

A hybrid correlative-mechanistic approach for modeling and mapping winter distributions of western bat species

Running title: Modeling western bat winter distributions

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Abstract

Aim: The fungal pathogen *Pseudogymnoascus destructans* and resultant white-nose syndrome (WNS) continues to advance into western North America, infecting new bat populations, species, and hibernacula. Western North America hosts the highest bat diversity in the U.S. and Canada, yet little is known about western hibernacula and western bats' hibernation behavior. An improved understanding of where bats hibernate in the West and the conditions that create suitable hibernacula is critical if land managers are to anticipate and address the conservation needs of WNS-susceptible species.

Location: United States and Canada

Taxon: bats

Methods: We estimated suitability of potential winter hibernaculum sites across the ranges of five bat species occurring in the West. We estimated winter survival capacity from a mechanistic survivorship model based on bat bioenergetics and climate conditions. Leveraging the Google Earth Engine platform for spatial data processing, we used boosted regression trees to relate these estimates, along with key landscape attributes, to bat occurrence data in a hybrid correlative-mechanistic approach.

Results: We show that winter survival capacity, topography, land cover, and access to caves and mines are important predictors of winter hibernaculum selection, but the shape and relative importance of these relationships vary among species. Our findings suggest that the occurrence of bat hibernacula can, in part, be predicted from readily mapped above-ground features, and is not only dictated by below-ground characteristics for which spatial data are lacking. Furthermore, our mechanistic estimate of winter survivorship was among the strongest predictors of winter occurrence probability across focal species.

Main conclusions: Our findings offer an improved understanding of the likely winter distribution of bats occurring in the West, and offers a valuable baseline for assessing the potential species-level impacts of *P. destructans* as well as future climate change.

Keywords: bat, bioenergetic model, hibernation, hybrid, species distribution model, western North America, white-nose syndrome, winter

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Introduction

Globally, bats are threatened by a wide range of human impacts, including habitat loss and fragmentation, mortality due to roads and energy development, loss of water sources, exploitation, and introduction of disease (Voigt & Kingston, 2016). In North America, one of the most pressing threats is white-nose syndrome (WNS), caused by a fungal pathogen introduced to New York state in 2006, which is rapidly spreading across the continent with dire consequences for hibernating bat populations (Leopardi et al., 2015, Frick et al., 2015). In response to this novel threat, hibernating bats have been studied intensively in eastern North America. In western North America (i.e., west of the Mississippi River, herein the West), where WNS has only recently begun to appear (USFWS, 2019), bat hibernation is far less understood. The West harbors considerably higher bat diversity than the East (Harvey et al., 2013), and western bats hibernate differently (Weller et al., 2018). Western bats generally do not form large colonies of thousands of individuals, but instead hibernate in much smaller numbers distributed widely across the landscape (Adams, 2003, Bachen et al., 2018). This hibernation behavior, along with the ruggedness and remoteness of much of the West, renders bats more difficult to study than in the East. This is important as WNS begins to reach the West (USFWS, 2019) and as climate change impacts bat populations (Adams, 2010), potentially interacting with the effects of WNS. Researchers and managers need new tools to understand how these combined stressors are likely to impact western bats, and how to allocate monitoring and management resources to minimize impacts to vulnerable populations.

When species are poorly understood, species distribution models (SDMs) help fill a wide variety of information needs (Rodriguez et al., 2007). A first step in building knowledge about these species and anticipating conservation needs is understanding where they are most likely to occur so that they can be better studied, monitored, and managed. SDMs use what we know about where a species occurs to predict where it is likely to occur over a broader area. These models can then serve many practical purposes, including: 1) informing sampling and monitoring efforts (Hauser & McCarthy, 2009, Jamevich et al., 2006, Williams et al., 2009); 2) elucidating movement patterns and metapopulation dynamics (Frey et al., 2012, Lawler et al., 2013, McClure et al., 2017); 3) reconstructing or predicting changes in distribution over time (Beans et al., 2012, Svenning et al., 2011); 4) assessing opportunities for reintroduction or assisted migration (Hällfors et al., 2016, Miranda et al., 2019); and 5) anticipating how the species may be impacted by climate change, land use change, and other stressors (Doherty et al., 2008, La Manna et al., 2008, Johnston et al., 2012).

Modeling species distributions is particularly challenging for subterranean species because observations tend to be rare and habitat selection is likely driven by landscape features that are not well-represented in existing geodatabases. To estimate the degree to which a species is associated with particular landscape characteristics, SDMs typically compare the characteristics of sites where a species has been observed to those of sites where the species has not been observed or to random sites across an area of interest (Elith & Leathwick, 2009). These models often use readily available data describing climate, land cover, and water availability, as these attributes are critical for defining species' physiological and ecological limits. However, the landscape attributes to which bats respond when selecting hibernacula are largely unknown, and key subterranean habitat attributes may not be captured by available spatial datasets. Efforts to model bat distributions, space use, and habitat selection have increased rapidly in recent years (e.g., Razgour et al., 2016, Zamora-Gutierrez et al., 2018, Burke et al., 2019, Delgado-Jaramillo et al., 2020). Few, however, have attempted to model distributions of winter hibernacula (but see Russell et al., 2014, Smeraldo et al., 2018, Weller et al., 2018), and none to our knowledge have predictively mapped occurrence probability or abundance in the West.

Climate is expected to be an important driver of bat winter distributions given that hibernaculum temperature and winter duration dictate the length of time that hibernating bats can survive on their fat stores (Thomas et al., 1990, Speakman & Thomas, 2003). Climate metrics (e.g., mean annual temperature, annual precipitation) are often included as predictors in SDMs (e.g., Kadmon et al., 2003, Peterson & Vieglais, 2001, Phillips et al., 2006). Yet, recent intensive study of bat hibernation physiology offers a far more detailed mechanistic understanding of how temperature and humidity affect bat metabolic rates and their ability to survive winter. Moreover, we now understand (and can predict) how bat physiology is affected when they are infected by *Pseudogymnoascus destructans*, the fungus that causes WNS (Langwig et al., 2012, 2016, Johnson et al., 2014, Hayman et al., 2016, Haase et al., 2019). We suggest that more fully and precisely integrating the relationship between climate and winter survivorship in SDMs can enhance our ability to model winter bat distributions and understand how they may be impacted by WNS.

Buckley et al. (2010, 2011) pioneered the concept of SDMs that integrate mechanistic understanding of how species respond physiologically to environmental conditions. They used correlative SDMs that fit observed locations of butterflies to empirically-derived numbers of degree-days required for each species' growth and survival (Buckley et al., 2011). They found that species-specific degree-day measures outperformed a fixed degree-day metric in predicting the current distribution of each species. However, the difference in performance was modest, suggesting that more detailed models and/or additional predictors may be helpful in refining predicted distributions. These hybrid correlative-mechanistic models, which integrate a mechanistic understanding of how a species responds to its environment into a more traditional correlative framework, allow incorporation of additional landscape attributes to which the species is likely to respond alongside physiology (e.g., Martinez et al., 2015, McClure et al., 2015).

Here, we integrated a bioenergetic model of bat hibernation (Hayman et al., 2016, Haase et al., 2019, Hranac et al. in prep) into a correlative species distribution modeling approach to predict winter distributions of western bat species. The bioenergetic model makes species-specific predictions of remaining fat stores and thus the likelihood of survival at the end of winter in a given location. Bringing bioenergetic model predictions into our analysis makes full use of what we know about bat hibernation physiology. We compiled bat winter occurrence data for five representative species from a variety of sources to inform our models. We used spatial predictions of winter survivorship from this mechanistic model as one predictor of bat occurrence probability across the areas encompassing our focal species' known range extents. We included this along with other landscape attributes (e.g., topography, vegetation cover, karst and mines) to fit species distribution models using a boosted regression tree (BRT) approach (Elith et al., 2008). Our objective was to better understand the distribution of suitable bat hibernacula across the West to inform targeted monitoring and management practices and provide a baseline for estimating which species and populations may be hardest hit by the advance of WNS and climate change.

Materials and Methods

Winter occurrence data

We selected five focal species for our analyses: *Corynorhinus townsendii*¹, *Myotis californicus*, *Myotis lucifugus*, *Myotis velifer*, and *Perimyotis subflavus*. These species were chosen because occurrence data and field-measured metabolic parameters were available for estimating survivorship, and because they were representative of variability in known distributions and habitat requirements among hibernating bats in the West, which we broadly define here as bats with all or a portion of their range extending west of the Mississippi River (Fig. 1; National Atlas of the United States, 2011).

