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A hybrid correlative-mechanistic approach for modeling winter distributions of North American bat species

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Abstract

Aim: The fungal pathogen *Pseudogymnoascus destructans* and resultant white-nose syndrome (WNS) continues to advance across North America, infecting new bat hibernacula. Western North America hosts the highest bat diversity in the United States and Canada, yet little is known about hibernacula and hibernation behaviour in this region. An improved understanding of the distribution of suitable hibernacula is critical for land managers to anticipate conservation needs of WNS-susceptible species in currently uninfected regions.

Location: United States, Canada.

Taxon: Bats.

Methods: We estimated suitability of potential winter hibernaculum sites across five bat species' ranges. We estimated winter survival capacity from a mechanistic survivorship model based on bat bioenergetics and climate conditions. We then used boosted regression trees to relate these estimates, along with key landscape attributes, to bat occurrence data in a hybrid correlative-mechanistic approach.

Results: Winter survival capacity, topography, land cover and access to subterranean features were important predictors of winter hibernaculum selection, but the shape and relative importance of these relationships varied amongst species. This suggests that the occurrence of bat hibernacula can, in part, be predicted from readily mapped above-ground features, not just below-ground characteristics for which spatial data are lacking. Furthermore, our mechanistic estimate of winter survivorship was, on average, the third strongest predictor of winter occurrence probability across focal species.

Main conclusions: Winter distributions of North American bat species were driven by their physiological capacity to survive winter conditions and duration in a given location, as well as selection for topographic and other landscape features but in species-specific ways. The influence of winter survivorship on several species' distributions, the underlying influence of climate conditions on winter survivorship and the anticipated influence of WNS on bats' hibernation physiology and survivorship together suggest that North American bat distributions may undergo future shifts as these species are exposed not only to WNS but also to climate change.

KEYWORDS
bat, bioenergetic model, hibernation, hybrid, North America, species distribution model, white-nose syndrome, winter

1 | 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 that is rapidly spreading across the continent with dire consequences for hibernating bat populations (Frick et al., 2015; Leopardi et al., 2015). In response to this novel threat, hibernating bats have been studied intensively in eastern North America. In western North America (an arbitrary distinction often defined as west of the Mississippi River, herein the West), where WNS has only recently begun to appear (United States Fish & Wildlife Service, 2021), bat hibernation is far less understood. The West harbours 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; Weller et al., 2018). This hibernation behaviour, 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 (United States Fish & Wildlife Service, 2021) and as climate change impacts bat populations (Sherwin et al., 2013), 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 minimise impacts to vulnerable populations.

When species ecology is poorly understood, species distribution models (SDMs) help fill a wide variety of information needs (Rodríguez et al., 2007). A first, necessary 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; Jarnevich 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; Johnston et al., 2012; La Manna et al., 2008).

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 quantify the characteristics of sites where a species has been observed, often comparing them 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 (i.e. shelters in which to hibernate, such as caves) are largely unknown, and because key subterranean habitat attributes are not visible to remote sensing platforms, continuous data over large extents are rarely available. Efforts to model bat distributions, space use and habitat selection have increased rapidly in recent years (e.g. Burke et al., 2019; Delgado-Jaramillo et al., 2020; Razgour et al., 2016; Zamora-Gutierrez et al., 2018). Few, however, have attempted to model distributions of winter hibernacula (but see Russell et al., 2014; Smeraldo et al., 2018; Weller et al., 2018) or focused on western North America (but see Rodhouse et al., 2012, 2015; Weller et al., 2018). 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 (Speakman & Thomas, 2003; Thomas et al., 1990). Climate metrics (e.g. mean annual temperature and 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 (Haase et al., 2019; Hayman et al., 2016; Johnson et al., 2014; Langwig et al., 2012, 2016). 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 fit correlative SDMs to relate 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. Martínez et al., 2015; McClure et al., 2015).

Here, we integrated a bioenergetic model of bat hibernation (Haase et al., 2019; Hayman et al., 2016; Hranac et al., 2021) into a correlative species distribution modeling approach to predict winter distributions of bat species whose ranges extend into the West. 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 (or habitat suitability) across the areas encompassing our focal species' known range extents. We included this along with other landscape attributes (e.g. topography, vegetation cover and karst and mines) to fit SDMs 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.

