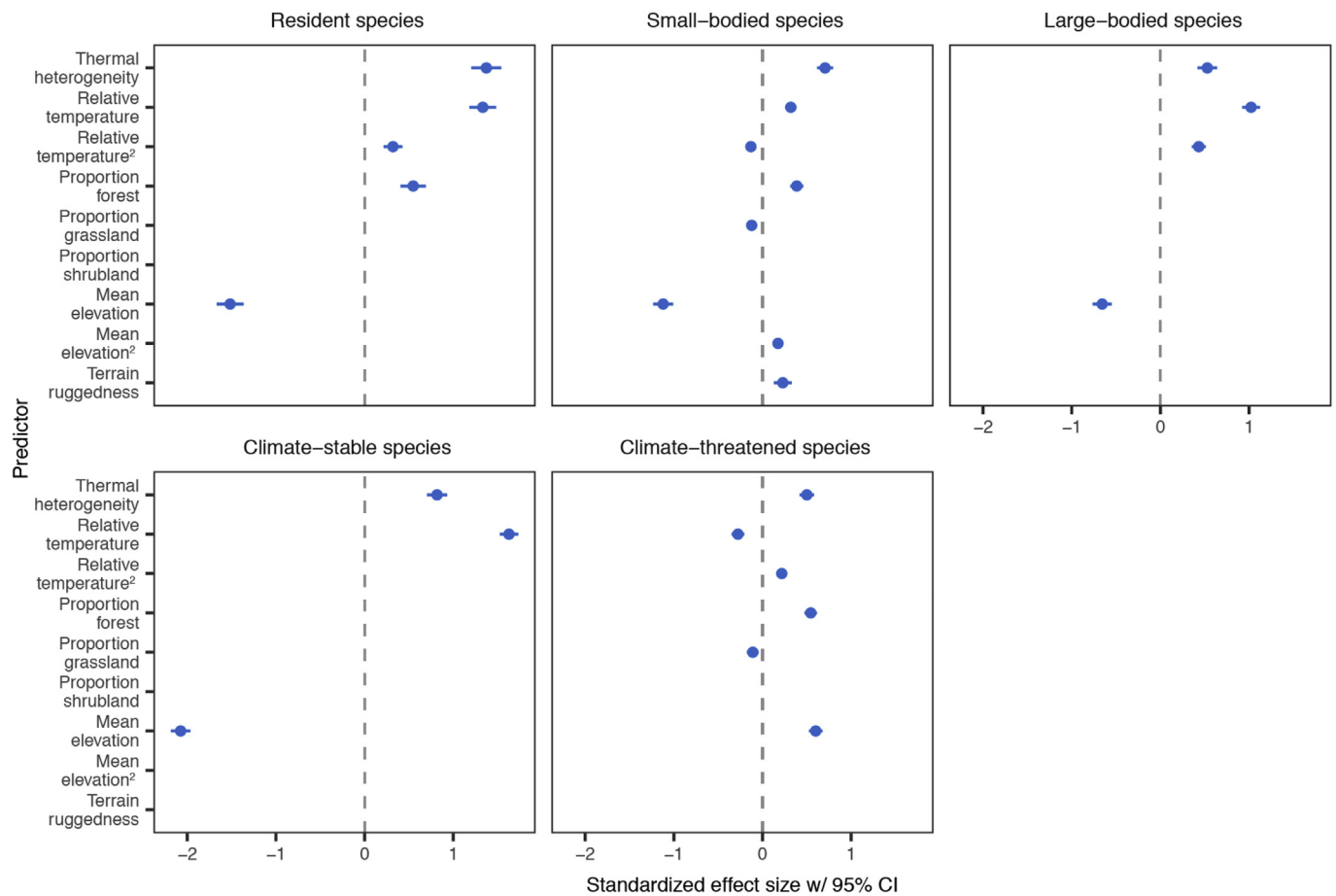


Fig. 2. Standardized effects sizes (points) with 95% confidence intervals (lines) for predictor variables in the top-ranked models of winter bird richness for all resident species and four subset groups (small-bodied, large-bodied, climate-stable, and climate-threatened species). Note that not all predictor variables are included in the top-ranked model for each species group.

