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Projecting the compound effects of climate change and white-nose syndrome on North American bat species

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ARTICLE INFO

Keywords:

Bats
Subterranean microclimate
Climate change
Hibernation
Species distribution model
White-nose syndrome

ABSTRACT

Climate change and disease are threats to biodiversity that may compound and interact with one another in ways that are difficult to predict. White-nose syndrome (WNS), caused by a cold-loving fungus (*Pseudogymnoascus destructans*), has had devastating impacts on North American hibernating bats, and impact severity has been linked to hibernaculum microclimate conditions. As WNS spreads across the continent and climate conditions change, anticipating these stressors' combined impacts may improve conservation outcomes for bats. We build on the recent development of winter species distribution models for five North American bat species, which used a hybrid correlative-mechanistic approach to integrate spatially explicit winter survivorship estimates from a bioenergetic model of hibernation physiology. We apply this bioenergetic model given the presence of *P. destructans*, including parameters capturing its climate-dependent growth as well as its climate-dependent effects on host physiology, under both current climate conditions and scenarios of future climate change. We then update species distribution models with the resulting survivorship estimates to predict changes in winter hibernacula suitability under future conditions. Exposure to *P. destructans* is generally projected to decrease bats' winter occurrence probability, but in many areas, changes in climate are projected to lessen the detrimental impacts of WNS. This rescue effect is not predicted for all species or geographies and may arrive too late to benefit many hibernacula. However, our findings offer hope that proactive conservation strategies to minimize other sources of mortality could allow bat populations exposed to *P. destructans* to persist long enough for conditions to improve.

Introduction

Climate change and infectious disease emergence are major threats to biodiversity [1,2]. Increasing temperatures, changes in the amount and timing of precipitation, increased frequency and severity of extreme conditions, and other changes in climate conditions [3] impact species and communities in a variety of ways. Climate change has already shifted distributions of a diverse range of species [4] and is projected to drive future shifts [5]. Some species' fundamental niches are

moving or disappearing altogether [6–8], while others may expand beyond range limits previously imposed by unsuitable climate conditions [9,10]. These range shifts may in turn drive changes in interspecific co-occurrence and population dynamics among competitors, predators, and prey [11,12], as well as diseases, parasites, and hosts [13–15].

All of these climate change impacts may be at play for bats and are expected to interact with the impacts of white-nose syndrome (WNS). WNS, caused by a cold-loving fungus (*Pseudogymnoascus destructans*) introduced to New York state in 2006, has killed millions of hibernating bats across eastern and central North America by

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<https://doi.org/10.1016/j.ecochg.2021.100047>

Received 26 May 2021; Received in revised form 15 December 2021; Accepted 20 December 2021

Available online 22 December 2021

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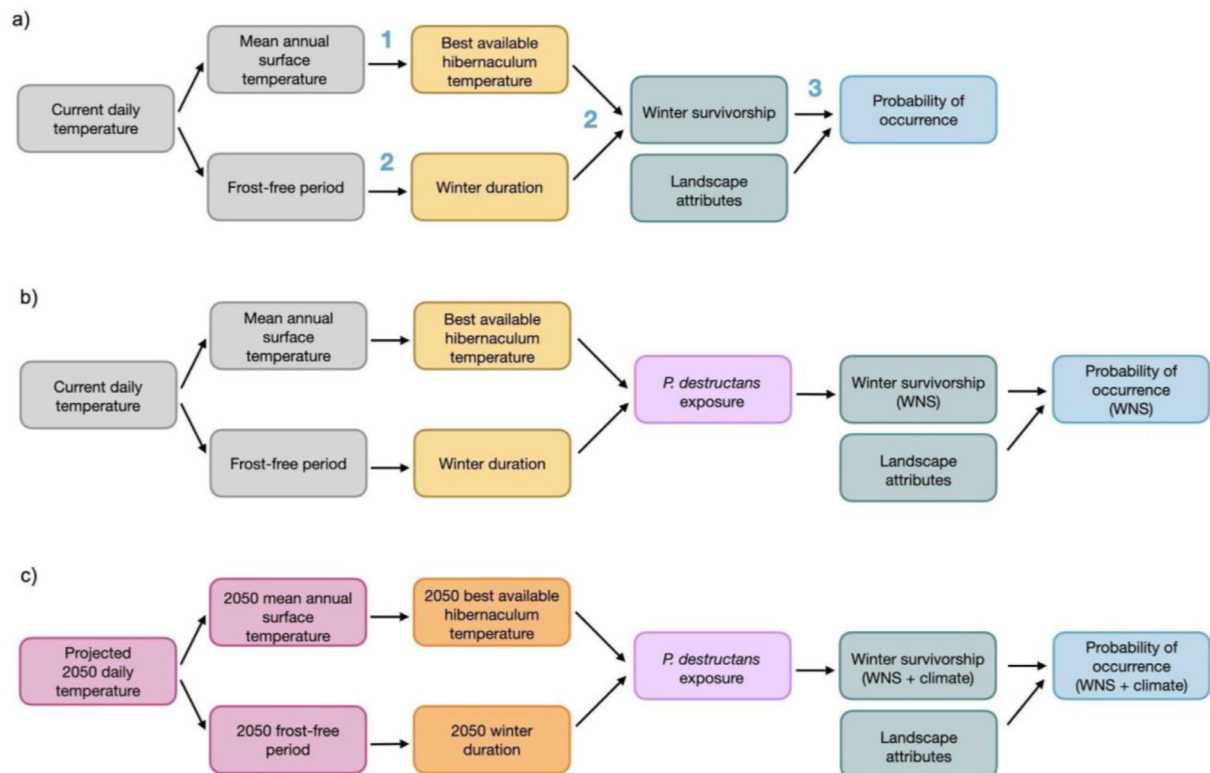