2 | MATERIALS AND METHODS

2.1 | 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 habitat requirements amongst hibernating bats whose ranges lie in whole or in part in the West, defined here as west of the Mississippi River (Figure 1; National Atlas of the United States, 2011).

We compiled species occurrence data from multiple sources, including online databases of museum records (VertNet, National Science Foundation (NSF), 2016, Biodiversity Information Serving Our Nation, United States Geological Survey (USGS), 2012), online repositories of vetted public and scientific observations (Global Biodiversity Information Facility, GBIF.org, 2018, Bat Population Database, United States Geological Survey (USGS), 2003), data associated with published literature (Dubois & Monson, 2007; Kuenzi et al., 1999; Ports & Bradley, 1996), data obtained from multiple Natural Heritage Programs (NHP; Montana Natural Heritage Program, 2020; NatureServe, 2019) 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.

We included only in-hand or visual observations (i.e. no acoustic detections) with dates of record since 1948 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 and hibernation-specific manner. We first used a generalised linear model informed by the timing of *M. lucifugus* immergence and emergence observations at hibernacula throughout North America (Hranac et al., 2021, Supporting Information) to estimate winter duration for each 1 km raster cell across the United States and Canada. Then, to estimate the start and end date of winter hibernation at a given grid cell, we centred this model-based winter duration estimate on the winter solstice. Finally, we selected only occurrence records observed between these spatially explicit start and end dates. Lastly, we removed repeat observations (e.g. across multiple studies or survey dates), retaining a single record for a given site (with unique sites defined to the nearest thousandth of a degree of latitude and longitude).

2.2 | Predictor variables

We identified landscape attributes that potentially influence hibernaculum conditions and selection from the published literature and our own knowledge (Table 1 and Figure SA1). 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 amongst species, attributes and locales (see Bellamy et al., 2013; Ducci et al., 2015; Razgour et al., 2011). We therefore derived predictor variables at multiple spatial scales (i.e. different neighbourhood sizes or the radius around each focal raster cell across which predictor values were smoothed) where applicable for comparison (Table 1). Our selection of neighbourhood sizes, which included 500 m, 5 km, and 25 km, was guided by those to which bats were found to respond in previous studies of multiscale