relative temperature had the strongest positive effect on richness of any predictor considered (Fig. 2). Mean elevation was a strong negative predictor in top-ranked models for all species groups except climate-threatened species, which showed positive relationships with mean elevation (Fig. 2). Proportion of forest and grassland cover showed positive and weak-negative relationships, respectively, with small-bodied and climate-threatened species (Fig. 2). Proportion of shrubland cover was never included in the top-ranked model for any species group, and terrain ruggedness was only included as a significant predictor of small-bodied species richness with a weak-positive influence (Fig. 2).

Hierarchical partitioning indicated that relative temperature had the greatest total and independent effect on bird richness patterns of large-bodied and climate-stable species (Fig. 3). Thermal heterogeneity had the greatest total and independent effect on small-bodied species, which were influenced to a slightly lesser degree by relative temperature, proportion of forest cover, mean elevation, and terrain ruggedness (Fig. 3). Relative temperature, thermal heterogeneity, and mean elevation had similar total and independent effects on richness patterns of climate-threatened species (Fig. 3).

Of the 512 models we tested for predicting bird richness for each of the five species groups, between two and four models had Δ BIC values within four of the top-ranked model of each, indicating similar levels of support (Table 2). In each case, similarly ranked models based on BIC explained similar amounts of variance as the top-ranked model (maximum difference in deviance explained = 0.03%; Table 2). Predictors in similarly ranked models had effect sizes with similar magnitudes and directions as top-ranked models (Figs. 2, S3). Furthermore, the

magnitudes of the independent and joint contributions of predictors in these models were largely consistent with those of the top-ranked model for each species group (Figs. 3, S4). Variance inflation factors (VIFs) for each term in top-ranked models for all species groups were < 5 (mean VIF = 1.85; Table S3), indicating minimal collinearity of factors included in top-ranked models (O'Brien, 2007). Correlograms of model residuals of total winter bird richness analyses indicated that richness among BBS routes exhibited only a small degree of spatial autocorrelation, and therefore that results were not strongly determined by their spatial configuration (Fig. S5).

Our BBS-based results were also largely consistent with those that we obtained when analyzing the CBC dataset (see Supplementary Material), which included a total of 213 winter species, including short-distance migrants and winter visitors not captured by the BBS. Relative temperature and thermal heterogeneity were again among the top predictors for all winter species, small-bodied species, and climate-stable species. Consistent with our predictions, and with the BBS-based results, thermal heterogeneity had a stronger influence on small-bodied species than on large-bodied species (Fig. S9). Similarly, richness of climate-threatened species was more strongly governed by thermal heterogeneity than relative temperature, while richness of climate-stable species was more influenced by relative temperature (Fig. S9). Overall, the effects of relative temperature and thermal heterogeneity for these species groups were consistent both in terms of direction and magnitude when comparing CBC- and BBS-based results. Results from the hierarchical partitioning analysis were also qualitatively similar for all species groups (Fig. S10), with the exception of small-bodied species, where relative temperature had a greater independent contribution