Fig. 1. Flowchart schematic detailing steps in development of species distribution models (SDMs) for five focal bat species under (a) current conditions, (b) exposure to *P. destructans*, and (c) exposure to *P. destructans* and projected climate change. Numbered steps are those detailed in previous related publications that support the work presented here: (1) McClure et al. [39], *Ecosphere*, (2) Hranac et al. [37], *Ecology and Evolution*, and (3) McClure et al. [38], *Journal of Biogeography*.

disrupting hibernation physiology [16,17]. It continues to spread widely and rapidly from its introduction site, including a 2016 novel introduction to Washington state [18,19] and is now invading western North America (herein the West). *Pseudogymnoascus destructans* grows on the skin of hibernating bats and, through a number of physiological mechanisms, causes them to arouse from their torpid state more frequently than healthy bats [17]. These arousals are energetically expensive [20], causing infected bats to expend fat stores before the end of winter. Impact severity varies geographically and among species, and has been linked to microclimate-dependent fungal growth [21,22], interspecific and microclimate-dependent differences in host physiology [23–26], as well as interspecific differences in hibernation behavior, including microclimate preferences [27,28].

Despite the growing understanding of these mechanisms, WNS impacts on bats remain difficult to predict, particularly as *P. destructans* spreads to novel environments supporting diverse species [29]. For example, it is common to find large aggregations of hibernating bats in eastern and central North America, but this is rarely observed in the West. Instead, western bats tend to hibernate in widely distributed small groups [30–32], which may affect their susceptibility to WNS as well as its spread. Understanding how WNS dynamics and impacts vary among species has been identified as a critical knowledge gap, and uncertainties remain around other key information needs, such as estimation of WNS survival rates and the genetic, physiological, behavioral, and environmental drivers of variability in survivorship [33].

Climate change presents an additional layer of uncertainty regarding WNS impacts on bats. Bat hibernation physiology and behavior, as well as *P. destructans* physiology, are closely linked to climate conditions. Hibernaculum temperature and humidity, along with winter duration, dictate healthy hibernating bats' success in surviving winter on their fat stores [20,34]; temperature and humidity also determine fungal growth rates [21,22]. WNS survivorship largely depends on whether fat

stores can sustain bats through winter given increased arousal frequencies and associated energy costs resulting from *P. destructans* infection [28,27,35,36]. A warming climate may shift bats' winter distributions through selection of different hibernacula to track changing availability of preferred hibernaculum conditions and/or through range expansion into areas where winter duration had previously been a limiting factor. In some hibernacula, higher temperatures may increase fungal loads by expanding availability of suitable growth conditions, while other hibernacula may experience the opposite trend. These warming temperatures may simultaneously alter bats' winter energy expenditures, to their benefit or detriment. Meanwhile, shorter winters could help to reduce mortality resulting from infected bats expending fat stores prior to spring emergence [37].

We modeled current winter distributions of five bat species using a hybrid correlative-mechanistic approach [38] (Fig. 1). We correlated observed winter occurrence of our focal species with landscape attributes expected to influence hibernaculum selection (e.g., topography, vegetation cover, water availability). As an additional predictor, we integrated a spatially explicit estimate of hibernation survivorship derived from a mechanistic bioenergetic model [36,37]. The bioenergetic model uses the hypothesized energetic requirements of bats during hibernation to dynamically model energy expenditure for the duration of a predicted winter under specified hibernaculum conditions. The model was parameterized for each of our focal species using field measurements of key aspects of hibernation physiology, and was run under current climate conditions, including model-based estimates of mean winter ambient temperatures experienced in hibernacula [39] and winter duration at a given location [37].

Here, we apply this bioenergetic model given the presence of *P. destructans*: we include parameters capturing *P. destructans*' climate-dependent growth as well as its climate-dependent effects on host physiology, under both current climate conditions and scenarios of future

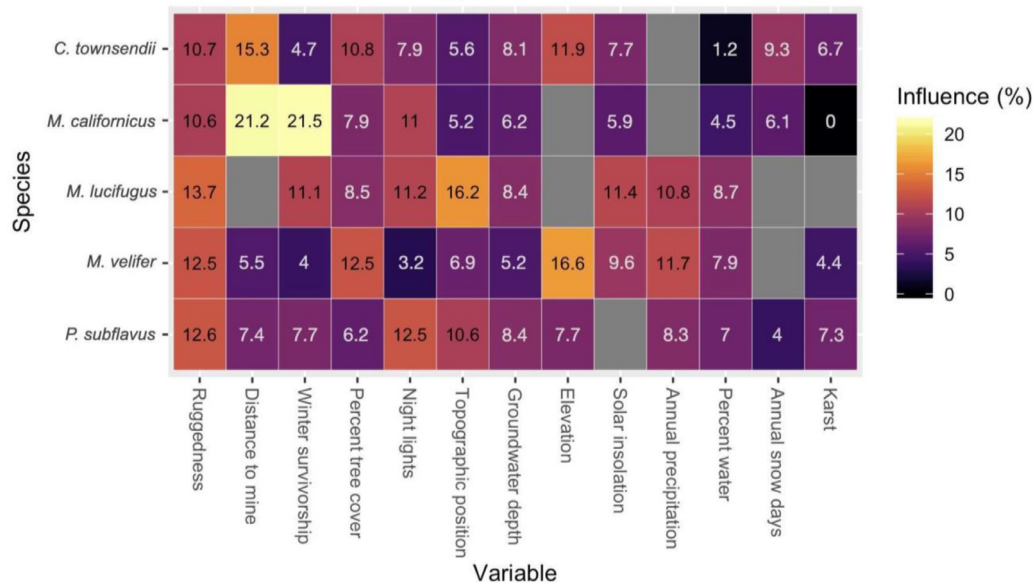


Fig. 2. Final predictor influences in boosted regression tree models estimating winter species distributions of bat species *Corynorhinus townsendii*, *Myotis californicus*, *Myotis lucifugus*, *Myotis velifer*, and *Perimyotis subflavus* across the United States and Canada. Brighter colors indicate 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).

climate change (Fig. 1). We then update our species distribution models [38] with the resulting survivorship estimates to predict changes in the distribution of suitable winter hibernacula under these projected future conditions. To our knowledge, there has been no attempt to model changing distributions of winter hibernacula in response to WNS exposure or climate change, let alone both. Our objective is to understand and predict the individual and joint effects of these two imminent stressors on North American bat populations. Our goal is to support researchers and managers in anticipating and planning for future impacts to bats. We expect this work will support managers in identifying species and geographies that are expected to be most affected by WNS, identifying populations for which WNS impacts may be either exacerbated or mitigated by climate change, and allocating monitoring and management resources accordingly.