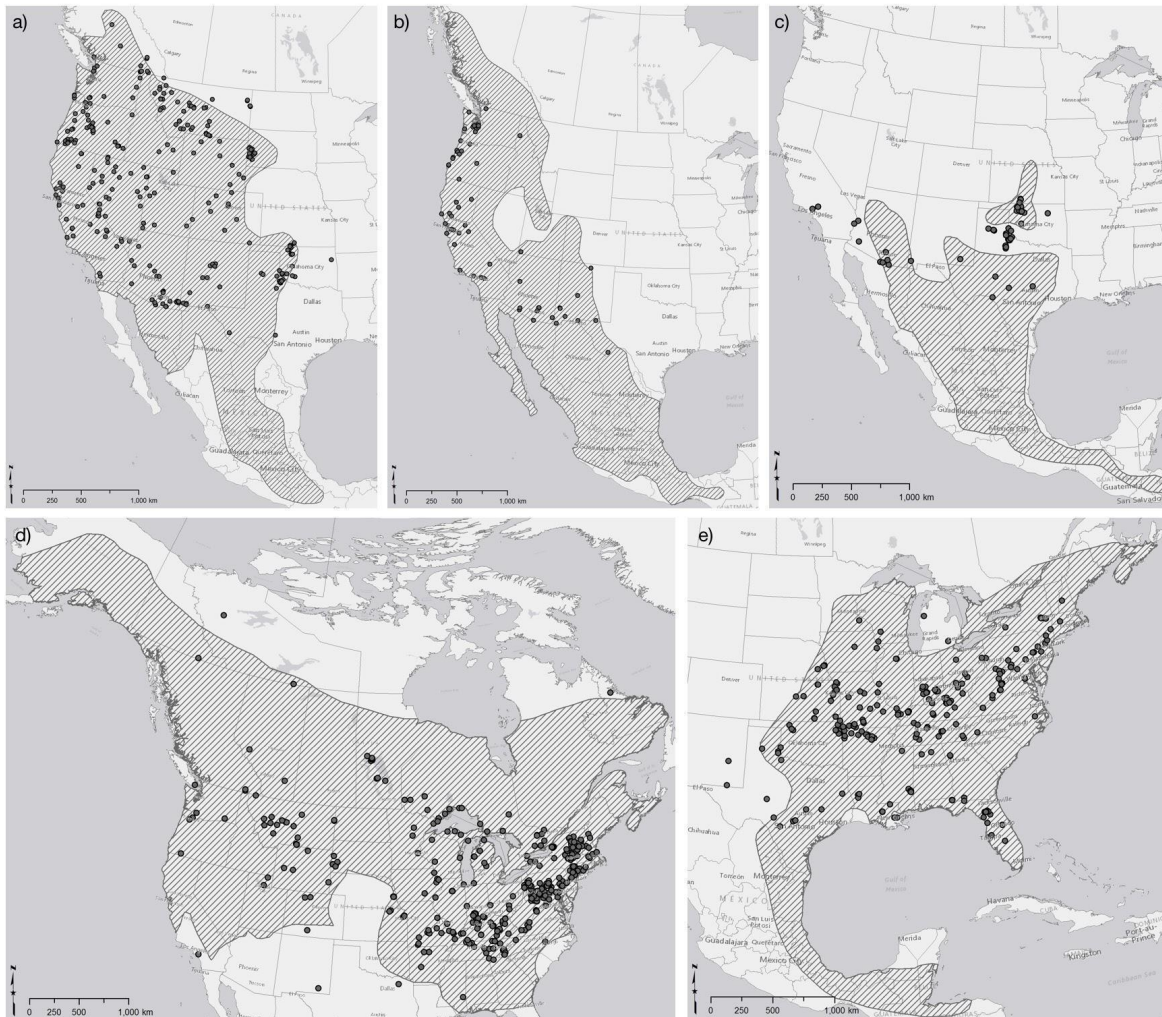


Figure 1. Current geographic range maps overlaid with winter presence locations available to inform species distribution models across the United States and Canada for five focal species: a) *Corynorhinus townsendii*, b) *Myotis californicus*, c) *Myotis velifer*, d) *Myotis lucifugus*, and e) *Perimyotis subflavus*.

We compiled species occurrence data from multiple sources, including online databases of museum records (VertNet [NSF, 2013], Biodiversity Information Serving Our Nation [USGS, 2012]), online repositories of vetted public and scientific observations (Global Biodiversity Information Facility [GBIF.org, 2018], Bat Population Database [USGS, 2003]), data associated with published literature (Ports & Bradley, 1996, Kuenzi et al., 1999, Dubois & Monson, 2007), data obtained from multiple Natural Heritage Programs (NHP; NatureServe, 2019, Montana

¹ Excluding isolated subspecies *C. townsendii ingens* and *virginianus* found in the Ozark and Appalachian Mountains

NHP, 2020), and data collected in our own field studies (unpublished data). We amassed thousands of occurrence records for each focal species, but the vast majority of records (>85%) were observed during summer or fall swarming, when bats are more readily observed. Even in bats that do not migrate seasonally, selection of hibernaculum microclimates and the surrounding habitat mosaic is expected to differ from selection of summer roosts (Smeraldo et al., 2018). Moreover, due to the sensitivity of hibernaculum locations to disturbance or exploitation, along with the difficulty of detecting torpid bats in hibernacula, winter bat location data were difficult to come by and limited in number (Table 2).

We included only in-hand observations (i.e., no acoustic detections) since 1948 (to match the earliest availability of gridded climate data) with location error < 5 km. Because we were interested only in winter distributions associated with hibernaculum use, we filtered the compiled dataset to observations recorded during what we defined as winter in a spatially explicit manner. Using a model of winter duration informed by immergence and emergence observations at sites throughout North America (Hranac et al. in prep, SI), we estimated the start and end of winter hibernation at a given location (at 1-km resolution) by centering this duration estimate on the winter solstice, then selected only occurrence records within this timeframe. Lastly, we dissolved repeat observations (e.g., across multiple studies or survey dates) to a single record for a given site (with unique sites defined to the nearest thousandth of a degree of latitude and longitude).

Predictor variables

We identified landscape attributes that potentially influence hibernaculum selection from the published literature and our own knowledge (Table 1, Fig. 2). We selected publicly available datasets representing these predictors with sufficient spatial extent to encompass our compiled occurrence data (United States and Canada south of the Arctic Circle). Where multiple candidate datasets were available, we chose those with the highest spatial resolution and/or temporal range that best encompassed our occurrence data. The scale at which bats perceive and respond to landscape attributes may vary among species, attributes, and locales (see Bellamy et al., 2013, Ducci et al., 2015). We therefore derived predictor variables at multiple spatial scales (i.e., over different neighborhood sizes) where applicable for comparison. All predictors were derived and/or sampled using Google Earth Engine, a cloud-based computing platform supporting large-scale analysis on an extensive catalog of remotely sensed, climatological, and other geospatial datasets (Gorelick et al., 2017).

Table 1. Summary of predictors considered in winter species distribution models for bat species *Corynorhinus townsendii*, *Myotis californicus*, *Myotis lucifugus*, *Myotis velifer*, and *Perimyotis subflavus* across the United States and Canada.

Predictor	Source data	Resolution	Neighborhood size
Winter survivorship	Haase et al., 2019, Hranac et al. in prep	1 km	--
Distance to mines	USGS MRDS ¹ , BC MinFile ²	1 km	--
Mine density	USGS MRDS, BC MinFile	1 km	25 km
Karst	Weary and Doctor, 2014, Salkeld and Walton, 2019	1 km	--
Elevation	ALOS ³ Digital Surface Model v2 (Tadono et al., 2014)	30 m	--
Ruggedness	ALOS Digital Surface Model v2 (Tadono et al., 2014)	30 m	500 m, 5 km, 25 km, multiscale
Topographic position	ALOS Digital Surface Model v2 (Tadono et al., 2014)	30 m	500 m, 5 km, 25 km, multiscale
Solar insolation	ALOS Digital Surface Model v2, Theobald et al., 2015	30 m	500 m, 5 km, 25 km, multiscale
Annual precipitation	DayMet v3 (Thornton et al., 2019)	1 km	--
Annual snow days	MODIS ⁴ Global Daily Snow Cover v6 (Hall et al., 2016)	500 m	--
Percent water	JRC ⁵ Yearly Water Classification v1 (Pekel et al., 2016)	30 m	500 m, 5 km, 25 km, multiscale
Groundwater depth	Fan et al., 2013	1 km	--
Percent tree cover	MODIS Vegetation Continuous Fields (NASA ⁶ , 2019)	250 m	5 km, 25 km
Night lights	DMSP Radiance-Calibrated OLS ⁷ v4 (NOAA ⁸ , 2016)	30 arcsec	--

1 United States Geological Survey Mineral Resources Data System; 2 British Columbia Mineral Inventory; 3 Advanced Land Observing Satellite; 4 Moderate Resolution Imaging Spectroradiometer; 5 Joint Research Centre; 6 National Aeronautics and Space Administration; 7 Defense Meteorological Satellite Program-Operational Linescan System; 8 National Oceanic and Atmospheric Administration

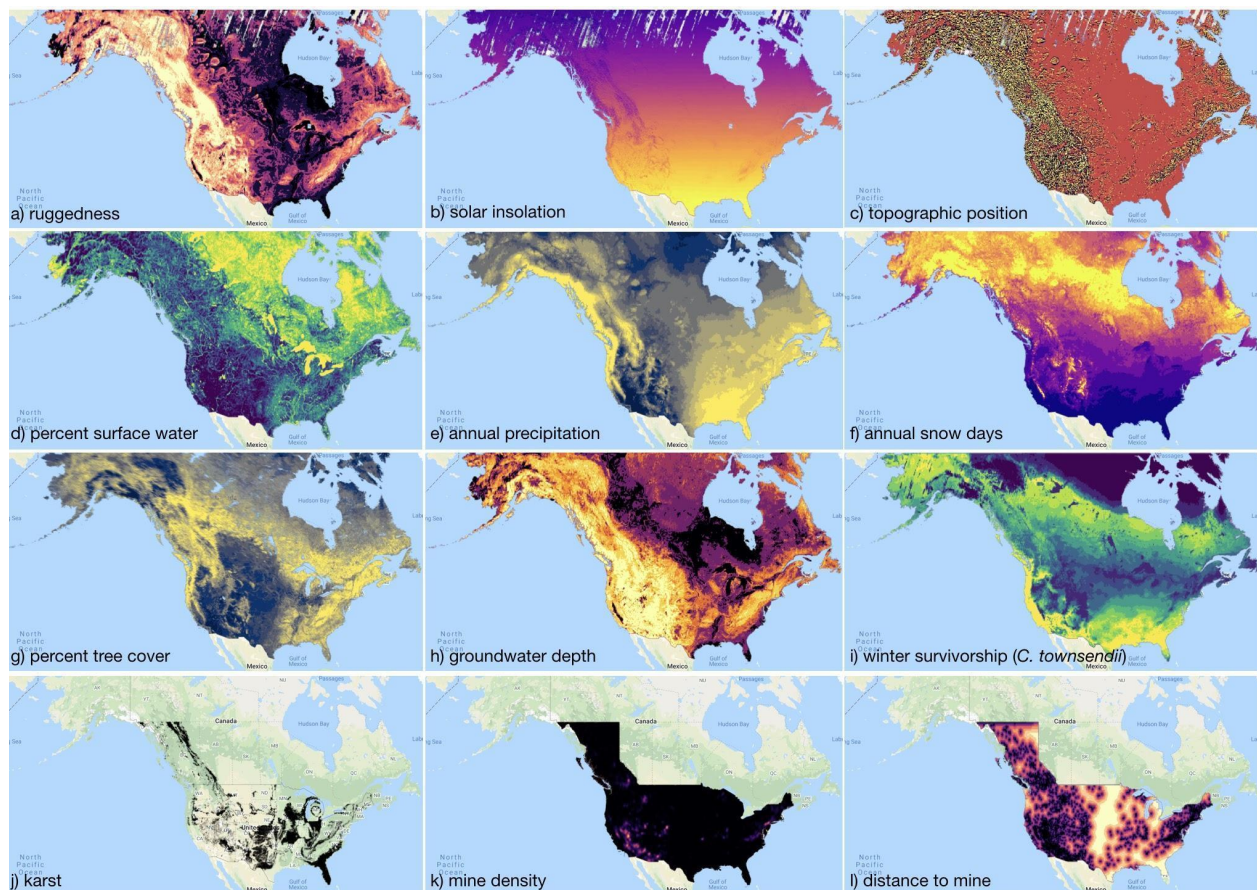


Figure 2. Maps of predictor variables used to fit winter species distribution models for bat species *Corynorhinus townsendii*, *Myotis californicus*, *Myotis lucifugus*, *Myotis velifer*, and *Perimyotis subflavus* across the United States and Canada (a - i) or, where continuous spatial data were not available for all provinces, across the U.S. and British Columbia (j - l). Data for karst and mines (j - l) was not available in other Canadian provinces, but this only impacts models for *M. lucifugus* as other focal species have either no, or only limited distribution in these provinces. In all panels, warmer, brighter colors represent higher values.

