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Research article

Snow cover dynamics: an overlooked yet important feature of winter bird occurrence and abundance across the United States

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Snow cover dynamics (i.e. depth, duration and variability) are dominant drivers of ecological processes during winter. For overwintering species, changes and gradients in snow cover may impact survival and population dynamics (e.g. facilitating survival via thermal refugia or limiting survival via reduced resource acquisition). However, snow cover dynamics are rarely used in species distribution modelling, especially for overwintering birds. Currently, we lack understanding of how snow cover gradients affect overwintering bird distributions and which functional traits drive these associations at regional and continental scales. Using observations from eBird, a global community science network, we explored the effects of snow cover dynamics on continental patterns of occurrence and counts for 150 bird species. We quantified the relative importance, species-specific responses and trait-based relationships of bird occurrence and abundance patterns to ecologically relevant snow cover dynamics across the United States. Snow cover dynamics were important environmental predictors in species distributions models, ranking within the top three predictors for most species occurrence (> 90%) and count (> 79%) patterns across the contiguous United States. Species exhibited a gradient of responses to snow cover from snow association to snow avoidance, yet most birds were limited by long, persistent snow seasons. Duration of winter and percent frozen ground without snow structured species distributions in the eastern USA, whereas snow cover variability was a stronger driver in the western USA. Birds associated with long, persistent snow seasons had traits associated with greater dispersal capacity and dietary diversity, whereas birds inhabiting regions with variable snow cover were generally habitat generalists. Our results suggest that various snow cover dynamics are important ecological filters of species distributions during winter. Global climate change is rapidly degrading key characteristics of seasonal snow cover. A changing cryosphere may elicit variable distributional changes for many overwintering birds, potentially accelerating range shifts and novel community assemblages.

Keywords: avian ecology, climate change, machine learning, remote sensing, species distribution modelling, winter climate, winter ecology

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Introduction

Winter is a season characterized by environmental constraints including reduced primary productivity, freezing temperatures and the presence of snow. These conditions can exceed the physiological limits for some species; consequently, winter is commonly a period of migration or senescence for many species as they actively avoid winter conditions. Species that remain active in winter face energetic and fitness challenges imposed by resource scarcities, winter climate and extreme weather events (Pauli et al. 2013). For overwintering species, snow is an important component of their winter habitat, because snow covers approximately 49% of all land in the Northern Hemisphere at some point during the year (Lemke 2007). Snow cover dynamics have major implications for ecological processes (Campbell et al. 2005, Williams et al. 2015, Slatyer et al. 2021), but their effects on species distributions remain poorly understood (Niittynen and Luoto 2018).

Several environmental factors constrain species distributions by directly and indirectly affecting demographic processes and resource acquisition (Elith and Leathwick 2009, Godsoe et al. 2017). Climate mediates species distributions directly, when it exceeds species' physiological limits (Kearney and Porter 2009), and indirectly through biotic interactions and food availability (Araújo and Luoto 2007, Alexander et al. 2015). In winter environments, organisms are confronted by two primary climate-mediated pressures: 1) lower temperatures, which influence metabolic and thermoregulatory rates (Root 1988, Zuckerberg et al. 2011, Stager et al. 2016), and 2) lower food availability, which reduces energy acquisition (Canterbury 2002). A third, climate-mediated pressure is precipitation (Boyle et al. 2020). Precipitation affects populations in all seasons through its effects on metabolic rates and resource availability (White et al. 2007, Martin and Maron 2012, Cohen et al. 2020). Winter precipitation in the form of freezing rain or snow can be challenging when thermal stress forces species to acquire more resources, but snow makes them inaccessible. Winter precipitation and temperature are considered important predictors of breeding bird distributions and abundance, and winter climate has carry-over effects on bird productivity in summer, even for migratory species (Illán et al. 2014).

Despite the importance of climate as a constraint of species distributions (Root 1988, Thuiller et al. 2004, Luoto et al. 2007), snow cover dynamics are rarely included in species distribution models. This is surprising, given that snow cover affects many organisms throughout the Northern Hemisphere (Pruitt 1960, Pauli et al. 2013, Williams et al. 2015, Rosvold 2016). For example, spatial variability of snow cover persistence determines Arctic plant distributions, taxonomic richness and functional diversity (Niittynen and Luoto 2018, Niittynen et al. 2018, 2020). Similarly, variability in snow cover conditions (e.g. duration and depth) has important implications for winter mammals and birds, affecting species directly, via movement related costs (Mahoney et al. 2018, McKinnon et al. 2019), and indirectly, such as phenotypic mismatch and corresponding increases in predation events (Mills et al. 2013, Wilson et al. 2019). Furthermore, variation in snow cover conditions determines competitive interactions between sympatric carnivore species (Manlick, et al. 2020), and reduces survival of prey species through predator release (Pokallus and Pauli 2015). Previous studies that integrated winter precipitation into distribution models often do not distinguish between different forms of precipitation among seasons and along rain-to-snow gradients (Barbet-Massin and Jetz 2014, Illán et al. 2014). Most snow data capture variation in characteristics of the snowpack (e.g. depth) or snowfall amount (Wang et al. 2016), but do not reflect ecologically relevant dynamics of snow cover such as its duration, variability and coupling with frozen ground (Gudex-Cross et al. 2021). Indeed, snow cover duration, variability and lack of subnivium (i.e. frequency of frozen ground without snow) strongly influence patterns of bird species richness (Gudex-Cross et al. 2021, 2022).

Species have evolved several adaptations that increase overwintering survival (i.e. functional traits, Voille et al. 2007) in snowy environments. For example, some bird and mammal species have evolved cryptic winter coloration that matches both the onset and disappearance of snow cover (Mills et al. 2018), which directly improves overwinter survival (Zimova et al. 2016, Wilson et al. 2019). Snow depth facilitates the persistence of cold-adapted species during winter because deeper snow establishes the subnivium (a thermally stable refugium beneath the snow), which is why snow depth is more important than both habitat structure and ambient temperature in explaining community composition of small mammal communities (Scott et al. 2022). Similarly, birds living in regions with harsh winter climates may have key functional traits related to snow conditions they experience. Enhanced dispersal capabilities (Jocque et al. 2010, Sheard et al. 2020), increased dietary plasticity (Sol et al. 2005, 2016), greater habitat breadth and larger body size (Bergmann 1847) may all balance the energetic costs associated with finding suitable food over larger areas during periods of persistent snow cover. For example, larger-bodied species may have an energetic advantage during both longer and more variable snow seasons because of their relatively lower metabolic rates, which can reduce the costs associated with thermal stress and energetic needs (Brown and Maurer 1989). Likewise, species with greater dispersal capacity may gain a fitness advantage if they can better access dispersed resources in snow covered landscapes. Finally, dietary and foraging strata diversity may serve as proxies for foraging innovativeness (Sol et al. 2005), which has been linked to overwinter residency in birds, whereas habitat generalism permits species to access diverse microrefugia and variable food resources during long, persistent snow seasons. Therefore, species functional traits that describe dispersal capacity, trophic plasticity, habitat breadth and body size may mediate how species respond to snow cover dynamics.

For birds, in particular, snow cover strongly influences behavior and survival. Ruffed grouse *Bonasa umbellus* use snow burrows as thermal refugia and deeper snow reduces stress hormones and mortality (Shipley et al. 2019, 2020).