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

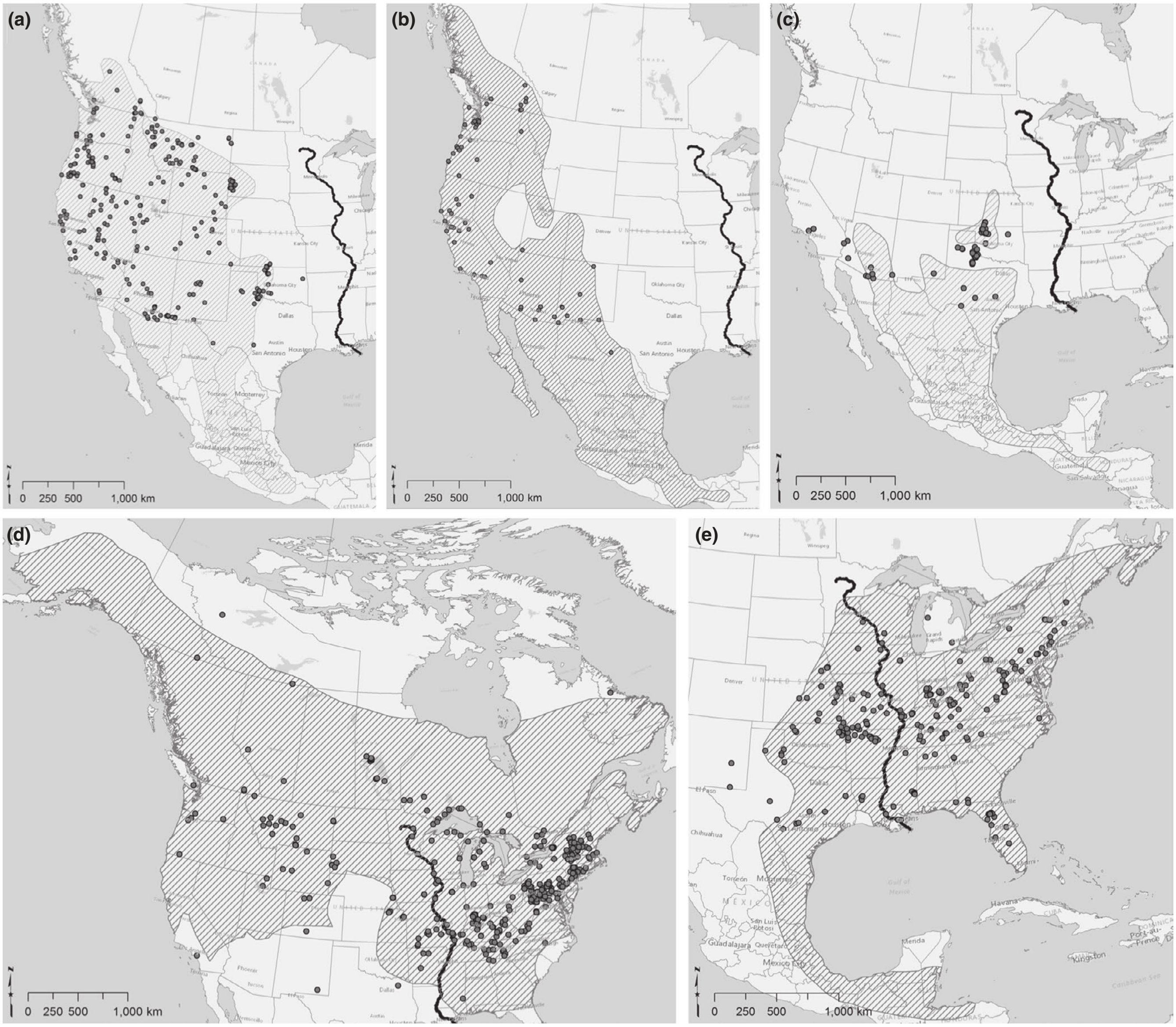

FIGURE 1 Current geographic range maps overlaid with winter presence locations available to inform species distribution models across the United States and Canada for five focal species (a) *Corynorhinus townsendii*, (b) *Myotis californicus*, (c) *Myotis velifer*, (d) *Myotis lucifugus* and (e) *Perimyotis subflavus*. The Mississippi River demarcating the West is shown in bold. All maps use the USA Contiguous Albers Equal Area Conic projection

habitat selection (100 m to 10 km; Bellamy et al., 2013; Ducci et al., 2015). However, these studies focused on response to the landscape during daily foraging bouts, and we felt it was important to consider a broader range of spatial scales for selection of a winter hibernaculum. All smoothing of predictor variables using each of the selected neighbourhood sizes was performed at the native resolution of each variable prior to sampling. Thus, for a variable with native resolution of 30 m, we summarised values within 500 m, 5 km and 25 km of each focal 30-m cell. Each layer was then aggregated to two scales, 1 and 10 km, for sampling. This step offered a means of exploring the scale of bats' response to those variables to which we could not reasonably apply the above range of neighbourhood sizes, either due to the coarse native resolution of the variables or because application of varying neighbourhood sizes did not make intuitive sense. All predictors were derived and/or sampled using Google Earth Engine, a cloud-based computing platform supporting large-scale analysis on an extensive catalogue of remotely sensed, climatological and other geospatial datasets (Gorelick et al., 2017). All final predictive maps were derived at a resolution of 1 km.

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 parameterised for western bat species. Full details are elsewhere (Haase et al., 2019; Hranac et al., 2021), but briefly, the model uses the hypothesised 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 80 times less energy per unit

