

RESEARCH PAPER

Global Ecology
and BiogeographyA Journal of
Macroecology

WILEY

Winter conditions structure extratropical patterns of species richness of amphibians, birds and mammals globally

David Gudex-Cross¹  | Likai Zhu²  | Spencer R. Keyser¹  | Benjamin Zuckerberg¹  | Jonathan N. Pauli¹  | Volker C. Radeloff¹

¹Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, Wisconsin, USA

²Laboratory of Geographic Information Science of the Ministry of Education, School of Geographic Sciences, East China Normal University, Shanghai, China

Correspondence

David Gudex-Cross, Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Room 240, Madison, WI 53706, USA.
Email: djgudexcross@gmail.com

Funding information

National Aeronautics and Space Administration, Grant/Award Number: 80NSSC19K0180; U.S. Geological Survey, Grant/Award Number: 140G0118C0009; National Natural Science Foundation of China, Grant/Award Number: 42001373

Handling Editor: Erica Fleishman

Abstract

Aim: The aim was to derive global indices of winter conditions and examine their relationships with species richness patterns outside of the tropics.

Location: All extratropical areas (>25° N and 25° S latitudes), excluding islands.

Time period: 2000–2018.

Major taxa studied: Amphibians, birds and mammals.

Methods: We mapped three global indices of winter conditions [number of days of frozen ground (length of frozen ground winter); snow cover variability; and lack of subnivium (below-snow refuge)] from satellite data, then used generalized additive models to examine their relationships with species richness patterns derived from range data.

Results: Length of frozen ground winter was the strongest predictor of species richness, with a consistent cross-taxonomic decline in species richness occurring beyond 3 months of winter. It also often outperformed other environmental predictors of species richness patterns commonly used in biodiversity studies, including climate variables, primary productivity and elevation. In areas with ≥3 months of winter conditions, all three winter indices explained much of the deviance in amphibian, mammal and resident bird species richness. Mammals exhibited a stronger relationship with snow cover variability and lack of subnivium than the other taxa. Species richness of fully migratory species of birds peaked at c. 5.5 months of winter, coinciding with low species richness of residents.

Main conclusions: Our study demonstrates that winter structures latitudinal and elevational gradients of extratropical terrestrial species richness. In a rapidly warming world, tracking the seasonal dynamics of frozen ground and snow cover will be essential for predicting the consequences of climate change on species, communities and ecosystems. The indices of winter conditions we developed from satellite imagery provide an effective means of monitoring these dynamics into the future.

KEYWORDS

climate, cryosphere, remote sensing, species richness, terrestrial vertebrates, winter ecology

1 | INTRODUCTION

Identifying the factors that structure species richness patterns over time and space is fundamental to the understanding of evolutionary and ecological processes. Numerous hypotheses have been put forward to explain macroscale patterns of species richness (particularly the latitudinal diversity gradient), including spatio-temporal dynamics (e.g., effective evolutionary time, mid domain effect), physiology–temperature relationships (e.g., metabolic theory, thermal niche), biotic interactions (e.g., interspecific competition, dispersal) and energy–water relationships (e.g., primary productivity) (Kinlock et al., 2018; Mittelbach et al., 2007; Worm & Tittensor, 2018). Although these hypotheses are not mutually exclusive (e.g., Tittensor & Worm, 2016) and each has some level of support, none of them has considered explicitly the role of winter conditions in structuring species richness gradients. Nonetheless, winter conditions are an important determinant of species distributions and life-history strategies. Prolonged cold coupled with frozen ground and variable snow cover place high thermoregulatory demands on organisms, given their need to generate heat for survival either endogenously (endotherms) or exogenously (ectotherms) during times when resources are typically scarce (Williams et al., 2015). On the one hand, winter constrains the distribution of many individual plant and animal species that are unable to cope with its extreme climatic conditions (Ashcroft et al., 2011; Šímová et al., 2011; Williams et al., 2015). On the other hand, many species have developed physiological, behavioural and life-history strategies (e.g., migration, hibernation) for surviving winter (Pauli et al., 2013; Penczykowski et al., 2017; Williams et al., 2015). That raises the question: how do winter conditions affect extratropical patterns of species richness of different taxa?

The biological effects of frozen ground and snow cover dynamics span trophic levels. Cycles of snow accumulation, ablation and melting mediate climate, biogeochemical processes, vegetation dynamics and species interactions (e.g., predator–prey relationships) (Niittynen et al., 2018; Penczykowski et al., 2017; Slatyer et al., 2021). For many plant and animal species, snow depths of 50 cm and greater (Kreyling, 2010) provide a crucial refuge from extreme winter temperatures and predators. The insulating properties of snow form a thermally stable environment (the subnivium) decoupled from air temperatures, providing organisms with protection from cold injury or death. Thermal stability in the subnivium is vital to the development, survival and fitness of hibernating animals, which include many species of freeze-tolerant amphibians and small mammals (Pauli et al., 2013; Petty et al., 2015). This means that large fluctuations in winter temperature that erode the subnivium and change the snowpack energy balance, such as freeze–thaw and rain-on-snow events, increase energy expenditure and lower survival rates of organisms during winter (Roberts et al., 2021; Slatyer et al., 2021). Snow-free winter days also expose species that rely on crypsis (white coat colour) or the subnivium for predator avoidance (Mills et al., 2013; Pauli et al., 2013; Roberts et al., 2021). Conversely, deep snow increases locomotive costs and water stress

(less available liquid water) for larger mammals that remain active during winter and can lower food availability for avian and mammalian predators (Penczykowski et al., 2017; Williams et al., 2015).

Another organismal response to harsh winter weather and lower food availability is seasonal migration. All major taxa have migratory species, but the majority of long-distance migrants are birds (Newton, 2010). Indeed, c. 20% of extant bird species migrate either short or long distances, and the number of breeding migrants in a given area has been linked strongly to resource seasonality and minimum temperature (Somveille et al., 2015, 2019). A major limitation in prior analyses of these relationships is the use of temperature measures (i.e., ranges and minima) to approximate winter conditions. Temperature data provide little information on one of the most important aspects of winter for migration, which is how long winter conditions last. However, the duration of winter may greatly affect macroscale patterns of bird species richness and the migration strategies of birds.

The ability to quantify winter conditions across broad spatial and temporal extents is facilitated by new advances in satellite remote sensing. Recently, indices of snow and frozen ground dynamics tailored specifically for biological studies have been developed at continental (Gudex-Cross et al., 2021) and global extents (Zhu et al., 2017, 2019). These “winter indices” (WIs) capture three biologically important aspects of winter: overall length (measured as either the duration of frozen ground or snow season length); snow cover variability (how often the ground transitions between being snow covered and not snow covered); and lack of subnivium (measured as the percentage of days of frozen ground without snow). A major advantage of the WIs over gridded climate products is that they are based on direct observations of the surface of the Earth and avoid the uncertainties and errors inherent in global temperature and precipitation data owing to interpolation among meteorological stations. However, one disadvantage of satellite data from optical sensors (e.g., MODIS) is cloud cover, which can create data gaps and, occasionally, erroneous snow cover detections (Stillinger et al., 2019). Cloud cover is not a problem for microwave sensors (used to determine frozen ground status) because they can penetrate clouds. The WIs are important predictors of species richness patterns in the USA (Gudex-Cross et al., 2021) and China (Zhu & Guo, 2022). Conducting similar analyses at a global extent and across more taxa is a powerful way to quantify the role of winter conditions in structuring contemporary patterns of terrestrial species richness.

Here, our primary goal was to examine macroscale relationships between winter conditions and species richness patterns of amphibians, mammals and birds. To accomplish this, we calculated the length of frozen ground winter (number of days of frozen ground; hereafter, “winter length”), snow cover variability and lack of subnivium globally and assessed their relationships with species richness derived from range maps. We asked three questions. First, to what extent does winter length constrain total species richness across taxonomic groups? Second, how does winter length affect the total number and percentage of bird species that are resident, partial migrants or full migrants? We predicted that species richness would be lower where

winters are longer across all taxa and that the total number and percentage of migratory bird species would be higher where winter is longer. Among migratory strategies, we predicted that areas with longer winters would support low resident and partial migrant species richness and high full migrant species richness. Third, within areas with ≥ 3 months of winter (i.e., areas where organisms face prolonged winter conditions and have adaptations for winter survival), how do snow cover variability and a lack of subnivism influence patterns of species richness of overwintering amphibian, mammal and resident bird species? We predicted that higher snow cover variability and lack of subnivism would be associated with lower species richness of these taxa. While addressing these questions, we also explored the importance of the WIs compared with other measures of winter climate (temperature and precipitation), seasonality and primary productivity that are commonly used to predict species richness patterns.

2 | METHODS

2.1 | Winter indices

We calculated three global WIs from optical (500-m resolution) and microwave (25-km resolution) satellite data: winter length (number of days of frozen ground); lack of subnivism (percentage of days of frozen ground without snow); and snow cover variability. Further detail on our WI processing steps and calculations is available in the paper by Zhu et al. (2017) for the frozen ground-based indices and the paper by Gudex-Cross et al. (2021) for snow cover variability. Here, we used MODIS Terra and Aqua 8-day snow cover products to determine snow cover (Hall & Riggs, 2016) and the NASA MEaSUREs freeze-thaw (Kim et al., 2017) and Daily Global Land Surface Parameters (Du et al., 2017) products to identify frozen ground. For snow, we developed an improved spatially and temporally continuous product by combining the Terra-Aqua snow data and applying spatial and temporal filtering methods to reduce cloud contamination (for more details, see Zhu et al., 2017). We derived all three WIs annually from 2000/2001 to 2017/2018 and calculated their mean values as input for our models. We used multiyear averages because our species range maps were also based on multiyear observations.

