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Winter Habitat Indices (WHIs) for the contiguous US and their relationship with winter bird diversity

David Gudex-Cross[a,*], Spencer R. Keyser[b], Benjamin Zuckerberg[b], Daniel Fink[c], Likai Zhu[d], Jonathan N. Pauli[e], Volker C. Radeloff[a]

[a] SILVIS Lab, Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA
[b] Zuckerberg Lab, Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA
[c] Cornell Lab of Ornithology, 159 Sapsucker Woods Rd., Ithaca, NY 14850, USA
[d] Shandong Provincial Key Laboratory of Water and Soil Conservation and Environmental Protection, College of Resources and Environment, Linyi University, Linyi, Shandong 276000, China
[e] Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA

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ABSTRACT

The seasonal dynamics of snow cover strongly affect ecosystem processes and winter habitat, making them an important driver of terrestrial biodiversity patterns. Snow cover data from the Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua and Terra satellites can capture these dynamics over large spatiotemporal scales, allowing for the development of indices with specific application in ecological research and predicting biodiversity. Here, our primary objective was to derive winter habitat indices (WHIs) from MODIS that quantify snow season length, snow cover variability, and the prevalence of frozen ground without snow as a proxy for subnivium conditions. We calculated the WHIs for the full snow year (Aug-Jul) and winter months (Dec-Feb) across the contiguous US from 2003/04 to 2017/18 and validated them with ground-based data from 797 meteorological stations. To demonstrate the potential of the WHIs for biodiversity assessments, we modeled their relationships with winter bird species richness derived from eBird observations. The WHIs had clear spatial patterns reflecting both altitudinal and latitudinal gradients in snow cover. Snow season length was generally longer at higher latitudes and elevations, while snow cover variability and frozen ground without snow were highest across low elevations of the mid latitudes. Variability in the WHIs was largely driven by elevation in the West and by latitude in the East. Snow season length and frozen ground without snow were most accurately mapped, and had correlations with station data across all years of 0.91 and 0.85, respectively. Snow cover variability was accurately mapped for winter ($r = 0.79$), but not for the full snow year ($r = -0.21$). The model containing all three WHIs used to predict winter bird species richness patterns across the contiguous US was by far the best, demonstrating the individual value of each index. Regions with longer snow seasons generally supported fewer species. Species richness increased steadily up to moderate levels of snow cover variability and frozen ground without snow, after which it steeply declined. Our results show that the MODIS WHIs accurately characterized unique gradients of snow cover dynamics and provided important information on winter habitat conditions for birds, highlighting their potential for ecological research and conservation planning.

1. Introduction

Snow cover is an important component of winter habitat across the mid to high latitudes. The seasonal dynamics of snow influence the physical and chemical processes that govern ecosystem structure and function. For example, snow cover dynamics regulate climatic conditions in the atmosphere and soil, as well as the stability of the subnivium (i.e., the area between the snowpack and the ground). The low thermal conductivity of snow also provides insulation against harmful freezing temperatures for soil organisms, plants, and animals (Edwards et al., 2007; Kreyling, 2010; Pauli et al., 2013). In temperate and polar ecosystems characteristics of snow cover such as duration, depth, and melt strongly affect water and nutrient cycling, and consequently influence vegetation composition patterns (Brooks et al., 2011; Jones, 1999). For

* Corresponding author.
E-mail address: djgudexcross@wisc.edu (D. Gudex-Cross).

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many cold-adapted animals, survival and fitness are directly linked to characteristics of the snowpack, which can increase or decrease energetic costs associated with thermoregulation, locomotion, predator avoidance, and foraging (Williams et al., 2015; Zuckerberg and Pauli, 2018). Snow cover dynamics are thus a major driver of terrestrial biodiversity patterns through their effects on primary productivity, winter habitat conditions, and species interactions (Niittynen et al., 2018; Penczykowski et al., 2017; Spehn et al., 2002).

Climate change is rapidly altering seasonal snow cover dynamics, particularly in the Northern Hemisphere. Warming temperatures during winter and early spring are causing shifts in snow phenology, especially earlier melt (Chen et al., 2015; Najafi et al., 2016; Xia et al., 2014), decreasing snow cover extent and duration (Brown and Robinson, 2011; Choi et al., 2010; Pulliainen et al., 2020), and decreasing snow depth (Dyer and Mote, 2006; Kunkel et al., 2016). Concomitant with snow cover decreases, the frequency of frozen ground without snow is increasing (Zhang et al., 2011; Zhu et al., 2019), meaning both the availability and the quality of the subnivium is in decline (Pauli et al., 2013; Zuckerberg and Pauli, 2018). Understanding how changes in seasonal snow dynamics will affect terrestrial biodiversity patterns requires data that accurately characterize these dynamics at varying temporal scales and across large areas.

Snow cover data products derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellites are ideal for quantifying large-scale snow cover dynamics. These products are available globally (Hall et al., 2002; modis.gsfc.nasa.gov/data/dataprod/mod10.php), continue to undergo extensive validation (e.g., Coll and Li, 2018), and have been used to map dynamics like snow cover duration and extent around the world (e.g., Notarnicola, 2020; Salomonson and Appel, 2004; Zhu et al., 2017). While meteorological stations offer longer and more detailed snow records than MODIS, their discrete locations and uneven distribution means they cannot sufficiently characterize spatial variability. Gridded datasets from data assimilation systems that incorporate data from satellites, stations, and climate models, e.g., SNODAS (Barrett, 2003), provide modeled estimates of snow cover and variables not directly quantifiable from MODIS (e.g., depth). However, these estimates come with higher uncertainties than observations from imagery, especially in complex terrains (Sirén et al., 2018), and have coarse spatial resolutions ($\geq$ 1 km). There are challenges associated with MODIS (and other optical-multispectral satellite) observations as well such as data gaps caused by clouds – especially problematic in winter months and around snowfall events when cloud cover is high – and polar darkness, as well as spectral similarities between snow, ice, water, and highly reflective clouds (Dumont and Gascoin, 2016; Stillinger et al., 2019). Yet, one of the biggest limitations of the use of MODIS snow data in biodiversity assessments and conservation planning is a lack of indices that capture ecologically important aspects of the snow season at spatiotemporal resolutions suitable for management decisions (Boelman et al., 2019).

Over the past decade, substantial progress has been made in the use of MODIS to characterize aspects of the snow season at different spatiotemporal scales. The most commonly derived metrics include snow cover duration, spatial extent, and phenology (e.g., first and last snow dates), which tend to be highly accurate even when mapped over broad spatial extents and complex topography (Dietz et al., 2012). However, because of their importance in watershed hydrology, these characteristics have been quantified almost exclusively in mountainous regions (e.g., Dariane et al., 2017; Malmros et al., 2018; Notarnicola, 2020). Indices that describe subnivium conditions, which affect a wide range of plant and animal species (Zuckerberg and Pauli, 2018), have been developed globally using a combination of MODIS snow data and frozen ground status derived from microwave sensors (NASA MEaSUREs; Zhu et al., 2017). Microwave satellite data have the advantage of being unaffected by clouds, but the frozen ground products are currently produced at spatial resolutions that are too coarse for many conservation applications (6 km pixels for the Northern Hemisphere and 25 km globally). Additionally, assuming the coarse pixels of microwave satellite data have homogenous freeze/thaw status when fusing with MODIS snow cover data might introduce error in the resulting indices (Zhu et al., 2017). Thus, while snow cover dynamics have been mapped with MODIS in the past, there is a need for indices designed specifically for conservation assessments and biodiversity modeling.

Accordingly, we developed indices that capture three characteristics of the snow season that are both important for biodiversity and quantifiable from MODIS at appropriate spatial scales: season length, cover variability, and the prevalence of frozen ground without snow (i.e., lack of subnivium). Snow season length is similar to cover duration, capturing both snow cover extent (total area) and phenology (first/last snow dates). Within-year variability in snow cover, or the frequency with which an area switches from snow-covered to not and vice versa, quantifies freeze-thaw events and identifies ecologically critical transition zones from snow- to rain-dominated systems. This metric has many important applications, with some examples being monitoring potential winter freeze-thaw damage in forests (Charrier et al., 2017); informing species range boundary mapping (La Sorte and Jetz, 2012); and identifying areas of phenotypic mismatch (e.g., for species that undergo seasonal colour molt to winter white as camouflage against snow (Mills et al., 2018). We are not aware of prior remote sensing studies on within-season (or intra-annual) snow cover variability, but there are examples of inter-annual variations in snow cover duration and extent (e.g., Li et al., 2017; Malmros et al., 2018). Finally, frozen ground without snow (sensu Zhu et al., 2017) approximates the frequency with which organisms lack thermal refugia (i.e., the subnivium) and thus face functionally colder climates (Fitzpatrick et al., 2019; Zhu et al., 2019).

Here, our primary goal was to develop a set of winter habitat indices (WHIs) from MODIS (500 m) that quantify snow season length, cover variability, and frozen ground without snow and assess their accuracy using meteorological station data. To highlight the potential of the WHIs for biodiversity assessments, we examined relationships between each WHI and winter bird diversity. Our specific research objectives were to:

1) calculate the WHIs for the full snow year (Aug – Jul) and winter months only (Dec – Feb), from 2003/04 to 2017/18, and for each year, across the contiguous US;
2) validate the MODIS WHIs with WHIs derived from meteorological station data;
3) evaluate errors in the WHIs geographically and by sensor (i.e., Terra vs. Aqua vs. Terra-Aqua combined);
4) examine spatial patterns in the MODIS WHIs to identify major gradients of snow cover dynamics and regions with distinct winter climate conditions; and
5) quantify relationships between the MODIS WHIs and winter bird species richness.

We predicted that areas with longer snow seasons would support fewer bird species compared to those with shorter ones because longer snow seasons have harsher winter conditions and lower food availability for most species (Somveille et al., 2015; Somveille et al., 2019). Conversely, we predicted that regions with higher snow cover variability and more frequent frozen ground without snow would support more bird species taking advantage of the transition zone from rain- to snow-dominated ecosystems, where temperatures are warmer and food availability is generally higher (Somveille et al., 2019).