Survivorship. We estimated species-specific, spatially explicit winter survivorship relative to the duration of winter. These estimates were based on an existing bioenergetic model of bat winter survivorship, recently updated and parameterized for western bat species. Full details are elsewhere (Haase et al., 2019, Hranac et al. in prep), but briefly, the model uses the hypothesized energetic requirements of bats in torpor to dynamically model torpor bouts for the duration of a predicted winter under specified hibernaculum conditions. For *M. lucifugus*, torpor consumes approximately eighty times less energy per unit time than euthermia, whereas the infrequent but periodic arousals to euthermic temperatures use the majority of energy stores, with each arousal consuming approximately 5% of total overwinter energetic costs (Thomas et al., 1990). In this model, ambient temperature and relative humidity were drivers of arousal frequency. We spatially interpolated the model results across the study extent to predict the fat mass expected to remain at the end of winter given mean ambient temperature and winter duration at each 1-km² raster cell. Higher, positive predicted values are expected to correspond

to high survivorship, while low or negative values indicate areas where bats are unlikely to survive. Further details regarding the bioenergetic model and spatial parameters are described in the Supplemental Information.

Topography. We derived topographic covariates from the global ALOS Digital Surface Model (DSM version 2.2; Tadono et al., 2014) at 30-m resolution, including elevation, topographic ruggedness, and topographic position. Topographic ruggedness was quantified as the standard deviation of elevation values within a given radius around each focal raster cell. Similarly, topographic position was quantified as the difference between the elevation of each focal raster cell and the mean of elevation values within a given radius, such that high values are associated with peaks and ridges and low values are associated with canyon bottoms (e.g., Guisan et al., 1999, Dickson & Beier, 2007). We also extracted Continuous Heat-Insolation Load Index, a surrogate for effects of solar insolation and topographic shading on evapotranspiration, also derived from the global ALOS DSM at 90-m resolution by Theobald et al. (2015). We used a moving window approach to derive topographic ruggedness and position at three spatial scales (diameter = 500 m, 5 km, 25 km), then the resulting values were averaged to create 'multiscale' metrics. We took the focal mean of solar insolation values over these multiple scales as well.

Surface attributes. We derived percent tree cover from the Terra MODIS Vegetation Continuous Fields product, which estimates sub-pixel-level surface vegetation cover globally, including percent tree cover, on an annual basis (250-m resolution; NASA, 2019). Because data were not available for the entire temporal range of our occurrence data, we used data for the most recent year available (2015). We estimated percent tree cover at two aggregated scales (diameter = 5 km, 25 km). We used global nighttime lights imagery from the Defense Meteorological Program Operational Line-Scan System (Radiance-Calibrated, V4) as a proxy for relative intensity of human development (30-arcsec resolution; NOAA, 2016). We estimated availability of surface water based on the Joint Research Center Yearly Water Classification History (V1), which maps the location and seasonality of surface water from Landsat 5, 7, and 8 imagery (30-m resolution; Pekel et al., 2016). We estimated the percent cover of seasonal or permanent surface water at three spatial scales (diameter = 500 m, 5 km, 25 km), focusing on the most recent year for which data were available (2015) because the data do not span the entire temporal range of our occurrence dataset. We estimated the frequency of snow cover based on the MODIS Global Daily Snow Cover product (V6; Hall et al., 2016), which estimates percent snow cover of each 500-m pixel on a daily basis. We counted the average number of days per year with at least 10% snow cover over the 5-year period from July, 2013 to June, 2018. We quantified precipitation using the DayMet dataset (V3; Thornton et al., 2019), which provides gridded daily precipitation data at 1-km resolution. We estimated mean annual total precipitation by summing daily values annually then averaging the most recent five years available (2013-2018) for consistency with the temporal range of other available predictor data.

Below-ground attributes. To represent potential availability of karst features that may provide suitable hibernacula, we relied on a map of karst and pseudokarst features across the United States produced by Weary and Doctor (2014) derived from State geological survey maps and USGS integrated geologic map databases (1:24,000 to 1:500,000 resolution). We merged this with an equivalent dataset for British Columbia provided by the Ministry of Forests, Lands, Natural Resource Operations and Rural Development (1:250,000 resolution) (Forest Analysis and Inventory, 2019). We did not differentiate among karst types, and instead created a simple binary indicator of karst presence vs. absence in raster format (1-km resolution). We also estimated availability of mines as potential hibernacula, using mine site locations available from the USGS Prospect- and Mine-Related Features database (v4, available for all but northeastern states; Horton & San Juan, 2019) and the Mineral Resources Data System (MRDS, used for

northeastern states; USGS, 2016), and from the MINFILE Production Database for British Columbia (BC Geological Survey, 2019). We included only mineral resource sites classified as mines (Mine-Related Features and MRDS) or as producing at one time (MINFILE). We derived two measures of mine availability: distance to the nearest mine and density of mines within 50 km of each focal raster cell (1-km resolution), calculated using a Gaussian kernel density function ($\sigma = 25$ km). Karst and mine data were not available for other Canadian provinces; these predictors were not included in models for *M. lucifugus*, whose range spans these areas. Finally, we estimated groundwater depth from a global water table depth model that gap-filled point observations with a mechanistic groundwater model (1-km resolution; Fan et al., 2013).

Model fitting

We estimated species-specific relative probability of occurrence during winter using boosted regression trees (BRT; De'Ath, 2007, Elith et al., 2008). A BRT (a.k.a. gradient boosting machine or stochastic gradient boosting) is an ensemble approach that combines regression trees, which relate a response to predictors by recursive binary splits of the data, and boosting, in which inference is drawn from the relative strength of many possible models rather than fitting a single parsimonious model. This method offers advantages over more traditional linear regression approaches in that a variety of response data and model forms can be accommodated (e.g., Gaussian, binomial, Poisson); different types of predictor variables (e.g., continuous, ordinal, categorical) can be included with no need for transformation or outlier removal; nonlinear relationships are easily captured; and interactions between predictors are handled automatically. Furthermore, overfitting is well-controlled through the use of cross-validation as BRT models are 'grown' (Elith et al., 2006, 2008). Importantly, a number of studies (e.g., Elith et al., 2006, Wisz et al., 2008, Oppel et al., 2012, Maiorano et al., 2013) have shown strong BRT predictive performance relative to other SDM approaches (e.g., generalized linear models, generalized additive models, climatic envelope models, maximum entropy).

We follow the approach detailed by Elith et al. (2008) for application of BRT to species distribution modeling. One key difference in our application is that we make use of presence-only data rather than presence-absence data. Use of presence-only data, in which sites where the focal species was absent are not known with certainty, requires a shift in model assumptions and inference. Presence-absence models compare landscape attributes of sites at which the species was known to be present and absent to estimate the absolute probability of occurrence at any unobserved site given its climate and/or landscape characteristics (Guisan & Zimmerman, 2000, Manly et al., 2007). Without absence data, attributes of presence locations must instead be compared to randomly-sampled 'background' (a.k.a. 'pseudo-absence') locations (e.g., Ferrier et al., 2002). In this case, presence is assessed relative to availability and the species' absence at sampled background locations is not guaranteed. This shift in comparison fundamentally alters the inferences that can be made from the model: we cannot estimate the *absolute* probability of focal species occurrence (i.e., 80% probability of occurrence at a given site), but we can estimate, or rank, the *relative* probability of occurrence (Keating & Cherry, 2004; but see Phillips & Elith, 2011, Royle et al., 2012).

We sampled 'background' locations from extents that were broadly inclusive of each species' known range in an effort to sufficiently capture the environmental conditions limiting their distributions (western U.S. and Canada for *C. townsendii*, *M. californicus*; U.S. and Canada for *M. lucifugus*; U.S. for *M. velifer*, *P. subflavus* [Razgour et al., 2016]). Because bats were more likely to have been observed in locations already known to harbor bats and that are more accessible (e.g., closer to population centers, accessible by roads, and in less rugged topography; Graham et al., 2004), we generated background points so as to replicate and thus control for this inherent spatial bias (after Hertzog et al., 2014). We first created a bias grid

based on the kernel density of occurrence locations (Venables, 2002) using the MASS package for R, then generated background points with probability dictated by occurrence density (e.g., Fig. 3). We generated three background points for every occurrence point as a balance between achieving coverage of available habitat and not swamping the presence locations or artificially inflating sample size. Finally, we sampled all candidate predictor variables at each presence and background location.