We calculated winter length as the total number of days within our determined frozen season. Importantly, defining winter length as the number of days of frozen ground differs from meteorological winter (December–February in the Northern Hemisphere and June–August in the Southern Hemisphere), and this definition constrains our analysis by excluding areas where cold temperatures and snow may occur, but the ground does not freeze (e.g., areas of the southwestern USA and southern Australia, and areas on the southern edge of major mountain ranges, such as northern Iraq, Syria, Pakistan and India). In the Northern Hemisphere, we defined the start of the frozen season as the middle date of the first 13 consecutive days of frozen ground from September to January, and the end as the middle

date of the first 13 consecutive days from February to August classified as thawed (Zhu et al., 2017). For the Southern Hemisphere, we used a March–July window to determine the start date and August–February to determine the end date. Given that our winter length calculation might be sensitive to different window sizes for determining the season start and end dates, we compared the 13-day window with two different sizes: 7-day and 21-day windows. We found that winter length estimates generated with different window sizes were highly consistent (Supporting Information Figure S1). The 7-day window estimates had slightly lower correlations with the 13-day window estimates than the 21-day window estimates. This was probably because of days when a brief freeze occurred and then thawed again before reaching the 13-day threshold.

We calculated the other two WIs by integrating information about freeze, thaw and snow cover status from the start to the end dates of the frozen season of each year. For example, if a pixel had frozen ground but no snow on a date within the frozen season, we added 1 day to the duration of frozen ground without snow cover. We then summed the number of days classified as frozen ground without snow and divided by the number of frozen ground days to obtain the percentage of days of frozen ground without snow. To calculate snow cover variability, we summed the number of transitions between snow and no snow that occurred within the frozen season and divided that number by the number of frozen ground days.

We validated the WIs on the basis of data from meteorological stations around the world. We only included stations that had a continuous and complete record of snow depth and minimum temperature throughout the study period (2000–2018), resulting in a total of 1,099 stations (Supporting Information Figure S2). To consider a station for use in our validation dataset, it needed to have snow and temperature data for every year and month, and $\leq 10\%$ of daily records missing within any year. However, for some stations we replaced blank snow records for summer months with zeros and did not count these instances as missing values. For stations with $< 10\%$ of their daily record missing, we interpolated the missing values by assigning them the average value of adjacent dates. If the value for one adjacent date was missing, we assigned the value of the other adjacent date. If both adjacent dates were missing, we interpolated the missing value using measurements 2 days away from it. If the missing value could not be interpolated using these steps, we excluded the station from our validation dataset.

We derived the WIs from the station data with the same calculations that we applied to the remote sensing data. We used Pearson's correlations and the slope of the regression line to assess the accuracy of the satellite-based WIs by comparing them with station-based WIs. In the station-based WI calculations, we considered the ground as frozen when the minimum temperature on a given day was $< 0^\circ\text{C}$ and snow covered when the snow depth was greater than zero. We used the 0°C threshold to facilitate direct comparisons with the accuracy assessments conducted in the development of the satellite-based freeze-thaw products (Kim et al., 2010, 2017). Furthermore, we tested how sensitive our station-based winter

length calculations were to different minimum temperature thresholds (0, -0.5, -1, -1.5 and -2°C) and how these thresholds affected the resulting accuracy of the remote sensing-based winter length index. We found nominal differences in the station-based winter length estimate using these different thresholds of minimum temperature, with lower temperature thresholds resulting in slightly shorter winter lengths (Supporting Information Figure S3). In terms of the effect of different minimum temperature thresholds (-0.5 and -1°C) on the accuracy of the remote sensing-based winter length estimates, we again detected only minor effects, although lower temperature thresholds did show slightly better agreement with the remote sensing estimates (Supporting Information Figure S4).

2.2 | Species richness calculations

We calculated species richness from range maps of individual species provided by BirdLife International (birds) BirdLife International and Handbook of the Birds of the World, (2019) and the International Union for the Conservation of Nature (amphibians and mammals) (IUCN, 2017; Radeloff et al., 2019). The BirdLife classification assigns the range of each bird species into mutually exclusive categories: resident populations (present year-round); breeding populations (present during the breeding season); and non-breeding populations (present during the non-breeding season). Given that we were only interested in populations that breed outside the tropics (residents and migrants), we excluded the non-breeding range polygons from our analysis. We applied the bird migration classification developed by Tobias et al. (2016) to the breeding population polygons only, separating them into partial migrant (<50% of populations migrate long distances or >50% of the populations migrate short distances) and full migrant (>50% of populations migrate long distances) classes.

To calculate species richness, we converted the range map polygons for every species to 110-km (c. 1°) grid cells, counted a species as present if its range overlapped a given cell, and summed the number of amphibians, mammals and birds (residents, partial migrants and full migrants separately) present in each cell (Radeloff et al., 2019). For birds, we also derived the percentage of species that are residents, partial migrants and full migrants in each cell. Additionally, we mapped the extratropical patterns of species richness of each taxon (Figure 1).

2.3 | Relationships between the winter indices and species richness

To test relationships between winter length (mean duration of frozen ground, 2000/2001–2017/2018) and species richness, we distributed stratified random points throughout the mid- to high latitudes, excluding the tropics (25° N–25° S) and islands (Supporting Information Figure S5). We stratified our samples by terrestrial biomes (Olson et al., 2001) to avoid oversampling areas

with particularly high or low numbers of species. Before stratification, we reduced the original 14 biomes to nine by excluding mangroves, which mainly occurred on islands, and generalizing related classes (e.g., we combined the temperate broadleaf and mixed forest and temperate conifer forest classes into “temperate forest”; Supporting Information Figure S5). Given that we were interested in quantifying species richness patterns across the full range of winter lengths, we sampled areas along a gradient from no frozen ground to almost year-round frozen ground. We maintained a minimum distance of 110 km between points to match the resolution of the species richness grids, resulting in 1,379 points for analysis (Supporting Information Figure S5). To examine relationships between winter length and species richness, we parameterized generalized additive models (GAMs; “mgcv” package in R; Wood, 2017), which can account for nonlinear relationships. We built the GAMs based on our prior work modelling relationships between winter bird species richness and the WIs in the USA (Gudex-Cross et al., 2021). These models assume that species richness follows a negative binomial distribution with a log-link mean function and use restricted maximum likelihood to estimate smoothing parameters. For the models of the percentage of bird species adopting a given migration strategy, we specified a quasibinomial distribution to account for overdispersion (Ives, 2018; Zuur et al., 2009), again with a log-link function and restricted maximum likelihood. To avoid overfitting, we applied an additional penalty to the smoothing parameter ($\gamma = 1.4$) and constrained the number of knots included in each smoothing function to 10 or fewer.

We followed the same steps to examine relationships between species richness and the within-season WIs (snow cover variability and percentage of days of frozen ground without snow) but limited these analyses to points where winter lasted for ≥ 3 months (≥ 90 frozen ground days) and overwintering species (amphibians, mammals and resident birds). Our final dataset consisted of 981 points. In these data, we examined the deviance in species richness of each taxon explained by GAMs that included all three WIs. We quantified the relative importance of the WIs by comparing the corrected Akaike's information criterion (AICc) of the full model (containing all three WIs) with all other possible models. We checked the amount of concurvity (nonlinear dependencies among predictor variables, akin to collinearity in linear models) among the WIs in our final models and, in cases where two variables had high concurvity (≥ 8), tested two alternative models with either variable and retained the model with the better fit.

2.4 | Comparisons of the winter indices with climate and primary productivity variables

To compare measures of climate with the WIs, we used four bioclimatic variables derived from WorldClim v.2.0 data (1-km resolution; Fick & Hijmans, 2017): minimum temperature, temperature seasonality, precipitation of the coldest quarter (3-month period) and precipitation seasonality. For primary productivity (“productivity”