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	Rationale (references)	Source data	Resolution	Neighbourhood size
Winter survivorship	Defines physiological response to climate conditions, seasonality (Hayman et al., 2016)	(Haase et al., 2019; Hranac et al., 2021)	1 km	—
Distance to mines	Hibernaculum availability (Weller et al., 2018)	USGS MRDS[1], BC MinFile[2]	1 km	—
Mine density	Hibernaculum availability (Weller et al., 2018)	USGS MRDS, BC MinFile	1 km	25 km
Karst	Hibernaculum availability (Burke et al., 2019; Cooper-Bohannon et al., 2016; Russell et al., 2014; Weller et al., 2018)	(Weary & Doctor, 2014; Forest Analysis & Inventory, 2019)	1 km	—
Elevation	Affects local climate, vegetation[a] (Burke et al., 2019; Cooper-Bohannon et al., 2016; Delgado-Jaramillo et al., 2020; Smeraldo et al., 2018; Weller et al., 2018)	ALOS[3] Digital Surface Model v2 (Tadono et al., 2014)	30 m	—
Ruggedness	Proxy for availability of crevices/caves, diverse exposure conditions (Perry et al., 2013)	ALOS Digital Surface Model v2 (Tadono et al., 2014)	30 m	500 m, 5 km, 25 km, multiscale
Topographic position	Affects local climate norms and variability (cold sinks, inversions; Perry et al., 2013)	ALOS Digital Surface Model v2 (Tadono et al., 2014)	30 m	500 m, 5 km, 25 km, multiscale
Solar insolation	Affects local climate norms & variability (de Boer et al., 2013; Perry et al., 2013)	ALOS Digital Surface Model v2 (Theobald et al., 2015)	30 m	500 m, 5 km, 25 km, multiscale
Annual precipitation	Affects local climate, vegetation, water availability (Weller et al., 2018; Zamora-Gutierrez et al., 2018)	DayMet v3 (Thornton et al., 2019)	1 km	—
Annual snow days	Insulation effect, water availability (Burke et al., 2019; Perry et al., 2013; Smeraldo et al., 2018; Zamora-Gutierrez et al., 2018, precipitation seasonality)	MODIS[4] Global Daily Snow Cover v6 (Hall et al., 2016)	500 m	—
Percent water	Water availability (Cooper-Bohannon et al., 2016; de Boer et al., 2013; Razgour et al., 2018; Smeraldo et al., 2018, distance from water)	JRC[5] Yearly Water Classification v1 (Pekel et al., 2016)	30 m	500 m, 5 km, 25 km, multiscale
Groundwater depth	Proxy for potential water flow within caves/mines (Perry et al., 2013)	(Fan et al., 2013)	1 km	—
Percent tree cover	Shade effect, roost availability in active seasons (de Boer et al., 2013; Perry et al., 2013; Russell et al., 2014)	MODIS Vegetation Continuous Fields[6] (DiMiceli et al., 2019)	250 m	5 km, 25 km
Night lights	Proxy for intensity of human development/activity; some bats hibernate in human structures (de Boer et al., 2013, cover by built-up areas, Razgour et al., 2018, distance from urban)	DMSP Radiance-Calibrated OLS[7] v4[8] (National Oceanic and Atmospheric Administration (NOAA), 2016)	30 arcsec	—

Note: The reasoning and precedence for consideration of each predictor are summarised under 'Rationale', noting (in parentheses) where cited studies used slightly different form of a predictor (e.g. percent water vs. distance from water).

[a] Surrounding vegetation composition may affect availability of insect prey and roost sites in active seasons. 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.

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. Using gridded spatial data, we applied the model to values of each 1 km grid cell 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 km^2 raster cell. Higher, positive predicted values are expected to correspond to high survivorship, whilst 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 Supporting Information.

2.2.1 | 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. Dickson & Beier, 2007; Guisan et al., 1999). 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.

2.2.2 | Surface attributes

We derived percent tree cover from the Terra MODIS Vegetation Continuous Fields product, which estimates subpixel-level surface vegetation cover globally, including percent tree cover, on an annual basis (250-m resolution; DiMiceli et al., 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; National Oceanic and Atmospheric Administration (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.

2.2.3 | 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 & Inventory, 2019). We did not differentiate amongst 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; United States Geological Survey, 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).

