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Research

Contrasting seasonal patterns of relative temperature and thermal heterogeneity and their influence on breeding and winter bird richness patterns across the conterminous United States

Paul R. Elsen, Laura S. Farwell, Anna M. Pidgeon and Volker C. Radeloff

P. R. Elsen (https://orcid.org/0000-0002-9953-7961) ✉ *(pelsen@wcs.org), L. S. Farwell (https://orcid.org/0000-0001-5829-8397), A. M. Pidgeon (https://orcid.org/0000-0002-0090-3352) and V. C. Radeloff (https://orcid.org/0000-0001-9004-221X), SILVIS Lab, Dept of Forest and Wildlife Ecology, Univ. of Wisconsin-Madison, Madison, WI, USA. PRE also at: Wildlife Conservation Society, Bronx, NY, USA.*

Environmental heterogeneity enhances species richness by creating niches and providing refugia. Spatial variation in climate has a particularly strong positive correlation with richness, but is often indirectly inferred from proxy variables, such as elevation and related topographic heterogeneity indices, or derived from interpolated coarse-grain weather station data. Our aim was to develop new remotely sensed metrics of relative temperature and thermal heterogeneity, compare them with proxy measures, and evaluate their performance in predicting species richness patterns. We analyzed Landsat 8's Thermal Infrared Sensor data, calculated two thermal metrics during summer and winter, and compared their seasonal spatial patterns with those of elevation and topographic heterogeneity. We fit generalized least squares models to evaluate each variable's effect in predicting seasonal bird richness using data from the North American Breeding Bird Survey. Generally speaking, neither elevation nor topographic heterogeneity were good proxies for temperature or thermal heterogeneity, respectively. Relative temperature had a non-linear relationship with elevation that was negatively quadratic in summer, but slightly positively quadratic in winter. Topographic heterogeneity had a stronger positive relationship with thermal heterogeneity in winter than in summer. The magnitude and direction of elevation–temperature and topographic heterogeneity–thermal heterogeneity relationships in each season also varied substantially across ecoregions. Remotely sensed metrics of relative temperature and thermal heterogeneity improved the predictive performance of species richness models, and both thermal variables had significant effects on bird richness that were independent of elevation and topographic heterogeneity. Thermal heterogeneity was positively related to total breeding bird richness, migrant breeding bird richness and resident bird richness, whereas topographic heterogeneity was negatively related to total breeding richness and unrelated to migrant or resident bird richness. Because thermal and topographic heterogeneity had contrasting seasonal patterns and effects on richness, they must be carefully contextualized when guiding conservation priorities.

Keywords: biodiversity, Breeding Bird Survey (BBS), conservation, environmental diversity, remote sensing, Thermal Infrared Sensor, thermal refugia, topographic heterogeneity

Introduction

Climate change is shifting species distributions and ecosystems across the globe (Scheffers et al. 2016, Pecl et al. 2017). As a result, recent conservation approaches have focused on protecting features of landscapes that promote biodiversity instead of targeting priority species or ecosystems (Tingley et al. 2014). By conserving the 'stage', or the abiotic and geophysical conditions of the environment that drive species richness patterns and adaptive evolution, conservation actions can protect the evolutionary underpinnings of biodiversity, rather than the current snapshot of it (Anderson and Ferree 2010). Such approaches are particularly advantageous when conserving species whose distributions are in flux due to climate change (Lawler et al. 2015, Elsen et al. 2018).

A major assumption underlying the suggestion to protect the 'stage' is that environmental heterogeneity (i.e. variation of environmental factors over space) is positively correlated with species richness because such variation increases niche space and provides refugia, thereby enhancing coexistence and persistence and promoting species diversity (Gómez et al. 2016). Environmental heterogeneity further provides refugia and increases adaptive capacity by bolstering species' ability to track climate change (Carroll et al. 2017). Indeed, empirical evidence does show positive relationships across taxonomic groups and at various spatial scales for a range of environmental variables (Field et al. 2009, Stein et al. 2014), suggesting that heterogeneity can predict patterns of biodiversity (Beier and De Albuquerque 2015). This is important for mapping biodiversity patterns, because species inventories are often incomplete, and species distribution data are orders of magnitude coarser than readily available environmental variables (Jetz et al. 2012).

The spatial patterns of abiotic and ecological features are commonly used to inform conservation strategies because they are easy to measure over large areas and are positively correlated with biodiversity (Tuanmu and Jetz 2015, Farwell et al. 2020). Among environmental factors, topographic heterogeneity has a particularly strong positive influence on biodiversity patterns (Davies et al. 2007, Antonelli et al. 2018), presumably because topographically heterogeneous landscapes contain a diversity of microclimates that promote niche diversification, speciation and species colonization (Price et al. 2014, Steinbauer et al. 2016), and provide refugia through climatic buffering that promotes species persistence (Scherrer and Körner 2010). Consequently, topographically complex regions are considered global conservation priorities (Brooks et al. 2006) and are recognized for their potential to guide conservation planning under climate change (Ackerly et al. 2010, Comer et al. 2015, Zarnetske et al. 2019).

The assumption that topographic heterogeneity (variation in topographic parameters such as elevation, slope and aspect over space) is a good proxy for thermal heterogeneity (variation in temperature over space) makes sense because elevational gradients strongly affect thermal gradients (Mokhov and Akperov 2006). Indeed, elevation and topographic heterogeneity are often used as proxies for temperature and thermal heterogeneity, respectively, in macroecological and gradient studies (Rahbek and Graves 2001, Lookingbill and Urban 2003, Zarnetske et al. 2019). Moreover, interpolated temperature surfaces from weather stations that are frequently used in biodiversity studies are often calculated using digital elevation models (DEMs) and are thus, in part, inherently driven by elevation (Hijmans et al. 2005). Importantly, interpolated weather station data do not capture fine-scale topographic effects directly, and only – at best – indirectly when modeling weather data based on elevation.

However, the validity of using elevation as a proxy for temperature may be questionable because temperature–elevation relationships can vary substantially throughout the year. For example, in the Rocky Mountains of North America, there is greater change in temperature over elevation in summer than in winter (Blandford et al. 2008). Similarly, elevation is more closely correlated with mean daily temperatures during spring than in other seasons in the Sierra Nevada due to temperature inversions and local physiography (Dobrowski et al. 2009). Yet this seasonal decoupling of temperature and elevation enables disentangling the effect of topographic versus thermal heterogeneity on biodiversity patterns and assessing their relative and independent contribution toward explaining diversity patterns. Such assessments are important for ensuring that coarse-filter conservation strategies focused on capturing environmental heterogeneity are targeted appropriately, but they require spatially-detailed, seasonal temperature data based on actual measurements.

Remotely sensed data from the Thermal Infrared Sensor (TIRS) onboard Landsat 8 provide temperature data independent from elevation (Jimenez-Munoz et al. 2014). Furthermore, TIRS data are collected year-round, making it possible to calculate thermal metrics for discrete seasons, aiding ecological inference into the processes governing species richness patterns and helping reveal the abiotic 'stage' on which species are acting, thus appropriately guiding conservation priorities.