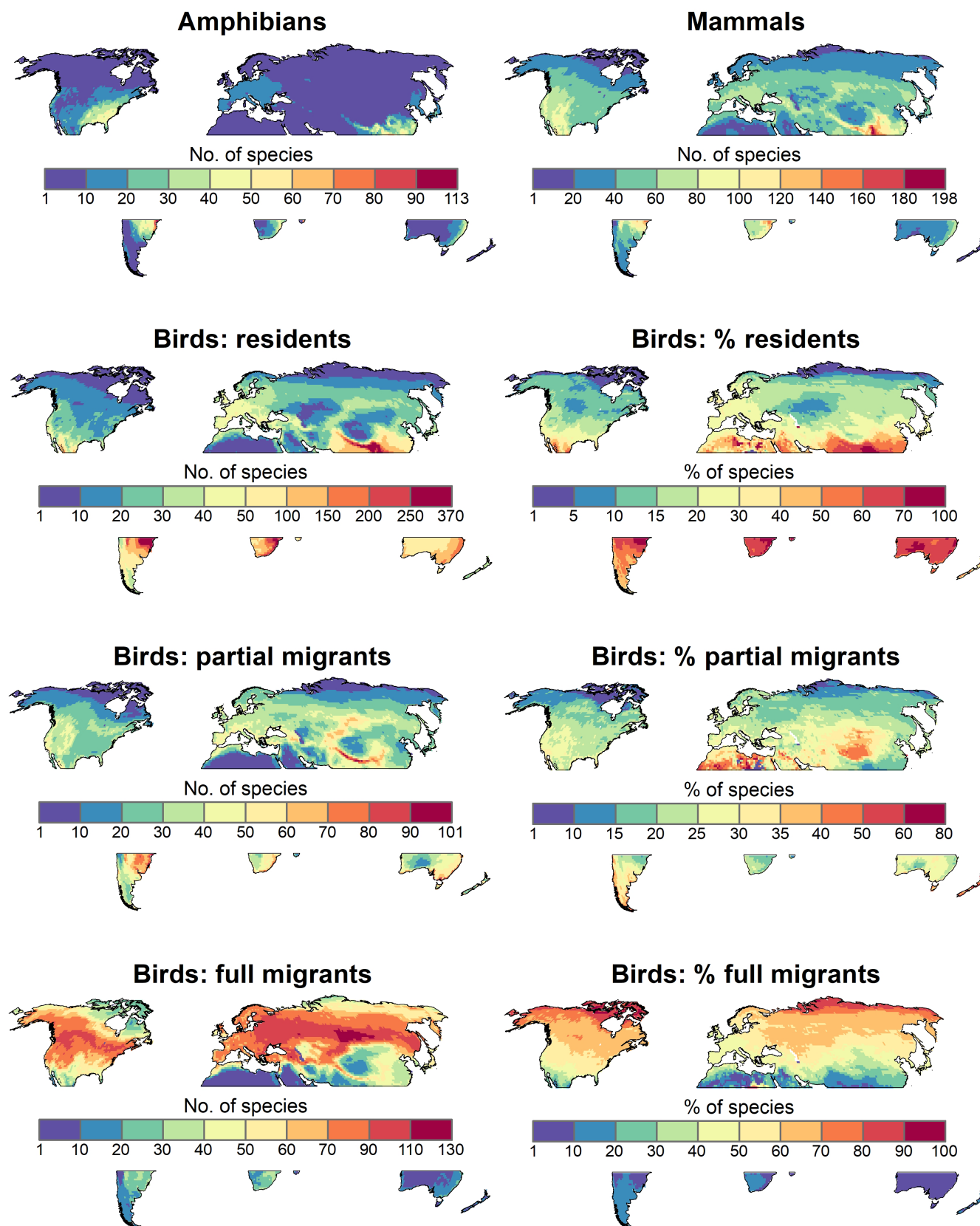


FIGURE 1 Species richness maps derived from the geographical ranges of individual species of amphibians, mammals, resident birds, partly migratory birds and fully migratory birds, and of the percentage of species richness for the bird migration strategies. We did not analyse the areas between 25° S and 25° N (tropics). Given the high numbers of species in the tropics, they are excluded here to highlight species richness patterns in other parts of the world

hereafter), we used the normalized difference vegetation index (NDVI)-based cumulative dynamic habitat index (DHI) derived from MODIS data (Radeloff et al., 2019). The cumulative DHI quantifies productivity annually by summing monthly median NDVI values over the course of a year, and we used the mean of the annual values from 2003–2018 here. Given its frequent use in species richness models as a proxy for climate and productivity, we also included elevation, derived from GMTED2010 data (Danielson & Gesch, 2011), in our comparisons to the WIs.

We used Pearson's correlation coefficient to quantify the correlations among the WIs and climate, productivity and elevation. Next, we compared the strength of the winter length index as a predictor of species richness for all taxa and the percentage of birds with a particular migratory strategy with the other variables (climate metrics, productivity and elevation). Here, and for the multivariate models, we used the same generalized additive modelling methods as described in the previous section. For the multivariate modelling of species richness of overwintering taxa (amphibians, mammals and resident birds) in areas with ≥ 3 months of winter conditions, we compared the explanatory power of the WI model with two other models: climate only and productivity only. We included elevation in the latter model. In instances where variables exhibited a high amount of concavity or were not significant, we determined the best alternative model by comparing the explanatory power of the models with one of the curving variables removed (e.g., minimum temperature instead of temperature seasonality for the climate-only model). After comparing these separate models, we examined the complementarity of the WIs, climate, productivity and elevation by combining them in a single model (combined models). Again, we determined the best alternative model by minimizing concavity and maximizing explanatory power. For our model comparisons, we evaluated the adjusted r^2 value and deviance explained. For the combined models, we examined the importance of the individual variables by quantifying the change in deviance explained when a given variable was removed from the full model.

3 | RESULTS

3.1 | Global winter indices

The WIs captured prominent gradients in global winter conditions (Figure 2). As expected, winter (measured as the number of days of frozen ground) was longest in high-latitude and alpine regions and shortest in low-latitude and coastal regions. The main gradient in winter length in both hemispheres was latitudinal, but in the Eastern Hemisphere, winter length also had a clear longitudinal component. In mountain ranges, there was a prominent gradient from shorter winters at lower elevations to longer winters at higher elevations. Both snow cover variability and lack of subnivium were highest in mid-latitude and coastal regions and lowest in polar and alpine regions. The lack of subnivium index also showed a distinct transition

zone at c. 45° N, where it was highest. Our validation based on data from 1,099 meteorological stations around the world (Supporting Information Figure S1) showed that all three WIs characterized conditions on the ground accurately (correlations ranged from .84 to .89; Supporting Information Figure S6).

3.2 | Winter length and species richness

Species richness of each taxon was strongly associated with winter length (Figure 3). Resident birds and mammals had higher levels of species richness (300 and 175 species, respectively) outside of the tropics than amphibians (59 species). Consistent with our first prediction, species richness generally decreased with increasing winter length for amphibians [41% deviance explained (d.e.)], mammals (30%), resident birds (46%) and the percentage of bird species that are residents (65%) (Figure 3a–d). However, species richness of these taxa was often as high or higher in areas with winters of short to moderate length (2–4 months) than in areas where the ground never freezes (winter length = 0). This was especially true for amphibians and mammals (Figure 3a,b). There was also an unexpected slight increase in the percentage of resident birds in areas with very long winters (10–12 months; Figure 3d), but these areas also had low numbers of bird species. The endothermic taxa (mammals and birds) had consistently higher numbers of species than the ectothermic amphibians across the full range of winter lengths (Figure 3a–c).

We found mixed support for our predictions about the relationship between winter length and bird migration strategies. For partial migrants (maximum species richness = 90), we found a slight peak in the number of species around 2–4 months of winter length and strong declines beyond that (d.e. = 23%; Figure 3e). However, the number of partial migrants was much higher than we expected in areas where the ground never freezes. We also found an unexpected bifurcation in the percentage of bird species that are partial migrants in areas with long winters (>8 months); some areas had a high percentage of partial migrants and others a low percentage (d.e. = 19%; Figure 3f). For full migrants (maximum species richness = 129), we found a strong curvilinear relationship with winter length (d.e. = 50%; Figure 3g). The number of fully migratory species increased substantially from areas where the ground never freezes to those with shorter winters, peaked between 5 and 8 months of winter and declined thereafter. The percentage of species that are full migrants also increased sharply from areas where the ground never freezes to areas with c. 5–8 months of winter, where it then began to taper off slightly but largely remained high (d.e. = 68%; Figure 3h). In most areas with at ≥ 3 months of winter, more than one-half of bird species were full migrants, and where winter lasted ≥ 8 months, this percentage reached a maximum of 80–90%. Yet, as with partial migrants, an unexpected bifurcation in the species richness of full migrants occurred in areas with long winters; some had high percentages and others low (Figure 3h).