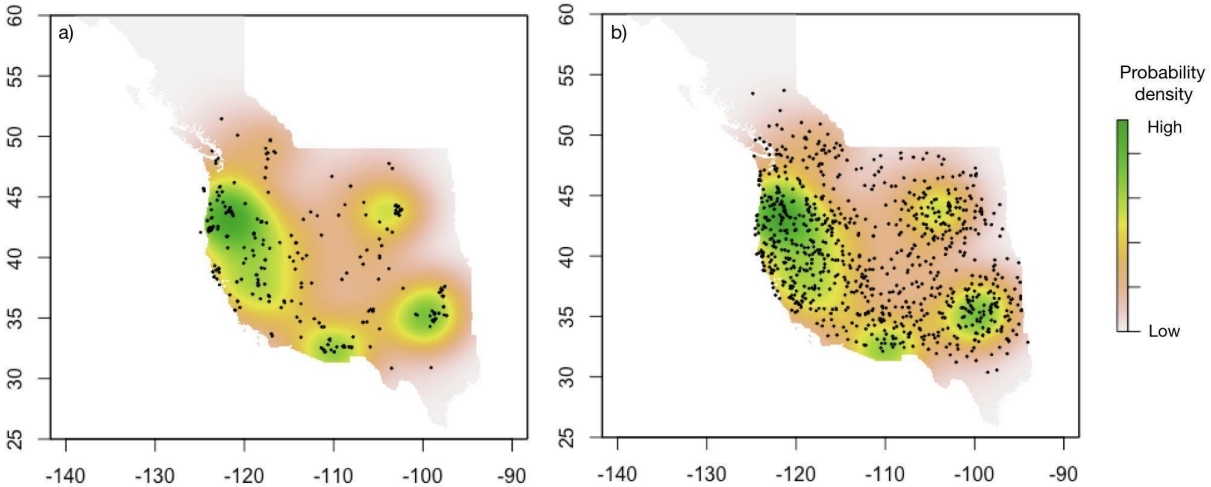


Figure 3. To correct for bias in species occurrence data used to fit winter species distribution models for bat species *Corynorhinus townsendii*, *Myotis californicus*, *Myotis lucifugus*, *Myotis velifer*, and *Perimyotis subflavus* across the United States and Canada, a) presence locations were used to generate a bias grid (i.e., kernel density surface), which was in turn used to b) probabilistically generate background locations that were subject to the same spatial patterns of bias. This example illustrates these steps for *C. townsendii*.

To identify the most appropriate scale for each predictor (i.e., the scale at which habitat selection was most evident), we first fit univariate generalized additive models (GAM; Yee & Mitchell, 1991) for each predictor. We chose GAM for this preliminary predictor selection step to not constrain the form of the response. We selected the best performing scale for each predictor based on a comparison of Akaike's Information Criterion (AIC) scores across each scale at which the predictor was sampled. We then assessed pairwise correlations and variance inflation factors across the resulting set of predictors and excluded those causing standard thresholds of 0.7 and 4.0, respectively, to be exceeded to avoid multicollinearity (Belsley, 1991, Booth et al., 1994). We also excluded mine density from further consideration due to its poorer AIC-based performance across all focal species compared to distance from mines.

We fit and calibrated each BRT model using the stepwise cross-validation process detailed by Elith et al. (2008) and accompanying R scripts (Elith et al., 2008 Appendix S3). We adjusted the model learning rate to ensure that a minimum of 1000 trees were fit, then calibrated the tree complexity (range: 3-5) and bag fraction (range: 0.5-0.7) to minimize deviance. We tested for benefits of dropping uninformative model terms based on estimated reduction in deviance. We then used this 'optimized' model to assess the relative contribution of each predictor, plot the relationship between each predictor and relative occurrence probability, and evaluate model performance. We evaluated the model's fit to the training data (iteratively partitioned in the cross-validation process) based on the mean proportion of deviance explained in each cross-validation iteration, and assessed predictive performance based on the predictive deviance (Elith et al., 2008). Because our models were fit using presence-background data, we do not

follow Elith et al. (2008) in reporting cross-validated area under the receiver operating curve (AUC), as use of this metric to evaluate presence-background models is flawed by ‘contamination’ of background sites with unobserved presence (Boyce et al., 2002, Jimenez-Valverde, 2012, Escobar, 2018). As a final modeling step, we applied the optimized model to predictor values in each 1-km cell of the extent of interest for each species to predict and map relative probability of occurrence (Elith et al., 2008 Appendix S3). We summarized the percentile ranks of occurrence probability values predicted for presence and background locations as an additional assessment of predictive performance. All model fitting and prediction were conducted in R (version 3.4.1; R Core Team, 2019).

Results

After filtering the compiled dataset to unique winter locations, an average of 240 presence locations per species (range: 72-450) were available to fit SDMs (Table 2). Of the neighborhood sizes compared, moderate to large neighborhoods (5-km, 25-km diameter) tended to capture the scale at which bats responded to landscape attributes better than a small neighborhood (500-m), but scale of selection for each attribute varied among species (Table A1). Sampling landscape predictors at finer resolution (1-km) tended to produce stronger relationships with bat occurrence than coarse-resolution sampling (10-km), and the tendency for each predictor to perform best at either a fine or coarse sampling resolution was fairly consistent across species (Table A1).

Table 2. Occurrence data available to inform winter species distribution models for five bat species across the United States and Canada after filtering to unique winter locations. Total records include all raw observations compiled from multiple sources. Winter records were selected based on a spatially explicit model of winter duration informed by bat immergence and emergence observations (Hranac et al. in prep, SI). Unique records were counted after dissolving repeat winter observations (e.g., across multiple studies or survey dates) at a given location.

Species	Total	Winter	Unique
<i>Corynorhinus townsendii</i>	8959	1637	355
<i>Myotis californicus</i>	5920	596	89
<i>Myotis lucifugus</i>	14946	2113	442
<i>Myotis velifer</i>	11152	1688	72
<i>Perimyotis subflavus</i>	7024	2722	284

Optimal BRT parameters varied among species, but higher tree complexity (4-5) and higher bag fractions (0.6-0.7) were favored (Table 3). Model performance was fairly similar across species, with a mean of 54.7-74.4% of the total deviance in the training data explained and predictive deviance of 0.753-0.881. The model for *M. californicus* had the best fit to the data (74.4% deviance explained), while the model for *C. townsendii* had the best predictive performance (0.753 +/- 0.027 predictive deviance). The model for *P. subflavus* had the poorest performance in terms of both fit (54.7% deviance explained) and predictive performance (0.881 +/- 0.027 predictive deviance).

Table 3. Final boosted regression tree (BRT) model parameters and performance metrics for winter species distribution models for bat species *Corynorhinus townsendii*, *Myotis californicus*, *Myotis lucifugus*, *Myotis velifer*, and *Perimyotis subflavus* across the United States and Canada.

Species	Tree complexity	Bag fraction	N trees	Mean total deviance	Mean residual deviance	Mean deviance explained	Predictive deviance (+/- SE)	Mean predicted percentile (presence)	Mean predicted percentile (background)
<i>C. townsendii</i>	5	0.7	3400	1.122	0.391	65.2	0.753 +/- 0.026	89.4	53.6

<i>M. californicus</i>	4	0.7	1850	1.106	0.283	74.4	0.782 +/- 0.072	94.6	56.8
<i>M. lucifugus</i>	5	0.6	4500	1.141	0.409	64.2	0.836 +/- 0.024	80.3	43.4
<i>M. velifer</i>	3	0.6	1800	1.125	0.318	71.7	0.759 +/- 0.041	83.7	38.7
<i>P. subflavus</i>	5	0.5	2300	1.126	0.51	54.7	0.881 +/- 0.027	88.0	58.1

We found considerable interspecific differences in the relative influence of each predictor on occurrence probability (Fig. 4). Ruggedness, topographic position, and percent tree cover were among the most consistently strong contributors, based on mean relative influence across species (11.64% +/- 1.96 SD, 9.62% +/- 4.14 SD, and 9.62% +/- 2.31 SD, respectively). Winter survivorship, on average, also had high influence, but its influence varied considerably across species (9.58% +/- 6.67 SD). Karst had the lowest influence overall (mean 4.6% +/- 3.31 SD, though it was not considered in the *M. lucifugus* model).