Montane birds use snow fields as foraging substrates, as arthropod fallout on snow increases foraging rates, and as microclimate refugia (Antor 1995, Scridel et al. 2018, Resano-Mayor et al. 2019). However, for many overwintering birds, snow cover imposes strong selective pressures by limiting access to food during an energetically stressful time. Indeed, in years with higher snow fall overwintering birds have reduced growth rates (Doherty and Grubb 2003), abundances (Greenwood and Baillie 1991, Jones et al. 2003), and survival (Doherty and Grubb 2002). Thus, snow cover may both facilitate and limit the occurrence and abundance of resident bird species, creating a gradient of responses to differences in the duration of snow cover, its intra-annual variability, and the prevalence of frozen ground without snow.

Given that large areas of the globe experience snow and snow affects a range of ecological processes, the question arises how snow cover structures the distributions of overwintering birds at regional and continental scales? Currently, most studies investigating ecological responses to snow cover dynamics are focused on plants, mammals and arthropods; birds were the focus of only 4% of studies according to a recent review (Slatyer et al. 2021). Additionally, most bird observation data have been collected during the breeding season (Marra et al. 2015) and information on birds in snow-covered environments is often only anecdotal (Rosvold 2016). One reason to explain the understudied effects of snow cover on bird distributions is the lack of reliable, fine-resolution information about seasonal snow cover across broad spatial and temporal extents (Niittynen and Luoto 2018). The recently developed 'winter habitat indices' (WHIs) may help fill this data gap (Gudex-Cross et al. 2021). The WHIs leverage direct observations of Earth's surface from satellites (Gudex-Cross et al. 2021), providing more reliable estimates of snow cover dynamics than gridded snow cover products that produce spatial biases (e.g. high uncertainty in complex terrains; Sirén et al. 2018) shown to impact wildlife modelling efforts (Brennan et al. 2013).

Our goal was to quantify how snow cover dynamics affect overwintering bird distributions at continental scales. To do so, we modeled bird distributions as a function of three remotely-sensed indices of snow cover dynamics: snow season length, snow cover variability and frozen ground without snow (WHIs; Gudex-Cross et al. 2021). We conducted our analysis across the contiguous United States based on ~2.8 million bird observations collected by community scientists using eBird (Sullivan et al. 2009). We predicted that snow cover would be an important driver of the occurrences and counts of overwintering birds. Specifically, we predicted that snow cover characteristics would outperform or complement temperature and land cover in models of species distributions. Alternatively, if snow cover dynamics are inconsequential factors of winter species distributions, we predicted that metrics capturing snow cover dynamics would contribute negligible information in our distribution models compared to temperature and land cover. If snow cover dynamics are important predictors of species occurrence and abundance patterns, we predicted that different birds can be placed on a gradient of responses from snow-associated to snow-avoidant. Lastly, we hypothesized that functional traits – diet diversity, foraging strata diversity (i.e. flexibility in foraging height/substrate), habitat breadth, dispersal capability and body mass – mediate species responses to seasonal snow cover. Specifically, we predicted species living in regions with long, persistent snow cover would be larger-bodied, use more foraging strata, have more diverse diets and be habitat generalists with greater dispersal capacities.

Methods

eBird data

We analyzed bird observation data from eBird, a global, semi-structured community science monitoring program (Sullivan et al. 2009, Kelling et al. 2019). We restricted the data to observations where the time, date and location were reported, and observers recorded the number of individuals of all bird species detected and identified during the survey period, resulting in a 'complete checklist' of species (Sullivan et al. 2009). Restricting the analysis to complete checklists allowed non-detections to be inferred and provide valuable information where search effort was expended but the species was not reported (Johnston et al. 2021). We further restricted checklists to those collected from 2005 to 2020 in the months of December, January and February to focus on the core of the northern hemisphere winter.

Because our goal was to quantify how snow cover dynamics affect overwintering bird distributions, we restricted the geographic extent of our study to states that experience an average snow season length of at least 30 days (mean snow season length of all pixels within a given state from 2005 to 2020; Zeng et al. 2018) using information from the WHIs (Gudex-Cross et al. 2021). We chose 30 days to maximize the spatial coverage of our analysis while minimizing spurious species-snow relationships in areas with erratic snow cover. This restricted the latitudinal extent of our study from 36°N to 49°N in the East and 31°N to 49°N in the West. We only included checklists with values for all three of the WHIs. After these pre-processing steps, we retained ~2.8 million checklists (~2 million checklists in the east and ~800 000 checklists in the West), covering mid to high latitudes and a range of elevations (Fig. 1D). We modeled all species that had ≥ 5000 detections within at least one region (East and West). We excluded species with marine or aquatic habitat requirements (orders: Anseriformes, Gaviiformes, Gruiformes, Pelecaniformes, Podicipediformes and Suliformes), because these species are strongly associated with bodies of water where snow cover can only occur when they are covered by ice, leaving us with 150 species across 10 orders.

Model covariates

We used five classes of data in our species distribution models: bird observations, snow cover dynamics, minimum