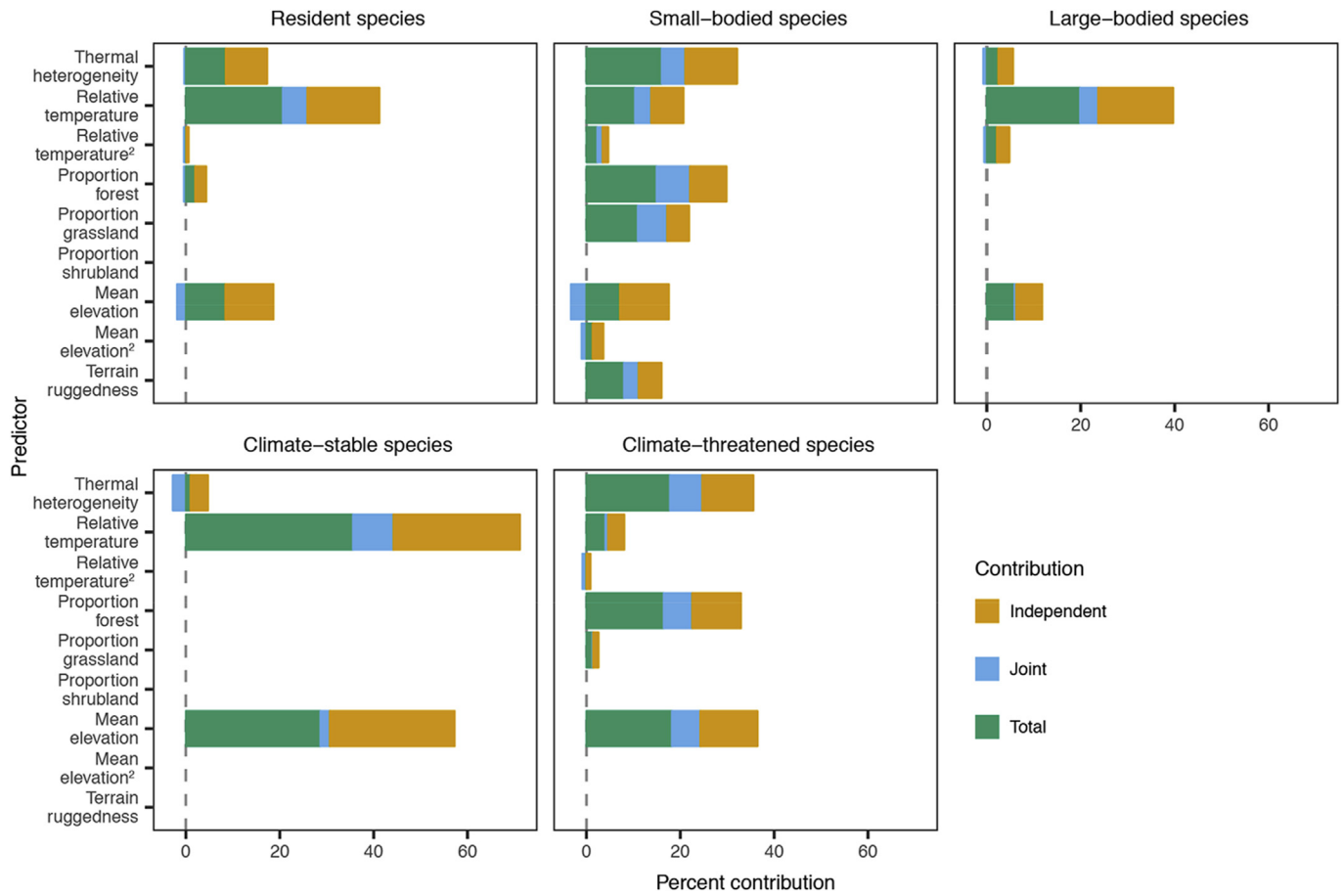


Fig. 3. Results of hierarchical partitioning analysis showing the independent, joint, and total contributions of predictor variables included in the top-ranked models of winter bird richness for all resident species and four subset groups (small-bodied, large-bodied, climate-stable, and climate-threatened species) towards the total variance explained by each model. Note that not all predictor variables are included in the top-ranked model for each species group.

than thermal heterogeneity in the CBC-based results, opposite from the BBS-based results.