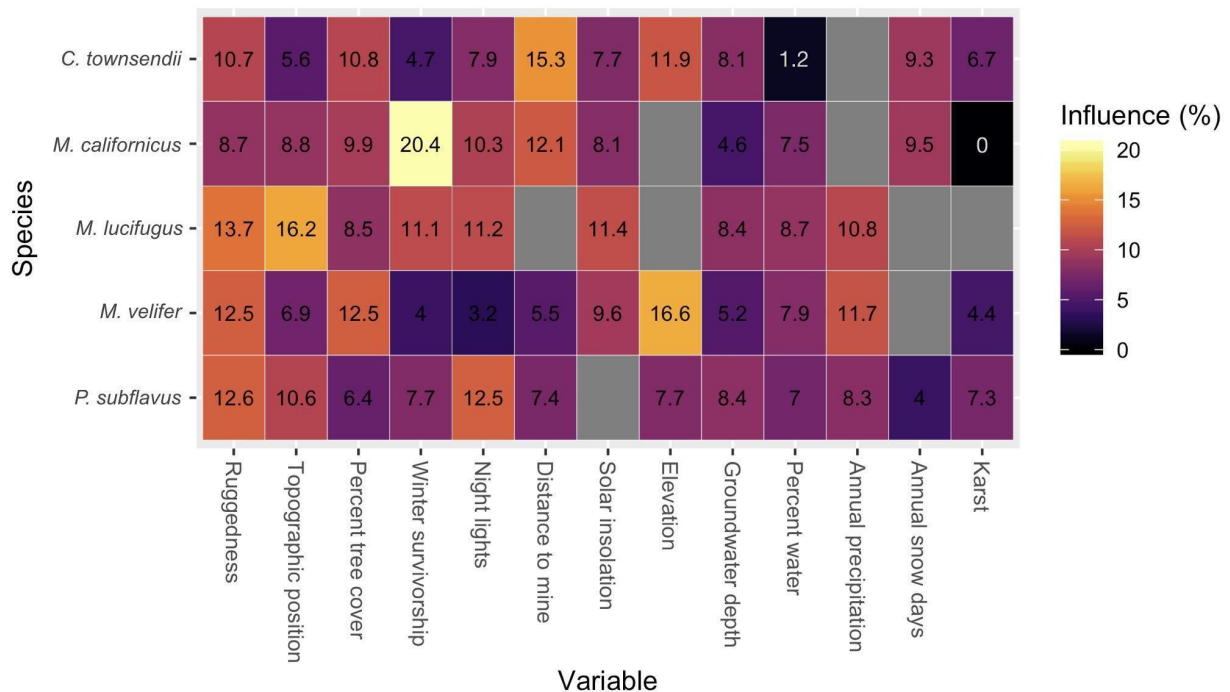
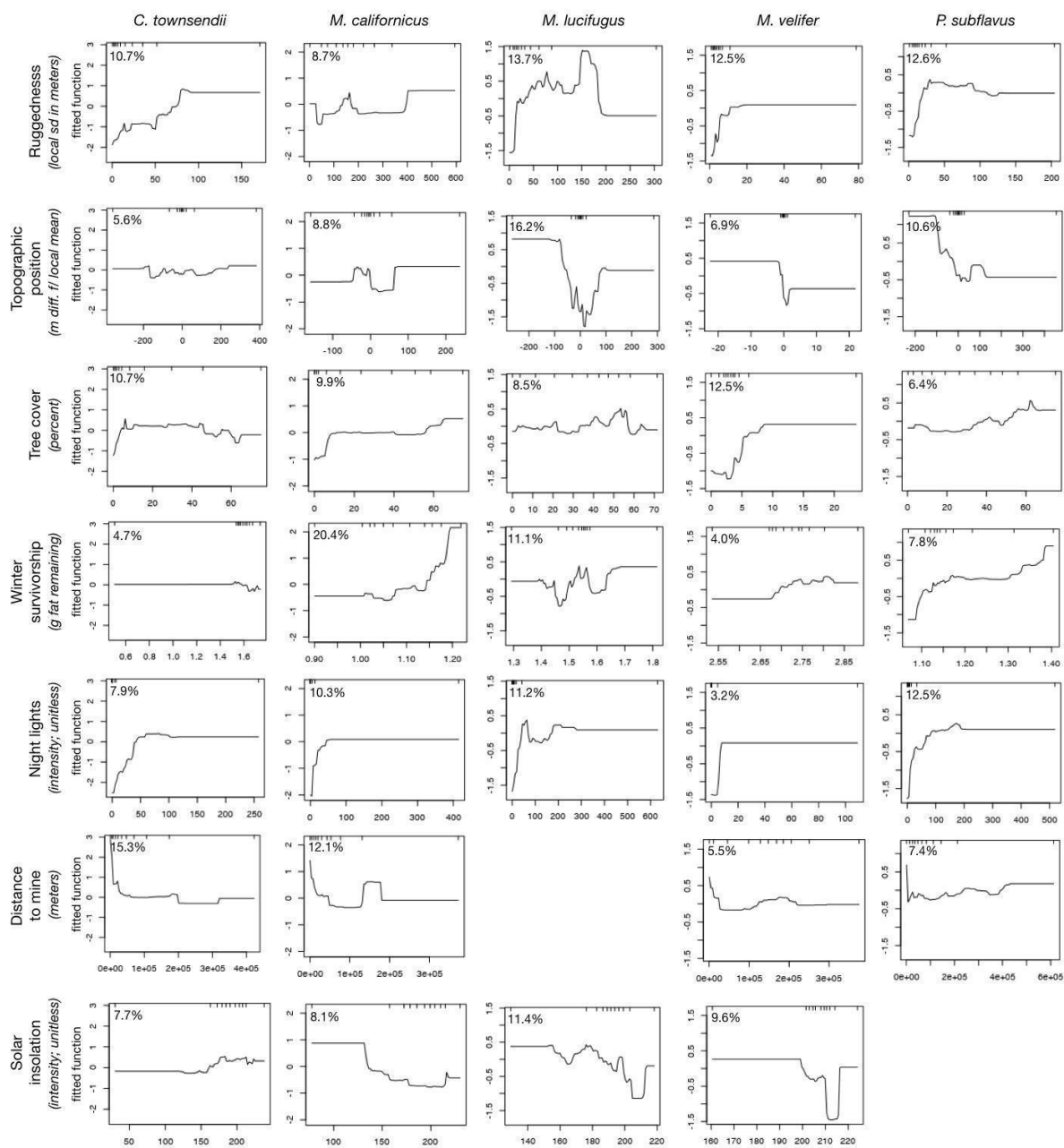


Figure 4. Final predictor influences in boosted regression tree (BRT) models estimating winter species distributions of bat species *Corynorhinus. townsendii*, *Myotis. californicus*, *Myotis. lucifugus*, *Myotis. velifer*, and *Perimyotis. subflavus* across the United States and Canada. Brighter colors indicate higher influence; predictors that were dropped from a given model are shown in gray. Variables are ordered by their average influence across species (decreasing left to right).

Consistency in a predictor's degree of influence across species did not necessarily correspond to similar relationships between that predictor and relative occurrence probability among species (Fig. 5). The effect of ruggedness was fairly consistent among species, with low relative occurrence probability predicted in very flat, open areas (very low ruggedness). *M. velifer*, and particularly *P. subflavus* appeared to favor low topographic positions (i.e., canyon bottoms); *M. lucifugus* also showed this pattern, in addition to an avoidance of open, flat topography (topographic position ~ 0). Relationships with solar insolation and elevation varied widely. For example, *C. townsendii* showed some preference for low elevations with high insolation, while *M. velifer* selected for low elevation, low insolation sites and *P. subflavus* preferred higher elevations (elevation was excluded from models for *M. californicus* and *M. lucifugus* due to high collinearity with other predictors). Occurrence probability generally increased with predicted winter survivorship, as expected, particularly in species for which survivorship had strong

influence (*M. californicus*, *M. lucifugus*, *P. subflavus*). Similarly, occurrence probability was generally higher with greater tree cover and fewer days of snow annually. The shape and direction of responses to groundwater depth, surface water, and annual precipitation (excluded from *C. townsendii* and *M. californicus* models due to collinearity) were highly variable. Before correcting for bias in presence locations, night lights were a strong predictor of most species' occurrence, but this relationship primarily reflected the distribution of sampling effort, not distribution of the species of interest. Still, even after correcting for sampling bias closer to human habitation, all species had very low relative probability of occurrence where night light intensity was lowest (darkest). However, in all species the rest of the response curve is quite flat, indicating minimal lingering effect of night lights in the models. Similarly, occurrence probability tended to be highest very close to mines, but beyond a minimum distance, the presence of mines had little effect on species distributions. Three species showed evidence of a preference for karst features (karst could not be considered for *M. lucifugus* due to missing karst data in portions of the species' range).



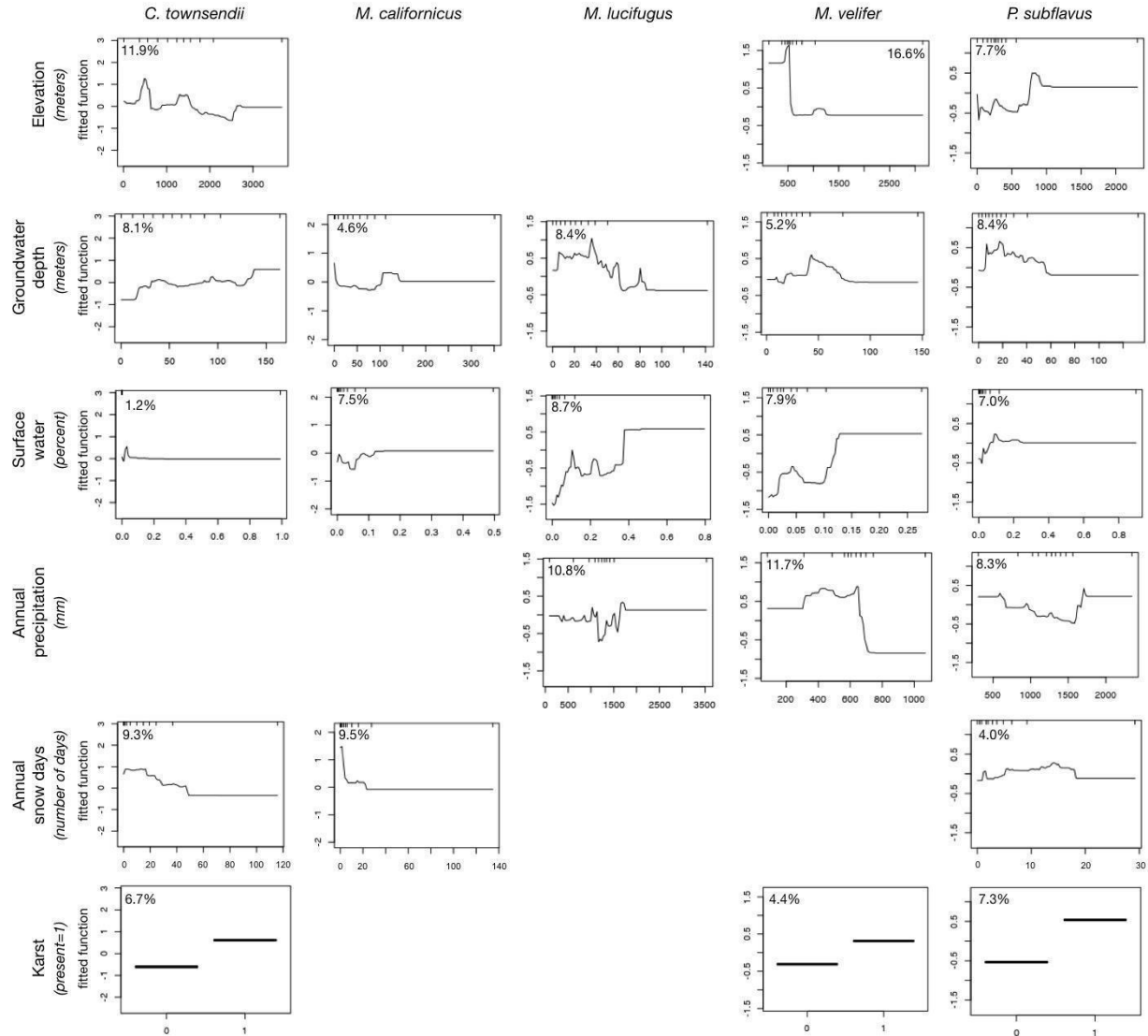


Figure 5. Fitted probability of occurrence functions for each predictor from boosted regression tree (BRT) models estimating winter species distributions of bat species *Corynorhinus townsendii*, *Myotis californicus*, *Myotis lucifugus*, *Myotis velifer*, and *Perimyotis subflavus* in the United States and Canada. Variables are ordered by their average influence across species; percentages indicate the relative influence of each predictor in the model. Rug plots (i.e., tic marks) indicate the deciles of the distribution of predictor values represented in the full presence/background location dataset.