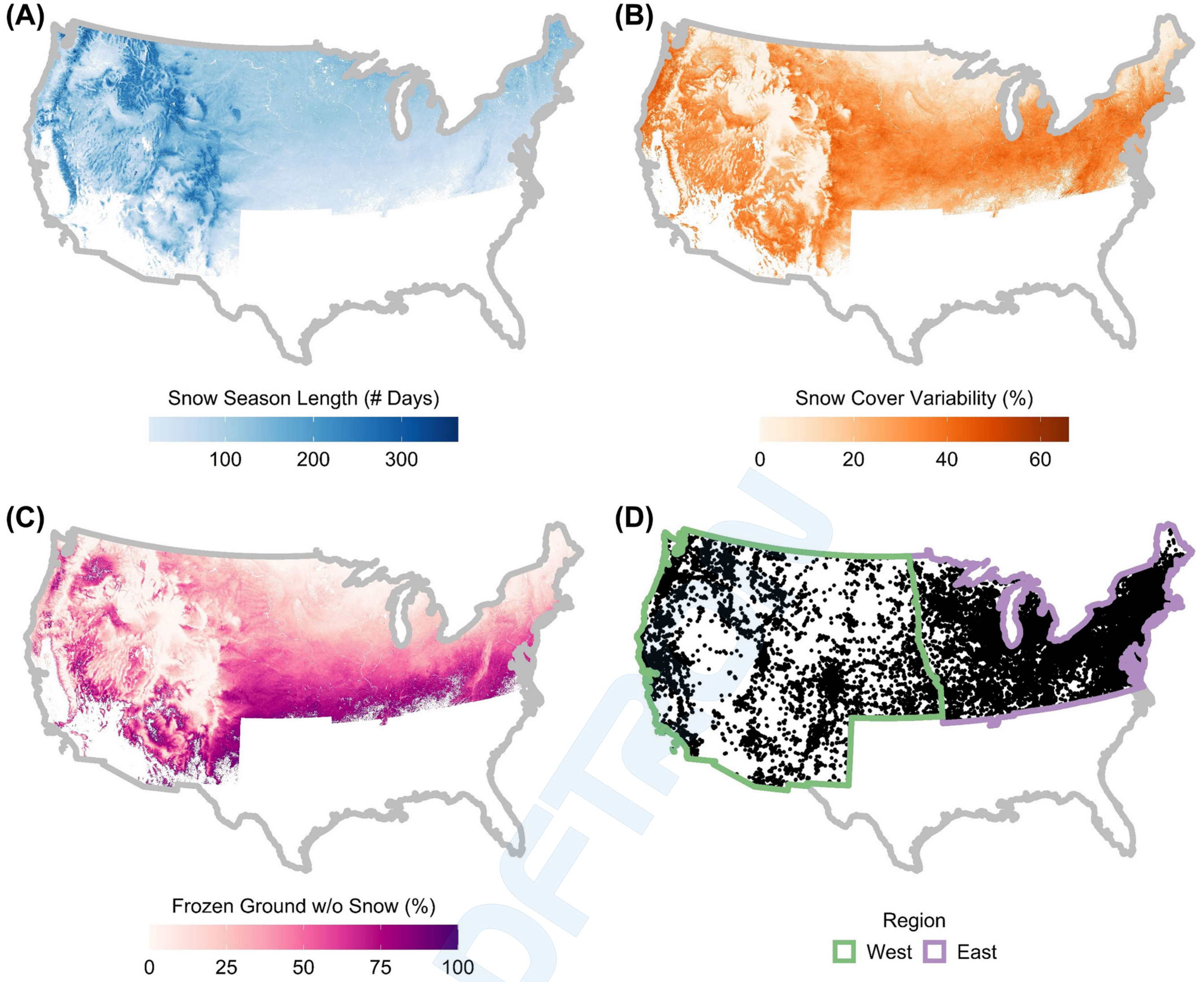

Figure 1. (A–C) The winter habitat indices and (D) spatial density of eBird checklists by region. (A) Snow season length, defined as the duration of snow-covered ground for a given snow season. Brighter colors indicate regions of long snow season length (e.g. mountainous regions). (B) Snow cover variability, defined as the percentage of snow cover change events (e.g. snow presence to absence) during the snow season derived from eight-day composite images. Brighter areas represent regions with higher snow cover variability. (C) Frozen ground without snow quantifies the percentage of days when snow is absent, but the ground is frozen. Brighter regions represent high proportion of such days. (A–C) Show the average winter habitat indices from 2005 to 2020. (D) Density of eBird checklists within each region (eastern USA, purple outline; western USA, green outline) used to model species distributions within the core of winter (Dec–Feb) from 2005 to 2020 from states within at least 30 days of snow cover. Species distributions were modeled separately based on checklists in the eastern or western regions of the USA.

temperature, landcover classes and survey-observer effort information. We averaged the spatial predictors at a 3-km resolution surrounding individual checklists, a resolution fine enough to capture important aspects of landscape composition and configuration across a large number of species using eBird data (Cohen et al. 2021, Fink et al. 2021).

We analyzed remotely sensed metrics of snow cover dynamics – the winter habitat indices (WHIs; Gudex-Cross et al. 2021) – to evaluate the importance of snow cover dynamics on the distributions of overwintering birds. The WHIs capture three distinct components of snow cover at a 500-m resolution: snow season length, snow cover variability and frozen ground without snow. Snow season length captures the length of the snow season, which relates to the duration of winter stress (e.g. length of energetic deficits) that species experience. Snow cover variability captures the intra-annual variability of snow cover using 8-day composite MODIS imagery. Snow cover variability relates to the frequency of favorable or hostile conditions and variability of thermal conditions that species experience. Finally, frozen ground without snow integrates temperature and snow presence/absence data to quantify the proportion of winter days during a snow season that the ground is frozen but lacks snow cover. Frozen ground without snow is a proxy for times when the subnivium is lacking (Pauli et al. 2013). Snow season length demonstrated the lowest interannual variation, followed by snow cover variability and, finally, frozen ground without snow. Frozen ground without snow likely exhibited the greatest interannual variation because it integrates information on both snow cover status and temperature. Both maximum and minimum values were represented for each WHI across all years included in our study. For each checklist, we extracted the WHIs for the corresponding winter. For more information on the interannual variation in the WHIs please see the Supporting information and refer to Gudex-Cross et al. (2021) for more details on the development and calculation of the WHIs.

We included minimum temperature as a separate predictor to account for the influence of winter temperatures on species occurrence and count. We extracted the 30-day average minimum temperature prior to each checklist from 1-km Daymet data (Thornton et al. 2020), following precedent studies (Cohen et al. 2020). Firstly, species respond to intra-annual variations in temperature extremes by modifying occurrence rates (e.g. via reduced/enhanced activity timing) and counts (e.g. via increased/decreased flocking; Cohen et al. 2020). By associating the average 30-day temperature with individual checklists we can account for species' intra-annual responses to temperature while characterizing average conditions at a given checklist (e.g. removing the influence of extreme days). Additionally, by capturing minimum temperature at this temporal resolution, we were able to reduce potential collinearity by partially decoupling monthly averages in temperature and seasonal snow cover dynamics (correlation between the WHIs and minimum temperature was moderate to low; snow season length versus minimum temperature $\rho = -0.54$; snow cover variability versus minimum temperature $\rho = 0.24$; frozen ground without snow versus minimum temperature $\rho = 0.33$).

We obtained annual landcover data from the MODIS Land Cover Type Dataset (MCD12Q1; https://lpdaac.usgs.gov/products/mcd12q1v006/), annual water cover from the MODIS water classification product (MOD44W) and intertidal wetland information from mudflat classified data (Murray et al. 2019). In place of the MODIS-based urban class, we used the 2016 NOAA VIIRS nighttime lights reflectance product (Cao and Bai 2014) to provide a detailed continuous index of the human-built environment along the urb-sub-exurban gradient. Lastly, we used the vector data on roads from the Global Roads Inventory Project (Meijer et al. 2018) to capture associations with road density (m per km^2). Similar to our climate data, we summarized cover classes and road densities within at a 3-km resolution around eBird checklist locations, to account for checklist locational errors (Cohen et al. 2020). We computed both the proportion of each class (PLAND) and edge density (ED) with the package landscape metrics in R (McGarigal et al. 2012, Hesselbarth et al. 2019, www.r-project.org). Only a few pairwise combinations of land cover edge density and land cover area (e.g. Cropland ED and Cropland PLAND) were highly collinear. This was not a concern because we only sought to describe response associations with the WHIs and collinearity does not adversely affect predictions from Random Forests.

To account for variation in detection rates, we included with each checklist several predictors describing how individual surveys were conducted. These include a) the duration spent searching for birds, b) the distance traveled during the search, c) the number of people in the search party and d) the checklist calibration index, a standardized measure of checklist-level variation in observer expertise (see Kelling et al. 2015 for development of the checklist calibration index and Johnston et al. 2018 for its use in distribution modelling). To account for variation in species-specific activity patterns and differences in time zones among observers, we included the time of day the survey was conducted coded as the difference from solar noon, the time of the day when the Sun is at the highest point in the sky at a given location. Additionally, we included 'Year' as a predictor to account for interannual variation in occurrence and counts not associated with variation in land cover, snow cover dynamics or temperature and to handle the exponential increase in eBird observations. For a complete list of all predictors included in the model refer to the Supporting information.

Species distribution modelling

We adopted a two-step hurdle model (similar to Johnston et al. 2015, Fink et al. 2020) to explicitly capture the effect of snow cover dynamics on both species' occurrences and counts. In the first step, we estimated the occurrence rate based on the binary detection/non-detection of a given species on surveys. Second, we estimated the median count of individuals of the species on surveys where the species was detected. Although our approach accounts for variation in detection rates, it does not directly estimate the absolute detection probability. For this reason, the estimates of occurrence should be considered as a relative measure of species occupancy. Similarly, the median count of species should be considered a measure of relative abundance, an index of the total count of the individuals of the species that are present in a given area and time.