2.3 | Model fitting

We estimated species-specific relative probability of occurrence (also interpretable as relative habitat suitability) 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 and Poisson); different types of predictor variables (e.g. continuous, ordinal and 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; Maiorano et al., 2013; Oppel et al., 2012; Wisz et al., 2008) have shown strong BRT predictive performance relative to other SDM approaches (e.g. generalised linear models, generalised additive models (GAM), climatic envelope models ad 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-background data rather than presence–absence data. Use of presence-background 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 & Zimmermann, 2000; Manly et al., 2007). Without absence data, attributes of presence locations must instead be compared to randomly sampled 'background' 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 geographic areas extending well beyond each species' known range in the United States and Canada (16 western states and British Columbia for *C. townsendii*, *M. californicus*; all states and provinces for *M. lucifugus*; all US states for *M. velifer*, *P. subflavus*). This choice aimed to sufficiently capture the full range of environmental conditions limiting bats' distributions (Razgour et al., 2016). Because bats were more likely to have been observed in locations already known to harbour bats and that are more accessible (e.g. closer to population centres, 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 & Ripley, 2002) using the MASS package for R, then generated background points with probability dictated by occurrence density, such that areas with high density of occurrences had high probability of background sampling, but all locations within the sampling extent had nonzero probability of sampling (e.g. Figure SA2). Our background sample consisted of three background points per occurrence point as a balance between achieving good coverage of available habitat and not artificially inflating sample size. Finally, we sampled all candidate predictor variables at each presence and background location.

To identify the most appropriate scale for each predictor (i.e. the scale at which habitat selection was most evident), we first fit univariate 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, which was then included in the final multivariate model (below), 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 (Appendix S3 in Elith et al., 2008). We adjusted the model learning rate to ensure that a minimum of 1,000 trees were fit, then calibrated the tree complexity (range: 3–5) and bag fraction (range: 0.5–0.7) to minimise deviance. We tested for benefits of dropping uninformative model terms based on estimated reduction in deviance. We then used this 'optimised' 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 (D^2), a pseudo-determination coefficient intended to be comparable to R^2 (Mateo & Hanselman, 2014; Nieto & Melin, 2017). We also assess predictive performance based on the cross-validated area under the receiver operating curve (AUC). Although use of this metric to evaluate presence-background models is flawed by 'contamination' of background sites with unobserved presence (Boyce et al., 2002; Escobar et al., 2018; Jimenez-Valverde, 2012), we report it here as an additional evaluation metric that supports comparison with other studies that frequently include it. As a final modeling step, we applied the optimised 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 (Appendix S3 in Elith et al., 2008). We summarised 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).

3 | RESULTS

After filtering the compiled dataset to unique winter locations, an average of 250 presence locations per species (range: 72–442) was available to fit SDMs (Table 2). Of the neighbourhood sizes compared, moderate to large neighbourhoods (5-km, 25-km diameter) tended to capture the scale at which bats responded to landscape attributes better than a small neighbourhood (500 m), but scale of selection for each attribute varied amongst species (Table SA1). 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 SA1).

Optimal BRT parameters varied amongst species, but higher tree complexity (4–5) and higher bag fractions (0.6–0.7) were favoured (Table 3). Model goodness of fit was fairly similar across species, with a mean of 54.7%–71.7% of the total deviance in the training data explained. Performance standards vary by application; here we considered values between 50% and 75% to demonstrate moderate support. Predictive performance based on AUC ranged from 0.814 to 0.873; scores between 0.8 and 0.9 are generally considered excellent (Hosmer & Lemeshow, 2000). The model for *M. velifer* had the best fit to the data (71.7% deviance explained) as well as the best predictive performance (0.873 AUC), followed by *C. townsendii* (0.867 AUC). The model for *P. subflavus* had the poorest performance in terms of both fit (54.7% deviance explained) and predictive performance (0.814 AUC).

We found considerable interspecific differences in the relative influence of each predictor on occurrence probability (Figure 2). Ruggedness, distance to mines, winter survivorship and percent tree cover were amongst the strongest contributors, based on mean relative influence across species (12.0%, 9.9%, 9.8% and 9.2%, respectively). Whilst the influence of ruggedness and percent tree cover was consistently quite high across species, distance to mines and winter survivorship had far more variable influence (Figure 2). Winter survivorship was the strongest predictor of *M. californicus* winter distributions but the second weakest predictor for *M. velifer*. On average, winter survivorship was the third strongest predictor (out of 11 to 13 predictors considered for each species). Karst had the lowest influence overall (mean 3.7%, though it was not considered in the *M. lucifugus* model).