Methods

We sought to estimate the change in five focal bat species' probability of occurrence (estimated under current conditions in McClure et al. [38]) given two future scenarios: (a) exposure to *P. destructans*, and (b) exposure to *P. destructans* and climate change. These species, including *Corynorhinus townsendii*, *Myotis californicus*, *M. lucifugus*, *M. velifer*, and *Perimyotis subflavus*, were selected based on data availability and representation of diverse distributions and habitat requirements among hibernating bats. To estimate bats' probability of occurrence given exposure to *P. destructans*, we ran the spatial bioenergetic model described in Hranac et al. [37] (also see Haase et al. [36]) to project winter survivorship from parameters capturing the influence of the hibernaculum environment (temperature and humidity) on fungal growth and the resulting impact of the fungus on bat hibernation physiology. To estimate bats' probability of occurrence given the additional impacts of climate change, we ran the bioenergetic model with the *P. destructans* growth parameters above as well as projected future climate parameters (winter duration and 'best available' temperatures, identified as the subterranean temperature closest to the species' preferred temperature as identified from published literature that was projected to be available in a given location; Fig. 1). The bioenergetic model, *P. destructans* growth parameters, and spatial application of the model are described fully in Haase et al. [36] and Hranac et al. [37] and summarized in Appendix 1. We therefore focus here on describing integration of future climate

scenarios into the bioenergetic model and subsequently SDMs for our five focal species.

We first projected daily temperatures at midcentury (2050) under a range of possible climate futures at high spatial resolution (1 km), which were then used to derive our climate parameters of interest. Global circulation models (GCMs) represent the energy budget of the earth system and the impact of external factors such as solar input and greenhouse gas emissions, simulating global patterns and processes across the earth's major climate system components (atmosphere, ocean, sea ice, and land surface) to project future climate attributes (e.g., temperature, precipitation) under possible future scenarios of carbon and other heat-trapping gas concentrations [40]. Regional climate models (RCMs) dynamically (i.e., mechanistically) downscale coarse GCM projections by resolving processes that occur at finer resolutions than GCM grid sizes (≥ 100 km) within a more limited geographic scope [41]. They account for the effects of local complexity, e.g., topography and coastlines, and simulate hydrologic processes at scales more relevant to decision-making (25–50 km). However, these outputs are still too coarse for many applications. GCM and RCM projections can be further statistically downscaled using a variety of approaches. Although many methods exist and vary considerably in their complexity, they all fundamentally aim to account for differences between model simulations applied to historical periods and observed climate attributes during those periods, then apply those statistical adjustments to future projections [41].

The NA-CORDEX Program data archive [42], hosted by the National Center for Atmospheric Research, contains output from RCMs run over a domain covering most of North America using boundary conditions from multiple CMIP5 GCMs (Appendix 2, Fig. A1). These projections span a range of possible climate futures in terms of greenhouse gas concentration scenarios and projected severity of future change, as well as performance in capturing regionally important drivers and processes.

The NA-CORDEX data archive includes outputs from two RCMs that offer 25 km spatial resolution and span the complete range (2.4–4.6 °C) of GCM equilibrium climate sensitivity (ECS), an emergent property of GCMs that serves as a metric of relative severity of projected change. These are the RegCM4 model [43] and the WRF model [44] (Fig. 2). These models differ in their underlying sub-models and -processes (see <https://na-cordex.org/rcm-characteristics>), which may mean that each best represents the meteorological phenomena driving future climate