We used Random Forest models for both steps of the hurdle model due to their ability to fit complex non-linear relationships, and strong predictive performance (Breiman 2001, Evans et al. 2011). Both steps were fit using all predictors. In the second step, we used quantile regression to estimate the median counts because of its robustness to the large counts that occur with winter flocking species (e.g. snow bunting).

For model assessment, we applied an 80/20 split for our training and testing datasets, respectively. Given spatiotemporal biases in eBird data, we implemented a spatiotemporal filter to reduce potential spatial and temporal autocorrelation. This filter randomly sampled a single checklist from each cell across a randomly placed 3-km × 3-km × 30-day grid. We selected these grid dimensions to match the spatiotemporal resolution of the predictors. Additionally, we implemented a case-weighting scheme conditional on the year that assigns higher probability of selecting checklists from years with less data to handle the exponential increase in eBird observations.

We examined a suite of predictive performance metrics to evaluate our models calculated using our withheld validation data. Specifically, we assessed the performance of our occurrence models using area under the curve (AUC), Kappa statistic (Cohen 1960), sensitivity and specificity and of our count models using Spearman rank correlation (SRC) and Poisson deviance explained (P-DE). We fit Random Forest models using the Ranger package (Wright and Ziegler 2017) and calculated PPMs using the PresenceAbsence package in R (Freeman and Moisen 2008). For more information on the predictive performance metrics used in model assessment see the Supporting information.

We quantified the importance of our environmental predictors using predictor importance scores, which determine the relative contribution of each predictor by evaluating differences in model performance between models with and without it (Breiman 2001). We then standardized predictor importance scores by computing the proportion of the total scores contributed by each environmental predictor ($PI_x/\sum PI_{Total}$). To identify the direction and magnitude of each variable, we calculated partial dependence plots. We estimated directionality (increasing/decreasing) by fitting a simple linear model and extracting the β coefficient using the purrr package (Henry and Wickham 2020).

Regional analyses

We subdivided our geographic extent into two broad regions – East and West – because these regions have strikingly different snow cover dynamics due to differences in topography and prevailing weather patterns (Fig. 1A–D; Gudex-Cross et al. 2021). We split the broad regions using the borders of Minnesota, Iowa and Missouri to capture the western boundary of the East and the Dakotas, Nebraska and Kansas to delineate the eastern boundary of the West. This divide broadly captures the 100th meridian, a biogeographic delineation in prevailing climate and biological conditions (Seager et al. 2018). Correspondingly, the east contained the largely mesic, primarily deciduous forested, low elevation ecoregions whereas the West captured the topographically complex, largely semi-arid/arid ecosystems (Fig. 1D). Further, we did this to account for: 1) non-stationarity in species distributional responses because species in the East likely respond to latitudinal gradients in snow cover dynamics whereas species in the West may respond to elevational gradients, 2) different bioclimatic drivers of winter conditions (latitude and lake effect snow in the East versus topography in the West) in each region, 3) different range in snow cover conditions species in each region may experience (e.g. up to ~364 days of snow in the west versus ~240 in the east) and 4) to avoid conflating environmental conditions species would not interact with due to dispersal barriers (e.g. Great Plains and Rocky Mountains; Machado et al. 2018). We modelled species that had more than 5000 occurrences in both regions separately for each region.

Functional trait analyses

To investigate how key functional traits mediate species responses to snow cover conditions, we used partial dependence plots to calculate a weighted mean for the average snow conditions that a species occurs in, conditional on occurrence probability and relative abundance. Conceptually, this is similar to the species thermal index (STI; Devictor et al. 2008), but for snow cover dynamics. For each species we calculated their optimal snow conditions across values of each winter habitat index, both for occurrence and relative abundance (see the Supporting information for a complete list of optimum WHI values for each species). We then parameterized OLS models to relate species-specific WHI values to the hand-wing index (Sheard et al. 2020), landscape diversity index (LDI; Zuckerberg et al. 2016), diet diversity (Shannon–Weiner index on food item proportions from Wilman et al. 2014), foraging strata diversity (Shannon–Weiner index on foraging strata proportions from Wilman et al. 2014) and body mass (Wilman et al. 2014). Body mass was log-transformed, and all functional traits were scaled prior to model fitting. Two sources of collinearity can arise in functional trait data: 1) correlations among species from phylogenetic relatedness and 2) different traits may be correlated with one another due to scaling (e.g. body mass and hand-wing index). Therefore, we inspected correlations between functional traits to verify functional traits were not colinear. Additionally, we fit phylogenetic generalized linear models (PGLMs) to account of phylogenetic correlations using a comprehensive avian phylogeny (Jetz et al. 2012). However, we found no evidence for phylogenetic correlation via Pagel's λ in fit PGLMs and therefore the results presented are from simple OLS models (Supporting information). We ran our trait-based models using the average snow conditions for each species from both occurrence and relative abundance partial dependences as the response variable. We found broad overlap between models fit using snow condition from both occurrence and count-based models. Therefore, we focus on results for the occurrence-based models only. For more information on the full functional trait model output and fitted PGLMs please see the Supporting information.

Results

Importance of snow cover for overwintering bird distributions

Snow cover dynamics were important in our models of both winter bird occurrence and counts. In our occurrence models, snow cover dynamics ranked within the top three predictors for 94% of species in east and 80% of species in the west. Similarly, snow cover dynamics ranked within the top three predictors of count-based models of > 79% of species in both regions (Fig. 2A). However, there were important differences between the eastern and western USA in terms of the relative importance of snow cover dynamics for bird distributions (Fig. 2A, B, 3 insets). More species in the East were associated with frozen ground without snow than in the West (Fig. 2B). Snow season length was more important for bird occurrences in the East versus the West (Fig. 2B, 3 insets). However, snow season length was equally important for bird counts in both regions. In contrast, in the west, snow cover variability was more important for both bird occurrence and counts (Fig. 2B, 3 insets). Snow season length and frozen ground without snow cover were also important predictors of occurrence and counts for many bird species in the west (Fig. 3).

When considering the mean relative importance scores of the combined WHIs for all bird species, the WHIs accounted for 19% (± 2.9%) and 17.5% (± 3.8%) of relative importance in our occurrence and count-based models, respectively, in the East, and 17.4% (± 3.5%) and 18.3% (± 4.3%) in the West, respectively. Considering the richness of our predictor space (62 environmental predictors) the inclusion of snow cover predictors was clearly important for many of the bird species in our study. If we assume equal importance of environmental predictors the cumulative expected importance of the three WHIs would be ~4.8%, but our results found that the WHIs contributed four times more predictive power than estimated by chance alone.

Species-specific responses to snow cover dynamics

Among species, both magnitude and direction of species responses to snow cover dynamics varied considerably (Fig. 3). Linear models fit to our partial dependence plots indicated that most species (80% in the East and 71% in the West) avoided regions with long snow seasons. Only a handful of species were clearly positively associated with long snow seasons in the east but many species avoided these conditions. The general pattern was similar in the West, but species association with long versus short snow seasons was more evenly distributed (Fig. 3 insets). Snow cover variability showed divergent patterns: a strong avoidance of highly variable winters in eastern species (80% of species) and a relatively even distribution (association and avoidance) of highly variable snow cover in western species (59% and 41% of species, respectively; Fig. 3 insets). Species from both regions responded uniformly to frozen ground without snow cover (Fig. 3 insets). In the East, 56% of species selected sites with higher frozen ground without snow, and in the West 50%. The magnitude and direction of species responses to each WHI reflected a gradient of responses from species with higher occurrence and counts in areas with long, stable snow seasons (e.g. mountain chickadee *Poecile gambeli*; Fig. 3) to those with higher occurrence and counts in areas with short, variable snow seasons (e.g. Carolina chickadee *Poecile carolinensis*; Fig. 3). Boreal and alpine species (e.g. pine grosbeak *Pinicola enucleator*) had strong positive associations with long snow seasons (Fig. 3). Likewise, many species that reside in open habitats during the winter were associated with high snow cover variability (e.g. Lapland longspur *Calcarius lapponicus*, Fig. 3).