We observed high relative probability of occurrence at presence locations compared to background locations, as expected (Table 3, Figs. 6-7, Figs. A1-A4). The mean percentile rank of predicted occurrence probability at presence locations ranged from 80.3 (*M. lucifugus*, *M. velifer*) to 94.6 (*M. californicus*), 29.9 - 45 percentile points higher than the mean values predicted for background locations. In some cases, conspicuous exclusions and inclusions evident in existing species range extents (e.g., exclusion of Great Plains for *C. townsendii*, exclusion of Texas panhandle and mid-Atlantic coast for *M. lucifugus*, inclusion of Great Salt Lake area for *M. californicus*, inclusion of Arizona's Sky Islands for *M. velifer*) are mirrored by low and high predicted probabilities, respectively. Often, areas outside the focal species' known ranges have high predicted occurrence probability, reflecting the similarity of landscape attributes in these areas to those of known presence locations. Conversely, areas with low

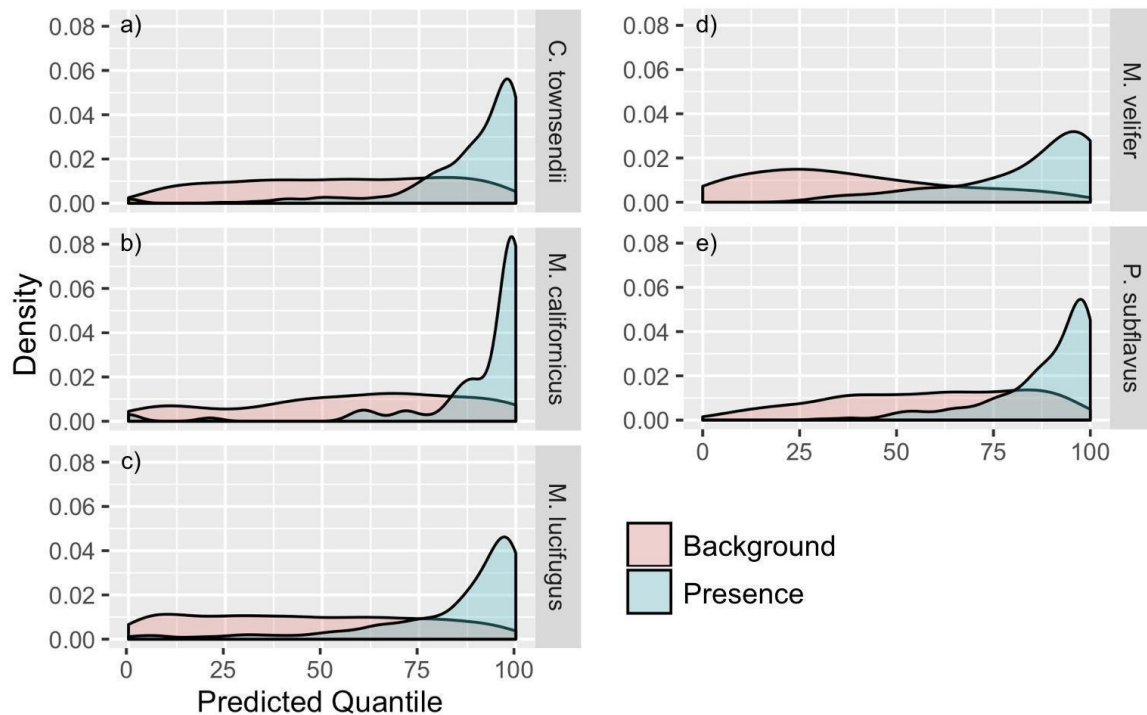


Figure 7. Distributions of predicted relative probability of occurrence of a) *Corynorhinus townsendii*, b) *Myotis californicus*, c) *Myotis lucifugus*, d) *Myotis velifer*, and e) *Perimyotis subflavus* in the United States and Canada at presence locations (green) compared to background locations (pink).

Discussion

This study provides insights into the drivers and spatial patterns of bat hibernaculum selection in the West - a topic that is poorly understood, yet critical for advancing bat research, conservation, and management of WNS impacts. We demonstrate that the nature and scale of bats' responses to the landscape when selecting hibernacula varies among species and across different landscape attributes. Our results point to ranges of landscape attribute values where each focal species may be most likely to hibernate and highlight the importance of protecting mine features as hibernacula for multiple species. Importantly, our findings indicate that topographic attributes are important predictors of hibernaculum selection, suggesting that bat winter occurrence can, in part, be predicted from readily mapped above-ground features. We also found that our mechanistic estimate of winter survivorship contributed to prediction of winter occurrence probability for all focal species; in one case (*M. californicus*), it was by far the strongest predictor.

Because so little is known about how bats choose winter hibernacula and bat winter distributions in the West have never been modeled, we felt it was important to use methods that allow for flexible, nonlinear relationships between predictors and relative probability of occurrence. Peaks in our modeled response curves may help to identify ranges of preferred attributes (e.g., preferred elevation bands or density of forest cover). Flat portions of response curves may indicate an absence of selection (e.g., beyond a threshold distance, bats don't care how far they are from the nearest mine) or they may indicate ranges of attribute values where we simply have no data (see wide gaps in decile rug plots on response curves, Fig. 5). Our use of bias correction when generating background locations (Hertzog et al., 2014) impacted model results and was important given the opportunistic sampling of winter bat locations reflected in

the public databases we relied on. Prior to bias correction, night lights were a strong predictor of most species' occurrence probability and suggested a preference for more intense night lights, but this uncorrected result would have reflected the distribution of sampling effort rather than the ecology of the focal species.

Although topographic attributes were often strong predictors of hibernaculum selection, preferred topographic characteristics (e.g., high versus low topographic position) varied among species. Karst presence was a weak predictor, perhaps because we did not consider differential selection among different types or depths of karst, or because the available map of karst features does not necessarily indicate where karst features are accessible to bats via caves or crevices. Mines were clearly important features for several species, and their relative influence appeared to scale sensibly with species' tendency to use mines: influence was lowest for *M. velifer* (Cave myotis), which is more frequently found in caves. Our models suggest the importance of generating and making public spatial karst and mine datasets in other Canadian provinces to better predict occurrence for *M. lucifugus* and other species frequently found in mines in these regions. Our results support the preservation of western mines as critical winter habitat for which there are significant opportunities to enhance existing protected area status (Weller et al., 2018).

Our mechanistic winter survivorship estimate (Hranac et al. in prep) contributed to all species' predicted occurrence, but to varying degrees. The direction of the relationship between survivorship and relative occurrence probability was positive overall, as expected, but its strength varied among species. This complex, model-based estimate of survivorship is unavoidably subject to uncertainty, but it has greater direct relevance to winter bat distributions than generic climate metrics (e.g., mean surface temperature) with no mechanistic link to bat physiology. Future quantitative comparisons between predictions from this mechanistic predictor and those generated using standard, off-the-shelf climate predictors may be of interest. We also see worthwhile opportunities to continue honing this survivorship model as additional empirical data for parameterization become available (e.g., for estimating species-specific, spatially explicit winter duration, better estimating subterranean temperatures and humidity experienced by hibernating bats and how they respond physiologically).

The maps of relative occurrence probability presented here (Figs. 6, A1-A4) should help to guide future work to survey and monitor western bat populations, inform future conservation efforts, and provide a baseline for understanding potential impacts of future change, namely the spread of WNS through the West and climate change. These maps should be interpreted with care outside the known range of each species, as places with predictor values similar to those currently occupied will be highlighted but other limits on species distributions (e.g., historic spread processes, species interactions) may exist that were not captured here. Occurrence probability of generalist species with broad geographic ranges is particularly difficult to model effectively (Hernandez et al., 2006, Razgour et al., 2016). Predictive maps for such species (e.g., *M. lucifugus*, *P. subflavus*), which have lower predictive performance, should be interpreted with caution. Still, we expect that these maps can be useful for considering the potential occurrence of the focal species in areas predicted to be suitable beyond their coarsely mapped range extents, which are likely inaccurate or out of date in some areas. Places that are predicted to have low occurrence probability may in fact be unlikely to support hibernacula, or they may simply have attributes not well represented in our presence data. These areas should be considered in the context of existing knowledge of the focal species and their hibernation patterns: Do these places lack karst or mine features, topographic relief, or trees to shelter hibernating bats? Or are they simply remote and characterized by rare landscape features that were underrepresented in our sample? It is also important to recognize that mapped occurrence

probabilities are relative values. We cannot estimate absolute occurrence probability from the available data, and our estimates may not be strictly proportional to absolute probability. The predicted values should be interpreted as rank probabilities, as reflected by the quantile symbology used in our maps (Fig. 6, Figs. A1-A4).

These are complex models based on relatively small sample sizes, so uncertainty remains and portions of the predictor space are undersampled. We may also be missing key predictors that we simply don't yet understand to be important for hibernaculum selection or cannot map continuously with currently available spatial data. Future efforts to improve on these models would benefit from additional winter location data (particularly for species other than *C. townsendii* and *M. lucifugus*) in novel locations. Future survey efforts could perhaps target places predicted to be highly suitable but where no occurrence data exist (e.g., *M. californicus* in the Great Salt Lake region, *M. velifer* in south Texas and northeast Arizona), or places with landscape characteristics not well represented in the current sample. Absence data would improve the robustness of distribution models considerably (e.g., in comprehensive survey and monitoring efforts, which species were searched for but not found?), although reliable absences would be extremely difficult to obtain (due to low detection probabilities that vary with survey techniques and site characteristics).

Winter hibernation is clearly a critical part of temperate bats' annual cycle, yet it is largely a black box for many species; we have only limited knowledge of where these widely-distributed species go for approximately half the year or what drives them there. This lack of understanding of the ecology of these species hinders conservation and management responses to ongoing and future threats to their persistence. Insights from SDMs are valuable for locating, studying, and managing species with low detectability (Razgour et al., 2016). SDMs may also help to define winter critical habitat for bats, as they have for other species (Heinrichs et al., 2010, Brotons et al., 2004). Unlike the East, there has simply not been a 'where' on which to focus conservation policy in the West; models like ours could begin to fill this gap.

Our study also paves the way for assessment of the potential impacts of WNS and climate change on western bats, as well as their interactions. Prediction of species distributions under altered spatial patterns of winter survivorship in the presence of *P. destructans* and future climate conditions may help to identify species and places most threatened by these stressors. We expect these predictions to have important implications for bat conservation and management in the West, such as informing placement of passive acoustic detectors for monitoring or understanding the distribution of at-risk and stable hibernacula across federal, state, and private lands to guide engagement strategies for conservation.