3.3. Spatial patterns in predicted bird richness across species groups

Mapping the predicted richness values resulting from the top-ranked model for the five species groups showed spatial patterns that largely mirrored observed richness patterns for each group from the BBS data (Figs. 4, S6). Deviations in predicted from observed richness for each

species group were largely random with respect to geographic location. Some underpredictions occurred along the west coast and throughout the southwestern US, and some overpredictions occurred in isolated regions of the western US and in Florida for all resident, large-bodied, and climate-stable species. We observed smaller deviations for small-bodied and climate-threatened species, which showed minor underprediction in California and the southwest and minor overprediction in the Appalachian Mountains. Predicted richness patterns of large-bodied and climate-stable species were most reflective of total resident species

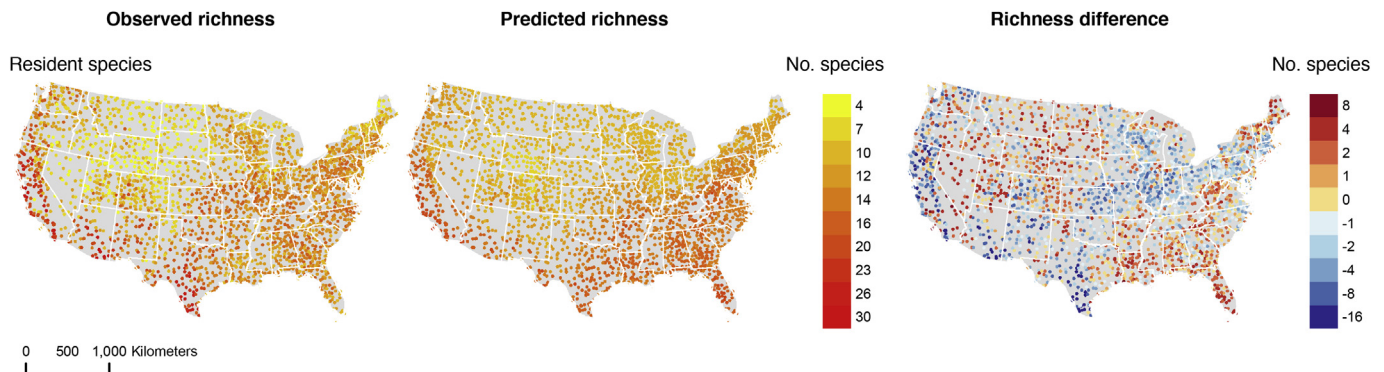


Fig. 4. Maps of observed richness (first column), predicted richness (second column), and richness difference (observed minus predicted; third column) for winter resident bird species across 2743 Breeding Bird Survey (BBS) routes in the conterminous US based on the top-ranked model. The left color ramp reflects observed and predicted richness values, while the right color ramp reflects richness differences from observed, such that bluer tones are under-predictions and redder tones are over-predictions. See Fig. S6 for analogous maps for small-bodied, large-bodied, climate-stable, and climate-threatened species. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

richness patterns during winter, while predicted climate-threatened species richness showed patterns that most strongly contrasted with total resident species richness.

4. Discussion

4.1. Predictive performance of relative temperature and thermal heterogeneity in explaining bird richness patterns

Our remotely-sensed measurements of the thermal environment representing relative temperature and thermal heterogeneity during winter were the two strongest predictors of total, small-bodied, large-bodied, and climate-stable winter bird richness patterns across the conterminous US. Both predictors had significant positive effects on bird richness when controlling for environmental factors related to elevation, topography, and land cover. Relative temperature explained more variance than any other predictor in our models for resident species, large-bodied species, and climate-stable species, confirming its role as a dominant factor predicting winter bird richness. These results linking fine-scale relative temperature gradients with winter bird richness support earlier, coarser-scale assessments showing tight associations between climatic factors and bird richness (Rahbek and Graves, 2001).

Our results also point to the important role of thermal heterogeneity in driving winter bird richness patterns, particularly of small-bodied and climate-threatened species. Inter-annual temperature variability can exert strong influence on species' range sizes (Chan et al., 2016), and regions of high temperature seasonality can filter out species that are not adapted to cope with wide temperature fluctuations (Janzen, 1967; Srinivasan et al., 2018). Yet thermal heterogeneity can act to bolster species richness by increasing the number of niches available and by supporting species with divergent adaptations to the thermal environment (Letten et al., 2013). Furthermore, regions of high thermal heterogeneity within a given season can buffer against exposure to temperature extremes (Scheffers et al., 2013), which is important for species with poorer thermoregulatory capacity or ranges more tightly governed by climatic factors.