Our study had three major objectives. Our first objective was to use TIRS data to calculate metrics of relative temperature and thermal heterogeneity for the conterminous US during summer and winter, the two seasons with the most contrasting temperature regimes and where most species typically experience the greatest temperature extremes and thermal stress. We refer to the TIRS data as 'relative temperature' throughout because TIRS provides brightness temperature rather than absolute land surface temperature values (Supporting information). We predicted that spatial patterns in relative temperature and thermal heterogeneity vary among seasons, given pronounced temperature seasonality in the US, which varies with latitude and elevation (Janzen 1967) (Table 1: P1).

Our second objective was to compare the seasonal spatial patterns of our thermal metrics with those of elevation and topographic heterogeneity across the conterminous US, and for each of its terrestrial ecoregions, to quantify the degree to which elevation and topographic heterogeneity can reliably

Table 1. Predictions and rationales related to the influence of thermal metrics on seasonal bird species richness patterns tested in this study, grouped by major objective.

No.	Prediction	Rationale
	Objective 1 – calculate seasonal metrics of relative temperature and thermal heterogeneity	
P1	Spatial patterns in relative temperature and thermal heterogeneity vary seasonally	Pronounced temperature seasonality in the US that varies with latitude and elevation
	Objective 2 – compare the seasonal spatial patterns of relative temperature and thermal heterogeneity with elevation and topographic heterogeneity	
P2	Relative temperature is more strongly correlated with elevation in the summer than in the winter	Greater variability in thermal lapse rates over elevation in winter
P3	Thermal heterogeneity is more strongly correlated with topographic heterogeneity in the winter than in the summer	Enhanced productivity and vegetation in summer create more microclimates
	Objective 3 – evaluate thermal and topographic variables in predicting breeding and winter bird richness patterns	
P4	Relative temperature is negatively related to species richness in the summer and positively related to species richness in the winter	Bird distributions are strongly governed by species' physiologies and thermal tolerances
P5	Relative temperature has a stronger effect on bird richness patterns in summer than in winter	Most species are living closer to their upper thermal limits than their lower thermal limits
P6	Thermal heterogeneity is a stronger predictor of richness patterns than topographic heterogeneity	Species richness and thermal heterogeneity patterns vary seasonally, while topographic heterogeneity is a constant
P7	Thermal heterogeneity has a stronger effect on resident bird richness patterns than migratory bird richness patterns	Migratory species can better track seasonal temperature fluctuations, whereas residents need to exploit microclimates arising from fine-scale thermal heterogeneity

serve as proxies for temperature and thermal heterogeneity, respectively. We predicted that spatial patterns of relative temperature would correlate more strongly with elevation in the summer than in the winter, given greater variability in temperature gradients arising from temperature inversions in winter, which could lead to a more pronounced decoupling of temperature and elevation in winter (Blandford et al. 2008) (Table 1: P2). Further, we predicted that spatial patterns of thermal heterogeneity would correlate more strongly with topographic heterogeneity in the winter than in the summer, because enhanced vegetation productivity in summer creates microclimatic conditions that could lead to a more pronounced decoupling of thermal and topographic heterogeneity (Scheffers et al. 2013) (Table 1: P3).

Our third objective was to evaluate the relative correlation of these variables in models of breeding and winter bird richness patterns across the conterminous US. We had four specific predictions related to this third objective. Our first prediction was that relative temperature would be negatively related to species richness in summer and positively related to species richness in winter (Table 1: P4). Bird distributions in northern latitudes often reflect species' physiologies and thermal tolerances (Root 1988, Khaliq et al. 2014) and are therefore correlated with temperature and productivity (Hawkins et al. 2003), so we expected bird richness to be limited by hot temperatures in summer and cold temperatures in winter. Second, we predicted that relative temperature would more strongly correlate with bird richness patterns in summer than in winter, because more species are living closer to their upper thermal limits and therefore their ranges should be more directly governed by warmer temperatures (Araújo et al. 2013) (Table 1: P5). Third, we predicted that thermal heterogeneity would be a better overall predictor of

richness patterns than topographic heterogeneity, because species richness and temperature patterns vary seasonally, while topography is constant (Table 1: P6). Fourth, we predicted that thermal heterogeneity would correlate more strongly with resident bird richness patterns than migratory bird richness patterns (Table 1: P7). While species undertake long-distance migrations for many reasons other than maintaining their thermal niche (Somveille et al. 2018), the underlying factor is access to resources, which are influenced by seasonal temperature fluctuations (Gómez et al. 2016, Srinivasan et al. 2018), and migration reduces the need to exploit fine-scale thermal heterogeneity. Resident species must endure both summer and winter temperatures, potentially resulting in a greater need for thermal heterogeneity that can provide microclimatic refugia and thermal buffering during winter (Latimer and Zuckerberg 2016).

Material and methods

Bird richness data

We analyzed data from the North American Breeding Bird Survey (BBS), the most extensive survey of breeding birds in the United States. In the BBS, breeding birds are surveyed annually by volunteers along 39.4 km routes (4027 in total), where the occurrence and abundance of all birds are recorded along with the date, time and weather conditions. Each route is surveyed once per year between late May and mid-July.

We identified each species' migratory status (migratory or resident) using designations from the USGS (<www.mbr-pwrc.usgs.gov/bbs/guild/guildlst.html>) and from the Birds of the World database when USGS data were unavailable

(Billerman et al. 2020). We considered breeding bird assemblages to include all resident and short- and long-distance migratory species recorded during the BBS, with the exception of select species outlined below. Because BBS data are collected during summer, we considered wintering bird assemblages to include only resident species, i.e. those species with stable year-round distributions that do not move between breeding and wintering periods, and excluded short- and long-distance migratory species. We ensured that patterns of resident species observed during the breeding season appropriately reflected winter richness patterns by assessing the movement patterns of all resident species included in our analyses using the Birds of the World database (Billerman et al. 2020) (Supporting information).

Prior to analysis, we filtered the BBS data to remove poor quality data and species not adequately surveyed by the BBS protocol (Supporting information). We then limited the filtered data to observations between 2013 and 2018 to align with the temporal extent of our remotely sensed data sources. To summarize bird richness, we used BBS routes as the spatial unit of analysis (2865 routes) and calculated species richness for each route as the total number of unique species identified across all years. For analyses of summer richness patterns that included all species, we analyzed 545 688 observations of 337 species (434 511 observations of 225 migratory species and 111 177 observations of 112 resident species). For analyses of winter richness patterns, we restricted our analyses to the 112 resident species for the reasons outlined above (Supporting information).

Remotely sensed thermal, elevation and land cover data

We build on our previous work developing metrics of relative temperature and thermal heterogeneity for winter using data from the Landsat 8 Thermal Infrared Sensor (TIRS) by developing these two metrics for distinct seasons (Elsen et al. 2020a). Doing so allowed us to compare seasonal patterns and better understand variability in their relationships to commonly used proxy measures of elevation and topographic heterogeneity. Developing season-specific thermal metrics also enabled us to investigate how the relationships of these thermal variables with biodiversity patterns change seasonally.