2. Methods

2.1. Preprocessing of the MODIS Normalized Difference Snow Index (NDSI) data

We analyzed daily MODIS NDSI data (Collection 6) from Terra (MOD10A1) and Aqua (MYD10A1) (Riggs et al., 2015) to calculate the WHIs in Google Earth Engine (Gorelick et al., 2017). MODIS NDSI data are highly accurate across all land cover types, but errors are greater in dense forests where snow cover on the ground is obscured, over large bodies of water, and at high elevations (Coll and Li, 2018; Zhu et al., 2017). Collection 6 products have improved accuracies over those from Collection 5 (Da Ronco et al., 2020; Masson et al., 2018; Zhang et al., 2019). We only analyzed pixels with the best snow cover retrievals (QA bit = 0) and applied an NDSI threshold ≥10 for snow presence, which characterize snow cover across large spatial scales and complex topographies more accurately than the commonly-used threshold of ≥40 (Coll and Li, 2018; Zhang et al., 2019). We initially applied a water mask derived from MODIS (MCD12Q1) to remove common misclassification errors between snow and water, yet noticeable errors persisted around inland lakes, so we applied a more aggressive Landsat-based mask from the European Commission's Joint Research Centre (Pekel et al., 2016). This step effectively removed water pixels misclassified as snow, but unfortunately also resulted in data losses in areas with abundant permanent and seasonal water (e.g., northern portions of the Great Lake states and Dakotas). We reordered the day of year (DOY) from August 1 (DOY 1) to July 31 (DOY 365) to analyze the full snow year and calculate snow season length. Finally, to focus our analyses on areas with biologically relevant snow seasons, we masked any pixel that had a median snow season length shorter than two weeks over the 14-year study period.

To minimize data gaps, we combined Terra and Aqua data using the daily observation with the highest NDSI value. We tested both mean and max value compositing of the daily observations and found that the results were very similar. We suggest this was because 1) the morning (Terra) and afternoon (Aqua) observations are taken on the same day, and 2) we had already applied a ≥ 10 NDSI threshold for snow presence to both datasets (as is done in the MODIS 8-day composite products). Thus, in the majority of cases, this step was simply retrieving whichever sensor had a cloud-free observation. Snow season length was derived from the Terra and Terra-Aqua combined data separately (see section 2.2). We did this because Aqua products usually have higher error rates due to a sensor malfunction necessitating the use of a different band in the NDSI calculation (Coll and Li, 2018; Zhang et al., 2019). For snow cover variability and frozen ground without snow, which require near-continuous observations of snow presence and absence, we created 8-day composites of snow cover (akin to a temporal filter) from the daily combined Terra-Aqua dataset. We used the same approach and compositing periods that are used to create the MODIS 8-day Maximum Snow Extent band in the MOD/MYD10A2 product (currently unavailable in Google Earth Engine). A pixel was considered snow-covered if any day in the 8-day period had snow. We chose an 8-day window, even though a longer window would have reduced data gaps even more (Coll and Li, 2018), to capture more transitional observations – i.e., when a pixel switches from snow-covered to not and vice versa.

Finally, because commission errors in the snow data are more prevalent during warmer months (namely July and August, Coll and Li, 2018), we constrained the dates when snow could theoretically occur. We did this by examining the historical first and last snow dates recorded in our ground-based validation dataset at different elevations (see section 2.3). Snow occurred year-round at high elevations (≥ 915 m or 3000 ft) so we did not constrain these areas by date. Mid elevations (458-914 m or 1500–2999 ft) were constrained to September 1st-July 31st and low elevations (≤ 457 m or 1499 ft) to October 1st-May 31st. We used the USGS's GMTED2010 dataset (Danielson and Gesch, 2011) to delineate elevation classes.

2.2. The MODIS WHIs

We calculated the three WHIs – snow season length, frozen ground without snow, and snow cover variability – for every year from 2003/04 to 2017/18, both for the full snow year (Aug – Jul) and for winter months only (Dec – Feb), except for snow season length, which is only meaningful for the full snow year. We included the full snow year calculations to characterize areas of the contiguous US that experience winter conditions outside the core winter months, namely high elevations. Because first and last snow detections are less affected by data gaps than the other WHIs, we derived snow season length from the daily data. We did this for both Terra and Terra-Aqua combined data to quantify the degree to which including Aqua increased coverages, but also introduced errors. Our calculation of snow season length used the following formula (note DOY 1 = Aug. 1):

$$\text{Snow season length (days)} = \text{DOY of last snow detection–DOY of first snow detection}$$

For the frozen ground without snow cover WHI (sensu Zhu et al., 2019), we combined daily minimum temperature from Daymet (1 km; Thornton et al., 2014) and the 8-day snow cover time-series so that each day's temperature estimate lined up with its associated 8-day composite snow cover estimate. We considered the ground as frozen when the daily minimum temperature was below −4 °C (∼25 °F, Riseborough (2001)). Because we were interested in quantifying the proportion of the 'frozen season' when there is no snow, we only analyzed 'frozen' pixels (with or without snow) in our calculation:

$$\text{Frozen ground without snow }(\%) = \left(\frac{\sum \text{Frozen days without snow}}{\sum \text{Total frozen days}}\right)*100$$

Our calculation derives a proportion rather than the absolute number of days of frozen ground without snow as in Zhu et al., 2019. We chose to calculate the proportion to put the absolute numbers into better ecological context. For example, five frozen days without snow in lower latitudes with short snow seasons is quite different from the same number of days in higher latitudes with longer snow seasons.

To derive snow cover variability from the 8-day composite snow presence/absence data, we first calculated the absolute backward-difference between each observation in the time-series (i.e., $|t_{365} - t_{364}|\ldots|t_2 - t_1|$) to detect 'change events' (new snow or snowmelt = 1) and no change (= 0). Change and no change events separated by a missing observation were not included in the calculation. We then calculated snow cover variability as the total number of change events divided by the total number of valid observations:

$$\text{Snow cover variability }(\%) = \left(\frac{\sum \text{Change events}}{\sum \text{Change\&no change events}}\right)*100$$

Finally, we examined the relatedness of the WHIs using Pearson's correlations. We then created a multiband composite image with the final WHIs used in our winter bird biodiversity analyses (see section 2.4) to identify regions/areas with unique snow cover dynamics across the contiguous US.

2.3. Accuracy assessment of the WHIs

To validate the accuracy of the MODIS WHIs, we obtained ground-based snow cover data from Global Historical Climatology Network (GHCN; Menne et al., 2012) and SNOwpack TELemetry Network (SNOTEL; Schaefer and Paetzold, 2001) meteorological stations and

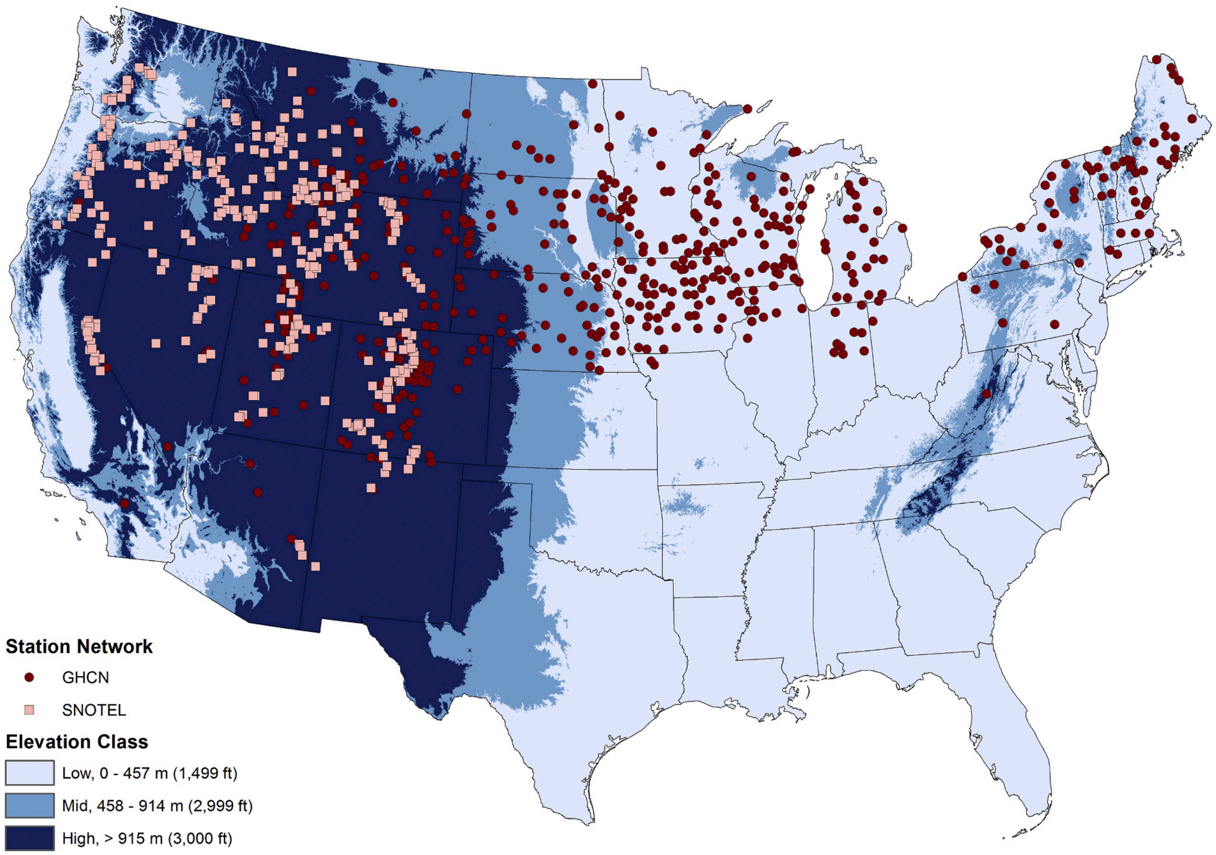

Fig. 1. The spatial distribution of 797 meteorological stations from the Global Historical Climatology Network (GHCN) and SNOwpack TELemetry (SNOTEL) Network used to validate the MODIS WHIs, across elevation classes. The final station list included stations that a) had a continuous snow data record from 2003/04–2017/18, b) had MODIS WHI observations for each year, and c) had a median snow season length of at least two weeks per year across the 14-year period.

calculated the WHIs from these data. We only included stations with continuous data from 2003/04 to 2017/18 (i.e., 797 stations, Fig. 1). However, our validation dataset was biased toward high elevations (~60% of stations) because SNOTEL is designed for hydrological monitoring in mountainous areas. We used a $\geq$ 3 cm snow depth (Snow Water Equivalent; SWE) threshold for snow presence, which is the lowest presence value reported in the SNOTEL data.