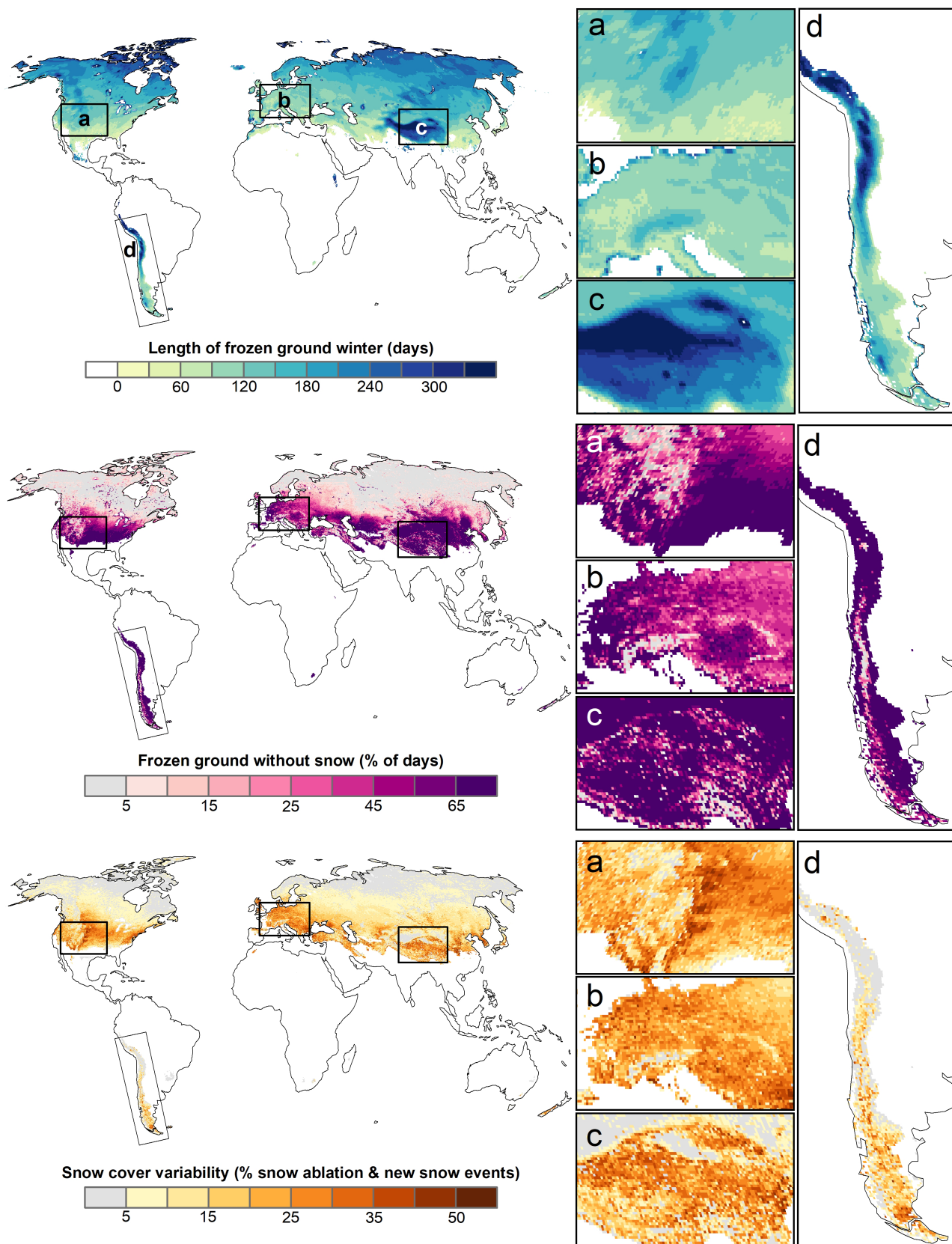
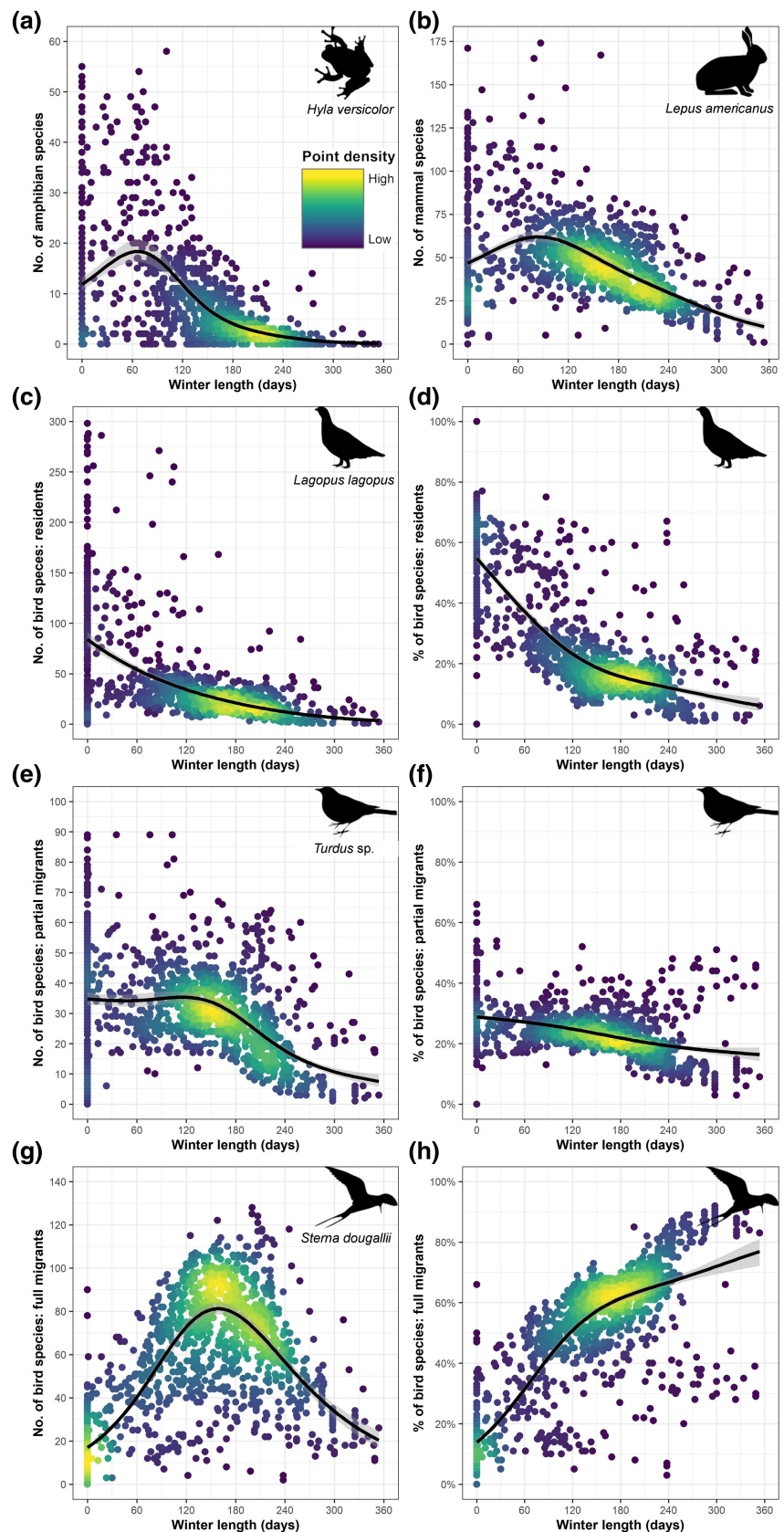


FIGURE 2 The 25-km global winter indices (WIs): (top) length of frozen ground winter (winter length); (middle) percentage of days of frozen ground without snow (lack of subnivium); and (bottom) snow cover variability. The panels on the right highlight regions with diverse topography, including (a) the Rockies in the North America; (b) the Alps in Europe; (c) the Tibetan Plateau in Asia; and (d) the Andes in South America

FIGURE 3 Global relationships between winter length (number of days of frozen ground) and species richness of (a) amphibians, (b) mammals and (c–h) birds. For bird migration strategies, relationships for the number of species are in the column on the left (c,e,g) and for the percentage of species in the column on the right (d,f,h)



3.3 | Winter indices and species richness in areas with ≥ 3 months of winter conditions

Contrary to our predictions, in areas with ≥ 3 months of winter conditions, both snow cover variability and lack of subnivium had positive, slightly curvilinear relationships with species richness of amphibians, mammals and resident birds (Figure 4). Snow cover variability explained more of the deviance in species richness of amphibians (d.e. = 18%) and mammals (d.e. = 34%) than lack of subnivium (d.e. = 13 and 22%, respectively; Figure 4a–d). The two indices had similar relationships with resident bird species richness (d.e. = 11% for both; Figure 4e,f). The effects of snow cover variability and lack of subnivium on species richness were consistent among taxa, with species richness increasing steadily from areas with little to no snow cover variability and percentage of days of frozen ground without snow to 20–30%, then plateauing or slightly declining (Figure 4).

Although snow cover variability and lack of subnivium each had limited explanatory power, including both substantially improved multivariate models of species richness of amphibians, mammals and resident birds (Supporting Information Table S1). All three indices were significant at the $p \leq .01$ level in each model, except for the percentage of days of frozen ground without snow in the mammal species richness model ($p = .12$). However, the snow cover variability and percentage of days of frozen ground without snow indices exhibited a high amount ($>.8$) of concavity, and the second-best models for all three taxa included only snow cover variability. The level of support for the second-best models, which contained winter length and snow cover variability, was similar ($\Delta AICc \leq 2$) to that for the full models, although the Akaike weights still favoured the full models (Supporting Information Table S1). The full models explained a substantial amount of the deviation in species richness of mammals (65%), resident birds (56%) and amphibians (52%), and the second-best models explained slightly less (65, 53 and 51%, respectively).

3.4 | Comparisons of the winter indices with other environmental variables

Outside the tropics, winter length was most strongly correlated with temperature ($r = -.87$ for minimum and $r = .71$ for seasonality) and much less strongly correlated with precipitation, productivity and elevation ($|r| < .3$) (Supporting Information Figure S7). However, in areas with ≥ 3 months of winter, winter length and temperature were less correlated ($r = -.70$ and $.47$ for minimum and seasonality, respectively), and winter length and productivity were slightly more correlated ($r = -.53$). In these areas, snow cover variability and lack of subnivium were more strongly correlated with temperature (r near $.5$ for both minimum and seasonality) than with the other variables we tested ($|r| < .4$ for all) (Supporting Information Figure S7).

Winter length explained more of the deviance in species richness outside the tropics than climate, productivity and elevation for mammals, partly migratory birds and fully migratory birds (Supporting Information Table S2). There were especially marked

differences in the deviance explained by winter length versus the next best predictor of species richness for fully migratory birds (50% vs. 32% explained by minimum temperature) and mammals (30% vs. 19% explained by productivity). For amphibians, only productivity explained slightly more deviance in species richness than winter length. For resident birds and the percentage of bird species adopting a given migration strategy, winter length explained as much deviance or slightly less deviance in species richness than our temperature measures, but outperformed the precipitation, productivity and elevation metrics.