TIRS has collected thermal imagery since it launched in February 2013. TIRS contains two bands (bands 10 and 11, centered on 10.9 and 12 μm, respectively) that collect land surface temperature data at 100 m resolution (Jimenez-Munoz et al. 2014). The data are resampled by the USGS to a spatial resolution of 30 m using cubic convolution and represent the highest resolution remotely sensed temperature data currently available for the conterminous US (Roy et al. 2014). We analyzed thermal data from band 10 to minimize bias introduced by out-of-field stray light that affects band 11 in particular (Barsi et al. 2014).

We calculated relative temperature and thermal heterogeneity for summer and winter separately to produce seasonal maps of relative temperature and thermal heterogeneity

(Fig. 1a–d; Supporting information). Relative temperature is derived by assigning to the central pixel of a 5 × 5 pixel moving window the mean value of all 25 pixels for each thermal image, and subsequently calculating the median value of those mean values across all images. Thermal heterogeneity is derived by assigning to the central pixel of a 5 × 5 pixel moving window the standard deviation of all 25 pixels for each thermal image, and subsequently calculating the median value of those standard deviation values across all images. For both variables, taking the median across all images within each season minimizes differences between adjacent Landsat paths and results in continuous and seamless maps across the conterminous US for both summer and winter. Our metric of thermal heterogeneity is not standardized by mean temperature because our aim was to include this metric together with relative temperature in species richness models and standardizing thermal heterogeneity would increase collinearity of predictors. We note that our approach results in warmer areas having higher heterogeneity values, and we control for this by directly incorporating relative temperature in our species models so that we can assess the independent association between species richness and thermal heterogeneity ('Modelling species richness' below).

We analyzed elevation data from a void-filled DEM produced by the NASA Shuttle Radar Topography Mission (SRTM) at 1 arc-second (30-m) resolution, which matches the spatial resolution of the TIRS data (Fig. 1g). We also derived a metric of topographic heterogeneity, analogous to thermal heterogeneity, by calculating spatial variation in the continuous heat-insolation load index (CHILI) (Theobald et al. 2015). CHILI is a modified version of the heat load index (HLI), which combines slope, aspect and latitude to estimate potential annual direct incident radiation and thereby captures microclimatic diversity (McCune and Keon 2002). In contrast to HLI, CHILI explicitly incorporates latitude and uses a 22.5° 'folding' to better capture evapotranspiration patterns than the original 45° of the HLI (Theobald et al. 2015). CHILI thus acts as a proxy for the effects of insolation and topographic shading on evapotranspiration. We calculated topographic heterogeneity by assigning the standard deviation of the CHILI values of all pixels in a 5 × 5 pixel moving window to the central pixel (Fig. 1h). The standard deviation of CHILI is highly correlated with a metric of spatial variability in elevation known as the terrain ruggedness index (Riley et al. 1999), but is a more direct proxy of thermal heterogeneity.

To investigate seasonal relationships between relative temperature and elevation, and between thermal heterogeneity and topographic heterogeneity across the conterminous US (Table 1: P2 and P3), we fit general linear models to 5000 randomly distributed data points across the US, with elevation and topographic heterogeneity as predictors of relative temperature and thermal heterogeneity, respectively. We included a squared term for elevation to accommodate nonlinearities, assessed the log–log relationship between topographic and thermal heterogeneity because data were skewed, and repeated this process in summer and winter for a total of
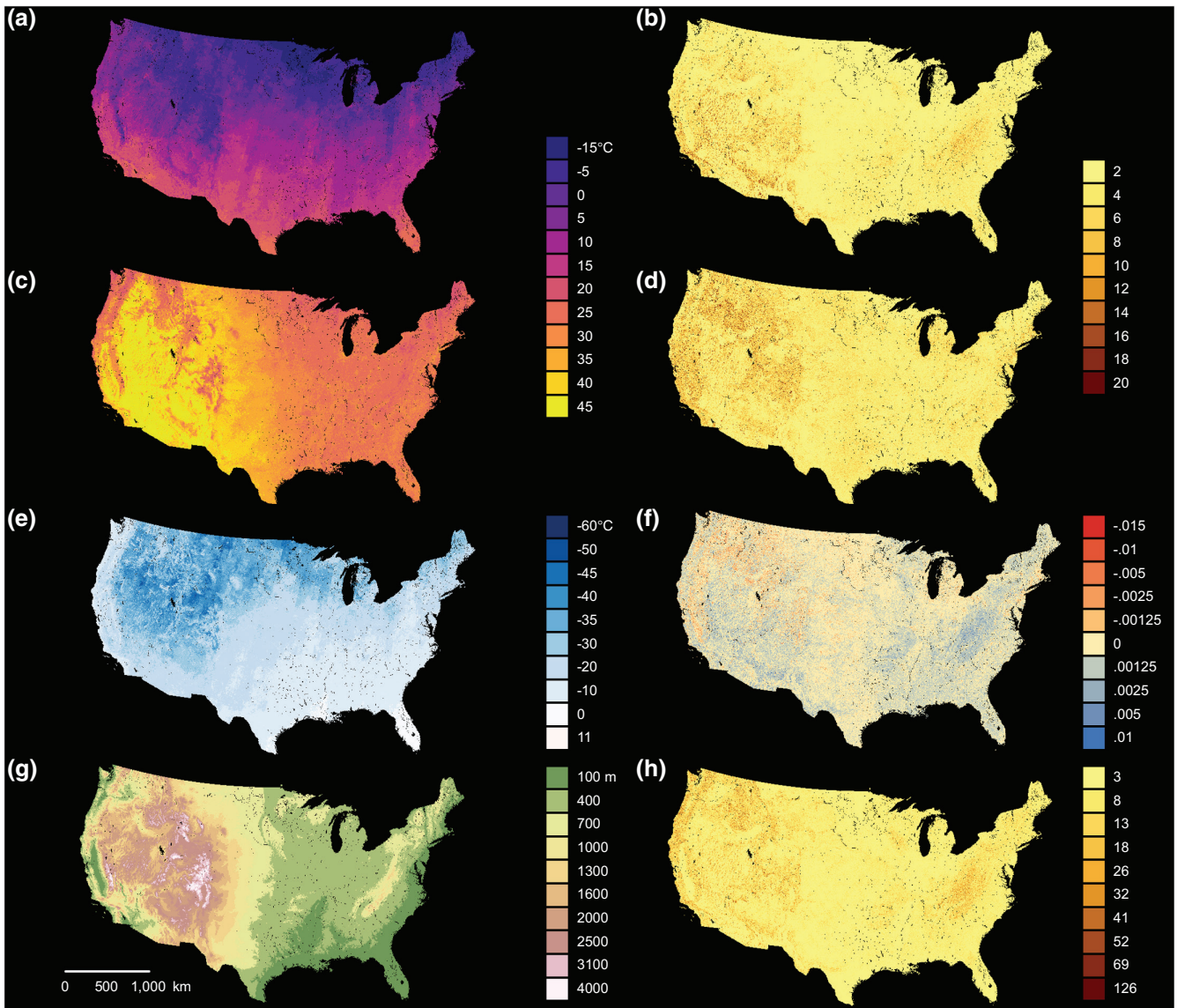
Figure 1. Maps of winter relative temperature (a), winter thermal heterogeneity (b), summer relative temperature (c), summer thermal heterogeneity (d), seasonal differences in relative temperature (e), seasonal differences in thermal heterogeneity (f), elevation (g) and topographic heterogeneity (h) for the conterminous US. Maps in (a–f) based on thermal satellite imagery from Landsat 8 (TIRS band 10), (g) based on satellite imagery from SRTM and (h) based on SRTM-derived continuous heat-insolation load index. Black areas in maps have no data due to masking out cloud, snow, ice and water bodies. Seasonal thermal heterogeneity differences in (f) are divided by mean relative temperature on the original brightness temperature scale (0.1 K) and are relative to summer thermal heterogeneity. Thus, the scale for (f) should be interpreted with respect to the relative, scalar differences among values (i.e. redder tones reflect pixels where thermal heterogeneity is greater in summer, while bluer tones reflect pixels where thermal heterogeneity is greater in winter).

