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Modeling climate-driven range shifts in populations of two bird species limited by habitat independent of climate

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Abstract

Ranges of species around the world are expected to contract in response to climate change. Species distribution models (SDMs) are a powerful tool for predicting changes in habitat availability, but the variables selected to create SDMs influence their performance. In addition to climate, habitat characteristics and species traits can play a role in predicting species distribution. In this paper, we consider how variable selection influences the accuracy of SDMs when applied to isolated subpopulations of two widely distributed bird species: great gray owl (*Strix nebulosa*) and willow flycatcher (*Empidonax traillii*). In the Sierra Nevada of California, these species are restricted largely to discrete patches of meadow habitat within a forest matrix, providing the potential to identify specific locations to target conservation efforts. We contrast predictions made by SDMs that consider climatic variables alone with those that incorporate both climate and geophysical variables. Adding geophysical variables resulted in differing model predictions. For willow flycatchers, adding geophysical variables improved predictive performance. In the case of great gray owls, models with and without geophysical variables had nearly identical performance under historical conditions but differed starkly in their predictions. The full model (climatic and geophysical variables) predicted habitat availability to decrease moderately, whereas the climate-only model predicted nearly complete loss of favorable habitat by 2099. The climate-only model is consistent with expectations based on previous SDMs of birds across North America, but previous studies also assumed homogeneity in species traits and range-wide habitat requirements. The full model appears more consistent with recent trends in great gray owl numbers in the Sierra Nevada specifically, where the population has remained relatively stable over recent decades. Given contradictions in our model predictions, care should be taken when trying to apply similar SDMs to other systems.

KEYWORDS

boosted regression tree, climate change, *Empidonax traillii*, montane meadow, Sierra Nevada, species distribution models, *Strix nebulosa*

INTRODUCTION

The range and distribution of species worldwide are shifting in response to climate change (Chen et al., 2011; Freeman et al., 2018; Hitch & Leberg, 2007; Kelly & Goulden, 2008; Thomas, 2010; Virkkala et al., 2010), which can affect species occupancy either directly by exceeding physiological constraints (e.g., heat tolerance) or indirectly by altering resource availability or other ecological conditions. Species distribution models (SDMs) that identify environmental predictors of species occurrence and predict changes in species ranges based on future climate scenarios have become a common conservation planning tool (Lawler et al., 2006; Morley et al., 2018; Schuetz et al., 2015; Siegel et al., 2014). Most species studied to date are predicted to shift ranges toward higher elevations or poleward under projected future climate scenarios to remain within the climatic conditions under which they evolved and are adapted to, and populations on the lowest latitude peripheries of species' ranges are generally predicted to disappear most rapidly (Hitch & Leberg, 2007; Langham et al., 2015; Morley et al., 2018; Rödder et al., 2021; Sagarin et al., 2006; Virkkala et al., 2010). Such range shifts have been observed in diverse taxa, including plants, invertebrates, and vertebrates (Bateman et al., 2020; Hitch & Leberg, 2007; Langham et al., 2015; McCain & Garfinkel, 2021; Reif & Flousek, 2012; Wilson et al., 2005).

However, many species have not demonstrated range shifts consistent with expectations based on observed changes in climate (McCain & Garfinkel, 2021; Rödder et al., 2021; Sofaer et al., 2018). Species that defy climate-based expectations may be limited by the availability of landscape characteristics that are independent of climate (Bradie & Leung, 2017; McHenry et al., 2019; Petitpierre et al., 2017; Platts et al., 2019; Virkkala et al., 2010). This is especially true for habitat specialists (Rödder et al., 2021). In such cases, the presence of relatively static geophysical features may be a greater predictor of a species' range, with climate playing a secondary role (Champion & Coleman, 2021; McHenry et al., 2019). For these species, modeling present or future distribution based on broad climate factors, without examining the contributions or constraints posed by geophysical characteristics of habitat or landscape configuration, can result in less robust predictions (Fourcade et al., 2017; McHenry et al., 2019; Pecchi et al., 2019; Petitpierre et al., 2017; Santini et al., 2021; Sofaer et al., 2018). Additionally, behavioral plasticity and physiological traits may mitigate or amplify the influence of climate change in some species (Beever et al., 2017; Donelson et al., 2019; MacLean & Beissinger, 2017; Santini et al., 2021).