Consistency in a predictor's degree of influence across species did not necessarily correspond to similar relationships between that predictor and relative occurrence probability amongst species (Figure SA3). The effect of ruggedness was fairly consistent amongst species, with low relative occurrence probability predicted in very flat, open areas (very low ruggedness). *M. velifer* and particularly *P. subflavus* appeared to favour 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, whilst *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 and 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. In preliminary models that did not correct for bias in presence locations (unpublished data), 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).

We observed high relative probability of occurrence at presence locations compared to background locations, as expected (Table 3 and Figure SA4). The mean percentile rank of predicted occurrence probability at presence locations ranged from 80.3 (*M. lucifugus*, *M. velifer*) to 94.8 (*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

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

Species	Total	Winter	Unique
Corynorhinus townsendii	8,959	1,637	355
Myotis californicus	5,920	596	97
Myotis lucifugus	14,946	2,113	442
Myotis velifer	11,152	1,688	72
Perimyotis subflavus	7,024	2,722	284

Note: 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., 2021, Supporting Information). Unique records were counted after dissolving repeat winter observations (e.g. across multiple studies or survey dates) at a given location.

those of known presence locations. Conversely, areas with low occurrence probability often occur within the species' known ranges, highlighting the generalised nature of simple polygon range extent estimates.

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 (D^2)	Cross-validated AUC	Mean predicted percentile (presence)	Mean predicted percentile (background)
C. townsendii	5	0.7	3400	1.122	0.391	65.2	0.867	89.4	53.6
M. californicus	4	0.7	1100	1.116	0.415	62.8	0.853	94.8	55.9
M. lucifugus	5	0.6	4500	1.141	0.409	64.2	0.839	80.3	43.4
M. velifer	3	0.6	1800	1.125	0.318	71.7	0.873	83.7	38.7
P. subflavus	5	0.5	2300	1.126	0.51	54.7	0.814	88.0	58.1

4 | DISCUSSION

This study provides insights into the drivers and spatial patterns of bat hibernaculum selection in western North America (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 amongst 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 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 do not 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, Figure A3). Our use of bias correction when generating background locations (Hertzog et al., 2014) was important given the opportunistic sampling of winter bat locations reflected in the public databases we relied on. Preliminary models that did not include bias correction (unpublished data) pointed to night lights as 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 amongst species. Karst presence was a weak predictor, perhaps because we did not consider differential selection amongst 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'

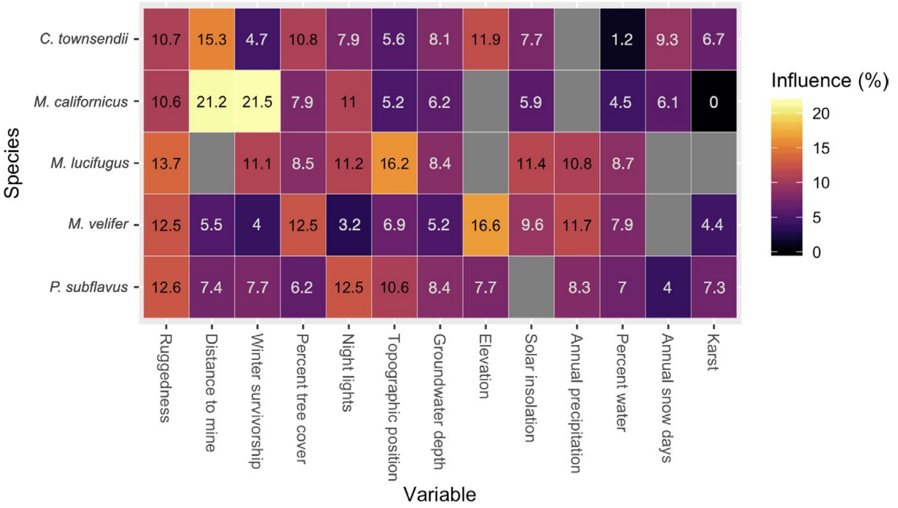

FIGURE 2 Final predictor influences in boosted regression tree (BRT) models estimating winter species distributions of bat species *Corynorhinus. townsendii*, *Myotis. californicus*, *Myotis. lucifugus*, *Myotis. velifer* and *Perimyotis. subflavus* across the United States and Canada. Brighter colours indicate higher influence; predictors that were dropped from a given model are shown in grey. Variables are ordered by their average influence across species (decreasing left to right)