We evaluated the accuracy of each MODIS-based WHI with scatterplots and Pearson's correlations with the station-based WHIs for both the full snow year and winter months. Here, it is important to note that the station-based WHIs pertain to a specific location on the ground, whereas the MODIS WHIs are for a 500 m pixel. Correlations were calculated for the means across the entire study period (2003/04–2017/18) and for each individual year, as well as for each elevation class. Finally, as a sensitivity analysis for the frozen ground without snow and snow cover variability WHIs, we quantified the information lost when downgrading daily station snow cover data to 8-day snow composites.

2.4. Relationships between the WHIs and winter bird diversity

We developed models to predict winter bird diversity based on three WHIs: snow season length (Terra) and the core winter frozen ground without snow and snow cover variability indices. Because we were interested in evaluating how winter habitat conditions captured by the WHIs relate to broad-scale winter biodiversity patterns, we modeled total bird species richness (highest number of species observed) during the core winter months (Dec – Feb) as our response variable (hereafter 'winter bird species richness'). We calculated winter bird species richness from eBird data (Sullivan et al., 2009), which were available from the winter of 2003 on throughout the US (Fig. S1). Raw eBird data consist of species counts ('checklists') collected in the field by citizen scientists. The raw data is processed with automated checks on data quality based on the date a given species was observed and the observer's geographic location, then vetted for accuracy by a regional expert (Sullivan et al., 2014). However, eBird data are unevenly distributed in space and time, with higher survey effort in and around areas of human activity and in recent years (the number of checklists has been increasing geometrically concomitant with smart phone and mobile app usage) (Cohen et al., 2020). To address these issues, we followed the best practices for maximizing eBird data quality detailed in Johnston et al., 2019 and Cohen et al., 2020. We only analyzed "complete checklists" where the observer recorded every species detected and identified, which allowed us to infer absences of undetected species and thus produce more accurate measures of species richness. To account for imprecise checklist locations, we summarized the mean WHI values within 2.5 km of a given checklist location. Finally, to account for the increase in the number of checklists over time and mitigate the uneven spatial distribution of eBird data, we created a uniform grid of 25 km cells across the contiguous US and extracted the checklist, along with its associated WHI values, with the highest winter bird species richness across all years (2003/04–2017/18) for each grid cell. We excluded areas that did not experience an appreciable snow season (e.g., the southernmost states) by only sampling from grid cells that had valid data for all three WHIs, resulting in a total of 7844 checklists (Fig. S1).

We evaluated relationships between winter bird species richness and the WHIs using generalized additive models (GAMs), which account for nonlinear relationships. To control for differences in survey effort across time and space detailed above, we also included the number of checklists within each grid cell as a covariate in our models (per Johnston et al., 2019). We assumed the maximum observed species richness in each grid cell would follow a negative binomial distribution with a log-link mean function that varied as additive combinations of smooth functions of the three WHIs and the number of checklists. To avoid overfitting the GAM, we restricted the flexibility of each smooth to have 5 knots (Wood, 2017). We constructed models for all combinations of the covariates and chose the best model based on the sample-size adjusted Akaike's Information Criterion (AIC_c). We used AIC_c instead of the non-adjusted AIC for model selection since their values converge at large sample sizes, and thus Burnham and Anderson (2002) recommend the use of AIC_c as standard practice. Additionally, we assessed model fit using the total deviance explained. Finally, we used partial effect plots to quantify and visualize the effect of each individual WHI, after accounting for the effects of survey effort and the other two WHIs in the model.

3. Results

3.1. The MODIS WHIs

3.1.1. Snow season length

The snow season length WHI captured prominent altitudinal and latitudinal gradients throughout the contiguous US (Fig. 2). The longest snow seasons (~8–11 months) occurred in the high elevations of the Sierra Nevada, Cascade, and Rocky Mountain ranges in the western US. Other notable gradients in the West included the short seasons (< 2 months) at lower elevations in the Four Corners (intersection of Arizona, New Mexico, Colorado, and Utah), Great Basin, and Pacific Northwest regions, but more moderate lengths (~4–7 months) with increasing elevation. Spatially, one of the most rapid changes in snow season length occurred from the border of the Front Range of the Rocky Mountains (longer) to the Central Plains region (shorter) in eastern Colorado (Fig. 2a). Most regions east of the Rocky Mountains were dominated by a distinct latitudinal gradient in snow season length, with very short seasons (< 1 month) in the southern states, slightly longer seasons (2–3 months) at mid-latitudes from the Central Plains to the Eastern Seaboard, and moderate length seasons (3–4 months) in the Upper Midwest and lower elevation areas of New England. The longest snow seasons in the eastern US occurred in the mountain ranges of New England (~5–7 months; Fig. 2b), followed by northern parts of the Great Lakes states and Maine (4–5 months).

The mean snow season length across all years agreed well with the station data, with estimates from Terra ($r = 0.91$) outperforming those from Terra-Aqua combined ($r = 0.87$) (Fig. 3). Terra snow season length had a mean difference of −20 days compared to the station data, with 72% of the observations falling within ±40 days. The mean differences for the three elevation classes showed consistent underestimations (low = −34 days, mid = − 46 days, and high = −10 days) and almost all of the overestimations occurred at high elevations in the western US

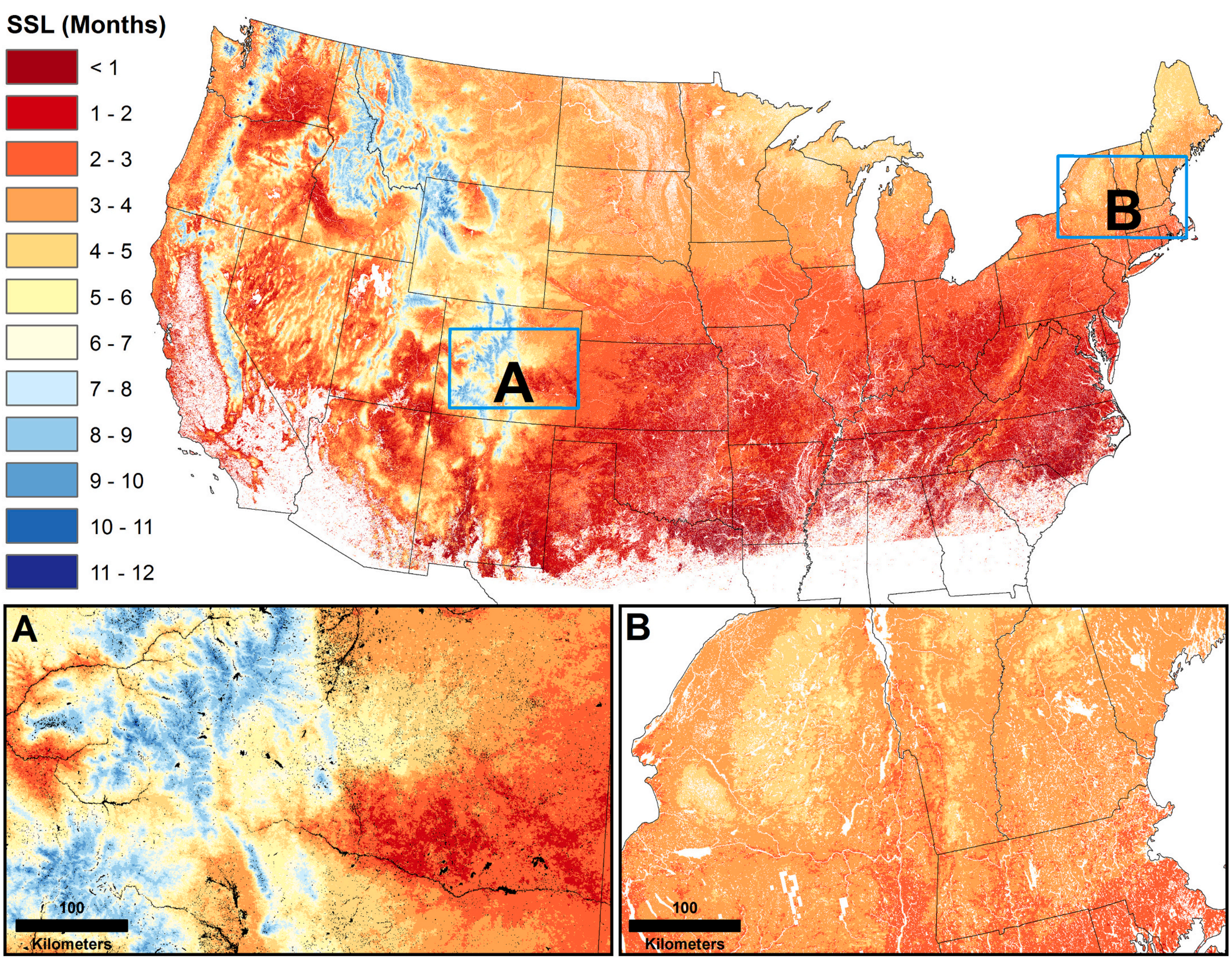

Fig. 2. Mean snow season length (SSL, months) estimated from daily MODIS Terra data from 2003/04–2017/18. The areas highlighted in (**A**) the Front Range of the Rocky Mountains and Central Plains and (**B**) New England show clear altitudinal and latitudinal gradients.