four models (Supporting information). To investigate these relationships at finer spatial scales, we parameterized these models for each Level III ecoregion (Omernik and Griffith 2014). To assess how the relationships varied between seasons, we calculated Spearman's correlation coefficients between elevation and relative temperature and between topographic heterogeneity and thermal heterogeneity for each ecoregion in each season.

To evaluate the relative effect of our thermal and topographic metrics in predicting breeding and winter bird richness patterns across the conterminous US (Table 1: P4–P7), we summarized each predictor variable at the scale of BBS routes. For each of our thermal and topographic variables, we calculated the mean value within a 19.7 km radius of each BBS route's centroid. We chose a 19.7 km radius because it encompasses an entire BBS route and because georeferenced maps of BBS routes were unavailable for all of our routes, which prohibited us from accurately circumscribing smaller areas from which to summarize environmental variables with confidence. Our approach is thus conservative by not making

additional assumptions about route locations, and follows convention used in route-level analyses of BBS data (Flather and Sauer 1996, Pidgeon et al. 2007, Rittenhouse et al. 2012, Elsen et al. 2020a).

We also summarized predictors related to land cover at the scale of BBS routes. The spatial distribution of land cover can drive bird richness patterns because most species tend to have strong habitat associations with one or more land cover types. We controlled for this variation by summarizing 2016 USGS National Land Cover Data (NLCD). We calculated the proportions of three land cover types that constitute natural habitat for most North American birds, i.e. forest (including deciduous, evergreen and mixed forest), grassland and shrubland, and excluded land cover types associated with human activities and development, including agricultural lands and urban areas. We also checked to ensure that the location of BBS routes were not significantly biased with respect to our environmental predictors (Supporting information).

Modelling species richness

We fit a series of generalized least squares (GLS) models with our environmental variables as predictors and different groups of species as five different response variables, for a total of five model sets using the 'mgcv' package (Wood 2017) in R ver. 3.6.1. Each model set included elevation, a squared term for elevation to account for established non-linear relationships between bird richness patterns over elevation (McCain 2009), topographic heterogeneity and land cover variables as predictors. Three model sets additionally included our summer-derived thermal metrics as predictors, and separately used breeding (migrant and resident) bird richness, migrant bird richness and resident bird richness as the response variable. A fourth model set included our winter-derived thermal metrics as predictors, and resident bird richness as the response variable. Finally, a fifth model set included all thermal predictors (summer and winter) and breeding bird richness as the response variable (Supporting information). All model sets included squared terms for relative temperature to account for non-linearities in richness patterns akin to those established for elevation.

For each model set, we fit models using all possible combinations of predictors, yielding 512 models for each of the first four model sets, and 4096 models for the fifth model set (a total of 6144 models). We assessed collinearity of our predictors prior to model fitting using Spearman's correlation coefficients (r) and retained all predictors in our model set because pairwise correlations were generally low (mean |correlation| = 0.31) (Supporting information). Additionally, we calculated variance inflation factors, which were < 5 in all cases, indicating an acceptable degree of multi-collinearity for use in our models (O'Brien 2007) (Supporting information). We centered and standardized all predictors to enable coefficient comparisons and initially fitted models using maximum likelihood estimation to enable ranking models based on Bayesian information criterion (BIC), which penalizes over-parameterized models.

Once we selected the top-ranked model for each model set based on BIC, we refitted each model using restricted maximum likelihood (REML) estimation to provide unbiased coefficient estimates (Züur et al. 2009). To directly account for spatial autocorrelation, we fitted models using exponential, spherical, linear, ratio and Gaussian spatial correlation structures with the geographic coordinates (latitude and longitude) of each BBS route centroid, and including a 'nugget' effect. We then compared models fitted with and without spatial correlation structures. In all cases, including spatial correlation structures improved model fit over models without spatial correlation structures (Supporting information), and inspection of variograms of the residual of the models with spatial correlation structures revealed that the residuals formed a horizontal band of points indicating spatial independence (Supporting information) (Züur et al. 2009). Using a multivariate framework and incorporating the spatial structure of our predictor variables through the use of spatial correlation structures helped to isolate the non-spatial effects of our predictors on bird richness and was important to reduce erroneous correlations arising from spatially-structured variables (Beale et al. 2010, Currie et al. 2020).

We selected top-ranked models with the best-fitting spatial correlation structure to compare effect sizes (with standard errors) of our predictor variables for each species group and predictor set as a means of assessing the contribution of each variable in predicting bird richness patterns. As a second way of investigating relative variable importance of our predictors, we applied hierarchical partitioning to calculate the independent and joint contributions of each predictor towards the total variance explained by the model (Supporting information).

Results

Consistent with our first prediction, patterns of both relative temperature and thermal heterogeneity varied considerably between winter and summer (Fig. 1). During winter, relative temperature exhibited a more prominent latitudinal gradient (Fig. 1a), whereas during summer it showed a more prominent longitudinal gradient (Fig. 1c). Across the conterminous US, relative temperature showed a significant negative quadratic relationship with mean elevation during summer and a slight negative relationship with mean elevation during winter, which was consistent with our second prediction. Differences in this relationship were strongest below 2000 m, where relative temperature increased markedly with elevation in summer, yet subtly declined with elevation in winter (Fig. 2a). We observed similar seasonal contrasts in elevation versus relative temperature correlations at the ecoregion scale, with the magnitude and direction of correlation being highly variable among ecoregions (Fig. 3, Supporting information). For example, several ecoregions in the mid-western US, in the Pacific Northwest, in parts of the eastern Rockies, and in the south had positive elevation–temperature relationships during summer, but negative relationships during winter (Fig. 3a, c).