Species relationships with snow cover dynamics separated species adapted to snowy winters from those that are not. For example, the WHIs captured the stark difference in the geographic transition between two sympatric chickadee species in the East (i.e. the black-capped chickadee *P. atricapillus* and Carolina chickadee *P. carolinensis*; Fig. 4). These two species differed greatly along the gradients of snow season length and frozen ground without snow, which captured a ~20% change

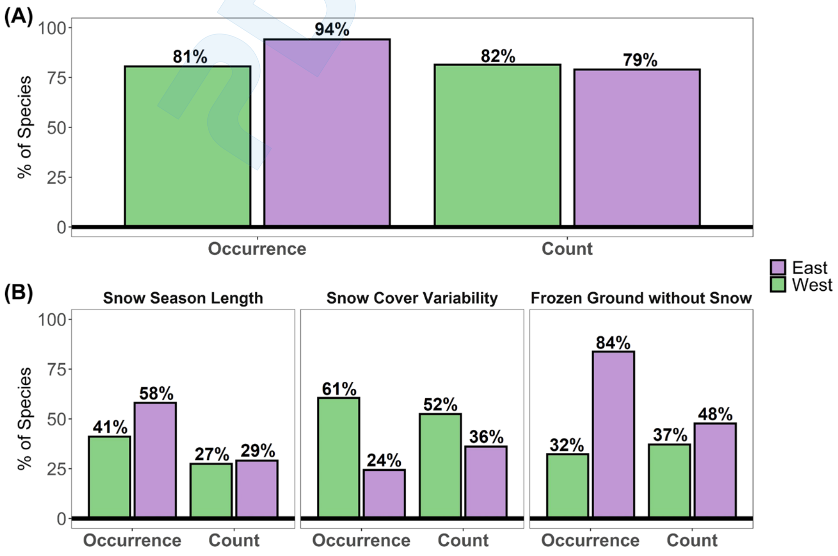

Figure 2. Snow cover dynamics are top predictors in winter bird occurrence and count-based models. Percent of species for which the WHIs were within the top three environmental predictors for patterns in occurrence and counts between the eastern (purple) and western (green) United States. (A) Percent of species for which any WHI was ranked with the top three environmental predictor. (B) Percent of species for which a given WHI was ranked within the top three environmental predictors.

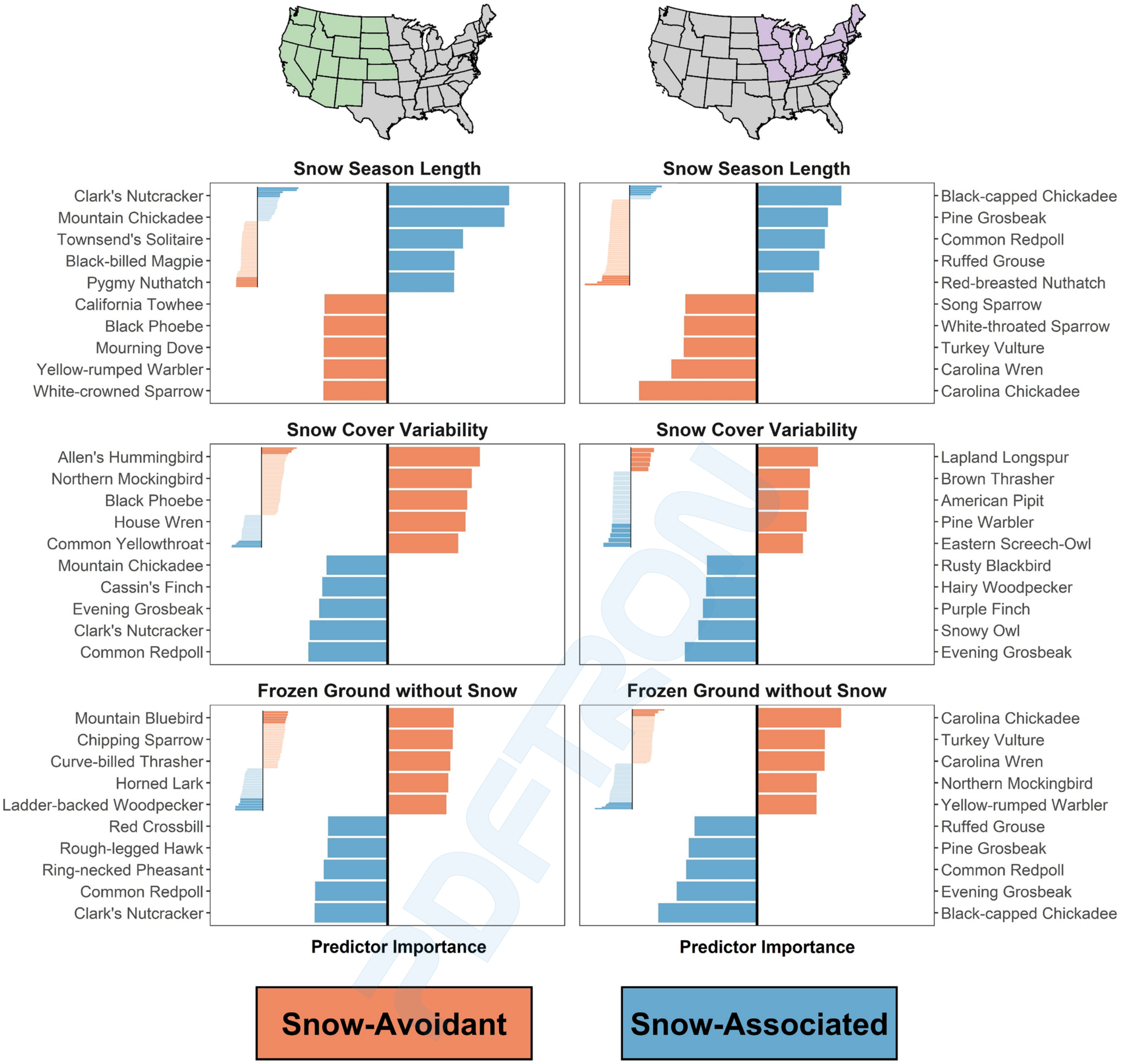

Figure 3. Species-specific snow response gradient. The length of each bars shows the relative importance for the specified WHI, species and region. The direction of the bars are shown according to the species response to the respective snow cover dynamics at the regional scale (left and right of the solid black line denote negative and positive relationship, respectively). Color of the bar indicates whether a species in snow-avoidant (orange) or snow-associated (blue). We selected the five species with the strongest positive and negative occurrence responses separately for each WHI and region East (right) and West (left). This was done to demonstrate exemplary responses while keeping the number of species tractable. Inset plots show the distributions of relative importances among all species where the corresponding WHI was a top-three spatial predictor for the region with bold colors to indicate the selected species.

in occurrence probability for both species (Fig. 4). In the West, we found similar species responses. Specifically, species strongly responded (positive and negative) to snow cover variability (Fig. 4). For example, black-billed magpie *P. hudsonia*, a resident species known to use snow cover for food-caching (Hendricks 2020), had higher probability of occurrence in low snow cover variability, whereas western meadowlark *S. neglecta*, a short-distance migrant, showed the opposite (Fig. 4).