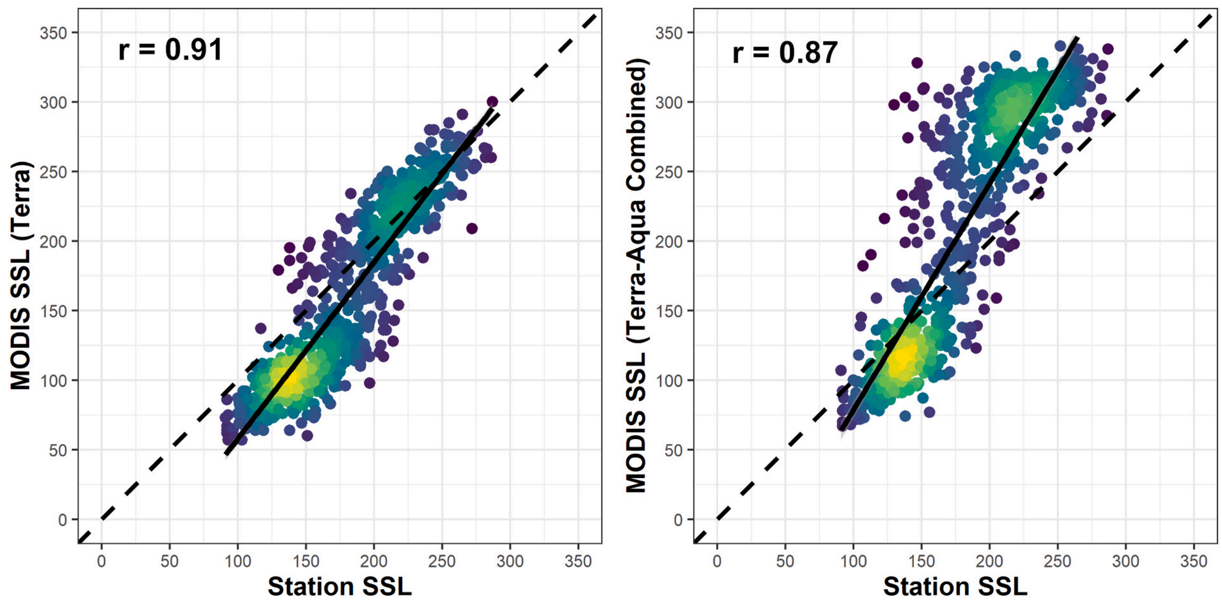

Fig. 3. The accuracy of mean snow season length (SSL, days) estimates, derived from daily Terra (left) and Terra-Aqua combined (right) data, across the study period (2003/04–2017/18) based on meteorological stations ($N = 797$). The bimodal distribution of the points is a reflection of our validation dataset: most stations were located at high or low elevations (long and short snow seasons, respectively) and few at mid elevations with moderate-length snow seasons. Points are colored by density from low (purple) to high (yellow). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Fig. S3). Conversely, the Terra-Aqua combined index had a mean difference of +28 days and over 40% of the observations overestimated snow season length by >50 days. Again, these overestimations occurred almost exclusively at high elevations in the West (mean difference with the station data = +58 days; Fig. S3). Terra snow season lengths had higher correlations than Terra-Aqua combined at low elevations ($r = 0.82$ vs. 0.65) and high elevations ($r = 0.67$ vs. 0.60), while both performed similarly at mid elevations ($r = 0.63$ vs. 0.64). Given their higher accuracies, we focused the rest of our analyses on the Terra-based estimates, which also had high annual accuracies ranging from $r = 0.70$–0.83, with only one year having moderate-level accuracy ($r = 0.59$ for 2014–2015; Table S1).

3.1.2. Frozen ground without snow

The frozen ground without snow indices for winter and the full snow year had virtually identical spatial patterns across the contiguous US, but estimates were higher in winter (Fig. 4). Areas with the highest frozen ground without snow percentages in the contiguous US occurred in the Central Plains region immediately east of the Front Range of the Rocky Mountains, with half or more of all winter observations being frozen without snow (Fig. 4a, c). Winter frozen ground without snow was also high in parts of the Colorado Plateau (Arizona and New Mexico) and the western Great Basin region (immediately east of the Sierra Nevada Mountains). Both indices had a strong latitudinal gradient east of the Rocky Mountains, with higher frozen ground without snow in the middle latitudes decreasing northward. Areas with the lowest frozen ground without snow percentage were those where frozen ground is snow-covered throughout much of the winter, including high elevation mountain ranges and northern parts of the Great Lakes states and New England, and those where frozen ground occurs less frequently, such as the low elevations of the Great Basin and areas with a strong lake effect (e.g., the Lake Champlain valley; Fig. 4b, d).

The mean frozen ground without snow estimates across all years were highly accurate for both the full snow year ($r = 0.85$) and winter ($r = 0.83$) according to the station data. Both indices generally underestimated the number of days of frozen ground without snow, but overall patterns were similar to the station-based data (Fig. 5). The winter estimates were often closer to the 'true' station-based value than those for the full season, though, the latter tended to underestimate frozen ground without snow prevalence in parts of the Midwest and the Front Range of the Rocky Mountains (Fig. S4). Notably, the winter estimates were highly correlated with the station-based full snow year frozen ground without snow estimates ($r = 0.84$), even more so than the full season correlation at low ($r = 0.61$ vs. 0.60) and mid elevations ($r = 0.81$ vs. 0.79). The full snow year correlation was only slightly stronger at high elevations ($r = 0.89$ vs. 0.88). Finally, both the winter and full season indices exhibited moderate to high annual accuracies ranging from $r = 0.62$–0.81 (Table S1).

3.1.3. Snow cover variability

We present the accuracy assessment results before describing spatial patterns in snow cover variability, because while the mean snow cover variability estimates across all years had good agreement with the station-based data for winter ($r = 0.79$), they did not for the full snow year ($r = -0.21$), making the full snow year maps unreliable. Both indices tended to overestimate variability by approximately 10–20% (Fig. 6). However, the full snow year index had much higher overestimations at high elevations in the West with low snow cover variability (0–5%) (Fig. S5). The full snow year data also had more uniform overestimations across all sites (i.e., with no discernible pattern mirroring the station data as in the winter index) (Fig. 6). Interestingly, the problematic sites featuring low variability were all the high elevation SNOTEL stations, resulting in the bimodal distribution of points in Fig. 6. Accordingly, the full snow year index performed very poorly at mid ($r = -0.03$) and high elevations ($r = 0.01$), and somewhat better at low elevations ($r = 0.18$). The exact opposite was true for the winter index, which performed best at high elevations ($r = 0.82$), followed by mid ($r = 0.45$) and low elevations ($r = 0.39$). The lower correlations for the latter two were mainly due to overestimations of variability in parts of the Midwest and the Front Range of the Rocky Mountains (Fig. S5). The winter index was also well-correlated with the station-based full snow year variability ($r = 0.77$). Annual correlations for the winter index were slightly lower than the correlation for the mean of all years, ranging from $r = 0.47$–0.67 (Table S1).

The winter snow cover variability patterns showed the highest values in the middle latitudes from the Central Plains to the Eastern Seaboard

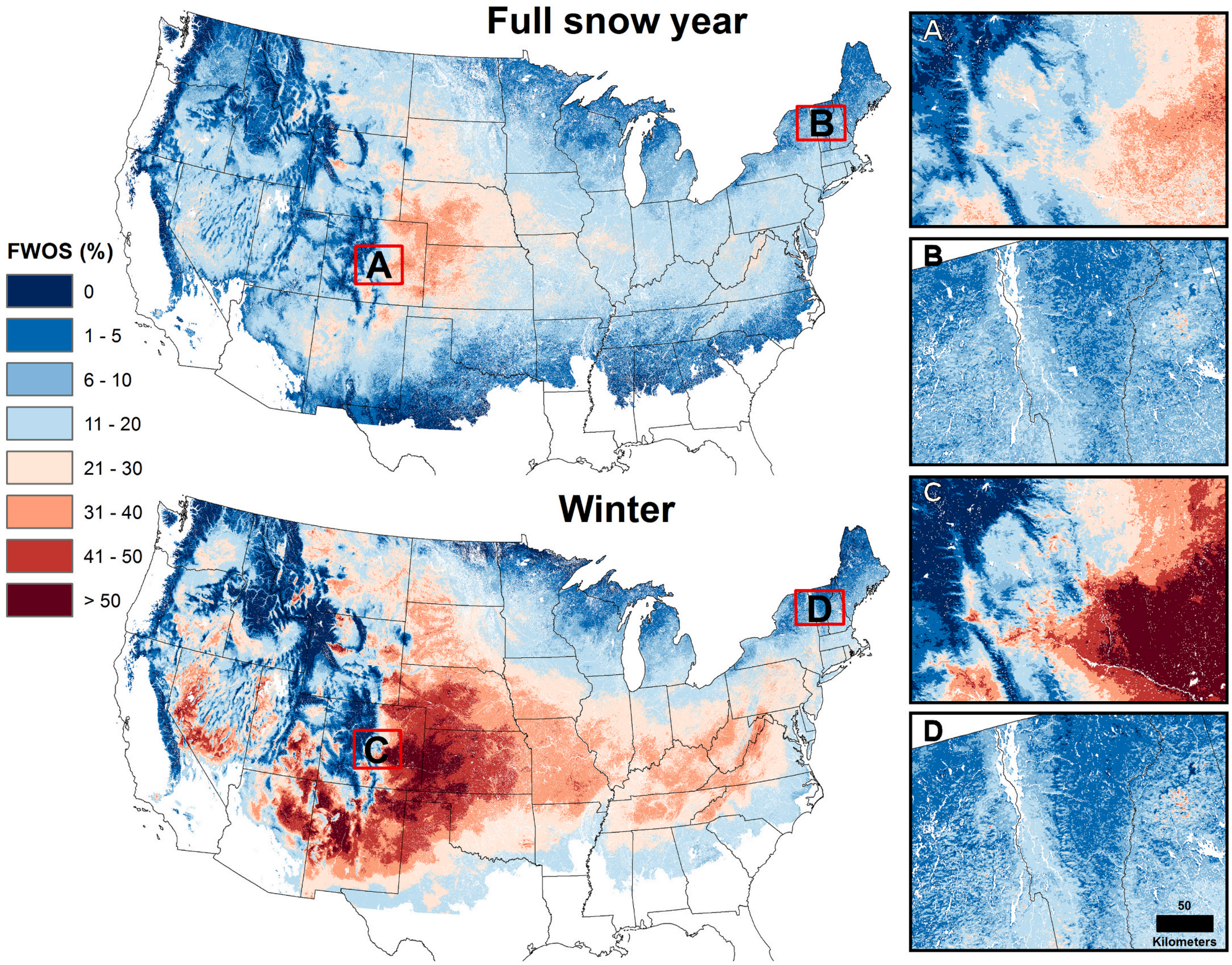

Fig. 4. Mean frozen ground without snow (FWOS, %) for the full snow season (top) and winter only (bottom) from 2003/04–2017/18. The right-hand panels highlight FWOS gradients across the Front Range of the Rocky Mountains and Central Plains (**A, C**) and New England (**B, D**). Areas where frozen ground was not recorded were removed to emphasize those where FWOS equaled zero (i.e., where the ground was always frozen and snow-covered).