Data Availability Statement

Original bat occurrence spatial data used in this analysis cannot be made available because they were obtained from third parties. While some of the data are available from public repositories and published literature (see Methods), others are protected by data sharing agreements due to the sensitive nature of hibernaculum location information to protect these sites from vandalism or exploitation. However, we make our complete analytical dataset, stripped of spatial identifiers, available via Dryad (link TBD). This includes all sampled predictor values and predicted relative occurrence probabilities for all bat presence points and accompanying bias-corrected background points.

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Biosketch

The members of the research team bring diverse interests and areas of expertise together - including disease ecology, physiology, wildlife health, behavioral ecology, landscape ecology, and conservation biology - to explore the ecology and management of WNS disease dynamics under non-stationary conditions.

Author contributions: SHO, LPM, DH, CLL, RKP, and BGD conceived the study, and MM and CGH developed the modeling approach. CRH, CGH, and DTSH developed the hibernation bioenergetic model; CRH spatially interpolated the results. CGH, NWF, SHO, and CLL collected a subset of the bat occurrence data, and DC compiled and supported analysis of the occurrence data. MLM derived and compiled predictor data, designed and conducted the final analyses, and drafted the manuscript, CGH and BGD supported design of the analyses, and all contributed to paper framing and revision.

Appendix

Table A1. Final predictor sets and their relative influences in boosted regression tree (BRT) models used to estimate winter species distributions of five focal bat species across the United States and Canada, including a) *Corynorhinus townsendii*, b) *Myotis californicus*, c) *Myotis lucifugus*, d) *Myotis velifer*, and e) *Perimyotis subflavus*.

a) *Corynorhinus townsendii*

Variable	Neighborhood size	Sample resolution	Relative influence
Distance to mine	--	10 km	15.32
Elevation	--	10 km	11.94
Percent tree cover	5 km	1 km	10.75
Ruggedness	500 m	1 km	10.65
Annual snow days	--	1 km	9.34
Groundwater depth	--	10 km	8.13
Night lights	--	1 km	7.92
Solar insolation	Multiscale	1 km	7.73
Karst	--	1 km	6.74
Topographic position	5 km	1 km	5.61
Winter survivorship	--	1 km	4.66
Percent water	500 m	1 km	1.2

b) *Myotis californicus*

Variable	Neighborhood size	Sample resolution	Relative influence
Winter survivorship	--	10 km	20.39
Distance to mine	--	1 km	12.13
Night lights	--	1 km	10.33
Percent tree cover	5 km	10 km	9.88
Annual snow days	--	1 km	9.53
Topographic position	Multiscale	10 km	8.83
Ruggedness	25 km	1 km	8.68
Solar insolation	5 km	1 km	8.1
Percent water	25 km	10 km	7.53
Groundwater depth	--	1 km	4.6

c) *Myotis lucifugus*

Variable	Neighborhood size	Sample resolution	Relative influence
Topographic position	Multiscale	1 km	16.22
Ruggedness	Multiscale	1 km	13.68
Solar insolation	25 km	10 km	11.36
Night lights	--	1 km	11.15
Winter survivorship	--	10 km	11.11
Annual precipitation	--	10 km	10.78
Percent water	5 km	1 km	8.73
Percent tree cover	25 km	1 km	8.54
Groundwater depth	--	10 km	8.44

d) *Myotis velifer*

Variable	Neighborhood size	Sample resolution	Relative influence
Elevation	--	10 km	16.57
Ruggedness	500 m	10 km	12.48
Percent tree cover	25 km	1 km	12.46
Annual precipitation	--	10 km	11.71
Solar insolation	25 km	1 km	9.61
Percent water	25 km	1 km	7.9
Topographic position	500 m	1 km	6.91
Distance to mine	--	10 km	5.51
Groundwater depth	--	10 km	5.24

Karst	--	1 km	4.44
Winter survivorship	--	1 km	3.99
Night lights	--	10 km	3.17

e) *Perimyotis subflavus*

Variable	Neighborhood size	Sample resolution	Relative influence
Ruggedness	5 km	1 km	12.61
Night lights	--	1 km	12.54
Topographic position	25 km	1 km	10.6
Groundwater depth	--	10 km	8.42
Annual precipitation	--	1 km	8.26
Winter survivorship	--	10 km	7.77
Elevation	--	10 km	7.74
Distance to mine	--	10 km	7.37
Karst	--	1 km	7.28
Percent water	5 km	1 km	7.05
Percent tree cover	5 km	1 km	6.4
Annual snow days	--	10 km	3.97

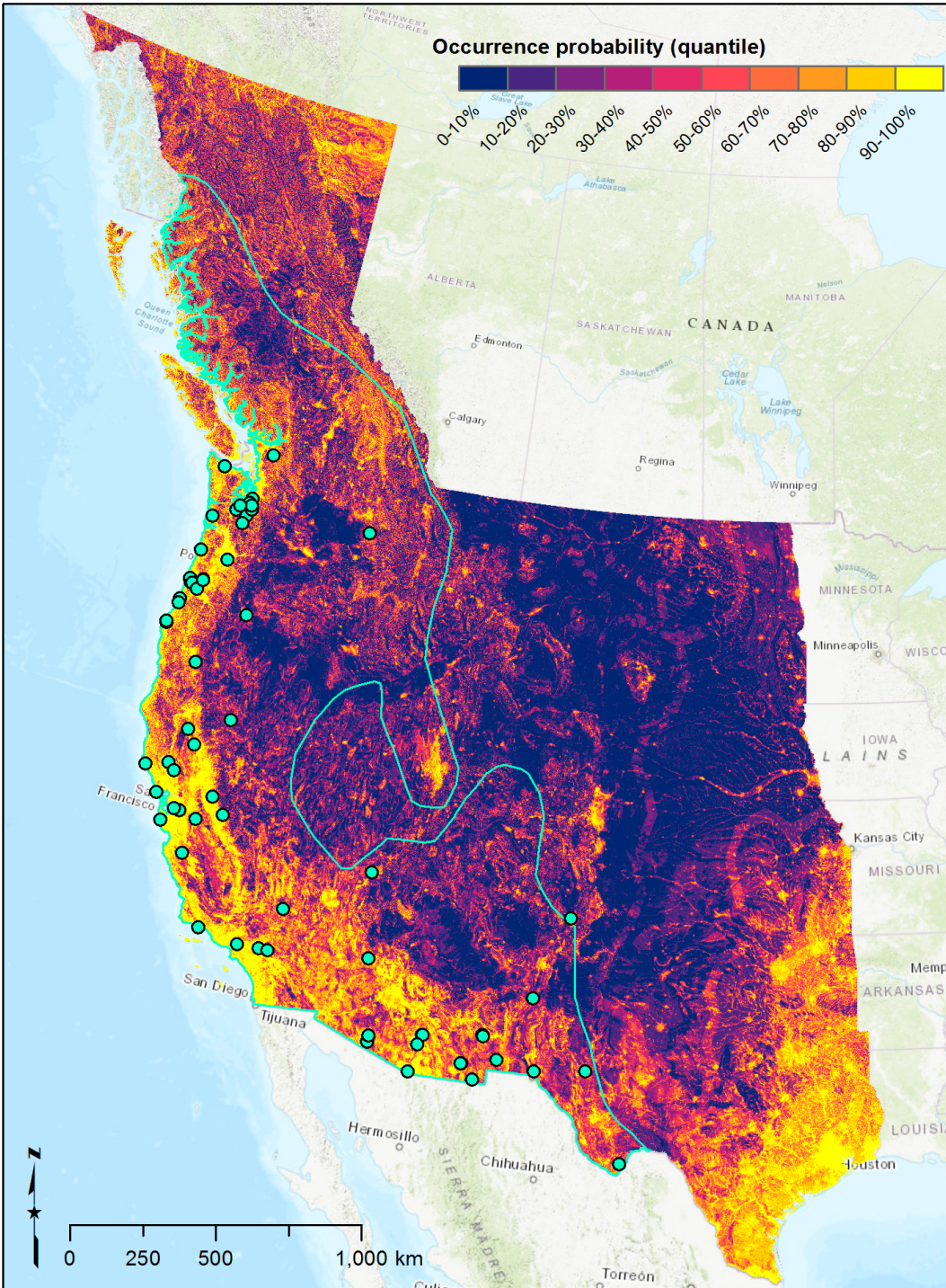


Figure A1. Predicted relative probability of occurrence of *Myotis californicus* (predictive deviance = 0.782 $\pm$ 0.072) across the western U.S. and British Columbia. The species' current range extent (turquoise outline) and winter occurrence locations used to fit the model are overlaid (turquoise points).