In areas with ≥ 3 months of winter, multivariate models containing the WIs explained more deviance in species richness patterns of the overwintering taxa (amphibians, mammals and resident birds) than models containing climate variables only, or productivity and elevation only, after variables with high concavity were removed (Supporting Information Table S3). Variables with high concavity in the WI model were frozen ground without snow and snow cover variability (with the latter always producing models with greater explanatory power), and minimum temperature and temperature seasonality in the climate model (with the former producing better models of species richness of amphibians and mammals and the latter producing better models of species richness of resident birds). In models containing the WIs, climate, productivity and elevation as predictors of species richness, we included either winter length or minimum temperature, owing to high concavity between the latter variables. Models with winter length outperformed those with minimum temperature (Supporting Information Table S4). The best model (without high concavity) contained the WIs, seasonality of both temperature and precipitation, productivity and elevation. In the final combined models, the WIs (winter length and snow cover variability) had the second and third strongest relationships with species richness of amphibians and mammals (productivity was strongest for the former and elevation for the latter) (Supporting Information Table S5). Winter length had the strongest relationship with species richness of resident birds, and snow cover variability had the weakest.

4 | DISCUSSION

Our results show that winter conditions structure extratropical patterns of species richness of amphibians, mammals and birds globally. Longer winters (more days of frozen ground) generally were associated with fewer species of amphibians, mammals and resident birds, and species richness of all declined markedly beginning at c. 3 months of winter. This consistent cross-taxonomic threshold indicates that winter length might be an influential environmental filter for species richness. The differences in the major gradients of winter length in the Western (latitudinal) and Eastern (both latitudinal and longitudinal) Hemispheres might also help to explain why the latitudinal diversity gradient is stronger in the Western Hemisphere for a broad range of organisms (Kinlock et al., 2018; Mittelbach et al., 2007). For species in areas with ≥ 3 months of winter, including

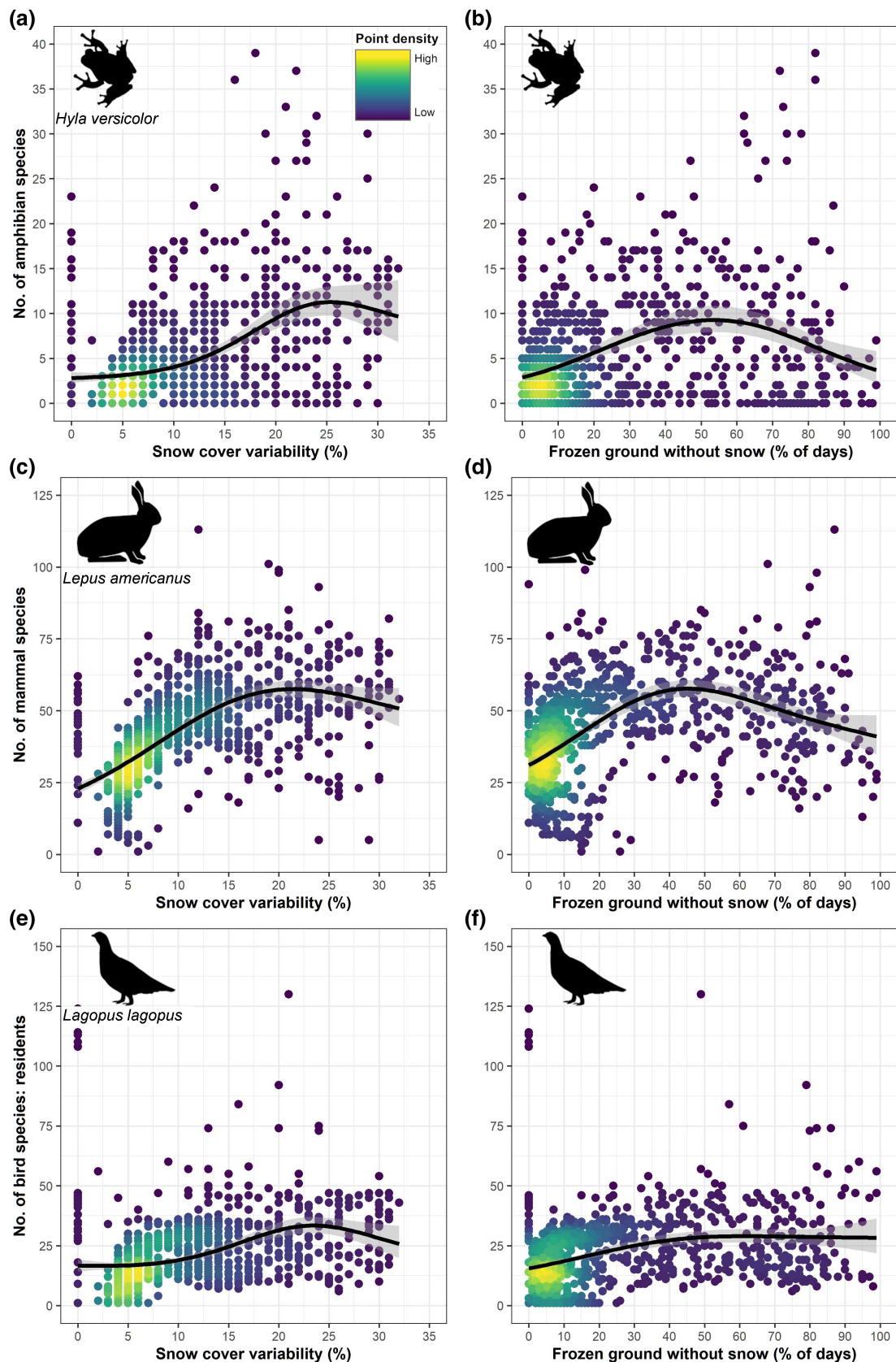


FIGURE 4 Global relationships between species richness in areas with prolonged winters (≥ 3 months) and (left column) snow cover variability and (right column) lack of subnivium (percentage of days of frozen ground without snow) for (a,b) amphibians, (c,d) mammals and (e,f) resident birds

multiple winter conditions resulted in better-fitting species richness models. Therefore, variation in frozen ground and snow cover patterns captured important additional information for explaining species richness gradients in temperate, boreal and polar ecosystems.

The limitation on species richness imposed by longer winters supports theories on the effects of climate and energy–water availability on macroscale species richness patterns (Worm & Tittensor, 2018). The most direct constraint that longer winters place on species richness is through colder and more variable temperature regimes. According to metabolic theory, organisms inhabiting colder environments have lower metabolism and longer generational times than those in warmer environments, hence lower rates of mutation and speciation (Allen et al., 2006; Currie et al., 2004; Stegen et al., 2009). However, there is evidence that relative to the tropics, speciation rates might be higher at higher latitudes, and that the lower number of species in these areas might instead be a product of higher extinction rates (Jetz et al., 2012; Weir & Schluter, 2007). Thermal tolerance is another physiological trait related to temperature that structures gradients of species richness (Carnicer et al., 2012; Khaliq et al., 2014; Sunday et al., 2012). The reason is that the thermal niche of a species (optimum range and critical limits of temperature) is highly conserved over time, and most extant species evolved under warm temperature regimes, which means that few species have evolved the adaptations required for overwinter survival (e.g., supercooling, thick fur or plumage, hibernation) (Bennett et al., 2021; Worm & Tittensor, 2018). Lastly, species inhabiting areas with longer winters face greater temperature variability than species in areas where winter is shorter and temperatures are rarely below freezing, and therefore require tolerance of both cold and heat (in summer). Thus, species richness is often lower at higher latitudes and elevations owing to colder and more variable temperatures, relative to lower latitudes and elevations, where temperature is warmer and more stable (Bennett et al., 2021; Gao & Liu, 2018; Polato et al., 2018). Our results showing fewer species for each taxon in areas with longer winters generally reaffirm that colder and more variable temperature regimes impose a major constraint on species richness. Furthermore, our finding that species richness of mammals and resident birds was consistently higher than that of amphibians throughout the range of winter lengths highlights the advantages of endothermy (internal temperature regulation decoupled from external sources) and higher potential activity time (endothermic organisms are more active than ectothermic organisms throughout the year) over ectothermy (internal temperature regulation dependent on external sources) for colonization and speciation in cold extratropical environments (Buckley et al., 2012; Khaliq et al., 2014; Weir & Schluter, 2007).

Although colder and more variable temperature regimes certainly limit species richness, our results for three major animal taxa suggest that the length of winter constrains extratropical species richness for several reasons that go beyond strict temperature thresholds. For example, one of our most surprising findings was that species richness of mammals, and to a lesser degree of amphibians, was often as high or higher in areas with prolonged periods of

frozen ground compared with areas where the ground never freezes (see Figure 3b), suggesting that the species richness of these taxa does not scale linearly with temperature. Furthermore, many species have not colonized all the areas within their lower thermal tolerance limits (Currie et al., 2004; Khaliq et al., 2014; Sunday et al., 2012). Taken together with the precipitous, cross-taxonomic decline in species richness beginning at 3 months of winter that we found here, it appears that the duration that temperatures are consistently at or near the extremes of species tolerances while access to resources (food, water and shelter) is severely limited owing to frozen ground or snow cover acts as a strong environmental filter on extratropical species richness. Longer winters entail less available energy and water for organisms because growing seasons are shorter, food resources are less abundant, and snow and ice restrict water access (Hawkins et al., 2003; Williams et al., 2015). Where these conditions extend for longer throughout the year, the metabolic and energetic trade-offs required for overwintering (e.g., shifts from specialist to generalist foraging strategies, larger thermal niches, hibernation) can become too costly for many species (Coops et al., 2019; Johnston & Bennett, 1996; Worm & Tittensor, 2018).