(Fig. 7), where a quarter or more of all the observations during winter were 'change events' (i.e., new snow or snowmelt). Winter variability estimates were lowest (~0–5%) in the Rocky Mountains, the northern parts of the Great Lake states and Maine, and the mountain ranges of New England. Again, a distinct latitudinal gradient occurred east of the Rocky Mountains, with higher winter variability in the middle latitudes decreasing to the north and south, as well as a stark transitional gradient from the Rocky Mountains (virtually no variability) to the Central Plains (high variability) (Fig. 7a, c). Contrasting the snow cover variability indices for the winter and full season revealed overestimations in the latter were greatest in areas with frequent cloud cover: mountain ranges and northern parts of the Great Lake states and New England (Fig. 7b, d).

3.1.4. Sensitivity of the WHIs: daily versus 8-day composite snow cover data

When we converted each station's continuous snow cover record from daily to 8-day composites in order to quantify how much the composited MODIS data affected our results, the frozen ground without snow estimates changed little for both the full snow year ($r = 0.94$) and winter ($r = 0.93$), albeit with systematic underestimations (46 vs. 365 observations) (Fig. 8). However, snow cover variability was greatly affected by this change for both the full season ($r = 0.80$) and winter ($r = 0.76$). Virtually all of the full snow year percentages >10% (ranging from approximately 10–30%) estimated from the daily data fell between 4 and 8% in the 8-day, with higher daily-derived variability estimates not always resulting in higher 8-day estimates. The same was true for winter variability, where daily-derived variability estimates ranging from approximately 5–30% consistently fell between 2 and 6%. Interestingly, the correlation between the MODIS-based (8-day) and station-based (daily) winter variability index was higher (0.79) than the daily versus 8-day relationship of the station data (0.76).

3.1.5. Composite patterns in the WHIs

Correlations between the MODIS WHIs showed that while they were closely related, each one captured unique aspects of snow cover dynamics across the contiguous US. Winter frozen ground without snow and snow cover variability had the strongest correlation ($r = 0.87$), followed by season length and winter variability ($r = -0.78$), then season length and winter frozen ground without snow ($r = -0.72$). Combining the WHIs in a composite image highlighted distinct zones of different snow cover dynamic dominated by either one WHI or a combination of them (Fig. 9). Notable examples include the high elevations of the Cascades and northern Rocky Mountains which are dominated by long snow seasons with near-continuous snow cover, and to a lesser

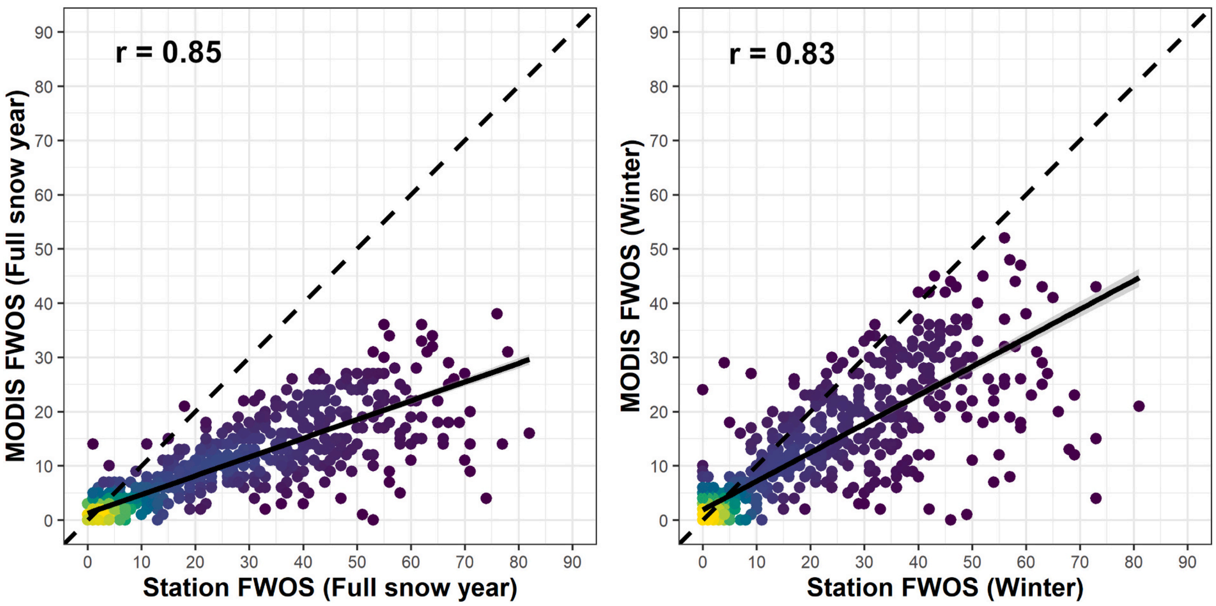

Fig. 5. The accuracy of mean frozen ground without snow (FWOS, %) estimates across the study period (2003/04–2017/18) based on meteorological stations (N = 797). Points are colored by density from low (purple) to high (yellow). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

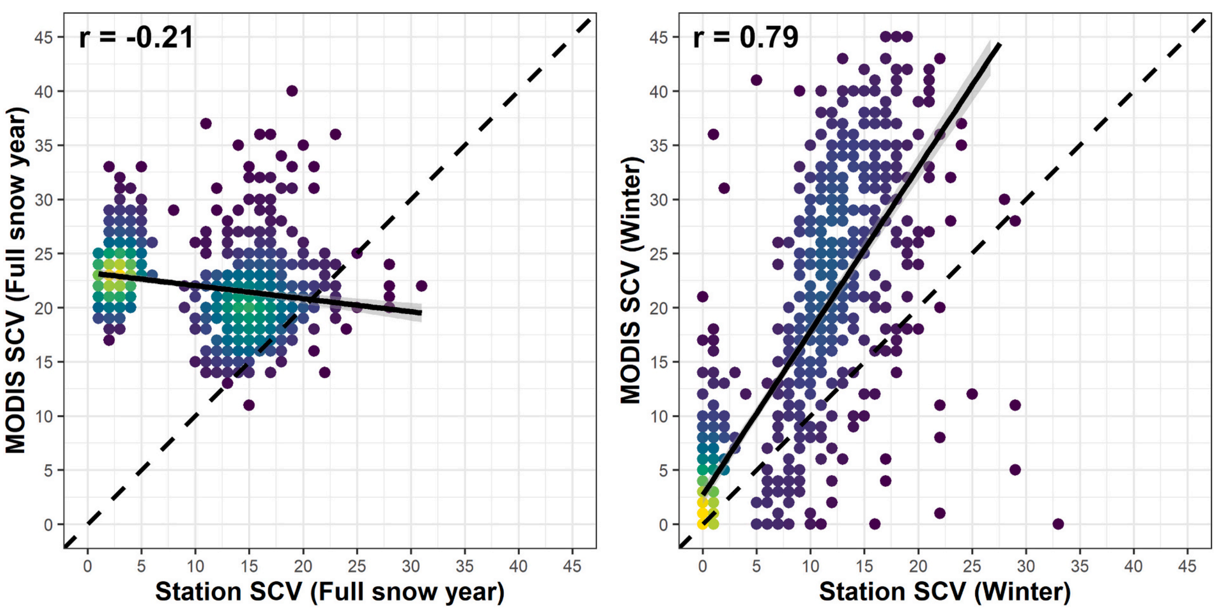

Fig. 6. The accuracy of mean snow cover variability (SCV, %) estimates across the study period (2003/04–2017/18) based on meteorological stations (N = 797). The grouping of points on the left-hand side of the graph (at low station-based SCV values) are all from high elevation SNOTEL stations, while those on the right-hand side are nearly all from low elevation GHCN stations. Points are colored by density from low (purple) to high (yellow). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

degree, the same is true for the mountains of New England and northern parts of the Great Lakes states and Maine. Snow seasons in the Central Plains east of the Rocky Mountains were some of the harshest, with high snow cover variability and frequent frozen ground without snow. This pattern graded into areas in the Midwest where frozen ground without snow was less frequent, but snow cover variability and season length were higher. Correlations between all the WHIs, both MODIS- and station-based, are available in Table S2.

3.2. *The WHIs and winter bird diversity*

Snow season length, winter snow cover variability, and winter frozen ground without snow prevalence were strong predictors of winter bird species richness across the contiguous US. Model comparisons consistently ranked the model that included all three WHIs as the best, and substantially so, with the next best model having a $\Delta AIC_c = 129.5$ (Table S3). The full model explained 34% of the total deviance, and of this 34%, the WHIs accounted for approximately 60% (20% of the total deviance).