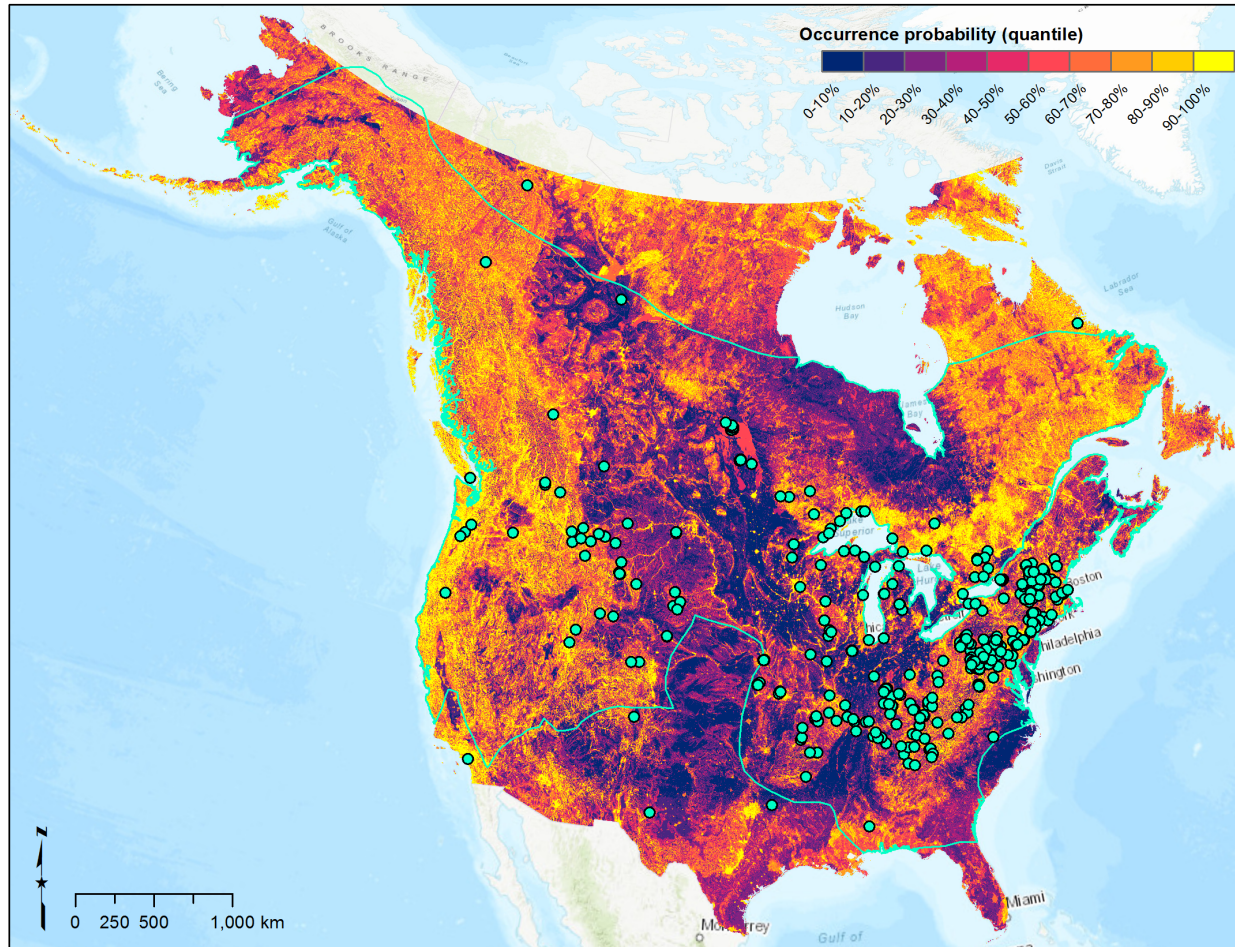


Figure A2. Predicted relative probability of occurrence of *Myotis lucifugus* (predictive deviance = 0.836 ± 0.024) across the U.S. and Canada (below the Arctic Circle). The species' current range extent (turquoise outline) and winter occurrence locations used to fit the model are overlaid (turquoise points).

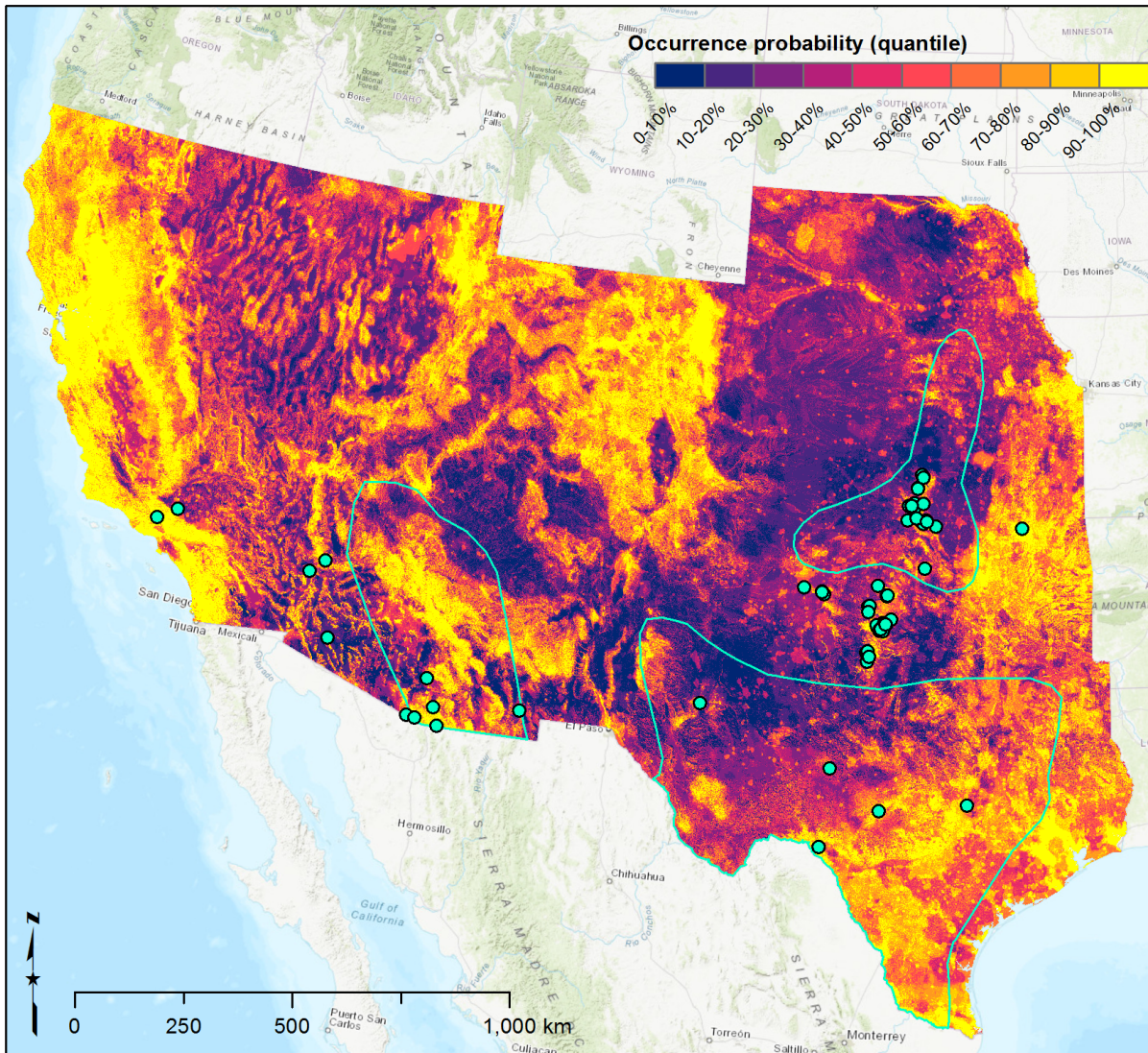


Figure A3. Predicted relative probability of occurrence of *Myotis velifer* (predictive deviance = 0.759 ± 0.041) across the southwestern U.S. The species' current range extent (turquoise outline) and winter occurrence locations used to fit the model are overlaid (turquoise points).

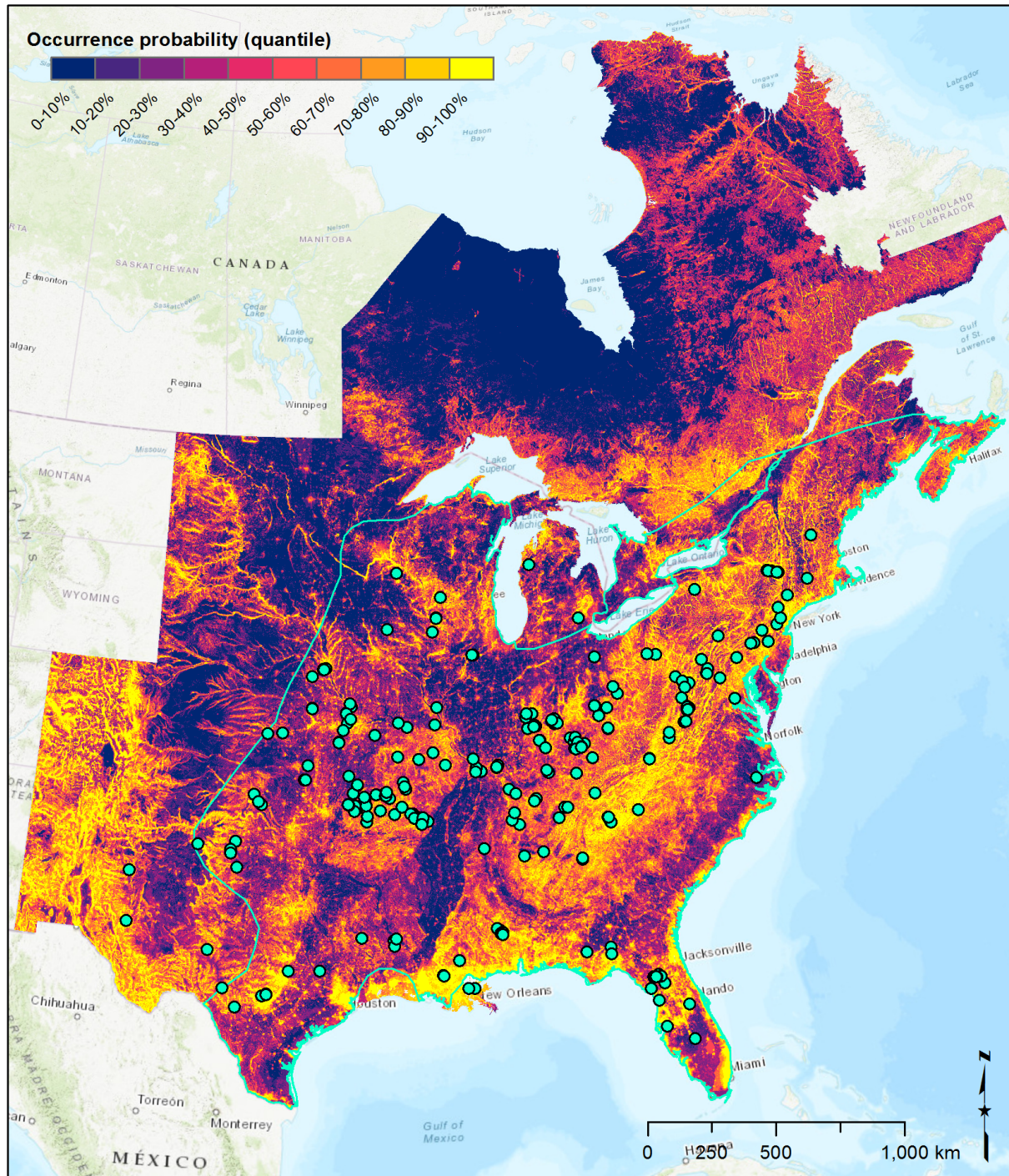


Figure A4. Predicted relative probability of occurrence of *Perimyotis subflavus* (predictive deviance = 0.881 +/- 0.027) across the eastern and central U.S. and eastern Canada. The species' current range extent (turquoise outline) and winter occurrence locations used to fit the model are overlaid (turquoise points).