The most striking relationships with winter length were for the number of bird species adopting a given migration strategy and their respective representation in the avifauna (see Figure 1c,d,g,h). We identified a clear peak in the number and percentage of fully migratory species at c. 5.5 months of winter, which coincided with low resident species richness. The hemispheric gradients in winter length (see Figure 2) that we found generally matched long-distance migration patterns in birds, which are largely latitudinal in North America and more longitudinal in Eurasia (Gill, 2007; Somveille et al., 2019). By breeding in areas that experience winter conditions for the majority of the year, full migrants might be both exploiting the resource-rich summer months and benefitting from reduced food competition in areas that support few resident species (Somveille et al., 2015, 2019). Although the relationship between winter length and species richness of partial migrants generally followed a pattern similar to that for full migrants, it was considerably weaker, suggesting other factors are at play (e.g., intraspecific competition; Chapman et al., 2011). Given that climate change is shifting the migratory dynamics and range boundaries of birds (Curley et al., 2020; Rushing et al., 2020; Thomas & Lennon, 1999), our winter length index offers a rigorous means to track and predict these shifts into the future, because current projections show that winters will be shorter, warmer and more susceptible to low- to no-snow conditions in the middle to high latitudes (Huning & AghaKouchak, 2020; Siirila-Woodburn et al., 2021; Wang et al., 2021).

Within areas that experience longer winters (≥ 3 months), snow cover variability and time without subnivism also influenced species richness patterns, particularly for amphibians and mammals. However, contrary to our expectations, species richness generally increased up to a point with increasing snow cover variability and lack of subnivism (c. 25% for snow cover variability and c. 50% for frequency of frozen ground without snow), then plateaued or declined slightly at higher values. This might be attributable to

regional climate variability, because these indices capture a latitudinal and elevational transition from rain- to snow-dominated ecosystems (both were highest at low elevations and along the coasts of the middle latitudes). This “trailing edge” of the cryosphere is important for species range limits and community assemblages, because it represents a transition zone from more warm-adapted to more cold-adapted species (Cahill et al., 2014). One potential reason why species richness might have been consistently higher in this zone for all three taxa is that it acts as an ecotone, where the northern range boundaries of warm-adapted species and southern range boundaries of cold-adapted species overlap. As such, this band of winter variability might promote species richness by increasing available niche space and thermal heterogeneity, which can be used by endothermic species, such as mammals and birds (Elsen et al., 2020; Stein et al., 2014, 2015). For temperate amphibians, which have ancestral origins in cool, moist climates and a high degree of niche conservatism tied to water availability (Buckley & Jetz, 2007; Kozak & Wiens, 2010), snow cover variability might increase species richness by providing a range of moisture regimes. For example, areas characterized by high snow cover variability, such as the mid-elevations of many mountain ranges (e.g., the Great Smoky Mountains in the USA, where global species richness of salamanders is highest), might be able to support more species than either lower elevations, where conditions are drier throughout the year, or higher elevations, where snow cover is too persistent.

Our study took a new approach to examine explicit links between winter conditions and macroecological gradients of species richness. The clear latitudinal and elevational gradients in winter conditions identified by our satellite-based WIs, particularly winter length, closely matched gradients of species richness of amphibians, mammals and birds, and the preponderance of different bird migration strategies. Additionally, the winter conditions captured by the WIs either outperformed or complemented other environmental variables, including climate, productivity and elevation, in explaining patterns of species richness. These results show that the WIs go beyond traditional measures of climate, productivity and spatial proxies for these (e.g., elevation, latitude), frequently used in macroecological studies of species richness (Hawkins & Diniz-Filho, 2004). For example, the winter length index describes how long cold temperatures and frozen ground persist in an area, which is more biologically meaningful than the meteorological (seasonal) definition of winter and more informative than measures of temperature (e.g., minimum) alone. Quantifying winter length as the number of days of frozen ground also provides a mechanistic link to stages of plant dormancy, vegetative growth and reproduction (Fadón & Rodrigo, 2018; Zohner et al., 2016), hence primary productivity. Indices that integrate different aspects of climate-energy dynamics, such as actual evapotranspiration, are powerful predictors of macroscale species richness patterns (Buckley & Jetz, 2007; Storch et al., 2006; Torres-Romero & Olalla-Tárraga, 2015), and we found the same to be true for the WIs. However,

one limitation of our study is the coarse spatial resolution of the WIs (25 km) and the species richness grids (c. 110 km or 1°), which obscure finer-scale patterns of variability in winter conditions and species richness that might be especially important in areas with complex topography (e.g., montane regions). Another limitation is that we could not account for the potential effects of interannual variability in winter conditions on species richness patterns because the IUCN range maps are static, and we did not examine potential interactions between the WIs (e.g., winter length and snow cover variability) and between the WIs and other environmental variables (e.g., winter length and productivity).

Despite these limitations, the strong relationships between the WIs and extratropical patterns of species richness suggest that tracking winter conditions in a rapidly warming world will be essential when predicting the ecological consequences of climate change. Our results and remote sensing products (the WIs; freely available for download at silvis.forest.wisc.edu) open many research questions in the field of winter ecology. Some potential avenues of future research that use the WIs include examining relationships between: (1) winter conditions, life-history strategies and functional traits within different taxa and for specific species; (2) the percentage of frozen ground and snow cover variability and the abundance and distribution of subnivium-dependent species; (3) the frequency of freeze-thaw events captured by the snow cover variability index and overwinter survival and fitness of organisms (especially plants); and (4) changes to winter conditions over time and species abundances and distributions.

COMPETING INTEREST

The authors declare that they have no competing interests.

ACKNOWLEDGMENTS

We gratefully acknowledge support by the NASA Biodiversity Program of the Earth Sciences Division (grant #80NSSC19K0180 awarded to B.Z., J.N.P. and V.C.R.), the USGS Landsat Science Team (grant #140G0118C0009 awarded to V.C.R.) and the National Natural Science Foundation of China (grant #42001373 awarded to L.Z.).

AUTHOR CONTRIBUTIONS

Conceptualization: D.G.-C., S.R.K., B.Z., J.N.P., V.C.R.; Methodology: D.G.-C., L.Z., S.R.K.; Investigation: D.G.-C., S.R.K., L.Z.; Visualization: D.G.-C., L.Z., V.C.R., S.R.K., B.Z., J.N.P.; Funding acquisition: B.Z., J.N.P., V.C.R.; Project administration: B.Z., J.N.P., V.C.R.; Supervision: V.C.R., B.Z.; Writing – original draft: D.G.-C.; Writing – review & editing: D.G.-C., S.R.K., L.Z., B.Z., J.N.P., V.C.R.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in DRYAD at: <http://doi.org/10.5061/dryad.9s4mw6mgs>. The DRYAD repository contains the three winter indices in raster format and the species richness modelling data and R code.