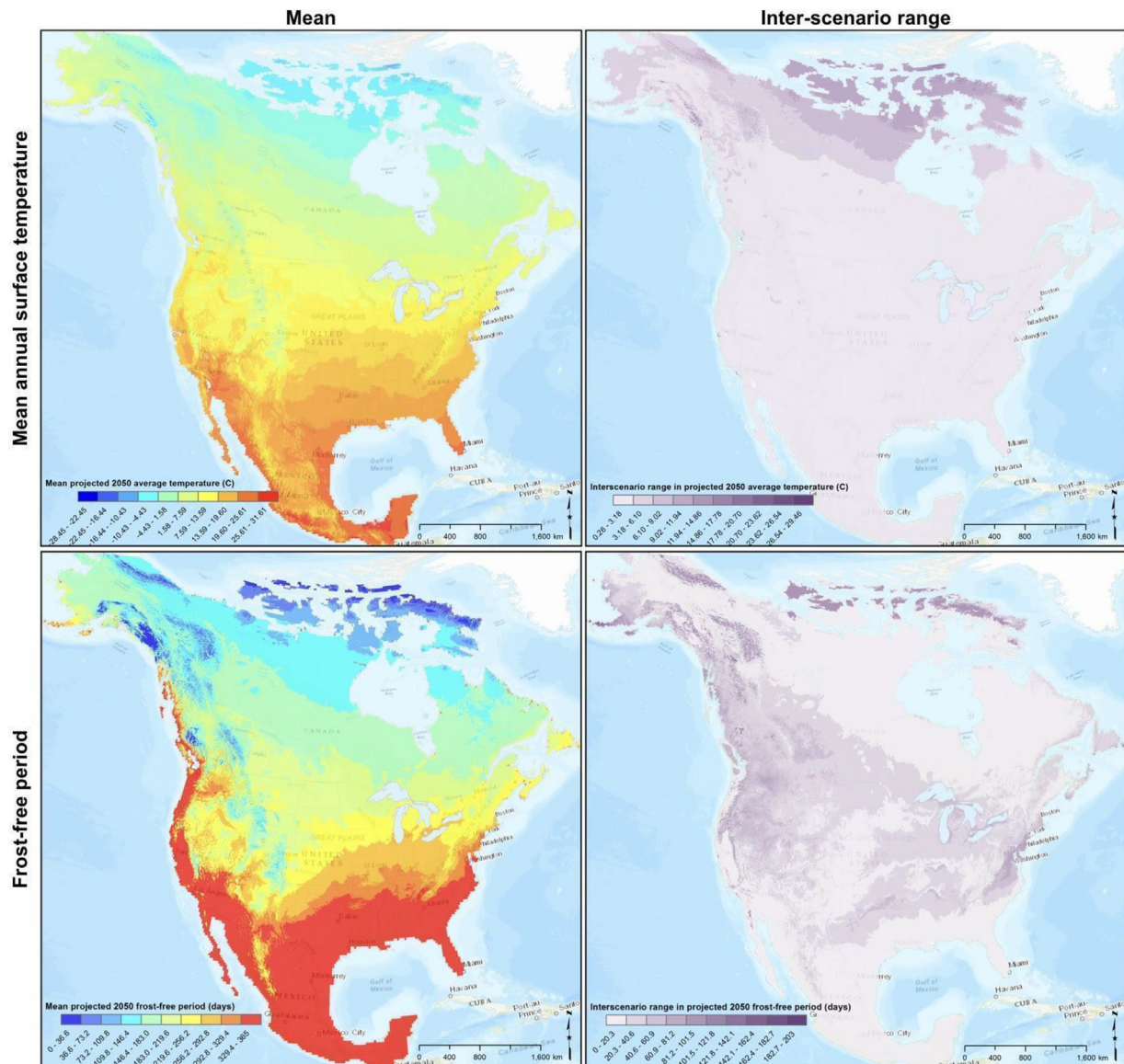


Fig. 3. Projected mid-century climate conditions (30-year averages centered on 2050) used to parameterize bioenergetic survivorship models: mean annual surface temperature (left) and duration of frost-free period (right). Winter survivorship estimates were subsequently used as predictors of occurrence probability in species distribution models for five focal bat species. Future climate scenarios were driven by each combination of two global circulation models (GCMs): GFDL-ESM2M and HadGEM2-ES, and two dynamically-downscaled regional climate models (RCMs): RegCM4 and WRF. We show the mean (top) and range (center) among the four scenarios as well as the mean projected change from current conditions (bottom).

change in different subregions of North America. Kotamarthi et al. [41] suggest that it is critical to understand the phenomena that are most relevant to climate impacts of interest when selecting the most appropriate downscaling tool. In the Mountain West, complex terrain is the primary driver of climate, with midlatitude cyclones, katabatic winds, monsoons, and associated air-mass thunderstorms being the most prominent resulting phenomena. The maritime climate along the Pacific coast also produces midlatitude cyclones, as well as orographic lifting and atmospheric rivers [41].

For each of the above RCMs, we selected downscaled outputs run on boundary conditions from two GCMs - GFDL-ESM2M (ECS = 2.4 °C) and HadGEM2-ES (ECS = 4.6 °C) - to span the range of available models' climate sensitivity (Appendix 2, Fig. A1). This approach is in keeping with the recommendation from Kotamarthi et al. [41] to use output from multiple GCMs with different physical parameterizations to cover a broader range of model uncertainty. Thus, in total, we consider four possible climate futures (2 RCMs x 2 GCMs).

We used versions of these outputs that were bias-corrected using a multivariate quantile mapping method [45] (MBCn), with Daymet temperatures as the observed dataset [46]. Because the dynamically downscaled RCMs were still considerably coarser (25 km) than our desired spatial resolution (1 km), we further statistically downscaled them by spatially interpolating the data to 1 km and applying an adiabatic lapse rate correction based on elevation [47].

To estimate survivorship under future conditions, we first derived 30-year means centered on the year 2050 for mean annual surface temperature (MAST) and duration of the frost-free period for each of the four climate scenarios. We then used projected MAST and a model linking surface and subterranean temperatures [39] to estimate the best available hibernaculum temperature likely to be available (i.e., the temperature closest to the mean ambient temperature at which each species has been observed during hibernation in the published literature) in any given location for a given species (see Appendix 1 for details). Similarly, projected frost-free period was used to estimate hibernation-