Indeed, the effect of temperature variability on species richness patterns depends on the spatial and temporal scale considered, in some cases tipping the balance towards higher rates of stochastic extinctions thereby reducing species richness, while in others promoting speciation rates and stabilizing competition, thereby increasing species richness (Shurin et al., 2010). We found that thermal heterogeneity acts to increase bird species richness at continental scales, at least during winter, potentially by creating thermal refugia that can support a greater number of species. We further provide evidence that spatial patterns in thermal heterogeneity more strongly predict richness patterns of small-bodied and climate-threatened species, two species groups that are thought to be more sensitive to cold temperatures or largely governed by climatic factors. Large-bodied and climate-stable species may have physiologies or other adaptations that enable them to occupy wider temperature gradients (Langham et al., 2015; Porter and Kearney, 2009). Consequently, such species may not be governed as strongly by thermal conditions (Srinivasan et al., 2018), lessening their need to exploit thermal heterogeneity during winter. Our results favor increased consideration of thermal heterogeneity to more accurately predict broad-scale species richness patterns, particularly of species sensitive to climate change.

4.2. Application of remotely-sensed thermal data for biodiversity conservation

More broadly, our analysis illustrates the promise of thermal data captured by satellite imagery to generate fine-scale thermal metrics with great utility for biodiversity conservation. Moderate-resolution thermal data are readily available across the globe. Capitalizing on the

rapid growth of species locality information from standardized surveys like the BBS, citizen science databases, and museum specimen collections (La Sorte et al., 2018), future work could evaluate whether the patterns we observe for wintering birds in the conterminous US are representative of patterns globally or in other biogeographic realms, and in other seasons when biodiversity patterns can show stark differences owing to migration (Elsen et al., 2018b; La Sorte et al., 2017). Thermal data in summer, for example, may reveal thermal refugia for birds during heat waves.

Our predictive maps of winter bird richness differ considerably from maps of total bird richness derived from static species range maps (Jenkins et al., 2015), making our maps valuable when identifying priority areas for conserving winter birds. Conservation priorities based on temperature gradients and thermal heterogeneity represent coarse-filter strategies that aim to protect features of landscapes that promote biodiversity (Tingley et al., 2014), which have advantages in conserving biodiversity under climate change (Elsen et al., 2018a; Lawler et al., 2015). Based on our analysis, such priority regions occur in California, coastal Florida, Texas, and throughout much of the southeast and Appalachian Mountains given their high levels of overall winter bird richness (Figs. 4, S6). For climate-threatened species, priorities include the Great Basin, Intermountain West, Pacific Northwest, and the Great Lakes region. Many of these same geographic regions are also priority regions for terrestrial vertebrates, freshwater fish, and trees, and correspond with areas where protection is largely lacking (Jenkins et al., 2015). Our results add support to calls for increased conservation attention in these threatened regions.

Another important consideration is the source of thermal heterogeneity. While terrain ruggedness can drive thermal heterogeneity, anthropogenic activities such as suburban and agricultural expansion can also significantly alter the thermal environment. For example, in the tropics, agricultural lands are 7.6 C warmer than primary forest on average (Senior et al., 2017), and temperate forests with greater tree densities have warmer and less variable microclimates than disturbed forests (Latimer and Zuckerberg, 2016). While agricultural lands are important for many bird species during winter (Elsen et al., 2017; Rosenblatt and Bonter, 2018), habitat conversion can negatively impact birds during breeding when they have different habitat requirements (Elsen et al., 2018b; Holmes, 2007). Thus, the positive influence of thermal heterogeneity on bird richness we observed during winter may be attenuated during breeding. Future work examining the interplay of thermal heterogeneity with land cover variables would help further inform the mechanism by which thermal heterogeneity influences species richness patterns.