Thermal heterogeneity also showed nuanced spatial patterns across the conterminous US across seasons, with patterns changing seasonally (Fig. 1). For example, the North American deserts, southeast and northeast generally exhibited greater thermal heterogeneity in winter, whereas summer thermal heterogeneity was more pronounced in the Central Valley of California, the Appalachian Mountains and the Pacific Northwest. This led to contrasting seasonal correlations between topographic and thermal heterogeneity in associated ecoregions, with negative correlations during summer and positive correlations during winter (Fig. 3b, d). Across the conterminous US, consistent with our third prediction, topographic heterogeneity had a stronger positive relationship with thermal heterogeneity in winter than in summer (Fig. 2b), but showed little directionality of change across seasons (Fig. 2d). The US-wide analysis also masks, to some degree, the complex and sometimes opposing relationships between both topographic and thermal variables that are apparent at the scale of individual ecoregions (Fig. 3, Supporting information).
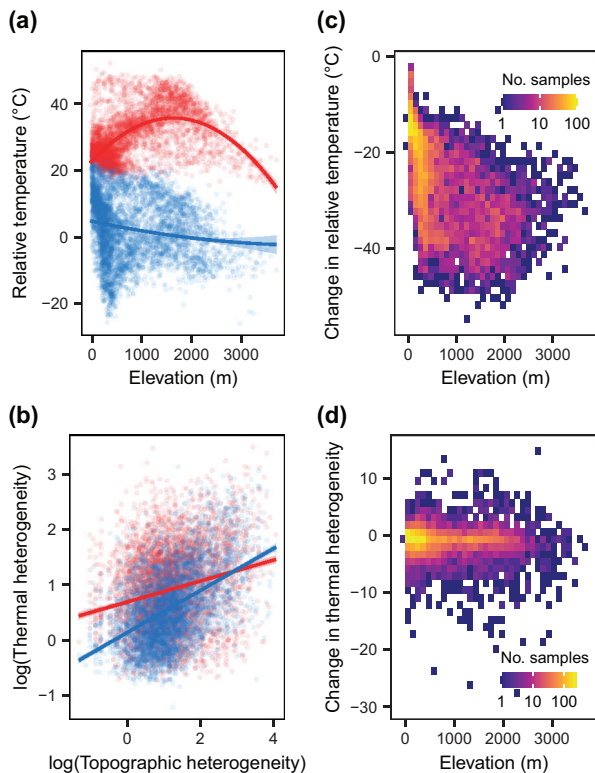

Figure 2. Seasonal relationships between elevation and relative temperature (a) and between log-transformed topographic heterogeneity and log-transformed thermal heterogeneity (b) based on 5000 random samples of predictors (summer points in red, winter points in blue). Colored lines are fits of a linear model (in (a), with a quadratic term for the independent variable), with shaded regions depicting 95% confidence intervals. Heat maps show seasonal change (with respect to summer) in relative temperature (c) and thermal heterogeneity (d) with elevation binned by 50-m of elevation and colored by the number of random samples.

Within each set of species richness models, there was no model that ranked as similar (ΔBIC < 2) to the top-ranked model, so we present results from the top-ranked model in each set (Burnham and Anderson 2002). Consistent with our fourth prediction, summer relative temperature was strongly negatively associated with breeding species richness, but counter to this prediction, winter relative temperature showed a weak negative association with resident species richness during winter (Fig. 4). In our model containing all thermal predictors from both seasons, we found that summer relative temperature had a stronger negative effect on breeding species richness than winter relative temperature, which was consistent with our fifth prediction (Fig. 4).

Compared with topographic heterogeneity, summer thermal heterogeneity was a stronger predictor of breeding species richness and winter thermal heterogeneity was a stronger predictor of resident species richness during winter, consistent with our sixth prediction (Fig. 4). While we had no a priori expectation as to the relative effect of thermal heterogeneity on breeding richness, we found that winter thermal heterogeneity had an effect size that was comparable to summer thermal heterogeneity. Counter to our final prediction, summer thermal heterogeneity had a larger effect on migrant species than on resident species, though both migrant and resident species richness were positively related to summer thermal heterogeneity, and resident species richness was also positively related to winter thermal heterogeneity.

Among the four model sets that incorporated summer thermal predictors, relative temperature consistently had a greater independent effect on richness patterns than thermal heterogeneity for all species groups (Supporting information). Furthermore, with the exception of resident species, relative temperature had a greater independent effect on richness patterns than mean elevation. The independent effect of summer thermal heterogeneity was similar to that of topographic heterogeneity for all species groups. However, winter thermal heterogeneity had a greater independent effect than topographic heterogeneity on resident species during winter.

Discussion

Using thermal satellite imagery from Landsat 8 TIRS, we developed new metrics of relative temperature and thermal heterogeneity, capturing distinct patterns across seasons. Our metrics are based on actual measurements, not interpolations of weather station data, which confers clear advantages over proxy variables such as elevation or topographic heterogeneity in models of bird species richness. While our metrics were correlated with elevation and topographic heterogeneity, we found that relationships were non-linear, that both the strength and the direction of these relationships differed profoundly between seasons (Fig. 1, 2), and that relationships varied considerably among ecoregions (Fig. 3). In other words, the suitability of elevation and topographic heterogeneity as proxies for relative temperature and thermal
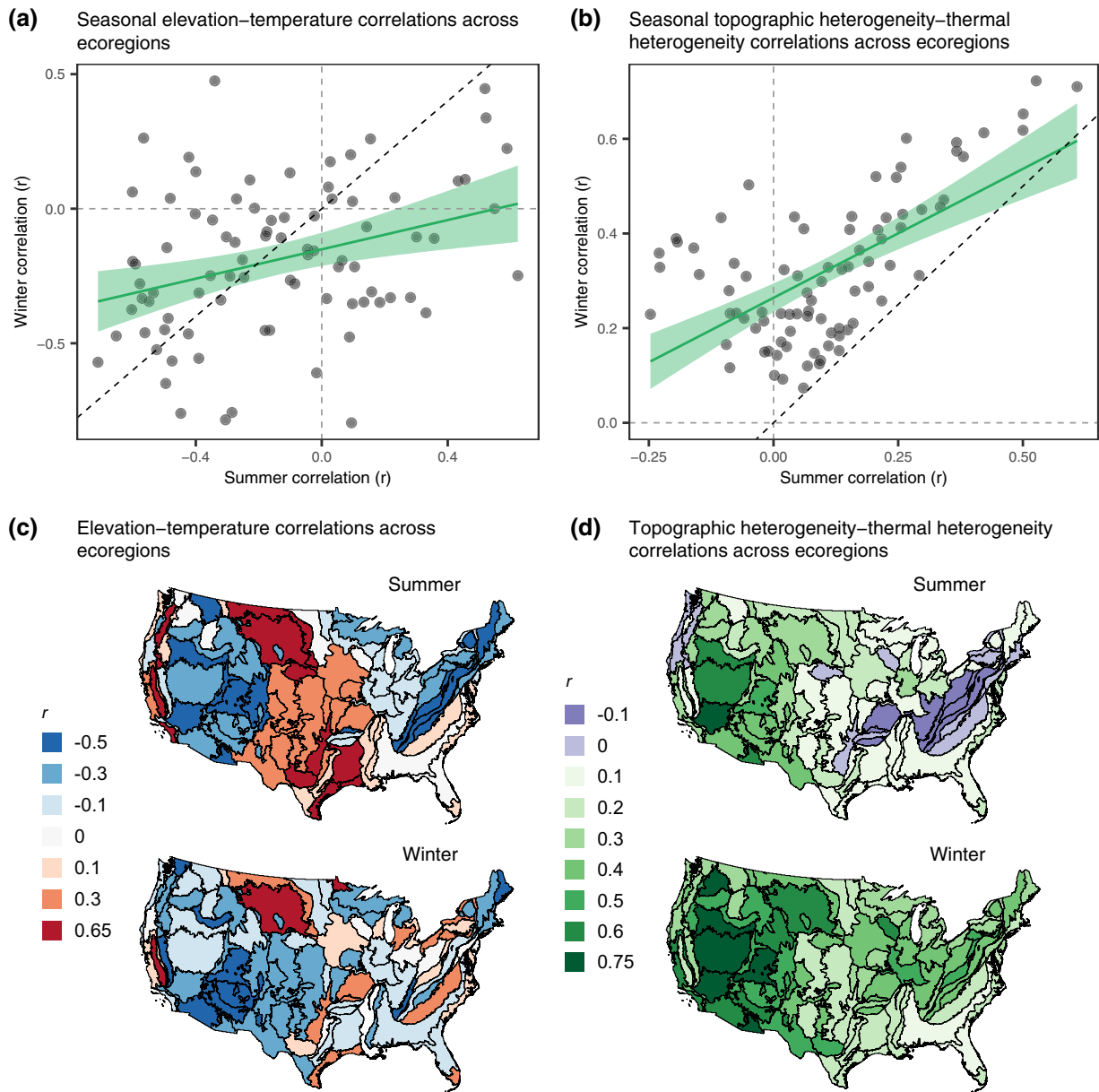
(a) Seasonal elevation–temperature correlations across ecoregions