Montane meadows within the greater Sierra Nevada region of California provide an example of a habitat type where a suite of geophysical characteristics may greatly constrain the range shifts of dependent species under future climate scenarios. These meadows are characterized by open areas of herbaceous vegetation interspersed with riparian shrubs where the soil remains saturated throughout the growing season (Drew et al., 2016; Kattelmann & Embury, 1996). Although montane meadows are profoundly influenced by climate-dependent variables such as water availability, the Sierra Nevada's meadows are a geologically stable habitat type that can only exist under a limited range of geophysical conditions (Benedict, 2014; Drew et al., 2016; Loheide et al., 2009) that include flat areas of fine soil located above impermeable (typically granitic) bedrock and bounded by steeper terrain where substantial runoff allows for saturated soils for most or all of the growing season (Benedict, 2014, Drew et al., 2016).

In this study, we investigate how incorporating fixed geophysical features alongside climate conditions influences model-based predictions of where favorable habitat will be available in the future within the Sierra Nevada region. We modeled future habitat availability for isolated populations of two bird species that are closely linked to riparian wet meadows in the region but differ in their natural history and predicted future climate vulnerability across their ranges: willow flycatcher (*Empidonax traillii*) and great gray owl (*Strix nebulosa*). Both of these species are distributed broadly across North America, but each has a geographically isolated population restricted to the greater Sierra Nevada that is ecologically distinct from other populations of these species in habitat type and behavior, with the Sierra Nevada populations of both species being largely restricted to montane meadows (Mathewson et al., 2012; Mendelsohn et al., 2020; Wu et al., 2016). Both species are designated as endangered by the state of California (California Department of Fish and Wildlife, 2022), are intermittently the subject of extensive monitoring efforts that have provided relatively complete documentation of all occupied habitat across the region, and breed in low densities within the region; each species has an estimated current population in the region of fewer than 200 breeding pairs (Loffland et al., 2022; Schofield et al., 2018; Wu et al., 2016). The Sierra Nevada lies within the southern portions of the overall breeding ranges of both species, with the Sierra Nevada population of great gray owls being the most southerly population of this primarily boreal species by a significant margin (Mendelsohn et al., 2020).

The willow flycatcher has been declining in the Sierra Nevada since formal surveys began in the 1970s (Harris et al., 1986; Serena, 1982), with observations of California-wide range contractions recorded as far back as the 1940s (Grinnell & Miller, 1944; Small, 1994). Once abundant throughout the entire state, willow flycatchers in California are now restricted to widely dispersed patches of wetland habitat (Grinnell & Miller, 1944; Small, 1994). According to Breeding Bird Survey data, the species declined nearly 4% annually between 1968 and 2015 in the Sierra Nevada (Chen et al., 2011; Freeman et al., 2018; Hitch & Leberg, 2007; Kelly & Goulden, 2008; Thomas, 2010; Virkkala et al., 2010). Although the species remains more abundant elsewhere in its range, especially where it uses a broader variety of habitat types, the decline of willow flycatcher populations is not limited to the Sierra Nevada; range-wide, the species is declining by about 1.5% annually (Langham et al., 2015).

Great gray owls in California are restricted primarily to a subregion of the Sierra Nevada that includes Yosemite National Park (YNP) and portions of two adjacent National Forests and nearby private lands and is geographically isolated from other populations of great gray owls. Population numbers in the region appear to be relatively stable, but historical detections are too sparse to accurately describe long-term population trends (Sauer et al., 2017; Wu et al., 2016). Unlike willow flycatchers, great gray owls in California will sometimes utilize nonmeadow herbaceous communities for foraging, such as clearcuts, postfire forest openings, and lava cap vegetation communities (Polasik et al., 2016). Across North America as a whole, great gray owls are predicted to lose up to 94% of their existing range by 2080 under a high emissions scenario (Langham et al., 2015). In addition to range contractions across the southern portion of their historical range, these models also predict that little new habitat becoming favorable for great gray owls in the future, leading to the species being classified as climate endangered (Langham et al., 2015).