Partial effects plots showed non-linear relationships between species

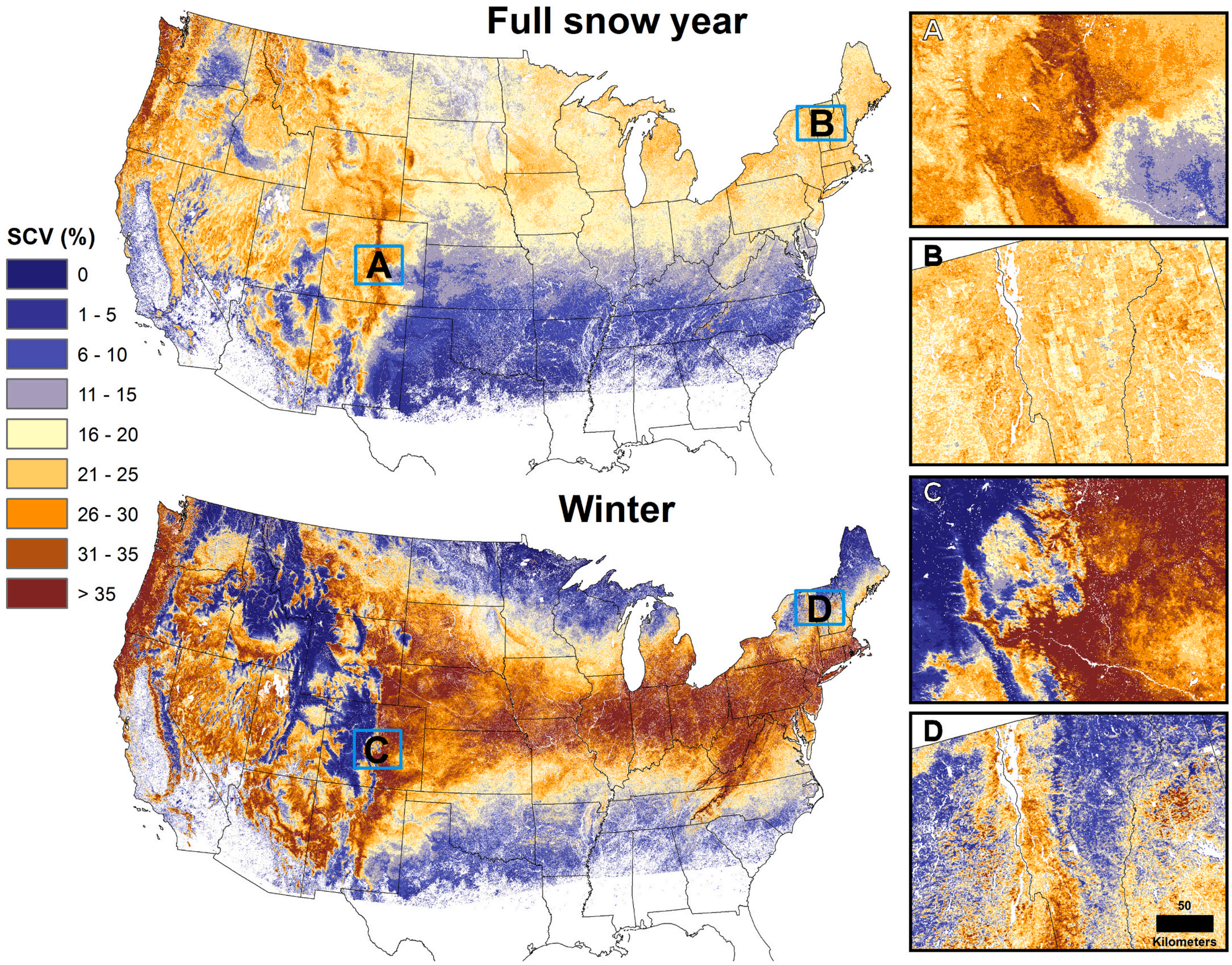

Fig. 7. Mean snow cover variability (SCV), in percent (number of change events/total valid observations), for the full snow season (top) and winter only (bottom) from 2003/04–2017/18. The right-hand panels show contrasting SCV estimations for the two time periods, and highlight important SCV gradients captured by the much more accurate winter index across the Front Range of the Rocky Mountains and the Central Plains (**A, C**) and New England (**B, D**).

richness and the model covariates (Fig. 10). Species richness had a strong unimodal relationship with survey effort, with maximum species counts occurring around 3000 checklists per grid. As expected, bird species richness was lower in regions with longer snow seasons (Fig. 10b). Species richness also had unimodal relationships with snow cover variability and frozen ground without snow. Richness was higher in regions where up to 25% of all the winter observations were 'change events' (i.e., new snow or snowmelt) and 40% of observations were of frozen ground without snow, but declined sharply in regions of greater variability (Fig. 10c, d).

4. Discussion

We derived the winter habitat indices (WHIs) from MODIS that characterize patterns of snow season length, snow cover variability, and frozen ground without snow across the contiguous US from 2003/04 to 2017/18. Accuracy assessment with data from 797 meteorological stations showed that the WHIs accurately captured snow cover dynamics, both across the 14-year study period and annually. The season length and frozen ground without snow indices were most accurate, followed by winter snow cover variability. For frozen ground without snow and for snow cover variability, the core winter indices were also highly correlated with the full snow year station data, and sometimes even more so than their full snow year counterparts. Thus, estimating these two WHIs for the core winter only appears to be an accurate portrayal of conditions over the entire snow year, and adding non-winter observations increases error. The ability of each WHI to capture winter habitat conditions that are important to wildlife was underscored by their individual importance in models predicting winter bird diversity across the contiguous US.

Though each MODIS WHI exhibited some degree of bias, only one – snow cover variability for the full snow year – showed poor agreement with the station data. Snow season length bias included underestimations at lower elevations with shorter seasons and overestimations at higher elevations with longer seasons, though most estimates were within 40 days of the station-based estimate. Frozen ground without snow was typically underestimated for both the full snow year and core winter indices, but more so in the former. Snow cover variability was mostly slightly overestimated in the core winter index, but this tendency was exacerbated in the full snow year index, where most of the MODIS WHI estimates were ~ 5–30% higher than the station-based ones (with greater differences at high elevation sites). The sources of error that may have biased our MODIS WHIs included: (1) incorrect snow detections, (2) data gaps due to cloud cover, (3)

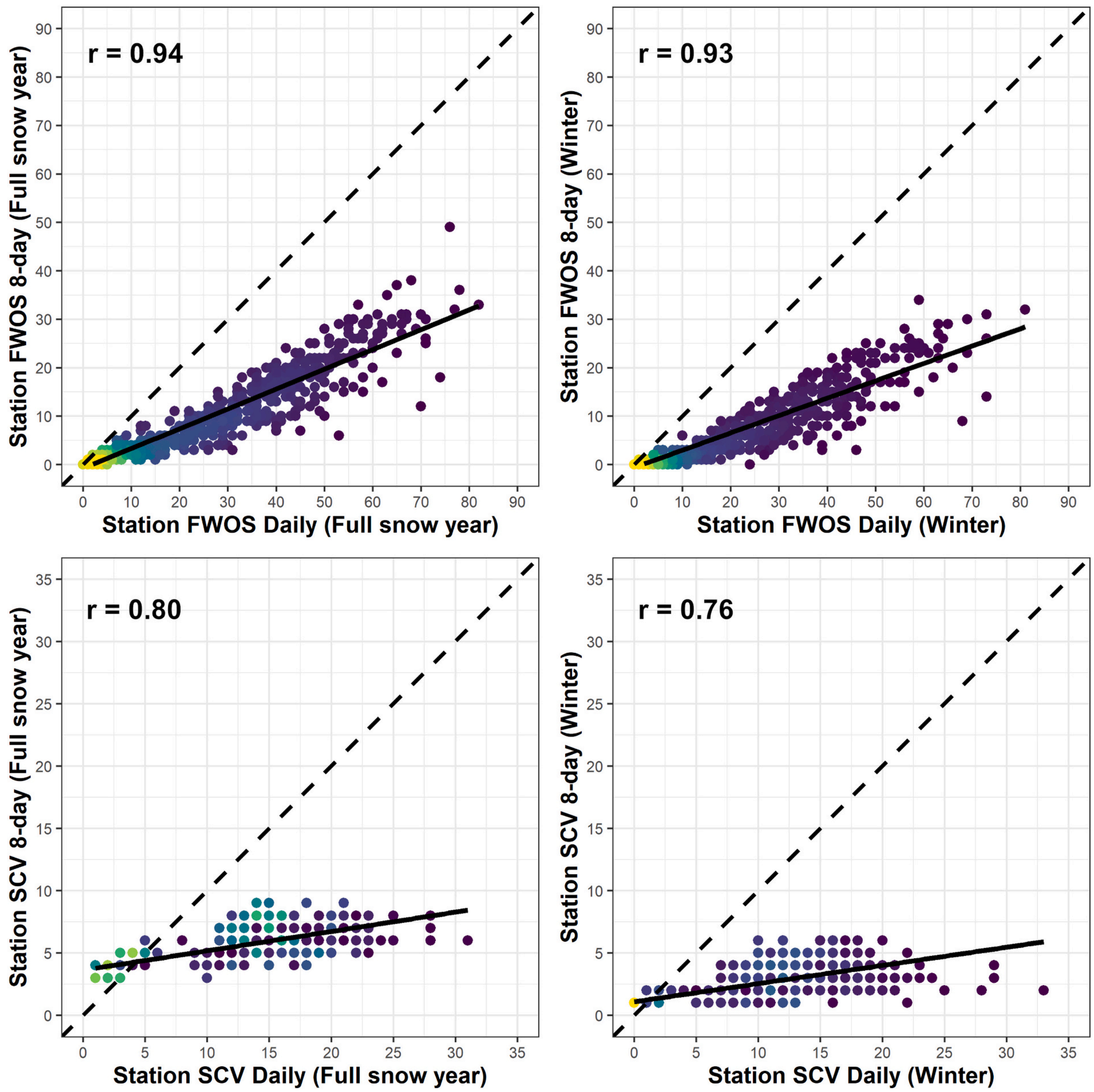

Fig. 8. Correlations between the station-based WHIs derived from daily versus 8-day snow cover data for frozen ground without snow (FWOS, %; top) and snow cover variability (SCV, %; bottom) from 2003/04–2017/18.

compositing of the snow cover data from daily to 8-day periods for the frozen ground without snow and snow cover variability WHIs, and (4) scale mismatch between meteorological stations (point-level) and MODIS (500 m) data. Incorrect snow detection in MODIS snow cover products is largely due to spectral similarities between certain cloud and snow conditions, which produce false positives (high NDSI values for clouds), and dampening of the spectral signal due to cloud and mountain shadows or patchy snow cover within a pixel, which produce false negatives (low NDSI values when they should be high) (Hall and Riggs, 2007; Rittger et al., 2013; Stillinger et al., 2019). Error rates in both the Terra and Aqua products are generally highest during the warmer shoulder season months when bright cirrus clouds and patchy snow cover are more common, and they are higher in the Aqua product than in the Terra products due to Aqua's sensor malfunction (Coll and Li, 2018; Hall and Riggs, 2007). Thus, while each WHI suffered from more than one of these errors, those that were both calculated for the full snow year and used combined Terra-Aqua data – i.e., the snow cover variability for the full snow year and combined Terra-Aqua snow season length and indices – performed worse relative to their counterparts (i.e., snow cover variability for winter only and snow season length from Terra only).