(b) Seasonal topographic heterogeneity–thermal heterogeneity correlations across ecoregions

(c) Elevation–temperature correlations across ecoregions

(d) Topographic heterogeneity–thermal heterogeneity correlations across ecoregions

Figure 3. Comparison of seasonal elevation-temperature (a) and topographic heterogeneity-thermal heterogeneity (b) correlations (Spearman's correlation coefficient, r) across 85 terrestrial ecoregions of the US. Correlations were calculated based on 5000 randomly sampled points per ecoregion (grey points, n = 85; grey vertical and horizontal dashed lines intercept the origin; black dashed lines show 1:1 line; colored lines show linear model fits with shaded region depicting 95% confidence intervals). The elevation–temperature and topographic heterogeneity–thermal heterogeneity correlations are also mapped spatially by ecoregion and season in (c) and (d), respectively.

heterogeneity vary considerably over space and time within the conterminous US.

Relative temperature was more strongly related with elevation during summer, showing a hump-shaped pattern during this season (Fig. 2a). This was somewhat surprising given that elevation is negatively correlated with temperature: globally, the wet adiabatic lapse rate varies between 3.5 and 6.5°C km^{-1} of elevation (compared to a dry adiabatic lapse rate of 9.8°C km^{-1} of elevation), with a global average of approximately 6.2°C km^{-1} of elevation (La Sorte and Jetz 2010). During winter, relative temperature declined nearly monotonically

with elevation, but with a lapse rate of roughly half the global average (Fig. 2b). Indeed, lapse rates are affected by a host of factors, including latitude, longitude, aspect, weather conditions and pollution, among others (Pepin et al. 1999, Whiteman et al. 1999, Blandford et al. 2008), and vary significantly among the mountain ranges of the world (Elsen et al. 2020b). A closer investigation of the relationship between relative temperature and elevation across ecoregions revealed that only a few individual ecoregions exhibited a hump-shaped pattern during summer (Supporting information), suggesting that the conterminous US patterns are
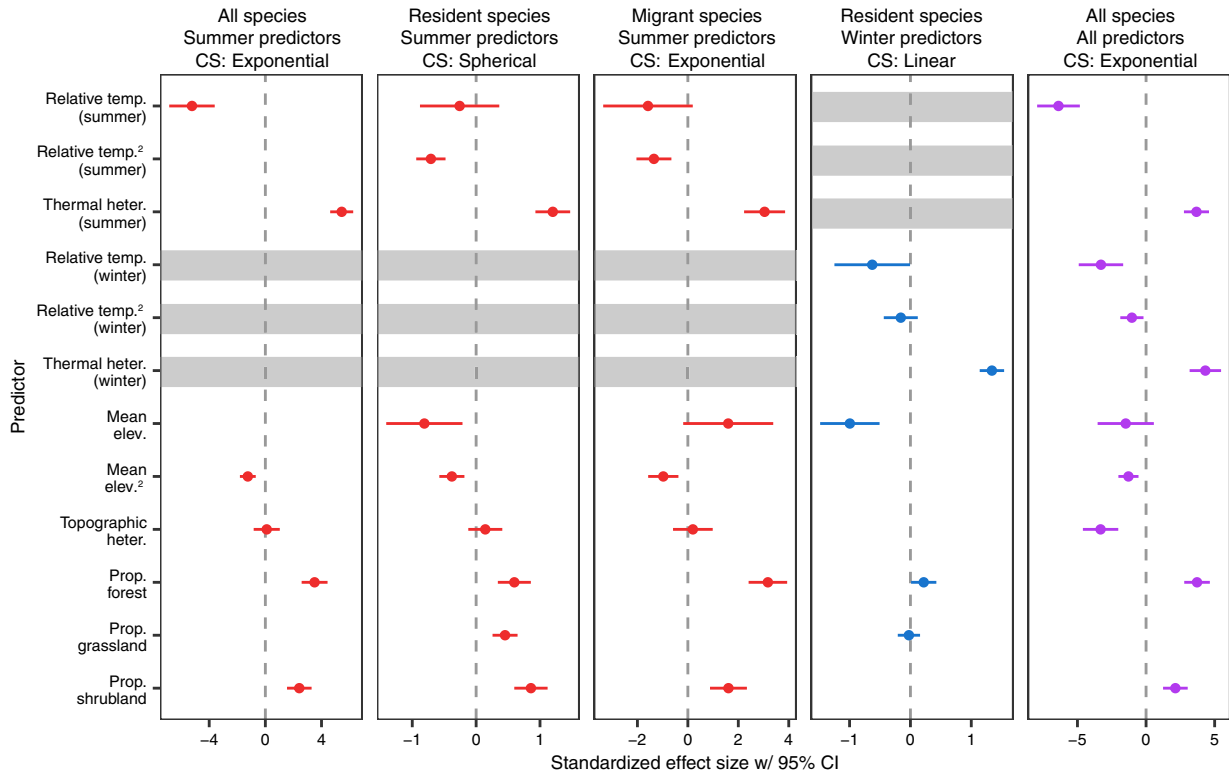
Figure 4. Standardized effect sizes (points) with 95% confidence intervals (lines) for predictor variables in the top-ranked GLS models with REML estimation of species richness for five species groups. Effect sizes account for spatial autocorrelation through fitting models with correlation structures (CS) as indicated. Colors of points and lines refer to predictor set included (red: summer predictors; blue: winter predictors; purple: all predictors). Grey horizontal bars indicate predictors that were not included in the model set for the given species group, while predictors with no given effects were not included in the top-ranked model.

likely mostly the results of interactions between differences in elevation and day length across longitude and latitude at the spatial scale of the US, and by influences associated with local weather (e.g. fog) and land cover.