Because the Sierra populations of these species have a limited, well-defined range and typically occupy discrete patches of meadow habitat, SDMs have the potential to make predictions on a scale that is relevant to making specific conservation decisions across the region, including identifying promising locations for habitat conservation and restoration so that they may serve as habitat refugia in the future. Ecological traits have been identified as predictors of future range shifts for many bird species (Reif & Flousek, 2012), so independently considering ecologically distinct populations of a species on a regional scale may yield more accurate predictions of range shifts than could be produced by geographically broader SDMs. Furthermore, SDMs created for this region—based on a finite set of locations known to support meadow habitat—will likely identify places to focus conservation efforts more effectively than predictions made based on the landscape as a whole.

Here we use boosted regression tree (BRT) models to describe recent and current habitat favorability for willow flycatchers and great gray owls in the Sierra Nevada. We apply those models to projected climate data under a high emissions scenario to predict future habitat favorability, with the goal of identifying sites that may be important for conservation both in the present and throughout the rest of the century. Machine learning techniques like BRT make it possible to create robust predictions about habitat favorability based on a broad suite of complex variables (Elith et al., 2008). BRT models are among the most robust predictive models for use in ecology because they are able to accommodate nonlinear data with interaction effects common to the complexities of natural systems, and combine elements from those methods identified as having the most robust predictive performance in identifying broader range shifts in other avian species (Elith et al., 2008; Virkkala et al., 2010). However, SDMs are susceptible to overfitting when a model indiscriminately includes ecologically irrelevant parameters, requiring some care to identify whether factors may be meaningful when creating models (Bradie & Leung, 2017; Colin et al., 2017; Petitpierre et al., 2017; Santini et al., 2021; Yackulic et al., 2013). We used two different approaches to create two separate BRT models for each species to predict locations that will support favorable habitat in the future. One model exclusively considered climate-influenced variables and was made using points distributed randomly across the greater Sierra Nevada region as a whole (climate-only model). The other model included both climatic and static geophysical variables and was made specifically using locations within existing meadow habitat (full model).

Given that willow flycatchers and great gray owls in the Sierra Nevada are primarily dependent on meadow habitats reliant on precipitation and runoff to persist, we expected that all models would predict an overall reduction in favorable habitat in the Sierra Nevada region in response to projected declines in precipitation (Diffenbaugh et al., 2015). We anticipated that models that include geophysical data alongside climate information and project specifically onto existing meadow locations would provide greater predictive power and have better capacity for identifying specific target locations for future conservation actions than models that exclusively consider climate variables across the region as a whole. We expected that full BRT models would identify habitat constraints not otherwise accounted for and also take into account the possible habitat distribution across the landscape (McHenry et al., 2019). We also expected that the full models incorporating both types of environmental variables and restricted to locations known to support meadow habitat would predict more severe range contractions than models with only climate variables projecting onto the landscape as a whole.

However, we also hypothesized that the influence of geophysical variables relative to climatic variables would differ between the two species we are examining, given their distinct life histories and the differences in the habitat characteristics they are most dependent on. We anticipated that geophysical variables would have less of an impact on model performance when making predictions regarding great gray owls relative to willow flycatchers. Great gray owls are a primarily boreal species that have a low heat tolerance and are adapted to hunting in deep snow (Bull & Duncan, 2020), making a warming climate likely to be a primary limiting factor, whereas willow flycatchers occupy more climatically diverse locations across their entire range and are likely to be able to withstand a broader range of climate conditions (Ruegg et al., 2018). For this reason, we also predicted that favorable habitat for great gray owls would primarily shift to higher elevations to track colder temperatures, while suitable habitat for willow flycatchers will primarily shift northward but downslope to track greater precipitation (Tingley et al., 2012).

METHODS

We combined survey data from multiple sources to identify the locations of willow flycatcher and great gray owl breeding habitat in the greater Sierra Nevada region. We defined the greater Sierra Nevada region as the Sierra Nevada, Sierra Nevada foothills, Modoc Plateau, Mono, and Southern Cascades ecological unit sections for California (note that some of the California ecological sections extend into Oregon and Nevada) as defined by the USDA Forest Service (Miles & Goudey, 1997). These ecological sections encompass all meadows described in the Sierra Nevada Multi-source Meadows Polygon Compilation, version 2.0 (SNMMPC; UC Davis, 2017). The SNMMPC is a comprehensive database of Sierra Nevada meadows that delineates the boundaries of meadows throughout the Sierra Nevada region and quantifies their geophysical characteristics (Figure 1).