ORCID

David Gudex-Cross  <https://orcid.org/0000-0001-6939-7753>

Likai Zhu  <https://orcid.org/0000-0003-4777-4129>

Spencer R. Keyser  <https://orcid.org/0000-0001-7524-9677>

Benjamin Zuckerberg  <https://orcid.org/0000-0001-7412-4354>

Jonathan N. Pauli  <https://orcid.org/0000-0001-5908-6628>

REFERENCES

- Allen, A. P., Gillooly, J. F., Savage, V. M., & Brown, J. H. (2006). Kinetic effects of temperature on rates of genetic divergence and speciation. *Proceedings of the National Academy of Sciences*, 103(24), 9130–9135. <https://doi.org/10.1073/pnas.0603587103>
- Ashcroft, M. B., French, K. O., & Chisholm, L. A. (2011). An evaluation of environmental factors affecting species distributions. *Ecological Modelling*, 222(3), 524–531. <https://doi.org/10.1016/j.ecolmod.2010.10.003>
- Bennett, J. M., Sunday, J., Calosi, P., Villalobos, F., Martínez, B., Molina-Venegas, R., Araújo, M. B., Algar, A. C., Clusella-Trullas, S., Hawkins, B. A., Keith, S. A., Kühn, I., Rahbek, C., Rodríguez, L., Singer, A., Morales-Castilla, I., & Olalla-Tárraga, M. Á. (2021). The evolution of critical thermal limits of life on Earth. *Nature Communications*, 12(1), 1198. <https://doi.org/10.1038/s41467-021-21263-8>
- BirdLife International and Handbook of the Birds of the World. (2019). *Bird species distribution maps of the world*. Version 2019.1. <http://datazone.birdlife.org/species/requestdis>
- Buckley, L. B., Hurlbert, A. H., & Jetz, W. (2012). Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and Biogeography*, 21(9), 873–885. <https://doi.org/10.1111/j.1466-8238.2011.00737.x>
- Buckley, L. B., & Jetz, W. (2007). Environmental and historical constraints on global patterns of amphibian richness. *Proceedings of the Royal Society B: Biological Sciences*, 274(1614), 1167–1173. <https://doi.org/10.1098/rspb.2006.0436>
- Cahill, A. E., Aiello-Lammens, M. E., Caitlin Fisher-Reid, M., Hua, X., Karanewsky, C. J., Ryu, H. Y., Sbeglia, G. C., Spagnolo, F., Waldron, J. B., & Wiens, J. J. (2014). Causes of warm-edge range limits: Systematic review, proximate factors and implications for climate change. *Journal of Biogeography*, 41(3), 429–442. <https://doi.org/10.1111/jbi.12231>
- Carnicer, J., Brotons, L., Stefanescu, C., & Penuelas, J. (2012). Biogeography of species richness gradients: Linking adaptive traits, demography and diversification. *Biological Reviews*, 87(2), 457–479. <https://doi.org/10.1111/j.1469-185X.2011.00210.x>
- Chapman, B. B., Brönmark, C., Nilsson, J. Å., & Hansson, L. A. (2011). The ecology and evolution of partial migration. *Oikos*, 120(12), 1764–1775. <https://doi.org/10.1111/j.1600-0706.2011.20131.x>
- Coops, N. C., Bolton, D. K., Hobi, M. L., & Radeloff, V. C. (2019). Untangling multiple species richness hypothesis globally using remote sensing habitat indices. *Ecological Indicators*, 107, 105567. <https://doi.org/10.1016/j.ecolind.2019.105567>
- Curley, S. R., Manne, L. L., & Veit, R. R. (2020). Differential winter and breeding range shifts: Implications for avian migration distances. *Diversity and Distributions*, 26(4), 415–425. <https://doi.org/10.1111/ddi.13036>
- Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guegan, J.-F., Hawkins, B. A., Kaufman, D. M., Kerr, J. T., Oberdorff, T., O'Brien, E., & Turner, J. R. G. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, 7(12), 1121–1134. <https://doi.org/10.1111/j.1461-0248.2004.00671.x>
- Danielson, J. J., & Gesch, D. B. (2011). *Global multi-resolution terrain elevation data 2010 (GMTED2010)*: US Department of the Interior, U.S. Geological Survey Open-File Report 2011-1073. USGS Publications Warehouse. 26 p. pubs.usgs.gov/of/2011/1073/
- Du, J., Kimball, J. S., Jones, L. A., Kim, Y., Glassy, J., & Watts, J. D. (2017). A global satellite environmental data record derived from AMSR-E and AMSR2 microwave Earth observations. *Earth System Science Data*, 9(2), 791–808. <https://doi.org/10.5194/essd-9-791-2017>
- Elsen, P. R., Farwell, L. S., Pidgeon, A. M., & Radeloff, V. C. (2020). Landsat 8 TIRS-derived relative temperature and thermal heterogeneity predict winter bird species richness patterns across the conterminous United States. *Remote Sensing of Environment*, 236, 111514. <https://doi.org/10.1016/j.rse.2019.111514>
- Fadón, E., & Rodrigo, J. (2018). Unveiling winter dormancy through empirical experiments. *Environmental and Experimental Botany*, 152, 28–36. <https://doi.org/10.1016/j.envexpbot.2017.11.006>
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(12), 4302–4315. <https://doi.org/10.1002/joc.5086>
- Gao, J., & Liu, Y. (2018). Climate stability is more important than water-energy variables in shaping the elevational variation in species richness. *Ecology and Evolution*, 8(14), 6872–6879. <https://doi.org/10.1002/ece3.4202>
- Gill, F. B. (2007). *Ornithology* (3rd ed.). W.H. Freeman and Company.
- Gudex-Cross, D., Keyser, S. R., Zuckerberg, B., Fink, D., Zhu, L., Pauli, J. N., & Radeloff, V. C. (2021). Winter Habitat Indices (WHIs) for the contiguous US and their relationship with winter bird diversity. *Remote Sensing of Environment*, 255, 112309. <https://doi.org/10.1016/j.rse.2021.112309>
- Hall, D. K., & Riggs, G. A. (2016). *MODIS/Aqua and MODIS/Terra snow cover 8-day L3 global 500m SIN Grid, version 6*. National Snow and Ice Data Center.
- Hawkins, B. A., & Diniz-Filho, J. A. F. (2004). "Latitude" and geographic patterns in species richness. *Ecography*, 27, 268–272. <https://doi.org/10.1111/j.0906-7590.2004.03883.x>
- Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guégan, J.-F., Kaufman, D. M., Kerr, J. T., Mittelbach, G. G., Oberdorff, T., O'Brien, E. M., Porter, E. E., & Turner, J. R. G. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, 84(12), 3105–3117. <https://doi.org/10.1890/03-8006>
- Huning, L. S., & AghaKouchak, A. (2020). Global snow drought hot spots and characteristics. *Proceedings of the National Academy of Sciences*, 117(33), 19753–19759. <https://doi.org/10.1073/pnas.1915921117>
- IUCN. (2017). *The IUCN red list of threatened species*. Version 2017-1. <https://www.iucnredlist.org>
- Ives, A. R. (2018). *Mixed and phylogenetic models: A conceptual introduction to correlated data*. Leanpub. https://leanpub.com/correlated_data
- Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, 491(7424), 444–448. <https://doi.org/10.1038/nature11631>
- Johnston, I. A., & Bennett, A. F. (1996). *Animals and temperature: Phenotypic and evolutionary adaptation*. Cambridge University Press.
- Khaliq, I., Hof, C., Prinzing, R., Böhning-Gaese, K., & Pfenninger, M. (2014). Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proceedings of the Royal Society B: Biological Sciences*, 281(1789), 20141097. <https://doi.org/10.1098/rspb.2014.1097>
- Kim, Y., Kimball, J. S., Glassy, J., & Du, J. (2017). An extended global Earth system data record on daily landscape freeze–thaw status determined from satellite passive microwave remote sensing. *Earth System Science Data*, 9(1), 133–147. <https://doi.org/10.5194/essd-9-133-2017>
- Kim, Y., Kimball, J. S., McDonald, K. C., & Glassy, J. (2010). Developing a global data record of daily landscape freeze/thaw status using satellite passive microwave remote sensing. *IEEE Transactions*