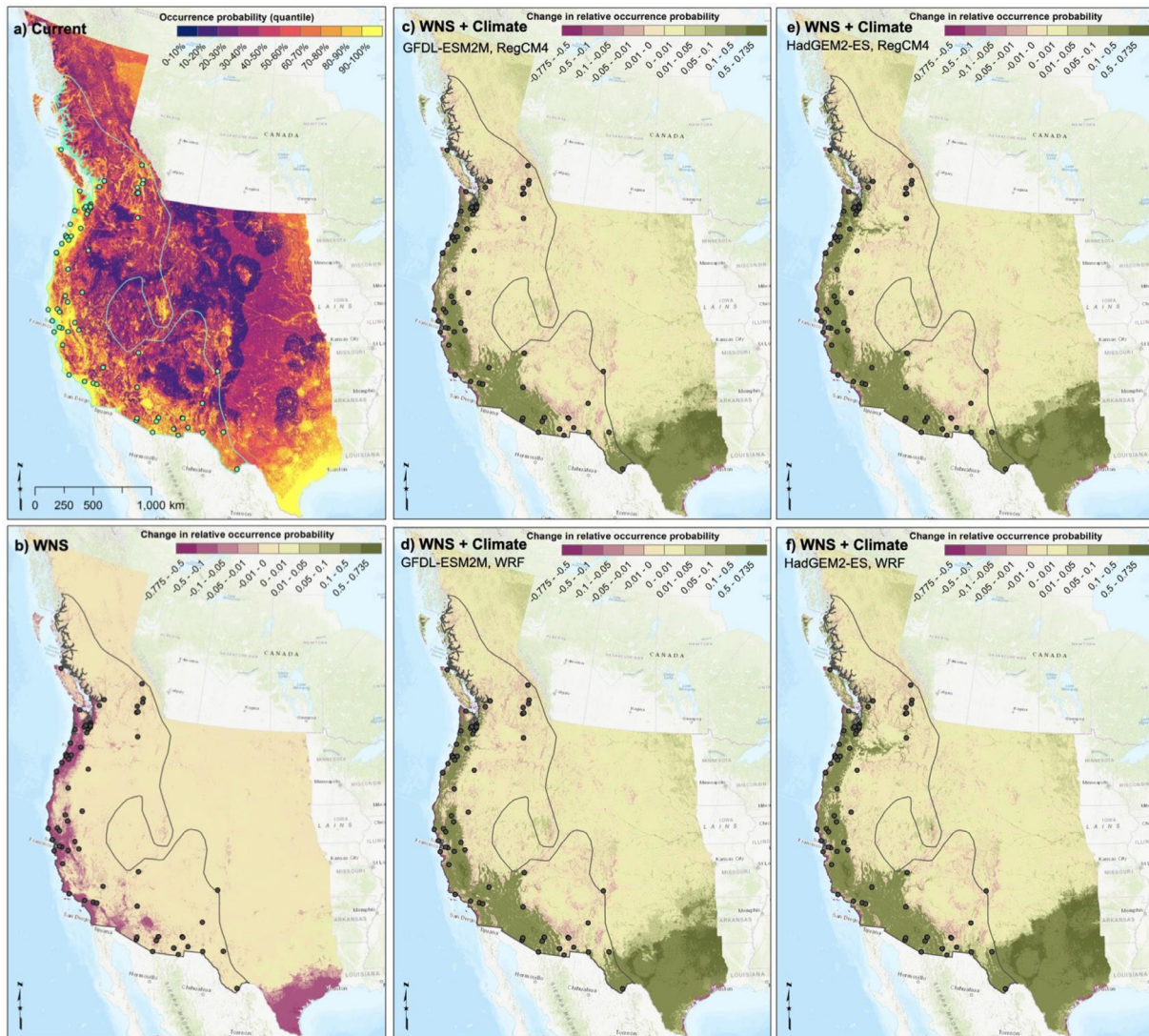


Fig. 4. Projected change in *Myotis californicus* relative probability of occurrence (a) under multiple future scenarios: exposure to white-nose syndrome (WNS) under current climate conditions (b) and exposure to WNS under projected mid-century climate conditions (c–f). Future climate scenarios were driven by each combination of two global circulation models (GCMs): GFDL-ESM2M (c,d) and HadGEM2-ES (e,f) and two dynamically-downscaled regional climate models (RCMs): RegCM4 (c,e) and WRF (d,f). Darker green indicates a projected increase in occurrence probability; darker purple indicates a projected decrease. The species' current known range (gray outline) and points of winter captures/observations (gray points) are overlaid.

specific winter duration (i.e., time between immergence and emergence from hibernacula) as described in Hranac et al. [37] (also see Appendix 1). We then ran the bioenergetic survivorship model for each of our five focal species under each future scenario using these projected future climate parameters.

Projections of future winter survivorship under each scenario were then used as predictors in species-specific SDMs that were previously derived under current conditions. These SDMs are fully described in McClure et al. [38], but briefly, we brought model-based, spatially-explicit estimates of winter survivorship together with landscape attributes hypothesized to influence hibernaculum selection (e.g., topography, precipitation, presence of karst and mines) as predictors of relative probability of occurrence (see McClure et al. [38] Section 2.3) throughout the states and territories encompassing each species' known range [48]. We used boosted regression trees [49] to link these predictors to our response data, which consisted of species occurrence records compiled from multiple sources (e.g., online databases of museum records and vetted observations, Natural Heritage Programs, our own field studies). The influence of each predictor on final predictive models for each species

are summarized in Fig. 2. We then applied the final model for each species to predictor values in each 1 km cell to predict and map relative probability of occurrence. Here, we essentially updated these models by replacing survivorship estimates under current conditions with projected survivorship under future scenarios. We then estimated and mapped the change in occurrence probability between current conditions and each future scenario simply as the difference in relative occurrence probability for each raster cell between each future scenario and the current scenario, with all relative occurrence probabilities scaled 0–1.

Results & discussion

Mean projected climate parameters (MAST and frost-free period) among the four climate scenarios assessed are mapped in Fig. 3, along with the inter-scenario range and the mean projected change in each parameter from current conditions. Spatial patterns in the mean parameter values reflect latitudinal, topographic, and coastal influences on temperature and frost-free period, as expected. We observed high