We extracted willow flycatcher occurrence data primarily from standardized broadcast surveys designed to elicit a response from territorial willow flycatchers (Bombay, Benson, et al., 2003), conducted sporadically throughout the region since the late 1970s (Serena, 1982) by staff at The Institute for Bird Populations (IBP), the US Forest Service (USFS) or California Department of Fish and Wildlife (CDFW), Point Blue Conservation Science, California State University Sacramento, University of

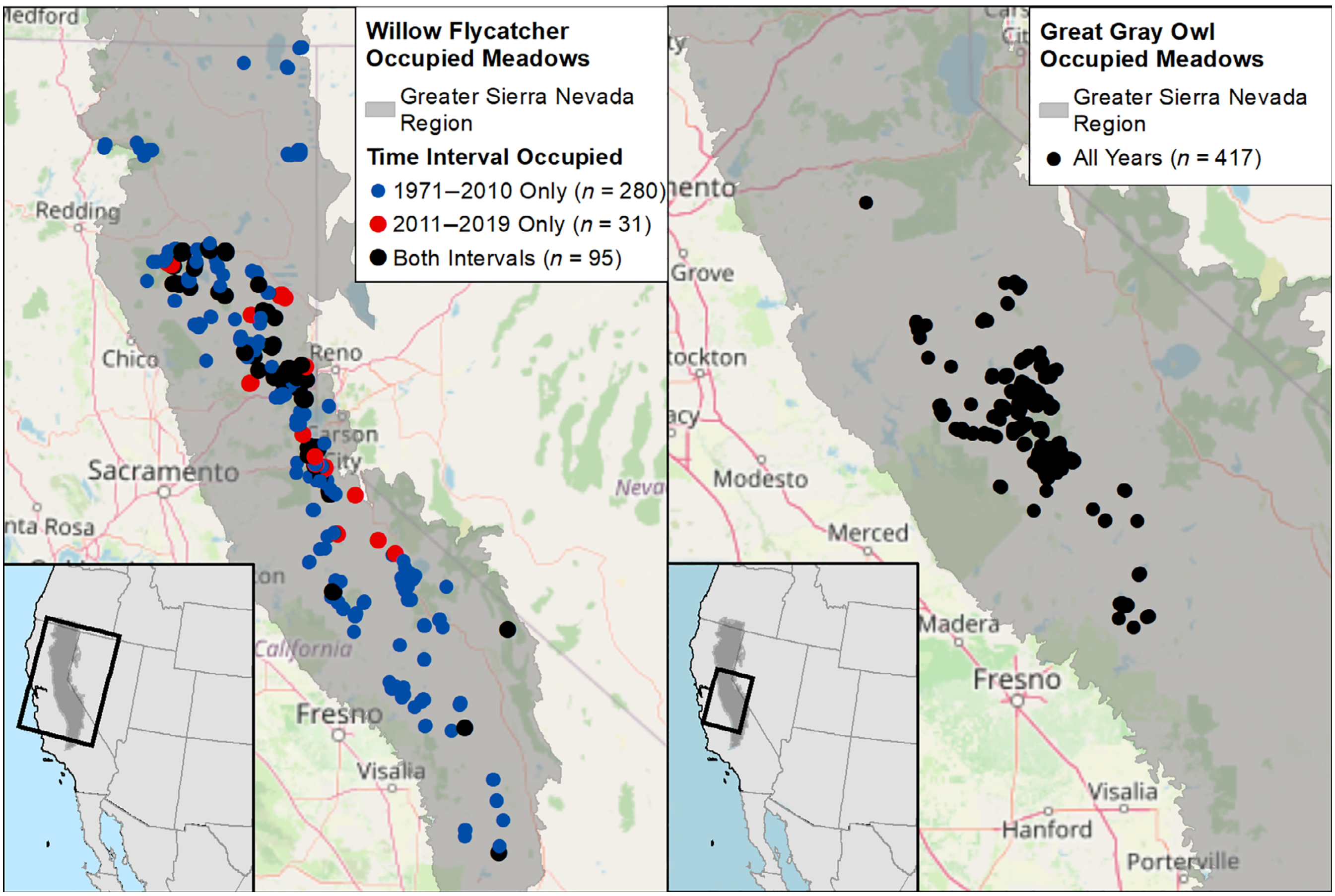

FIGURE 1 Locations of meadows observed to be occupied by territorial willow flycatchers or great gray owls during one or more years between 1971 and 2019 in relation to the greater Sierra Nevada region.

Nevada Reno, Utah State University, and others. Although surveys have covered a wide geographic area across a substantial timespan, few meadows have received consistent survey efforts sufficient for determining colonization and extinction probabilities (Loffland et al., 2022). We also included high-quality observations reported to eBird (Sullivan et al., 2009) and observations archived in the California Natural Diversity Database (CNDDB; California Department of Fish and Wildlife, 2016) at meadows that were not otherwise known to be occupied. Consistent with established willow flycatcher survey protocol (Bombay, Benson, et al., 2003), we filtered the datasets to obtain all observations within the great Sierra Nevada region during the peak breeding season (June 15–July 15) of any year where singing or other behavioral observations indicated resident breeding status or if an active nest or fledglings were directly observed at any time during the season (Bombay, Benson, et al., 2003). Because willow flycatchers are visually similar to other closely related flycatchers, we further restricted our analysis to observations in which the distinctive "fitz-bew" vocalization unique to the species was heard; visual observations alone were not considered sufficient to confirm willow flycatcher presence. Notably, only one eBird record met these criteria outside of meadows already found to be occupied during standardized surveys. Based on these data and criteria, we designated meadows with records of territorial or breeding willow flycatchers as being historically occupied, currently occupied, or both. We considered any meadow to be historically occupied if a territorial willow flycatcher was detected at least once prior to 2011 or currently occupied if a territorial willow flycatcher was detected at least once after 2010.