Functional trait responses

Our analysis of functional traits identified several key traits that were most closely associated with the typical snow conditions each species inhabits (Table 1). Species inhabiting environments with longer snow seasons had higher dispersal capabilities, as captured by hand-wing index. In contrast, species inhabiting areas with more frozen ground without

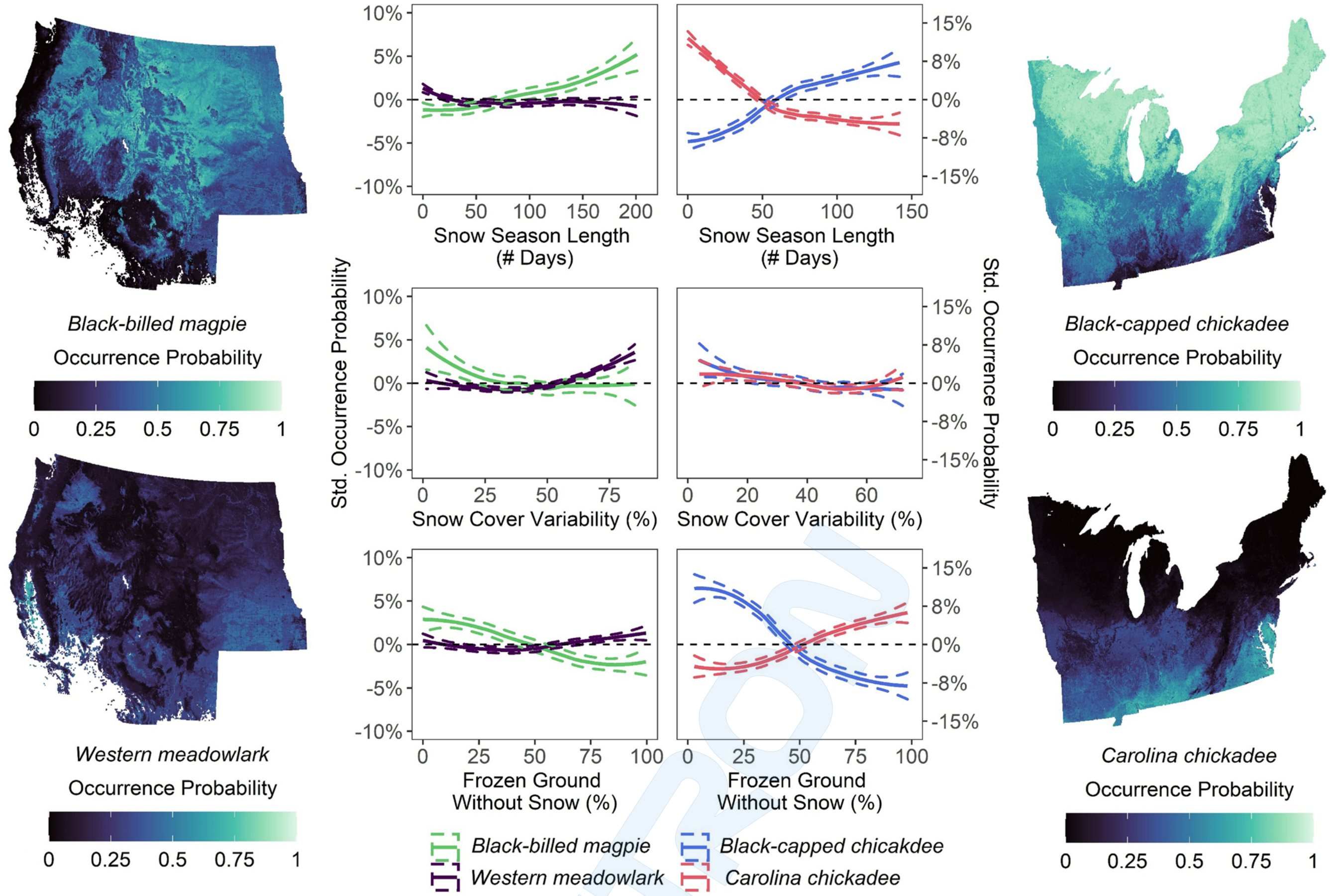

Figure 4. Species' winter occurrence distributions and associations with WHIs. The predicted winter distribution maps and partial dependence plots for all three WHIs are shown here for two eastern species: black-capped chickadee (*P. atricapillus*; top-right) and Carolina chickadee (*P. carolinensis*; bottom-right) and two western species: black-billed magpie (*P. hudsonia*; top-left) and western meadowlark (*S. neglecta*; bottom-left). The distribution maps show the predicted probability of occurrence of each species on a standardized survey performed by a skilled eBird participant on a 1-km transect for 1-h at the time of day when the given species is most detectable based on the land cover and average minimum temperatures for winter 2020. The partial dependence plots in the center show how each species' predicted occurrence varies with changes in a given WHI. To facilitate comparisons, each partial dependence function is centered to have zero mean. The dotted lines around the solid lines denote 95% confidence intervals calculated across resampling replicates. In the example of the two chickadee species the northern blackcapped chickadee shows a strong positive association with increased snow season lengths and reduced frequency of frozen ground without snow compared to opposite trends for the Carolina chickadee, a sympatric sister species.

snow had lower dispersal capability, but only for occurrence in the east. Habitat breath, measured via landscape diversity index, was related to the variability of snow cover and frozen ground without snow. Specifically, species in areas of high snow cover variability were typically habitat generalists, but only in the East. Conversely, species in areas with less frozen ground without snow had narrower habitat preferences. Dietary diversity was lower for species in areas with higher snow cover variability, but only in the West.

Predictive performance metrics

Our occurrence models had high predictive performance for all species (mean AUC = 0.92 ± 0.05) in both regions. Mean AUC was slightly higher for the western USA compared to the eastern USA. (0.93 versus 0.90, respectively). The mean Kappa statistic was 0.45 ± 0.13 with higher values in the west (0.49 ± 0.12) compared to the east (0.4 ± 0.12).

Likewise, our count-based model performed adequately and across the USA, mean P-DE was 0.47 (± 0.17), with higher value in the west (mean P-DE = 0.52 ± 0.16) relative the east (mean P-DE = 0.42 ± 0.16). Positive values for P-DE demonstrated our ability to accurately capture the spatial patterns of species counts. Mean SRC was positive and differed little between regions (mean SRC = 0.30 ± 0.15). Positive values of SRC confirmed that predicted counts were positively correlated with observed counts. For a complete list of the regional values of computed predictive performance metrics, please see the Supporting information.

Table 1. Results from ordinary least squares regression models. All results included in the table below were deemed important using a $\alpha = 0.05$. R^2 is the global model fit. Hand-wing index, landscape diversity index and dietary diversity are significant predictors of average snow conditions species inhabit based on occurrence PDs. Results are ordered by the snow cover dynamics of interest (SSL = snow season length, SCV = snow cover variability, FWOS = frozen ground without snow). For complete list of full model output, please refer to the Supporting information.