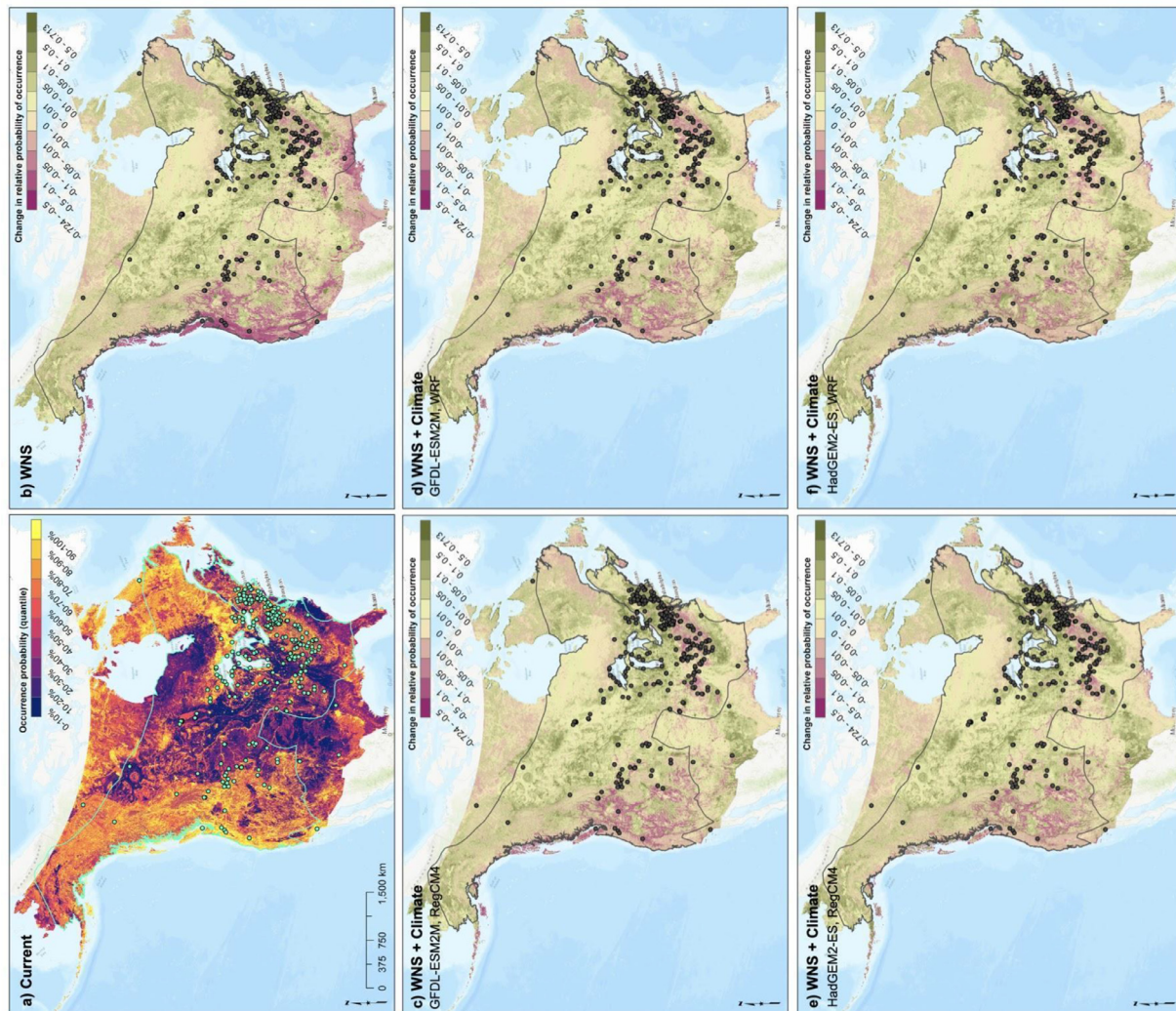


Fig. 5. Projected change in *Myotis lucifugus* relative probability of occurrence (a) under multiple future scenarios: exposure to white-nose syndrome (WNS) under current climate conditions (b) and exposure to WNS under projected mid-century climate conditions (c–f). Future climate scenarios were driven by each combination of two global circulation models (GCMs): GFDL-ESM2M (c,d) and HadGEM2-ES (e,f) and two dynamically-downscaled regional climate models (RCMs): RegCM4 (c,e) and WRF (d,f). Darker green indicates a projected increase in occurrence probability; darker purple indicates a projected decrease. The species' current known range (gray outline) and points of winter observations/captures (gray points) are overlaid.

agreement among climate scenarios (i.e., low inter-scenario range) for projected MAST, with increasing disagreement at very high latitudes. Disagreement among climate scenarios in length of the frost-free period was higher in some areas and more sporadic than that seen in MAST projections, which may reflect a stronger influence of topography. Projected change in MAST increased with latitude and with elevation, while projected change in frost-free period was more spatially variable, with the largest increases in the Appalachian region and localized portions of the West coast.

Projected changes in probability of occurrence for each of five focal species under future scenarios are mapped in Figs. 4–6 and A2–A3 (Appendix 2). We focus on projections from SDMs in which the survivorship predictor accounted for at least 5% of the boosted regression tree model fit under current conditions [38] (Fig. 2), which included models for *M. californicus*, *M. lucifugus*, and *P. subflavus*. Projections from SDMs to which survivorship contributed less than 5% (*C. townsendii*, *M. velifer*) are expected to be less useful because little clear relationship between known species occurrences and survivorship emerged.

Generally, probability of occurrence was projected to decline following exposure to *P. destructans* (with the exception of *C. townsendii*, Appendix 2, Fig. A2). However, projected occurrence probability increased

for most species in most places when climate change was also considered. The greatest projected declines with *P. destructans* exposure were typically in areas with the highest occurrence probability under current conditions (i.e., the areas currently expected to be most suitable for a given species). Spatial patterns in change in occurrence probability after considering climate impacts were more variable. For *M. californicus*, we projected moderate declines in occurrence probability in British Columbia, but a strong increase in other high occurrence probability portions of the range (Fig. 4). For *M. lucifugus*, we projected decreases in the severity of declines, but climate change had little impact on areas already expected to remain stable or experience increased occurrence probability (Fig. 5). In contrast, we observed thresholding behavior in *P. subflavus* such that projected rangewide declines under *P. destructans* exposure were replaced by a marked increase in occurrence probability in the southeast given climate change (Fig. 6). This threshold appears to follow and is thus probably driven by spatial patterns in the frost-free period (Fig. 3). We do not interpret projected changes under each future scenario for *C. townsendii* or *M. velifer* because the low contribution of winter survivorship estimates to SDM fits appear to result in unreliable and counterintuitive behavior of models for these species (Appendix 2, Figs. A2–A3).