Great gray owl occupancy data compiled for the Sierra Nevada Great Gray Owl Conservation Strategy (Wu et al., 2016) consist primarily of observations made by YNP and USFS during occupancy surveys following a standardized protocol (Beck & Winter, 2000; S. Stock, unpublished data). Data compiled by Wu et al. also included other great gray owl detections archived by the CDFW in the CNDDB (which incorporates observations included in the USFS internal wildlife observation databases) and those compiled from private land owners and local researchers where a nest or fledglings were observed (J. Keane, J. Medley, K. Roberts, M. Reno, C. Stermer, and J. Wu, unpublished data). All meadows with both published and unpublished observations are compiled in Schofield et al. (2022). The majority of observations and survey efforts occurred between 2001 and 2011, with relatively sparse data available before 2001. We also reviewed eBird data for great gray owl observations not present in the data compiled by YNP, although we found none where evidence of breeding was specifically noted at sites outside of those already known to be occupied based on formal survey data or CNDDB records.

We intersected willow flycatcher and great gray owl detections that met our criteria with the 18,780 meadows in the SNMMPC, classifying any meadow as being occupied by willow flycatchers if it was contained within or overlapped polygons designated as being occupied during formal surveys or, following conventions established for defining functionally contiguous meadow habitat at scales used by willow flycatchers in previous research (Schofield et al., 2018), was within 300 m of the point locations of individual observations. We considered meadows to be occupied by breeding great gray owls if they were contained within or overlapped polygons designated as occupied activity centers within the YNP database, or if a nest, fledgling, or adult great gray owl identified as a breeding individual outside YNP was otherwise detected within 750 m (Wu et al., 2016) between 2000 and 2020 (Figure 1). For both willow flycatchers and great gray owls, we considered multiple adjacent meadows in the SNMMPC to be occupied if a single territory was observed to overlap multiple meadows. For the purposes of this paper, we considered all other locations as unoccupied. Although SNMMPC is relatively comprehensive, some degraded, tree-encroached meadows and other types of wetlands are not included within the data layer. In addition, meadows below the mixed conifer zone in elevation, especially those on large private land inholdings, were not always included (UC Davis, 2017). A small number of locations where territorial willow flycatchers ($n = 22$) or great gray owls ($n = 14$) were found were not associated with a meadow in the SNMMPC and were not included in this analysis.