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., 2021) 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, and survivorship was the third strongest predictor of occurrence overall (9.8% mean influence), but its influence varied considerably amongst species (4%–21.5%, Figure 2). This interspecies variability is likely to reflect some real ecological differences in the degree to which species distribution limits are defined by the physiological response to ambient temperature and winter duration captured in our winter survivorship model. Winter survivorship was a poor predictor of winter distribution for *M. velifer*, whose U.S. distribution is limited to Texas and the desert southwest where winters are relatively short and winter temperatures are generally mild. In contrast, winter survivorship was the strongest predictor of the winter distribution of *M. californicus*, whose range encompasses strong latitudinal and elevational gradients. Here, we would expect a strong 'signal' in terms of relative probability of occurrence of *M. californicus* along these gradients driving winter survivorship predictions.

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 parameterisation 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 (Figure 3) 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 and all aspects of underlying models for such species (e.g. *M. lucifugus* and *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 characterised by rare landscape features that were underrepresented in our sample? It is also important to recognise 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 (Figure 3).

These are complex models based on relatively small sample sizes, so uncertainty remains and portions of the predictor

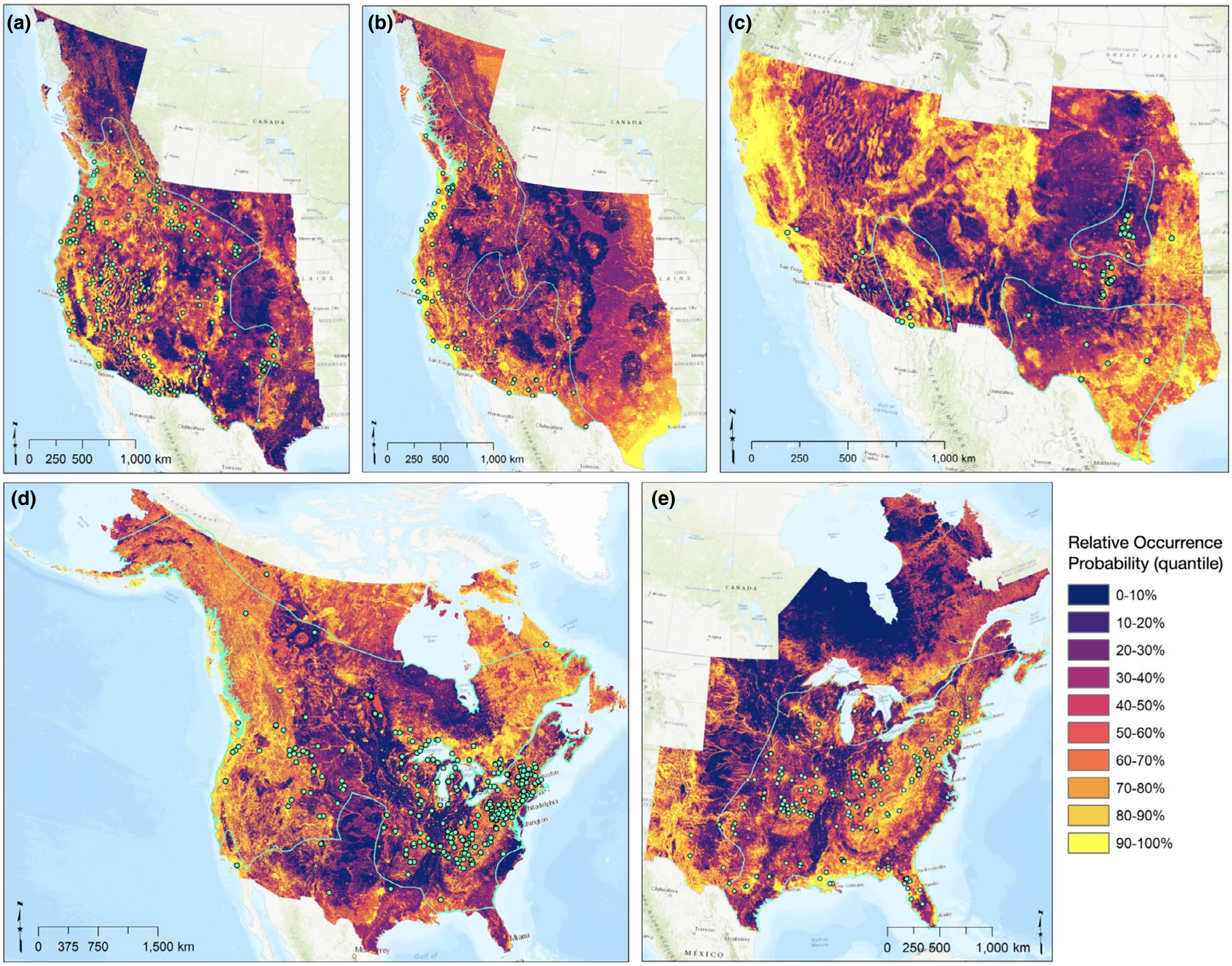

FIGURE 3 Predicted relative probability of occurrence of (a) *Corynorhinus townsendii* (deviance explained = 65.2%, AUC = 0.867); (b) *Myotis californicus* (deviance explained = 62.8%, AUC = 0.853) across the western United States and British Columbia; (c) *Myotis velifer* (deviance explained = 71.7%, AUC = 0.873) across the southwestern United States; (d) *Myotis lucifugus* (deviance explained = 64.2%, AUC = 0.839) across the United States and Canada (below the Arctic Circle) and (e) *Perimyotis subflavus* (deviance explained = 54.7%, AUC = 0.814) across the eastern and central United States and eastern Canada. Each species' current range extent (turquoise outline) and winter occurrence locations used to fit the model are overlaid (turquoise points). Occurrence probability is scaled using a quantile symbolisation to reflect the fact that predictions represent relative occurrence probability; whilst absolute values cannot be reliably interpreted relative to one another, percentile ranking is permitted (i.e. yellow areas of the maps represent the 10% by area of the mapped landscape with the highest occurrence probability, regardless of the underlying distribution of values). All maps use the USA Contiguous Albers Equal Area Conic projection