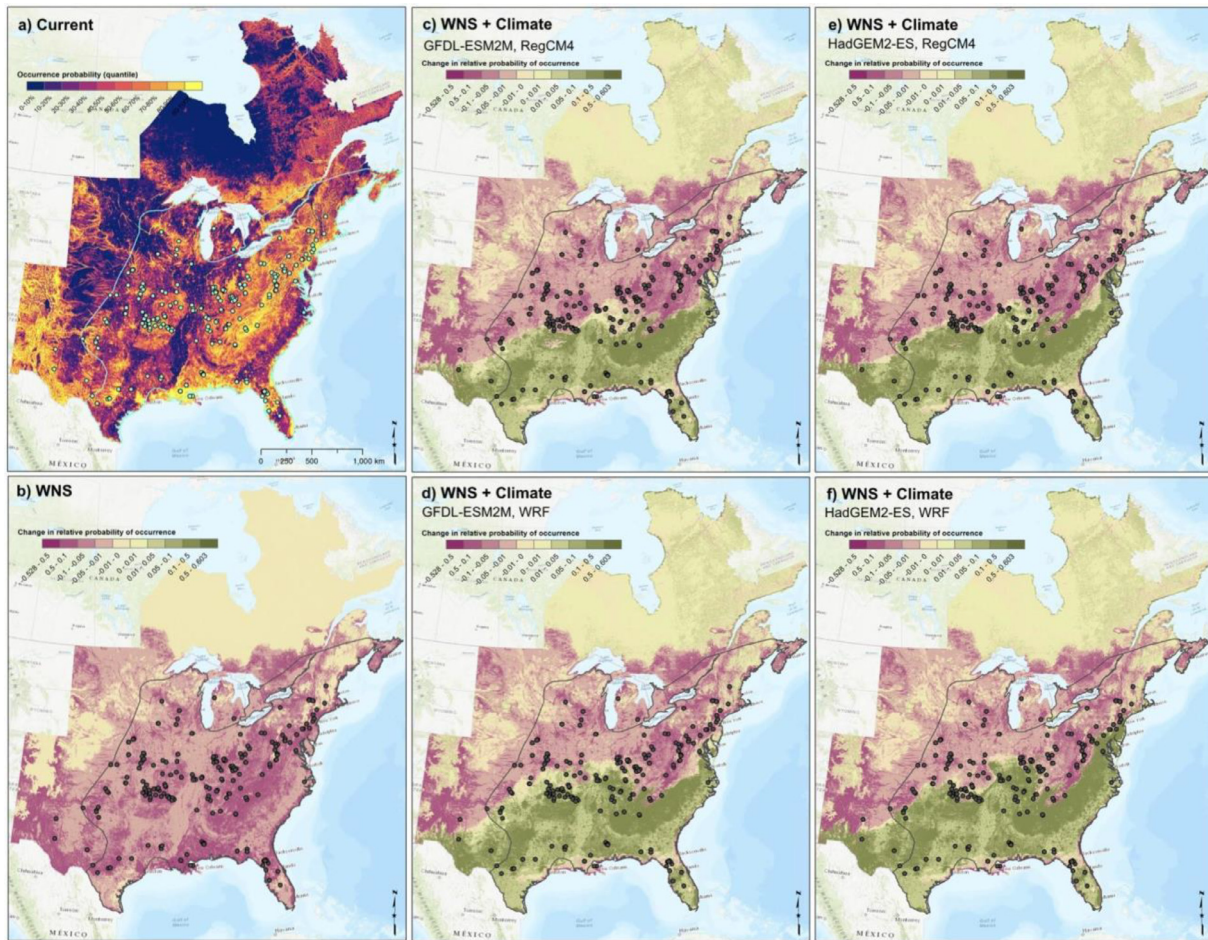


Fig. 6. Projected change in *Perimyotis subflavus* relative probability of occurrence (a) under multiple future scenarios: exposure to white-nose syndrome (WNS) under current climate conditions (b) and exposure to WNS under projected mid-century climate conditions (c–f). Future climate scenarios were driven by each combination of two global circulation models (GCMs): GFDL-ESM2M (c,d) and HadGEM2-ES (e,f) and two dynamically-downscaled regional climate models (RCMs): RegCM4 (c,e) and WRF (d,f). Darker green indicates a projected increase in occurrence probability; darker purple indicates a projected decrease. The species' current known range (gray outline) and points of winter captures/observations (gray points) are overlaid.

Table 1

Percent of points of winter capture/observation for each of five focal species that are projected to exhibit decreased relative probability of occurrence following exposure to WNS and climate change. Future climate scenarios were driven by each combination of two global circulation models (GCMs): GFDL-ESM2M (Scenarios 1, 2) and HadGEM2-ES (Scenarios 3, 4) and two dynamically-downscaled regional climate models (RCMs): RegCM4 (Scenarios 1, 3) and WRF (Scenarios 2, 4).