To examine predictions that account for all available habitat and climate conditions, rather than those limited to known meadows, we created a dataset that consisted of the occupied willow flycatcher and great gray owl meadow locations and random unoccupied locations independent of mapped meadow boundaries. To do this, we combined locations of the geometric mean of occupied meadows as described above with randomly distributed points across the full extent of the greater Sierra Nevada region (total = 18,780 points). We chose these two different methods to represent unoccupied habitat to allow us to compare two distinct strategies for modeling future species distribution: one strategy ("full model") considers future distribution specifically within discrete habitat patches based on geological features associated with montane meadows, combined with projected climate conditions, and another strategy (climate-only model) considers climate conditions across the landscape as a whole and is not restricted to specific habitat patches (meadows).

We associated historical and projected climatic variables and static geophysical characteristics (in the case of the full models) with occupied and unoccupied meadows in the SNMMPC based on the pixel value at the geometric center of the meadows, and historical and projected climatic variables with the randomly distributed points across the greater Sierra Nevada region (in the case of the climate models) based on the pixel value at that immediate location. The climate data used, both the historical summary data (1981–2010) and model projections (2010–2099), were taken from the California Basin Characterization Model (BCM) Downscaled Climate and Hydrology 30-year Summaries 270-m pixel resolution rasters (Flint & Flint, 2017; accessed from http://climate.calcommons.org). We used the projected climate data that were derived by the BCM using four climate models (the geophysical fluid dynamics laboratory [GFDL], parallel climate model [PCM], community climate system model [CCSM], and French National Center for Meteorological Research [CNRM]) projected over three separate time intervals (2010–2039, 2040–2069, and 2070–2099) under the higher emissions scenario (A2). Although some BCM variables were initially derived with the use of geological data (soil water runoff and recharge), we consider these climatic variables because they are nonstatic and vary based on climate. We retrieved geophysical data from the SNMMPC and the STATSGO2 datasets (Soil Survey Staff, 2020; UC Davis, 2017), although some of the values that we accessed from the SNMMPC were derived from data originally compiled by the US Geological Survey (USGS). Geophysical data were recorded at a resolution of 100 m (Soil Survey Staff, 2020; UC Davis, 2017). We did not include elevation as a predictor variable in SDMs for either species because we use elevation as a way to quantify the location of favorable habitat rather than as a trait of favorable habitat.

We assume that existing meadows will maintain the overall geophysical characteristics that are needed to support a meadow and that a negligible number of new meadows, if any, will form through 2099. By extension, we assume that the meadows in the SNMMPC will continue to represent a comprehensive sample of available habitat patches with the potential to support a meadow and associated meadow species. We also assume that the specific geophysical variables (e.g., catchment area or dominant rock type) included in our analyses will remain functionally constant during the interval being considered. We excluded variables that are likely to change during that period, such as total meadow size, dominant vegetation type (Lubetkin et al., 2017), or soil organic matter (Ankenbauer & Loheide, 2017). Overall, our predictive models included 15 covariates for each time interval: 6 static geophysical variables and 9 historic/projected climatic variables (Table 1).

With these data, we created BRT models for each species, following the methods described by Elith et al. (2008), using the "gbm*" functions in the "dismo" R package (Hijmans et al., 2017), to describe the relative probability of occupancy (which acts as a proxy for habitat favorability at each location) for each species at each location under historical conditions. We then used these BRT models to predict relative probability of occurrence under projected future climate conditions. BRT iteratively creates a series of random decision tree models and then merges the results of these models in a forward stepwise progression such that the first tree is the one with the greatest predictive power and all subsequent trees fit residuals not yet explained within the model. This process yielded a value for each species at each location that is a continuous variable from 0 to 1, quantifying the likeliness the species will be present in a location.