There are several potential mechanisms for the variation in thermal lapse rates that we found. Seasonal differences in thermal lapse rates also occur in other regions, e.g. in China (He et al. 2018), the Himalayas (Kattel et al. 2015), Mexico (Xiang et al. 2014) and the US (Dobrowski et al. 2009, Minder et al. 2010). Yet there is large variability in seasonal lapse rate patterns: summer lapse rates are higher than winter rates in China, and differences are related to aspect, solar zenith angle and radiation, and vegetation cover. As vegetation and solar zenith angle increases, surface temperature lapse rate decreases, and lapse rates are highest on southern aspects (He et al. 2018). The influence of solar radiation on thermal lapse rates interacts with elevation and season: high solar radiation at high elevations during summer in the Himalayas reduces the thermal lapse rate compared to winter (Kattel et al. 2015). In the Cascade Mountains of the US, lapse rates are smallest in late-summer minimum temperatures and largest in late-spring maximum temperatures, and strongly related to aspect (Minder et al. 2010). We found a similar pattern for the Cascades ecoregion, with a more pronounced lapse rate in winter compared to summer (Supporting information), reflective of the overall US pattern

(Fig. 2b). Elevational differences in humidity, radiative cooling and cold air flows can also affect lapse rates (Kattel et al. 2015, Córdova et al. 2018).

Because seasonal lapse rates vary due to vegetation, aspect, latitude, elevation and longitude (e.g. with respect to the proximity to maritime versus continental circulation patterns), it is perhaps not surprising we found such wide variation in thermal lapse rates across the ecoregions of the US (Supporting information), which vary significantly in these and other parameters. This wide variation may also help explain why the continental US pattern showed striking non-linearities in summer (Fig. 2a). Our results therefore suggest that elevation is not a good proxy for temperature – especially at the scale of the conterminous US – because their relationship is sensitive to the regional abiotic and biotic context and differs among seasons.

We found that patterns of thermal heterogeneity differed markedly between winter and summer (Fig. 1). For example, thermal heterogeneity was more pronounced in mountainous regions such as the Great Basin, the Coastal Range of California, the mountains of the southwest, and throughout the Appalachian Mountains in winter (Fig. 1f). During summer, thermal heterogeneity was pronounced in the Central Valley of California, in the northern Rockies and in portions of the Cascades (Fig. 1f). While we found a positive relationship between topographic and thermal heterogeneity across

seasons at the scale of the US, this relationship was stronger in the winter than in the summer (Fig. 2b) and varied considerably across seasons and by ecoregion (Fig. 3d, Supporting information).

Topographic heterogeneity also captures spatial patterns of abiotic factors other than temperature, such as variation in slope, aspect, solar radiation, precipitation, hydrology and geomorphology, among others (Peterson 2003, Luoto and Heikkinen 2008). Furthermore, thermal heterogeneity can be influenced by differences in land cover, such as roads, agriculture and human development. This helps explain why, for example, thermal heterogeneity can be high both in flat regions such as the California Central Valley (where fine-scale variation in land cover associated with field edges and a diversity of crop types increases thermal heterogeneity) and in mountainous regions such as the Sierra Nevada (where steep elevational gradients drive thermal gradients and associated thermal heterogeneity). However, when comparing thermal heterogeneity among land cover classes, we found large variation within classes, but no consistent differences among land cover classes driving thermal heterogeneity at a continental scale (Supporting information). The high amount of variation may be one additional reason why topographic heterogeneity does not fully capture patterns of thermal heterogeneity.

Because relative temperature and thermal heterogeneity capture environmental variations that are distinct from elevation and topographic heterogeneity, these variables contributed independently and significantly to explaining variation in bird richness across the conterminous US (Fig. 4, Supporting information). We found that, for most of the species groups we considered, relative temperature was a better predictor of richness than elevation, and thermal heterogeneity was as good as or better than topographic heterogeneity (Fig. 4). This finding is generally in line with conclusions reached in a global study using coarser-resolution data that found that topographic heterogeneity and temperature were the most important predictors of bird richness patterns (Davies et al. 2007). It is also consistent with recent research assessing the predictive performance of winter thermal heterogeneity on richness patterns of climate sensitive species across the conterminous US (Elsen et al. 2020a). Our results highlight the value of including variables related to both relative temperature and thermal heterogeneity in models of broad scale richness patterns.

Thermal heterogeneity was positively correlated with bird richness patterns in both winter and summer, making it a promising new metric for conservation planning. Similar conclusions have been reached for related but coarse-resolution metrics of thermal heterogeneity and their influence on mammal richness patterns (Stein et al. 2015). Areas with high thermal heterogeneity can act as important refugia to buffer species against cold spells during winter (Latimer and Zuckerberg 2016) and heat waves during summer (Albright et al. 2011). Yet, we found that patterns of thermal heterogeneity shift among seasons (Fig. 1f), and these shifts vary strongly among regions (Fig. 2d), suggesting there may be tradeoffs in conservation prioritizations based

on patterns of thermal heterogeneity from one season only, or when using proxy variables such as topographic heterogeneity (Supporting information). Our models including both summer and winter thermal heterogeneity suggest that both variables had significant and distinct positive effects on bird richness. Consequently, prioritizing areas characterized by high thermal heterogeneity in both seasons would best capture areas of greater overall breeding bird richness, while also supporting resident species. In the US, the Californian mountains and parts of the Rocky Mountains, Great Basin and southwest deserts have exceptionally high thermal heterogeneity year-round (Ackerly et al. 2010) (Fig. 5). Many of these regions closely align with priority regions for other terrestrial vertebrates, freshwater fish and trees (Jenkins et al. 2015). Protecting and restoring habitat in these areas would likely provide particularly large benefits for biodiversity, especially for species threatened by climate change (Heller and Zavaleta 2009, Elsen et al. 2020a).

While data availability was generally high for calculating our thermal metrics during summer, the presence of clouds in winter in some geographical areas – such as the Midwest around Michigan, the northeastern US and parts of the northern Rockies – resulted in few images with which to make calculations (Supporting information). While our data processing workflow took several steps to minimize spatial and temporal biases in calculations (Supporting information) and gives confidence in our species richness model results at the spatial scale considered (i.e. within 19.7 km BBS buffers), it should be noted that applying our thermal metrics at finer spatial scales in geographies with poorer data coverage during winter should be done with care.