4.3. Caveats and considerations

Though many factors limit species ranges and determine biodiversity patterns (Sexton et al., 2009), advances in remotely-sensed data are rapidly increasing our ability to investigate their roles directly (Estes et al., 2018; Radeloff et al., 2019). We focused here on the thermal environment, complementing other studies showing that remotely-sensed data, such as metrics of productivity (Coops et al., 2009; Hobi et al., 2017), cloud cover (Wilson and Jetz, 2016), and texture measures as proxies of habitat structure (Culbert et al., 2010; Tuanmu and Jetz, 2015), are useful in predicting biodiversity patterns. While incorporating such variables into models would likely increase predictive performance, the resulting model complexity potentially limits interpretability and the ability to directly test ecological hypotheses (Merow et al., 2014). Consequently, we opted to limit our input variables to focus on testing the roles of relative temperature and thermal heterogeneity in explaining species richness patterns. In doing so, we have demonstrated the profound influence of both variables on winter bird richness across the conterminous US, while providing an analytical framework that can readily be applied to other taxonomic groups and other regions.

Secondly, the TIRS data represent surface-level temperatures, which may not precisely reflect the conditions experienced by birds, especially in forests. In winter, closed canopy forests can provide thermal buffering of cold temperatures by filtering radiation exchange (Norris et al., 2011) and altering microclimatic conditions in the understory (Latimer and Zuckerberg, 2016). While sub-canopy temperatures are correlated with interpolated temperatures from weather stations, the degree of correlation is influenced by topography and landscape features such as the amount of urban area and forest edge (Latimer and Zuckerberg, 2016). Methods of combining air temperature, digital elevation model, and light detection-and-ranging (LiDAR) data have been proposed to more accurately capture microclimatic variability and thermal refugia (Lenoir et al., 2016), but such data are at present unavailable over broad spatial scales. Given our continental scale analysis of thermal data at the BBS route level (i.e., averaged within a 19.7 km buffer), we suggest that TIRS data provide the best broadly available approximation of relative temperature and thermal heterogeneity.

Finally, our analysis took advantage of data from the most extensive bird monitoring program in the US, the Breeding Bird Survey (Sauer et al., 2017), providing us with nearly 100,000 observations with which to model bird richness patterns. However, because these surveys are conducted during the breeding season, they do not directly capture winter bird communities, and our analysis excludes species that a) undergo short-distance migrations while still wintering in the US, and b) breed further north, but overwinter in the US. Our approach of considering only resident species that have stable annual distributions is hence conservative given the nature of the data, but we recognize that true winter bird richness patterns likely differ to some degree. However, we have no reason to believe that focusing on these species qualitatively changed our results, given the limited number of species that were potentially omitted. Indeed, analyzing data from the CBC, which contains short-distance migrants and winter visitors in addition to permanent residents, yielded qualitatively similar results (Figs. S9 and S10). This independent validation gives us increased confidence in our conclusions that relative temperature and thermal heterogeneity are important predictors of winter bird richness patterns.

5. Conclusion

We show that temperature gradients and fine-scale thermal heterogeneity strongly drive winter bird richness patterns, especially for species with greater sensitivities to the thermal environment. Our findings highlight the exciting potential of TIRS data to capture both gradients in relative temperature and intra-seasonal thermal heterogeneity that can be used to predict species richness patterns over broad scales. Our results have important implications for conservation planning under global change and underscore the importance of protecting regions with high thermal heterogeneity. The global availability of TIRS data enables future studies to investigate the predictive performance of the thermal environment on other taxonomic groups and in different spatial and temporal contexts, and to understand how the thermal environment interacts with other abiotic and biotic factors to govern species richness. Such studies are needed to bolster the generality of our findings and to better understand when and where the thermal environment plays pivotal roles in driving species richness patterns.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.rse.2019.111514>.

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