WHI	Trait	Region	β	p	R^2
SSL	Hand-wing index	East	2.36	0.005	0.25
SSL	Hand-wing index	West	1.28	0.032	0.07
SCV	Landscape diversity index	East	0.29	0.010	0.15
SCV	Landscape diversity index	West	0.30	0.048	0.15
SCV	Diet diversity	West	−0.37	0.013	0.15
FWOS	Hand-wing index	East	−1.34	0.012	0.16
FWOS	Landscape diversity index	West	−0.80	0.019	0.13

Discussion

Snow cover dynamics were strong predictors of broad-scale patterns of occurrence and counts for the majority of the 150 bird species we examined across the contiguous United States. We found consistent snow cover–species relationships in both the eastern and western USA, but species-specific responses to individual snow cover dynamics varied by region. The direction and magnitude of species responses to snow cover characteristics reflected a gradient where most species avoided long, persistent snow seasons, yet a suite of overwintering species favored regions of longer, stable snow cover. These snow-adapted species tended to be habitat specialists and dietary generalists with higher dispersal capabilities, but the strength of these responses varied with region and the snow cover dynamic examined. Our continental analysis affirms that snow cover, independent of land cover and temperature, serves as an important environmental filter of species occurrences and the count of individuals.

On average, the cumulative importance of snow cover exceeded the importance of minimum temperature, suggesting snow is a major and understudied, determinant of species distributions. Although minimum temperature was the strongest individual predictor of bird distributions, each individual aspect of snow cover (duration, variability and frozen ground without snow cover) remained highly influential, outranking all predictors besides temperature. This suggests that the duration, variability and harshness of the snow season, in conjunction with temperature, captures an important environmental filter (Root 1988, Zuckerberg et al. 2011). Together, these findings supported our first hypothesis that snow cover dynamics are important features describing patterns of winter bird occurrence and abundance. Our results support work that highlights the importance of snow cover dynamics determining species distributions and community composition across disparate taxonomic groups and levels of biological organization (Williams et al. 2015, Niittynen et al. 2018, Gudex-Cross et al. 2021, Slatyer et al. 2021). One potential explanation for the broad importance of snow cover is that snow affects foraging efficiency for many species. Species that lack adaptations for efficient foraging in snow-covered areas (e.g. ground foragers) may be limited by long, persistent snow seasons (Link and Sauer 2007), whereas species adaptations to snow (e.g. arboreal caching species) gain a competitive edge there (Osborne and Green 1992). Alternatively, snow cover dynamics may interact with habitats that species use throughout winter, such as forests and associated food resources (Boonstra et al. 2016, Hankin and Bisbing 2021), that are missed by coarse land cover classifications and temperature alone.

Species demonstrated a gradient of responses to snow cover dynamics. However, the skewness of this gradient depended on both the region and snow cover dynamic in question. In the eastern USA, species distributions were strongly influenced by frozen ground without snow and snow season length, whereas snow cover variability was most important in the West. In the East, snow cover dynamics vary latitudinally and in proximity to major water bodies (e.g. the Great Lakes), whereas in the West, they are more strongly influenced by topographic complexity (Gudex-Cross et al. 2021). This difference in gradients of snow cover may impart differences in migratory strategies employed by overwintering birds in each region. Birds in the West predominantly migrate along elevational gradients, whereas birds in the East migrate latitudinally (Boyle 2017). Snow cover variability is inversely related to elevation, where lower elevations have higher variability, generating an elevational gradient (Gudex-Cross et al. 2021). Therefore, many western species may use steep elevational clines to move and settle along this snow cover variability gradient, resulting in strong distributional ties to snow cover variability. Selection for areas of high snow cover variability may increase foraging opportunities relative to permanently snow laden areas (Summers and Underhill 1996), while reducing risk of extreme weather events (Boyle et al. 2010, Boyle 2017) and distance to breeding grounds for short distance migrants (Hsiung et al. 2018). Minimum temperature is also inversely related to elevation, and overwintering birds may select both milder temperatures and higher snow cover variability to reduce metabolic costs. In the East, the frequency of frozen ground without snow follows a strong latitudinal gradient that separates species adapted to long, snowy winter conditions (e.g. black-capped chickadee) from those that are not (e.g. Carolina chickadee). Frozen ground without snow may capture an important climatic interaction, the coupling of presence or absence of snow cover with severe cold, which may exert greater energetic demands on species lacking adaptations for cold, snowy environments (Rogers and Reed 2003, Stager et al. 2016, Zhu et al. 2019).

Though frozen ground without snow was the most universally important component of snow cover across species wintering in the east, snow season length was the most pronounced ecological filter limiting most species' occurrences in regions with long snow seasons. This suggests the regions with exceptionally long snow seasons likely impose the greatest energetic limitations on winter birds, reducing the number of species that can persist in these regions (Gudex-Cross et al. 2022). The dominance of species' avoidance to long snow seasons aligns well with recent work suggesting that winter length structures extratropical richness, particularly limiting resident and partial migratory bird richness in regions with long winter lengths (Gudex-Cross et al. 2022). Interestingly, this pattern was not as pronounced for species in the West, suggesting that 1) topographic complexity increases thermal heterogeneity reducing negative energetic burdens during long snow seasons for species in the West (Elsen et al. 2020, 2021) or 2) these mountainous regions have facilitated evolutionary dynamics (e.g. rapid evolution) necessary for species to adapt to long, persistent snow seasons (e.g. high-elevation species; Igea and Tanentzap 2021).

The strong link between snow cover dynamics and patterns in species occurrence rate and median count in our results is an indication of the selective pressures shaping species winter distributions. For example, we found that ruffed grouse *Bonasa umbellus* had higher probability of occurrence in areas with long, stable snow seasons, which may limit stress by supporting roosting in deep, low-density snowpack (Shipley et al. 2019, 2021). Grouse in areas with shallow snow cover have lower survival probabilities, providing a direct link between demography and snow cover (Shipley et al. 2020) that likely explain the correspondence between higher grouse occurrence rates and counts in regions of longer, persistent snow cover. Other species have indirect, yet important connections to variable snow cover conditions. For example, snowy owls *Bubo scandiacus* avoided highly variable snow conditions and sites with intermediated frozen ground without snow. Snowy owls may select for persistent snow cover that facilitates higher abundance of subnivium dependent prey resources or occupy snow-less coastal regions to hunt overwintering waterfowl (Robillard et al. 2018). Similarly, several species in the west, including Clark's nutcracker *Nucifraga columbiana*, mountain chickadee *Poecile gambeli* and Townsend solitaire *Myadestes townsendii*, were associated with long, persistent snow seasons. In montane environments, longer snow seasons foster vegetative communities that alpine birds use for winter food resources, resulting, for example, in increased regeneration of whitebark pine (*Pinus albicaulis*; Hankin and Bisbing 2021). Additionally, tolerating long snow seasons in alpine regions may enable these species to access to breeding sites earlier in summer, avoid costs associated with long-distance migration, and maintain year-round territories (Hsiung et al. 2018). However, most species avoided long, persistent snow seasons, most likely because long and persistent snow cover restricts foraging (Rogers and Smith 1993), subsequently limiting growth (Doherty and Grubb 2003) and lowering survival (Doherty and Grubb 2002).