space are undersampled. We may also be missing key predictors that we simply do not yet understand to be important for hibernaculum selection or cannot map continuously with currently available spatial data. Furthermore, varying degrees of temporal mismatch between occurrence records (mid-century to present) and climate and land cover variables (recent average conditions to temporally align all predictors) mean that conditions for older records may not be fully and accurately captured. This may have contributed to low predictive influence of climate variables (e.g. precipitation and snow). Future efforts to improve on these models would benefit from additional winter location data (particularly for species other than *C. townsendii* and *M. lucifugus*). Not only could spatial coverage be improved but additional recent records would allow exclusion of older records without resulting in prohibitively small sample sizes. 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. Underrepresented characteristics are evident in the 'flat' portions of the partial dependence plots and 'empty' portions of associated rug plots shown in Figure A3 (e.g. high elevations, high ruggedness, high number of snow days and high percent surface water). 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 (Brotons et al., 2004; Heinrichs et al., 2010). 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.

Significance Statement.

Bats are threatened worldwide by human impacts. In North America, WNS, caused by an introduced fungal pathogen, decimates hibernating bats and is rapidly spreading westward. Bat diversity is highest in the West, yet we know little about where these species go in winter or why, hindering conservation responses. We estimate winter occurrence probability across five western bat species' ranges by integrating mechanistic understanding of hibernating bats' physiological responses to climate conditions into SDMs. This work can inform targeted monitoring and management and provide a baseline for assessing impacts of advancing WNS and climate change on bats.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Original bat occurrence spatial data used in this analysis cannot be provided in the interest of protecting sensitive hibernacula locations from vandalism and exploitation. However, we make our complete analytical dataset, including all sampled predictor values for all bat presence points and accompanying bias-corrected background points, available via Dryad (https://doi.org/10.5061/dryad.crjdfn32r). It has simply been stripped of spatial identifiers (latitude, longitude and site names, where applicable).

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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, behavioural 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.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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