Biases in our MODIS-based estimates of snow season length, which are based on daily data, were caused by data gaps and incorrect snow detections. Because we constrained the period when snow could occur by elevation class (low = Oct. 1st – May 31st, mid = Sep. 1st – June 31st, high = no date constraint), the lower elevations were less affected by false positives during warmer months. Thus season length was largely underestimated in these areas due to missed snow cover days from clouds or shadows, and overestimated in higher elevation areas where false positives were more common. Unsurprisingly, season length estimates derived from the daily Terra data outperformed those from Terra-Aqua combined, especially at higher elevations, because the latter contained the aforementioned snow detection errors that are most prevalent in the Aqua data. Other studies that have mapped and validated snow cover duration, which is closely related to our season length metric, using MODIS products have found similar results in Europe (Dietz et al., 2012; Foppa and Seiz, 2012), China (Xu et al., 2017), the

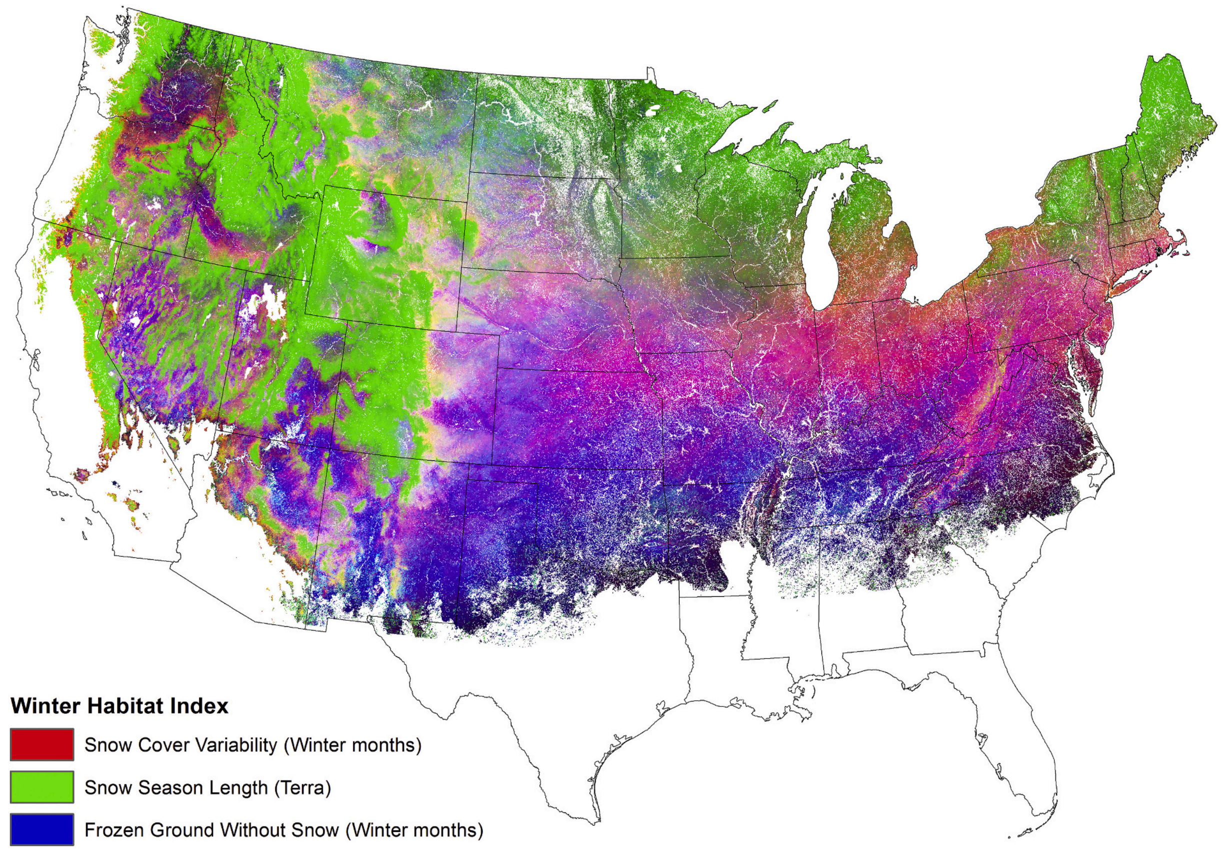

Fig. 9. Composite spatial patterns in the MODIS WHIs from 2003/04–2017/18, highlighting zones with distinct snow cover dynamic across the contiguous US. The winter snow cover variability (%) WHI is in red, the snow season length (days) WHI in green, and the winter frozen ground without snow (%) WHI in blue. Thus, for example, bright green areas represent long snow seasons with little snow cover variability and rarely any frozen ground without snow. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Pacific Northwest in the US (Gao et al., 2011), and across mountain ranges globally (Notarnicola, 2020).

While data gaps and incorrect snow detections also affected the MODIS-based estimates of frozen ground without snow and snow cover variability, our 8-day compositing introduced additional bias by reducing the number of valid observations available for the WHI calculations, e.g., from 94 possible observations in the daily data to 12 in the 8-day data for the core winter calculations. Our sensitivity analysis based on the continuous data from meteorological stations (representing 'true' conditions) showed that condensing the data record from daily observations to 8-day composites led to consistent underestimations in the estimates of frozen ground without snow and snow cover variability (refer to Section 3.1.4 and Fig. 8). Compositing the snow record overestimated the amount of time the ground is frozen with snow and hence underestimated the prevalence of frozen ground without snow. Similarly, extending snow presence or absence to 8-day periods removed the variability within those periods, leading to underestimations in areas where snow cover is more variable versus those that remain snow-covered for long periods of time (e.g., high elevations). However, because frozen ground without snow and snow cover variability require a near-continuous data record (whereas snow season length only requires a first and last observation), we found that creating 8-day composites with the MODIS data was necessary to produce them at an annual timescale. Using only the daily data resulted in substantial data gaps in parts of the country where cloud cover is especially prevalent in winter (e.g., the Upper Midwest and Northeast). Even after compositing data from two sensors (Terra and Aqua), having a valid MODIS observation for each 8-day period in a given year was rare.

That data gaps remained in our 8-day composite snow product is the reason our accuracy assessment results for the MODIS-based estimates differ from those of the station-based sensitivity analysis (Figs. 5 and 6 vs. Fig. 8), since the MODIS calculations were based on fewer observations. This was particularly true for the snow cover variability indices, which were biased toward overestimation in the MODIS estimates (data gaps) and underestimation in the station-based sensitivity analysis (no data gaps). Because we only counted a 'change event' (new snow or snowmelt) as valid if it occurred between two clear, adjacent observations – if a pixel had snow the first period, was masked due to cloud cover the next, then had no snow cover on the following period, no change event was recorded – reducing the number of valid observations progressively increases the impact of one change event on the variability estimate (increases it). Nevertheless, three of the four MODIS WHIs derived from 8-day composites were still highly correlated with the 'true' conditions represented by the station data. The exception to this was the snow cover variability for the full snow year index, which was almost universally overestimated due to a combination of false positive snow detections in warmer shoulder season months and fewer valid observations, inflating the variability estimate. We suspect the false positive during warmer months issue was drastically reduced in the frozen ground without snow for the full snow year index, because valid observations for this index also require the minimum temperature to be below -4 °C ($\sim$25 °F).

Despite the known shortcomings of Aqua snow cover data, we decided to test if they could provide supplemental information to the Terra data for the WHI calculations. Our question was whether the increase in spatiotemporal coverage due to more frequent snow observations, particularly in the core winter months and for annual estimates, outweighed the resulting decrease in accuracy. Maximizing

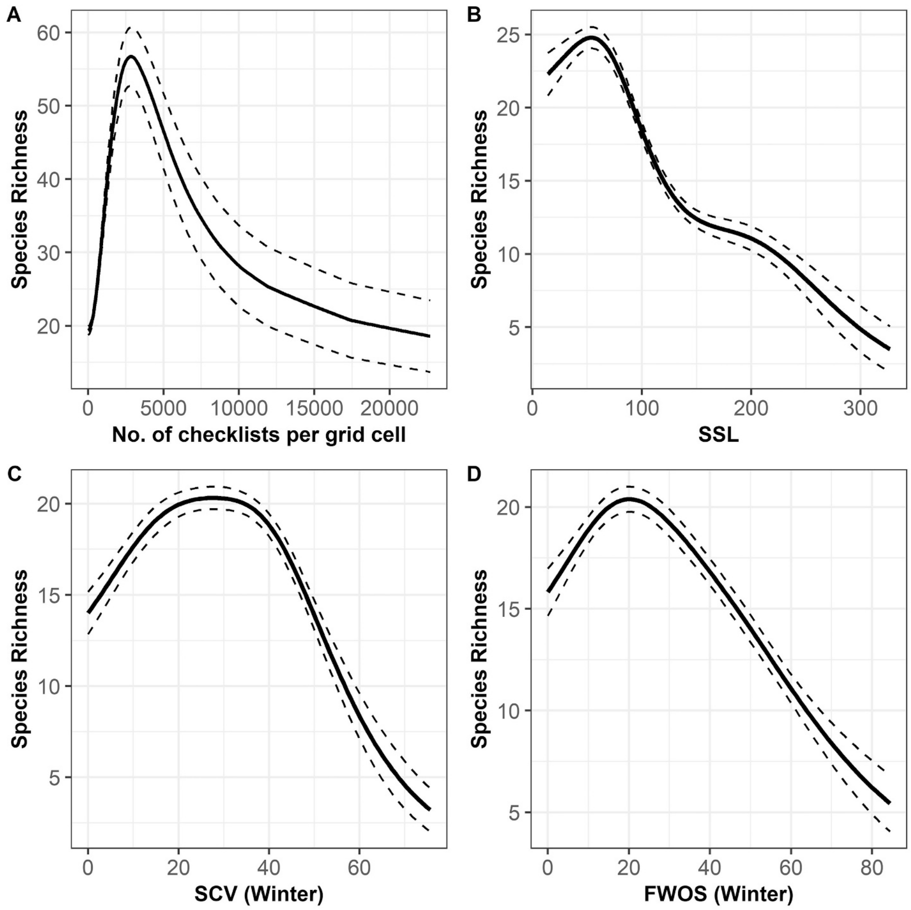

Fig. 10. Partial effects plots showing the modeled predictions of winter bird species richness as a function of the number of eBird checklists per grid cell (**A**), snow season length (SSL, days; **B**), winter snow cover variability (SCV, %; **C**), and winter frozen ground without snow (FWOS, %; **D**). Solid black lines show the predicted relationship between species richness and each WHI when all other variables are held constant. Dashed lines represent 95% confidence intervals.