- on *Geoscience and Remote Sensing*, 49(3), 949–960. <https://doi.org/10.1109/TGRS.2010.2070515>
- Kinlock, N. L., Prowant, L., Herstoff, E. M., Foley, C. M., Akin-Fajiye, M., Bender, N., Umarani, M., Ryu, H. Y., Şen, B., & Gurevitch, J. (2018). Explaining global variation in the latitudinal diversity gradient: meta-analysis confirms known patterns and uncovers new ones. *Global Ecology and Biogeography*, 27(1), 125–141. <https://doi.org/10.1111/geb.12665>
- Kozak, K. H., & Wiens, J. J. (2010). Niche conservatism drives elevational diversity patterns in Appalachian salamanders. *The American Naturalist*, 176(1), 40–54. <https://doi.org/10.1086/653031>
- Kreyling, J. (2010). Winter climate change: A critical factor for temperate vegetation performance. *Ecology*, 91(7), 1939–1948. <https://doi.org/10.1890/09-1160.1>
- Mills, L. S., Zimova, M., Oyler, J., Running, S., Abatzoglou, J. T., & Lukacs, P. M. (2013). Camouflage mismatch in seasonal coat color due to decreased snow duration. *Proceedings of the National Academy of Sciences*, 110(18), 7360–7365. <https://doi.org/10.1073/pnas.1222724110>
- Mittelbach, G. G., Schemske, D. W., Cornell, H. V., Allen, A. P., Brown, J. M., Bush, M. B., Harrison, S. P., Hurlbert, A. H., Knowlton, N., Lessios, H. A., McCain, C. M., McCune, A. R., McDade, L. A., McPeck, M. A., Near, T. J., Price, T. D., Ricklefs, R. E., Roy, K., Sax, D. F., ... Turelli, M. (2007). Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. *Ecology Letters*, 10(4), 315–331. <https://doi.org/10.1111/j.1461-0248.2007.01020.x>
- Newton, I. (2010). *The migration ecology of birds*. Academic Press, Elsevier.
- Niittynen, P., Heikkinen, R. K., & Luoto, M. (2018). Snow cover is a neglected driver of Arctic biodiversity loss. *Nature Climate Change*, 8(11), 997–1001. <https://doi.org/10.1038/s41558-018-0311-x>
- Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P., & Kassem, K. R. (2001). Terrestrial ecoregions of the world: A new map of life on Earth. *BioScience*, 51(11), 933–938.
- Pauli, J. N., Zuckerberg, B., Whiteman, J. P., & Porter, W. (2013). The subnivium: A deteriorating seasonal refugium. *Frontiers in Ecology and the Environment*, 11(5), 260–267. <https://doi.org/10.1890/120222>
- Penczykowski, R. M., Connolly, B. M., & Barton, B. T. (2017). Winter is changing: Trophic interactions under altered snow regimes. *Food Webs*, 13, 80–91. <https://doi.org/10.1016/j.fooweb.2017.02.006>
- Petty, S. K., Zuckerberg, B., & Pauli, J. N. (2015). Winter conditions and land cover structure the subnivium, a seasonal refuge beneath the snow. *PLoS One*, 10(5), e0127613. <https://doi.org/10.1371/journal.pone.0127613>
- Polato, N. R., Gill, B. A., Shah, A. A., Gray, M. M., Casner, K. L., Barthelet, A., Messer, P. W., Simmons, M. P., Guayasamin, J. M., Encalada, A. C., Kondratieff, B. C., Flecker, A. S., Thomas, S. A., Ghalambor, C. K., Poff, N. L. R., Funk, W. C., & Zamudio, K. R. (2018). Narrow thermal tolerance and low dispersal drive higher speciation in tropical mountains. *Proceedings of the National Academy of Sciences*, 115(49), 12471–12476. <https://doi.org/10.1073/pnas.1809326115>
- Radeloff, V. C., Dubinin, M., Coops, N. C., Allen, A. M., Brooks, T. M., Clayton, M. K., Costa, G. C., Graham, C. H., Helmers, D. P., Ives, A. R., Kolesov, D., Pidgeon, A. M., Rapacciuolo, G., Razenkova, E., Suttidate, N., Young, B. E., Zhu, L., & Hobi, M. L. (2019). The dynamic habitat indices (DHIs) from MODIS and global biodiversity. *Remote Sensing of Environment*, 222, 204–214. <https://doi.org/10.1016/j.rse.2018.12.009>
- Roberts, K. T., Rank, N. E., Dahlhoff, E. P., Stillman, J. H., & Williams, C. M. (2021). Snow modulates winter energy use and cold exposure across an elevation gradient in a montane ectotherm. *Global Change Biology*, 27(23), 6103–6116. <https://doi.org/10.1111/gcb.15912>
- Rushing, C. S., Royle, J. A., Ziolkowski, D. J., & Pardieck, K. L. (2020). Migratory behavior and winter geography drive differential range shifts of eastern birds in response to recent climate change. *Proceedings of the National Academy of Sciences*, 117(23), 12897–12903. <https://doi.org/10.1073/pnas.2000299117>
- Siirila-Woodburn, E. R., Rhoades, A. M., Hatchett, B. J., Huning, L. S., Szinai, J., Tague, C., Nico, P. S., Feldman, D. R., Jones, A. D., Collins, W. D., & Kaatz, L. (2021). A low-to-no snow future and its impacts on water resources in the western United States. *Nature Reviews Earth & Environment*, 2(11), 800–819. <https://doi.org/10.1038/s43017-021-00219-y>
- Šimová, I., Storch, D., Keil, P., Boyle, B., Phillips, O. L., & Enquist, B. J. (2011). Global species–energy relationship in forest plots: Role of abundance, temperature and species climatic tolerances. *Global Ecology and Biogeography*, 20(6), 842–856. <https://doi.org/10.1111/j.1466-8238.2011.00650.x>
- Slatyer, R. A., Umbers, K. D., & Arnold, P. A. (2021). Ecological responses to variation in seasonal snow cover. *Conservation Biology*, 36(1), e13727. <https://doi.org/10.1111/cobi.13727>
- Somveille, M., Manica, A., & Rodrigues, A. S. (2019). Where the wild birds go: Explaining the differences in migratory destinations across terrestrial bird species. *Ecography*, 42(2), 225–236. <https://doi.org/10.1111/ecog.03531>
- Somveille, M., Rodrigues, A. S., & Manica, A. (2015). Why do birds migrate? A macroecological perspective. *Global Ecology and Biogeography*, 24(6), 664–674. <https://doi.org/10.1111/geb.12298>
- Stegen, J. C., Enquist, B. J., & Ferriere, R. (2009). Advancing the metabolic theory of biodiversity. *Ecology Letters*, 12(10), 1001–1015. <https://doi.org/10.1111/j.1461-0248.2009.01358.x>
- Stein, A., Beck, J., Meyer, C., Waldmann, E., Weigelt, P., & Kreft, H. (2015). Differential effects of environmental heterogeneity on global mammal species richness. *Global Ecology and Biogeography*, 24(9), 1072–1083. <https://doi.org/10.1111/geb.12337>
- Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17(7), 866–880. <https://doi.org/10.1111/ele.12277>
- Stillinger, T., Roberts, D. A., Collar, N. M., & Dozier, J. (2019). Cloud masking for Landsat 8 and MODIS Terra over snow-covered terrain: Error analysis and spectral similarity between snow and cloud. *Water Resources Research*, 55(7), 6169–6184. <https://doi.org/10.1029/2019WR024932>
- Storch, D., Davies, R. G., Zajíček, S., Orme, C. D. L., Olson, V., Thomas, G. H., Ding, T.-S., Rasmussen, P. C., Ridgely, R. S., Bennett, P. M., Blackburn, T. M., Owens, I. P. F., & Gaston, K. J. (2006). Energy, range dynamics and global species richness patterns: Reconciling mid-domain effects and environmental determinants of avian diversity. *Ecology Letters*, 9(12), 1308–1320. <https://doi.org/10.1111/j.1461-0248.2006.00984.x>
- Sunday, J. M., Bates, A. E., & Dulvy, N. K. (2012). Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, 2(9), 686–690. <https://doi.org/10.1038/nclimate1539>
- Thomas, C. D., & Lennon, J. J. (1999). Birds extend their ranges northwards. *Nature*, 399(6733), 213. <https://doi.org/10.1038/20335>
- Tittensor, D. P., & Worm, B. (2016). A neutral-metabolic theory of latitudinal biodiversity. *Global Ecology and Biogeography*, 25(6), 630–641. <https://doi.org/10.1111/geb.12451>
- Tobias, J. A., Sheard, C., Seddon, N., Meade, A., Cotton, A. J., & Nakagawa, S. (2016). Territoriality, social bonds, and the evolution of communal signaling in birds. *Frontiers in Ecology and Evolution*, 4, 74. <https://doi.org/10.3389/fevo.2016.00074>
- Torres-Romero, E. J., & Olalla-Tárraga, M. Á. (2015). Untangling human and environmental effects on geographical gradients of mammal species richness: A global and regional evaluation. *Journal of Animal Ecology*, 84(3), 851–860. <https://doi.org/10.1111/1365-2656.12313>

- Wang, J., Guan, Y., Wu, L., Guan, X., Cai, W., Huang, J., Dong, W., & Zhang, B. (2021). Changing lengths of the four seasons by global warming. *Geophysical Research Letters*, 48(6), e2020GL091753. <https://doi.org/10.1029/2020GL091753>
- Weir, J. T., & Schluter, D. (2007). The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science*, 315(5818), 1574–1576. <https://doi.org/10.1126/science.1135590>
- Williams, C. M., Henry, H. A., & Sinclair, B. J. (2015). Cold truths: How winter drives responses of terrestrial organisms to climate change. *Biological Reviews*, 90(1), 214–235. <https://doi.org/10.1111/brv.12105>
- Wood, S. N. (2017). *Generalized additive models: An introduction with R*. Chapman and Hall/CRC Press. <https://doi.org/10.1201/9781420010404>
- Worm, B., & Tittensor, D. P. (2018). *A theory of global biodiversity* (MPB-60). Princeton University Press. <https://doi.org/10.23943/9781400890231>
- Zhu, L., & Guo, Y. (2022). Remotely sensed Winter Habitat Indices improve the explanation of broad-scale patterns of mammal and bird species richness in China. *Remote Sensing*, 14(3), 794. <https://doi.org/10.3390/rs14030794>
- Zhu, L., Ives, A. R., Zhang, C., Guo, Y., & Radeloff, V. C. (2019). Climate change causes functionally colder winters for snow cover-dependent organisms. *Nature Climate Change*, 9(11), 886–893. <https://doi.org/10.1038/s41558-019-0588-4>
- Zhu, L., Radeloff, V. C., & Ives, A. R. (2017). Characterizing global patterns of frozen ground with and without snow cover using microwave and MODIS satellite data products. *Remote Sensing of Environment*, 191, 168–178. <https://doi.org/10.1016/j.rse.2017.01.020>
- Zohner, C. M., Benito, B. M., Svenning, J.-C., & Renner, S. S. (2016). Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Climate Change*, 6(12), 1120–1123. <https://doi.org/10.1038/nclimate3138>
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R* (Vol. 574). Springer. <https://doi.org/10.1007/978-0-387-87458-6>

BIOSKETCH

Our research team is broadly interested in understanding how environmental conditions influence species distributions and biodiversity patterns through time and space. Much of our current work focuses on winter ecology and the use of big data (e.g., satellite imagery, eBird) to elucidate macroecological patterns and processes. **David Gudex-Cross** (silvis.forest.wisc.edu/staff/gudex-cross-david/), **Volker C. Radeloff** (silvis.forest.wisc.edu/staff/radeloff-volker/) and **Likai Zhu** (silvis.forest.wisc.edu/staff/zhu-likai/) specialize in ecological remote sensing and macroecology, and **Benjamin Zuckerberg** (zuckerberg.russell.wisc.edu), **Jonathan N. Pauli** (pauli.russell.wisc.edu) and **Spencer R. Keyser** (zuckerberg.russell.wisc.edu/spencer-keyser/) specialize in climate change ecology and wildlife ecology.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Gudex-Cross, D., Zhu L., Keyser S. R., Zuckerberg B., Pauli J. N., & Radeloff V. C. (2022). Winter conditions structure extratropical patterns of species richness of amphibians, birds and mammals globally. *Global Ecology and Biogeography*, 31, 1366–1380. <https://doi.org/10.1111/geb.13511>