Species	n locations	Percent locations with projected decrease in Pr(Occ)				
		WNS	WNS + Scenario 1	WNS + Scenario 2	WNS + Scenario 3	WNS + Scenario 4
<i>M. californicus</i>	95	92.6	44.2	45.3	41.1	42.1
<i>M. lucifugus</i>	442	41.2	41.4	43.0	42.1	45.9
<i>P. subflavus</i>	284	98.9	77.1	58.1	73.2	52.8
<i>C. townsendii</i>	355	45.6	61.1	65.6	64.2	66.2
<i>M. velifer</i>	72	90.3	79.2	50.0	75.0	62.5

It may be important to consider patterns in projected changes in occurrence probability not just across the known range of each species, but also more specifically at known hibernacula. We summarized projected changes in relative probability of occurrence at the points of winter capture or observation that informed development of species distribution models (Table 1). For *M. californicus* and *P. subflavus*, the vast majority of winter locations are projected to exhibit decreased occurrence probability with exposure to WNS (92.6 and 98.9% of locations, respectively), but climate change scenarios reduce these figures to 43.2 and 65.3%, respectively, on average. Thus, although climate change is projected to significantly mitigate the impacts of WNS on these species, approximately half of known hibernaculum locations may still experi-

ence declines in occurrence. In the case of *M. lucifugus*, WNS exposure is projected to result in decreased occurrence probability at 41.2% of winter locations, and climate change is anticipated to have little effect on this pattern (projected declines at 43.1% of locations, on average).

All four climate scenarios showed close agreement regarding future changes in occurrence probability. This agreement may be driven by one or more factors. First, derived estimates of MAST and frost-free period may not be sensitive to differences among scenarios in projected daily temperatures. This appears to be more likely for MAST than for frost-free period (Fig. 3) and is not surprising given that calculation of the frost-free period is threshold dependent (i.e., definition of the frost-free period is dependent on the first and last day of the year on which

a precise threshold temperature is reached). Second, the subterranean temperature model and/or winter duration model may not be sensitive to MAST and frost-free period parameters, respectively (see Fig. 1). This is unlikely in the case of the subterranean temperature model, given that MAST is the model's strongest predictor [39]. It is also unlikely in the case of the winter duration model given that inclusion of frost-free period as a predictor improved the model by 25.39 AIC units [37]. Third, the survivorship model may not be sensitive to variation in the best available temperature estimate derived from the subterranean temperature model and/or our estimate of winter duration. We suggest that derivation of the 'best available' temperature for a given species at a given location from the subterranean temperature model likely absorbs the majority of the variability among climate scenarios [37] (see Appendix 1). Finally, for some species, SDMs may not be sensitive to variation in winter survivorship estimates. SDM sensitivity to survivorship is expected to be directly related to the contribution of the survivorship predictor to the boosted regression tree model for a given species (see McClure et al. [38]).

Although all climate scenarios produced very similar projections of future change in occurrence probability, differences were apparent in some places for most species. For *M. californicus*, differences were most apparent along the Pacific coast near the California-Oregon border and around the state of Oklahoma (Fig. 4). For *P. subflavus*, the location of the threshold between increasing and decreasing occurrence probability fluctuated across the Appalachian region among scenarios (Fig. 6). Model disagreement was also evident in Oklahoma for *C. townsendii* and *M. velifer*, as well as the Columbia Plateau of eastern Washington and the Sierra Nevada range of California, respectively (Appendix 2, Figs. A2–A3).

We suggest that our predictions of species distributions in the presence of *P. destructans* and future climate conditions can help managers to better anticipate the species- and place-specific impacts of these stressors, individually and synergistically, across North America. Our results may help to inform placement of passive acoustic detectors for monitoring known hibernacula as *P. destructans* continues to spread and the climate continues to warm. For example, monitoring of bat populations could be targeted in hibernacula where our projections suggest that suitable hibernation conditions are likely to be lost and that occurrence probability is likely to decline (vulnerable hibernacula). Conversely, monitoring as well as protection efforts could target hibernacula that are likely to be retained (potential refugia). Our predictions may also enable assessment of the distribution of at-risk and stable hibernacula across federal, state, and private lands to guide engagement strategies for conservation. Additionally, they may help managers to prepare for possible range expansions into or contractions from their jurisdictions under future climate conditions.

Our findings suggest that by mid-century, changing temperatures may offer a 'rescue' effect for many bat populations from the deleterious effects of *P. destructans*. However, given the pace of *P. destructans*' spread from the East and its recent detection in New Mexico and Montana [19], this rescue effect may arrive too late for many hibernacula. It is also important to note that integration of the temporally dynamic spread of WNS across North America, including the impacts it has already had on exposed hibernacula, was beyond the scope of this effort. Clearly any potential climatic rescue effects will arrive far too late for populations already decimated by WNS. Furthermore, a warming climate is not predicted to shield all species in all areas (e.g., *M. californicus* in British Columbia, *M. lucifugus* in mountainous regions, *P. subflavus* in the northeastern United States), and climate change may have other deleterious impacts on bats that are beyond the scope of our models (e.g., increasing aridity, driving declines in insect populations). It is therefore important that managers continue to strive for effective proactive conservation strategies to combat the devastating impacts of *P. destructans* as the fungus continues to spread. Even in the absence of a 'cure' for WNS, conservation and management actions that minimize

other sources of mortality may allow bat populations to persist long enough for conditions to improve.

Required disclosure

Any opinions, findings, and conclusions or recommendations expressed in this publication are those of the author(s) and do not necessarily reflect the views of the Government.

Declaration of Competing Interest

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

Acknowledgments

This project has been funded in part with Federal funds from the Department of Defense Environmental Research and Development Program (SERDP), under Contract Number W912HQ-16-C-0015. DTSH is funded by Royal Society Te Aparangi, grant number MAU1701. We are grateful to Linda Mearns for input on appropriate selection and application of projected climate data. We thank Nathan Justice, Eric Stofferahn, and Tony Chang for valuable technical support. Finally, we are indebted to the many individuals and organizations who generously provided raw data that made possible the studies supporting this paper, including subterranean microclimate data, bat species occurrence locations, hibernaculum immergence and emergence observations, and bat physiology records (see Haase et al. [36], McClure et al. [39], Hranac et al. [37], and McClure et al. [38] for further details).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecoche.2021.100047.

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