Species' affinity towards certain snow characteristics were related to functional traits. Generally, overwintering birds with higher dispersal capacity (i.e. greater hand-wing index) and greater dietary diversity were more likely to occur in areas with longer, more persistent snow cover. Species with greater flight efficiency can search for resources over larger areas in harsh winter climates to fulfill their energy budgets while minimizing costs associated with locomotion. Globally, the bird hand-wing index of breeding bird distributions is greater in regions with high temperature seasonality and low precipitation seasonality (Sheard et al. 2020). That matches our results for overwintering species: areas with long snow seasons (high seasonality) support species with greater dispersal capabilities. Hand-wing index has been positively linked to migratory propensity (Phillips et al. 2018, Sheard et al. 2020) suggesting it may represent migratory tendency rather than dispersal. In the context of our study we would expect a negative relationship between hang-wing index and snow season length during winter because migrants should avoid long snow seasons in wintering grounds (Newton and Dale 1996, Somveille et al. 2015). However, we found a positive association between hang-wing index long snow seasons, suggesting this relationship is not driven by migratory behavior alone. One possible mechanism linking dispersal to snow cover is that low food availability and reduced territoriality in harsh winter environments has selected for species with enhanced flight efficiency to optimize foraging in areas with patchy, low resource availability (Jocque et al. 2010, Sheard et al. 2020).

We also found that birds in areas with low snow cover variability had higher dietary diversity and narrower habitat breadth. This partially supported our predictions of higher dietary diversity during persistent snow cover, but we expected this in conjunction with expanded habitat breadth. Persistent snow cover may require foraging plasticity by obscuring access to preferred food sources thereby necessitating the use of diverse resources (Sonerud 1986). For example, resident palearctic birds have greater foraging innovativeness in winter compared to non-winter seasons to avoid winter starvation (Sol et al. 2005). If higher dietary diversity is a proxy for innovativeness for acquiring food, then this may explain why dietary diversity was higher in areas with less variable snow cover. Alternatively, because our trophic traits did not include species winter-specific diets, low dietary breadth may arise via species tracking important dietary items by moving to areas of high snow cover variability in winter (Robillard et al. 2018). This may explain the importance of trophic diversity in the West as species can track resources altitudinally, but not in the eastern USA where birds must migrate south of the snowline. Interestingly, diet diversity and habitat breadth were associated with opposite responses to snow cover variability. This suggests that a potential tradeoff between dietary diversity and habitat breath. In variable snow conditions, species may not need to shift dietary preferences if food supplies are frequently available, and the use of diverse habitats nearby may facilitate resource tracking. However, it is worth noting that our functional trait models did not explain a large amount of variation in the snow conditions species inhabit. Species possess several unique adaptations that likely promote their survival in snow covered regions such as cryptic winter coloration (Mills et al. 2018), higher metabolic summit temperatures (Stager et al. 2016), snow roosting behaviors (Shipley et al. 2019) and caching (Sutton et al. 2016) that we were not able to incorporate into our functional trait analysis. Behavioral and physiological adaptations that species possess in harsh environments and the tighter coupling of body mass to temperature may partially explain why body mass did not emerge as a significant predictor in our functional trait models. Further, we did not detect an effect of foraging strata diversity. The reason for this may be that some foraging strata are more directly tied to snow cover dynamics than others (e.g. arboreal species will have an advantage over ground-dwelling species). For example, the abundance of ground foraging species abundance in farmlands is lower during deep snow years (Deshpande et al. 2022). Therefore, examining the dominant foraging strata rather than strata diversity for winter birds may yield further insights into species functional responses to snow cover. Our results point to the potential importance of habitat breadth, dietary diversity and dispersal capabilities, but warrant further investigation into other functional traits that may link individual fitness to snow cover dynamics.

Minimum temperature is one of the strongest determinants of range margins for overwintering bird species (Root 1988, Stager et al. 2016). However, we propose that snow cover dynamics are equally important and complement temperature metrics in explaining overwintering bird distributions. Importantly, we found only moderate to low correlation between the WHIs and minimum temperature and the consistent importance of snow cover dynamics in our models that included minimum temperature. Snow cover, land cover and temperature likely interact in complex ways to influence species distributions. The occurrence and count-based Random Forest models used here had enough flexibility to fit high order interactions. The ranger parameters, 'min.node.size' and 'max.depth', were set to default values leading to very deep trees given the large sample sizes used in this study. Thus, these models were capable of fitting interactions between snow cover, land cover and temperature. Therefore, models could express context dependent temperature and snow effects. For example, subnivium-dependent birds may be less negatively impacted by low temperatures in the presence of optimal snow conditions (Shipley et al. 2019) whereas other species may exceed expected thermal limits in the absence of snow and presence of supplemental feeding (Job and Bednekoff 2011). Our Random Forest model accounted for interactions during model fitting, but the nature of these interactions is often difficult to disentangle. Carefully designed field studies (Rogers and Reed 2003) and advancements in statistical techniques (e.g. iterative forests; Basu et al. 2018) will provide key insights into the interactions between winter climate and species distributions.

The importance of snow in structuring overwintering bird distributions hints to the importance of including snow cover projections when predicting species responses to climate change. For example, the northern range boundary of Carolina wrens *Thryothorus ludovicianus* has shifted northward, supposedly due to warming winters (Huang et al. 2016). However, population dynamics of Carolina wrens are driven by winter severity (no. of days with snow cover ≥ 4 cm; Link and Sauer 2007, Huang et al. 2016). This may explain why our measures of snow cover dynamics (i.e. snow season length) were among the strongest environmental variables predicting Carolina wren occurrence and count patterns. Accordingly, future changes in snow cover may be just as important as temperature for predicting the future vulnerability of species to winter climate change. Indeed, diminishing snow cover duration is predicted to drive loss in arctic plant habitat, richness and functional composition (Niittynen et al. 2018, 2020). Similarly, reductions in snow cover duration, changes in snow depth and increases in freeze-thaw dynamics can alter animal food webs through altered predator–prey dynamics, resource availability and phenology (Penczykowski et al. 2017). One possible outcome for bird communities is that future warming will increase variability and reduce the duration of seasonal snow cover alleviating a critical abiotic filter for many species. This may explain why both winter bird assemblages demonstrate faster rates of change than summer assemblages and why regional trends in temperature do not adequately capture change in composition (Lehikoinen et al. 2020). Explicitly linking trends in seasonal snow cover to shifts in bird distributions is a critical next step to assess the impacts of global climate change on winter bird communities and identify conservation targets, such as identifying climate refugia for high elevation species (Brambilla et al. 2022).

Snow cover dynamics appear to be an integral abiotic filter structuring patterns of occurrence and counts for overwintering birds with important consequences in a warming world increasingly characterized by longer, more intense snow droughts (Huning and AghaKouchak 2020). Warming temperatures are changing many aspects of winter snowpacks, including decreased snow cover duration (Notaro et al. 2011), increased rain-on-snow events (Bintanja and Andry 2017) and changes in the amount of snow (Zeng et al. 2018, Siirila-Woodburn et al. 2021). The increased variability of snow cover and overall shortening of the snow season will create opportunities for many species that are currently limited by persistent snow, but also constrain snow-specialist species (Sultaire et al. 2016, Zhu et al. 2019, Melin et al. 2020). Furthermore, as species respond differently to snow cover dynamics, future alterations in seasonal snow cover will likely generate novel bird communities. The strong macroecological responses to snow cover for overwintering birds highlight the need for more studies identifying the direct and indirect mechanisms mediating species-specific responses to snow cover.

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Data availability statement

eBird data used in this study is freely available online at https://ebird.org/science/download-ebird-data-products. Code generated to conduct the analyses is available upon request. Data on the Winter Habitat Indices (WHIs) is freely available online at http://silvis.forest.wisc.edu/data/whis/. Further details of data used in the analyses is located in the Supporting information.

Supporting information

The Supporting information associated with this article is available with the online version.

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