spatiotemporal coverage and resolution of the WHIs is important for many conservation and biodiversity applications, such as species distribution modeling, identifying areas of phenotypic mismatch (e.g., for species that rely on snow cover for cryptic coloration, like snowshoe hare), and for management decisions at local or regional scales over relatively short timeframes (e.g., 10-year management plans). The core winter indices are of particular importance because snow and frozen ground conditions affect wildlife especially during colder months. We found that the daily Terra data alone was sufficient to characterize snow season length without substantial gaps in spatial coverage for most years. Yet, even after creating 8-day composites from the daily data, Terra data alone was insufficient to calculate frozen ground without snow and snow cover variability. Further, we found that the Aqua errors mainly occurred during the shoulder seasons and not in the core winter months, which was reflected in the high accuracies of the winter frozen ground without snow and snow cover variability indices derived from the combined Terra-Aqua data, similar to what others have found (e.g., Wang et al., 2009). Ultimately, the answer to the question if Aqua data adds useful information depends which index is of interest, for which parts of the US the WHIs are calculated, and whether the core winter months or full snow year is more appropriate. Based on our results, we recommend that users do not include the Aqua data in 1) calculations of snow season length for the western US, and 2) calculations of snow cover variability and frequency of frozen ground without snow for the full snow year regardless of location.

The accuracies of our WHIs compare favorably with other studies that have developed and extensively validated similar MODIS-derived snow cover metrics across broad spatiotemporal scales. For example, 87% of snow cover duration estimates (pixels) across Europe (2000−2011) using a combined Terra-Aqua fall within ±36 days of ground-based duration estimates (Dietz et al., 2012). This result is slightly more accurate than our season length index (72% of pixels within ±40 days), and we suggest that more complex topography in the US may be the cause. Mean snow cover duration (2000–2018) has also been mapped across major mountain ranges of the world, with high accuracy in North America based on station data ($r = 0.80$) (Notarnicola, 2020). While our overall season length accuracy was higher ($r = 0.91$), our correlation for the high elevation class was quite a bit lower ($r = 0.67$). We suspect this is due to the use of fewer validation stations by Notarnicola (2020) and their focus on the Rocky Mountains in the US, which have less frequent cloud cover than mountain ranges in the Northeast and Pacific Northwest. These two differences in our validation dataset, which included 489 high elevation sites spanning several major mountain ranges, may have made the Notarnicola (2020) high elevation estimates likely more accurate than ours, but less precise. In a global study that was the inspiration for our frozen ground without snow indices, Zhu et al. (2017) mapped the duration of frozen ground with and without snow (akin to our frozen ground without snow WHI, but expressed in days rather than as a percentage) using a combination of MODIS 8-day snow cover and microwave sensing-based freeze/thaw status data and had higher overall accuracies ($r = 0.91$ vs. our 0.85), but with important caveats. First, their frozen ground estimation was limited by the coarse resolution of the microwave data (25 km). We improved upon this by using 1-km data from Daymet and achieved similar results at a much finer spatial resolution. Second, their validation of frozen ground status was not independent of the data used to calculate their metrics, as they extracted the microwave data for each station (rather than using minimum temperature-based thresholds), and thus overall accuracy is only capturing snow cover duration accuracy. Caveats aside, the spatial patterns in their frozen ground without snow metric (see Figs. 3b and 4c in Zhu et al., 2017) largely matched those of ours. The main difference was their index had higher estimates of frozen ground without snow in the southcentral and southeastern portions of the US, most likely due to differences in the spatial resolution of our frozen ground status data.

Our WHIs identified distinct spatial patterns in snow cover dynamics across the contiguous US. These spatial patterns summarize dynamic winter conditions that are of potential importance for many winter-adapted species and ecosystems by capturing interactions between ground status (frozen or not, snow-covered or not) and gradients of temperature (latitude, elevation) and precipitation (longitude, elevation, near large bodies of water). Unsurprisingly, snow season length is longer in high elevation areas nationwide and, in general, the highest elevation mountain ranges experience long snow seasons with little variability in snow cover. One exception to this is the Allegheny Mountains in the eastern US, which have snow seasons of moderate length (~3–5 months) characterized by high variability. This mountain range is in the transition zone from rain- to snow-dominated winters, and we suspect rainfall on warmer days during the core winter months causes the high rates of snow cover variability, and also of frozen ground without snow, since minimum temperatures at night remain low. East of the Mississippi River, there is a strong latitudinal gradient in snow cover dynamics, where the percentage of frozen ground without snow is high in the southernmost latitudes, snow cover variability high in mid-latitudes, and snow season length in the north. Snow cover variability is also higher near large bodies of water, such as Lake Champlain in New England and the Great Lakes. Finally, the WHIs highlighted the Central Plains region east of the Rocky Mountains as having arguably the harshest winters, where frozen ground without snow is highest reflecting cold, dry winters.

The ecological relevance of the WHIs was underscored by our assessment of winter bird species richness, where we found that each WHI had a significant, independent contribution in explaining variation in patterns of winter bird species richness across the contiguous US. The large percentage of total deviance explained by the WHIs (~60%) suggests that snow cover dynamics strongly influence the spatial distribution of winter bird diversity in the mid to northern latitudes. As far as we know, our study is the first to explicitly examine relationships between broad-scale snow cover dynamics and winter bird diversity. Most related studies to date have focused on quantifying relationships between winter bird assemblages and measures of temperature, total precipitation, and productivity (e.g., Elsen et al., 2020; Evans et al., 2006; H-Acevedo and Currie, 2003; Meehan et al., 2004).

Overall, regions with longer snow seasons supported fewer bird species. This is unsurprising given longer snow seasons occur at higher elevations and latitudes where winter minimum temperatures are lower, snow depths are typically greater, and food availability is limited, resulting in high energetic demands for endotherms (Evans et al., 2006; Kawamura et al., 2019; Williams et al., 2015). Indeed, the majority of bird species that breed in North America have evolved migratory strategies to escape such harsh winter conditions (Somveille et al., 2019; Somveille et al., 2015). However, species richness did not increase linearly with the snow cover variability WHI. Variability tends to peak in middle latitude and coastal areas of the country where rain occurs in winter and freeze/thaw events occur more frequently, and higher winter temperatures can result in more bird species (Elsen et al., 2020; Evans et al., 2006). We found that while initial increases in snow cover variability and frozen ground without snow were associated with increased species richness, once these indices cross a certain threshold (~40% and 25%, respectively), species richness declines precipitously. These relationships suggest a geographic optimum may exist for wintering birds between long, harsh snow seasons and those characterized by high temperature and precipitation fluctuations, where short-distance migrants may still find resources and resident birds benefit from reduced competition. Similarly, intermediate levels of temporal heterogeneity in snow cover may facilitate coexistence of species that utilize aspects of snow cover (e.g., for foraging) and those that do not, effectively increasing species richness (Adler and Drake, 2008; White et al., 2010). In regions of high variability, a possible explanation for lower species richness is the costs associated with highly variable temperatures, leading to unpredictable environmental conditions (H-Acevedo and Currie, 2003). For birds, climatic stability in winter can be a major determinant of winter species richness patterns across North America, with more species preferring areas where temperature is relatively stable but precipitation varies (H-Acevedo and Currie, 2003). Diminished species richness in extremely cold, dry conditions (higher frozen ground without snow) may be due to the lack of a subnivium or other thermal refugia (Pauli et al., 2013; Petty et al., 2015) for birds themselves (e.g., roosting habitat; Shipley et al., 2019; Shipley et al., 2020) and for the resources they depend on (e.g., low productivity, food availability; Antor, 1995). However, land cover may mediate species responses to winter weather. For example, we would expect fewer species in grasslands where extremely cold, dry conditions are harder to escape, which raises energetic costs and requires higher cold tolerance compared to land cover types such as forest. That said, birds utilize overwintering habitat more dynamically than breeding habitat, moving to and from different land cover types in response to fluctuating weather conditions and resource availability (Latimer and Zuckerberg, 2020). Thus, winter habitat conditions may be more important for mediating winter bird diversity than land cover types per se, and the MODIS WHIs can support future comparisons of the relationships of snow and species richness among and within different land cover types.

In summary, the MODIS WHIs that we derived for the contiguous US offer a novel dataset to examine relationships between winter habitat conditions and biodiversity patterns. Their 500-m resolution allows for investigations that span from single species (e.g., snowshoe hares) to functional guilds (e.g., snow-adapted species) to entire taxa (e.g., birds) at regional or nationwide scales. As climate change continues to affect seasonally snow-covered ecosystems across the mid to high latitudes, the WHIs are essential to understanding the potential effects of these changes on the abundance, distribution, and fitness of species. To facilitate such studies, the WHIs are available for download on the University of Wisconsin-Madison SILVIS Lab's website (silvis.forest.wisc.edu/data/whis).

Credit

David Gudex-Cross: Conceptualization, Writing – Original draft preparation, Methodology, Investigation, Formal analysis, Validation, Visualization; **Spencer Keyser**: Methodology, Formal analysis, Visualization, Writing – review & editing; **Benjamin Zuckerberg**: Conceptualization, Funding acquisition, Supervision, Writing – review & editing; **Daniel Fink**: Methodology, Funding acquisition, Resources, Writing – review & editing; **Likai Zhu**: Conceptualization, Methodology, Writing – review & editing; **Jonathan Pauli**: Funding acquisition, Project administration, Writing – review & editing; **Volker Radeloff**: Conceptualization, Funding acquisition, Project administration, Methodology, Resources, Supervision, Writing – review & editing.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rse.2021.112309.

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