For each species, we assessed outputs from two models: a "full model" that includes all 15 variables described above (6 geophysical and 9 climatic) within all meadows defined by the SNMMPC, and a "climate-only" model using the same nine climatic variables from the same source but no geophysical variables at unoccupied locations distributed randomly across the greater Sierra Nevada region and the locations of occupied meadows. We chose to use unoccupied meadow locations to represent absences in the full model to examine how predictions of habitat favorability within discrete locations of possible habitat contrasted with predictions made by models built using points dispersed across the landscape and independent of both the locations of discrete habitat patches or the locations' geophysical attributes as a whole.

For willow flycatchers, we trained a model using randomly selected data from 50% of all historically occupied locations and 50% of all historically unoccupied locations (pre-2011) and data from historical climatic conditions (1981–2010). For great gray owls, we trained the model using the same methodology but did not divide the training and test data by period due to the comparatively sparse survey data prior to 2000. We optimized hyperparameter values by using 10-fold cross-validation to minimize residual deviance. We trained the model using a learning rate of 0.005, a tree complexity of 4, and a bag fraction of 0.5. We then tested the performance of each model under historical conditions using the remaining 50% of the data and used the area under the curve (AUC) to assure that it was not overfitted to the original training data, which would result in poor predictive performance when applied to the full dataset. The BRT models generated values representing the relative probability of occupation of each location by each species under historic climate conditions and under conditions projected by each of the four climate models at all three

TABLE 1 Covariates included in boosted regression tree models to identify meadows in the greater Sierra Nevada region that are likely to support favorable or highly favorable habitat for willow flycatchers or great gray owls under projected climate scenarios.

Variable	Description	Variable type	Data source
Catchment area	Area of the upstream catchment exiting through the meadow	Geophysical	Sierra Nevada Multi-source Meadow Polygon Compilation (SNMMPC v2)
Rock type	Most abundant lithology (rock type)	Geophysical	Sierra Nevada Multi-source Meadow Polygon Compilation (SNMMPC v2)
Kf	K factor/soil erodibility	Geophysical	Sierra Nevada Multi-source Meadow Polygon Compilation (SNMMPC v2)
Meadow slope	Median meadow slope based on USGS digital elevation model (DEM)	Geophysical	Sierra Nevada Multi-source Meadow Polygon Compilation (SNMMPC v2)
Clay total	Percent clay composition in soil	Geophysical	Sierra Nevada Multi-source Meadow Polygon Compilation (SNMMPC v2)
Soil type	Dominant first order soil type	Geophysical	US General Soils Map (STATSGO2)
Aet	Actual evapotranspiration	Climatic	2014 California Basin Characterization Model (BCM) Downscaled Climate and Hydrology 30-year Summaries
Aprpck	April snowpack	Climatic	2014 California Basin Characterization Model (BCM) Downscaled Climate and Hydrology 30-year Summaries
Cwd	Climate water deficit	Climatic	2014 California Basin Characterization Model (BCM) Downscaled Climate and Hydrology 30-year Summaries
Pet	Potential evapotranspiration	Climatic	2014 California Basin Characterization Model (BCM) Downscaled Climate and Hydrology 30-year Summaries
Ppt	Total precipitation	Climatic	2014 California Basin Characterization Model (BCM) Downscaled Climate and Hydrology 30-year Summaries
Rch	Recharge	Climatic	2014 California Basin Characterization Model (BCM) Downscaled Climate and Hydrology 30-year Summaries
Run	Runoff	Climatic	2014 California Basin Characterization Model (BCM) Downscaled Climate and Hydrology 30-year Summaries
Tmax	Mean annual maximum monthly temperature	Climatic	2014 California Basin Characterization Model (BCM) Downscaled Climate and Hydrology 30-year Summaries
Tmin	Mean annual minimum monthly temperature	Climatic	2014 California Basin Characterization Model (BCM) Downscaled Climate and Hydrology 30-year Summaries

Note: Geophysical variables were assumed to be constant over the temporal domain of the study; climatic variables were assessed over historic as well as projected time periods.

time intervals (2010–2039, 2040–2069, and 2070–2099) for both the full model and the climate-only model. We also calculated the mean of the relative probability of occupation with the four climate models combined at each time interval.