Another important consideration of our study is that we were unable to assess the degree to which short-distance, altitudinal and partial migrants might select features of the thermal environment for occupancy during winter. We had to restrict the portion of the analysis focusing on winter patterns to resident species to ensure BBS data appropriately reflect richness patterns in winter, but this process inherently excludes these migratory groups and prevents us from assessing how their richness dynamics might be influenced by the thermal environment. For example, altitudinal migrants track thermal conditions across seasons to occupy the same thermal niche throughout the year, whereas residents tend to have broader thermal niches, owing to them experiencing large seasonal fluctuations in temperature (Srinivasan et al. 2018). Excluding short- and long-distance migrants from the winter analysis acts to artificially reduce richness in some portions of the US, most notably the southernmost and northernmost portions of the country, and these exclusions may have affected our results. It is possible that migrants, having different sensitivities to the thermal environment than residents, could be more strongly structured by relative temperature than thermal heterogeneity. We are unable to test this prediction directly using BBS data, but a previous study using data from the Christmas Bird Count, which contains short-distance migrants and winter visitors in addition to permanent residents, also found that thermal heterogeneity strongly
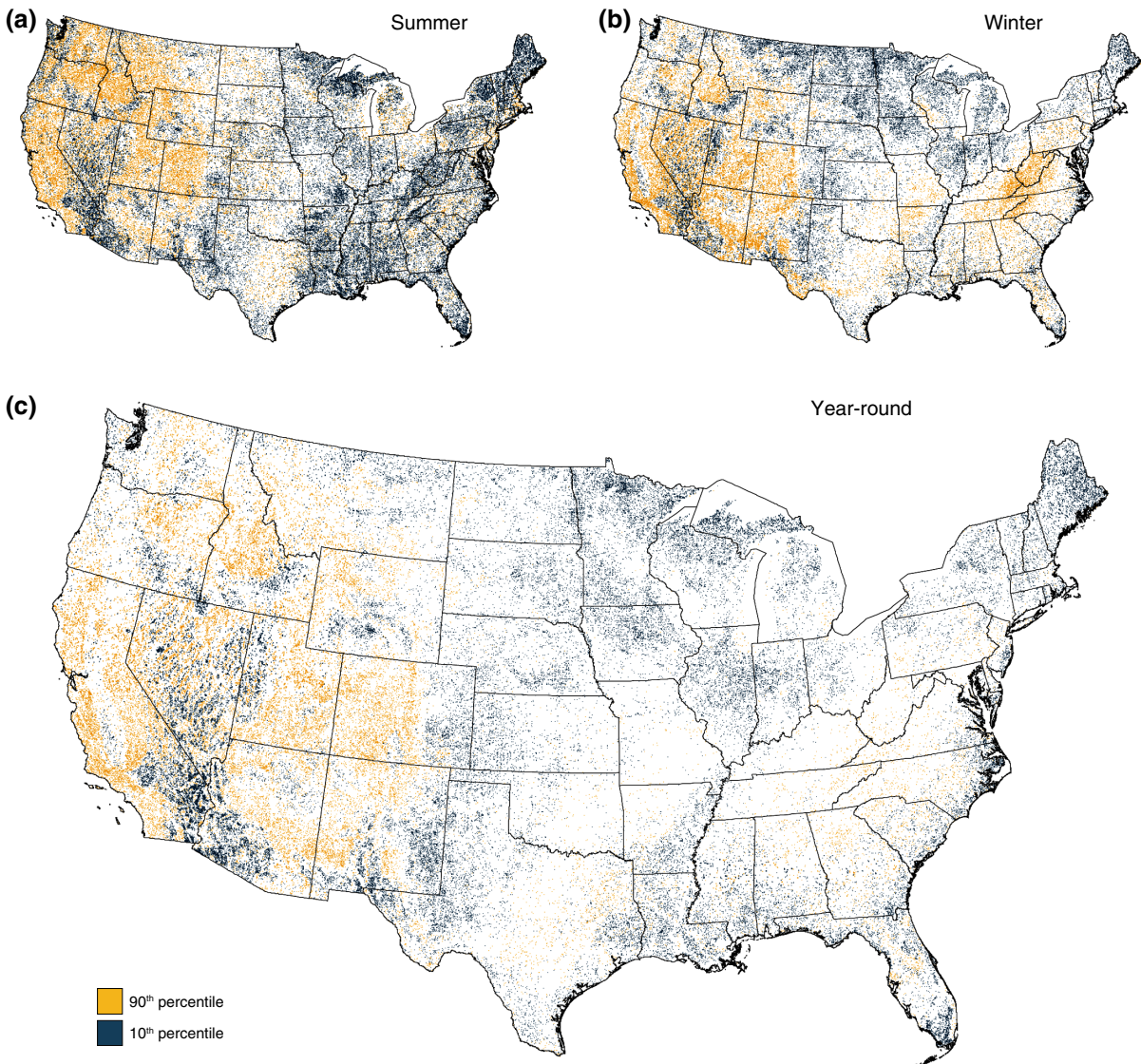
Figure 5. Map of 90th and 10th percentiles of thermal heterogeneity values for summer (a), winter (b) and year-round (c). Regions in the 90th percentile year-round constitute conservation priorities due to their positive correlations with species richness patterns in both summer and winter and likely high adaptation potential. By contrast, regions in the 10th percentile year-round reflect areas of risk because they offer few thermal niches, have a persistent lack of thermal refugia, and thus likely have low adaptation potential. Regions with 90th percentile in one season and 10th percentile in the other are rare and are mapped separately in the Supporting information.

predicted richness patterns (Elsen et al. 2020a). While these independent results give confidence in our conclusions, further research linking fine-scale movement patterns of birds to thermal occupancy dynamics would help discern the importance of thermal heterogeneity for migrant species.

An additional caveat is that BBS data are collected along roads, which tend to be in less topographically complex portions of the landscape, and thus it is possible that our topographic heterogeneity metric summarized within 19.7 km of the route centroid overestimates the topographic heterogeneity of the effective survey area. This could have resulted in underestimates of the effect of topographic heterogeneity on bird richness. Developing predictive models using more precise species occurrence records spanning elevational and

thermal gradients would help further reveal their links with biodiversity.

High resolution digital elevation models have been available and widely used by ecologists to investigate biodiversity patterns for decades (Turner et al. 2003). Yet medium-resolution (30-m) thermal data from satellites have very rarely been used in biodiversity studies (Elsen et al. 2020a). Our results illustrate their potential for broad applications in future studies. The global availability of Landsat 8 TIRS data means that our metrics and analytical framework can easily be applied elsewhere on the globe to understand, for example, how the relative importance of the thermal environment for biodiversity changes across geographical gradients (Srinivasan et al. 2018). Further research is needed to understand how thermal

heterogeneity influences richness patterns of other taxonomic groups (Stein et al. 2014). Such studies would be important to understand the generality of utilizing thermal heterogeneity as a robust prioritization tool in conservation planning.

Data availability statement

Data from the Breeding Bird Survey are available at <www.mbr-pwrc.usgs.gov/bbs>. Landsat 8 TIRS data, SRTM elevation data, NLCD land cover data are also freely available (Methods and Supporting information). Level III ecoregion data are freely available at <www.epa.gov/eco-research/level-iii-and-iv-ecoregions-continental-united-states>.

Data deposition

Data are freely available at <http://silvis.forest.wisc.edu/maps-data/>.

Author contributions

Paul R. Elsen: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (lead); Software (lead); Validation (lead); Visualization (lead); Writing – original draft (lead). **Laura S. Farwell**: Data curation (supporting); Methodology (supporting); Writing – review and editing (supporting). **Anna M. Pidgeon**: Conceptualization (equal); Funding acquisition (equal); Supervision (equal); Writing – review and editing (supporting). **Volker C. Radeloff**: Conceptualization (equal); Funding acquisition (equal); Supervision (equal); Writing – review and editing (supporting).

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