In addition to AUC, we assessed overall model performance using Mathew's correlation coefficient (MCC; Brown, 2018), which is a more robust metric of model fit than AUC and other common metrics where there are a large proportion of absences in a dataset (Chicco & Jurman, 2020; Chicco et al., 2021). MCC requires that relative probability of occupancy be converted to a binary of occupied/unoccupied and uses the contingency table of true/false positives and negatives to calculate a Pearson correlation coefficient, so its interpretation is similar to that of r^2 values (Paszko & Padzik, 1975). We defined the threshold at which a location was predicted to be occupied based on the classifier value that maximized the MCC of the model (Virkkala et al., 2010). Hereafter, we refer to the values above that threshold as "favorable" habitat rather than occupied because these models are identifying and predicting locations with characteristics consistent with historically occupied habitat and not the true occupancy. For willow flycatchers, we assessed the predictive power of the mean occupancy probability for all four climate-only 2010–2039 SDMs using the observed locations of willow flycatchers found after 2010.

For each climate projection, we assessed how the mean elevation and latitude of favorable locations for each species differed between historic conditions and projected conditions based on the mean of the relative occupancy probability of the four climate models during each time interval (2010–2039, 2040–2069, and 2070–2099). We performed a post hoc Tukey's honest significant difference (HSD) test to assess changes in the elevation and latitude of favorable locations through time using the TukeyHSD function in R (R Core Team, 2017). To visualize the spatial change in habitat for each species, we mapped the favorable locations predicted under historical conditions and for the 2070–2099 projection made by the climate model that was most statistically similar in predicted changes in elevation and latitude to the four climate models as a whole (based on Tukey post hoc tests).

RESULTS

Willow flycatcher

We identified 406 of the 18,780 meadows classified by the SNMMPC as occupied by territorial willow flycatchers during one or more years between 1971 and 2019 (Figure 1). Of these, 280 were known to be occupied only in 2010 or earlier, 31 were known to be occupied only after 2010, and 95 were known to be occupied in both eras (Figure 1). The BRT model that incorporated both geophysical and climatic variables for predicting willow flycatcher presence within meadows in the greater Sierra Nevada region (full model) had an AUC of 0.927 when applied to the test data and an overall MCC of 0.646 (Table 2). The BRT model that used only climatic variables to predict willow flycatcher presence at randomly distributed points across the greater Sierra Nevada region (climate only) had an AUC of 0.899 and an overall MCC of 0.525 (Table 2). When predicting locations occupied by willow flycatchers after 2010, the full model had an AUC of 0.890 when applied to the full dataset and an MCC of 0.229, and the climate-only model had an AUC of 0.886 and an MCC of 0.184.

In the full model, meadow catchment area, soil water runoff, and meadow slope were the three variables with the highest relative influence in explaining a location's favorability for willow flycatchers, and, combined, these variables had a relative influence of 31.2% on the model's predictive power (Table 3). In total, geophysical variables had a relative influence of 36.6% with climate variables accounting for the remaining 63.4%. For the climate-only model, April snowpack, maximum temperature, and minimum temperature had the greatest relative influence on the model at 40.1% (Table 3). Both the full and climate-only BRT models predicted that under conditions projected by all four climate models (GFDL, PCM, CCSM, and CNRM), the number of locations that reach the threshold values considered favorable for willow flycatcher will progressively decrease between the historic period and the three time intervals examined (Figure 2).

TABLE 2 Model performance for predicting historical occupancy (1981–2010) for willow flycatchers and great gray owls based on historical climate and occupancy data, and for predicting recent willow flycatcher occupancy (since 2010) using projected climate data for the 2010–2039 interval alongside the threshold value for a location to be considered favorable habitat that maximizes Mathew's correlation coefficient (MCC).

Interval	Species	Model	MCC	AUC	MCC favorable location threshold
1981–2010	Willow flycatcher	Full	0.646	0.927	0.243
1981–2010	Willow flycatcher	Climate only	0.525	0.899	0.213
1981–2010	Great gray owl	Full	0.796	0.978	0.321
1981–2010	Great gray owl	Climate only	0.832	0.984	0.315
2010–2039[a]	Willow flycatcher	Full	0.229	0.890	0.243
2010–2039[a]	Willow flycatcher	Climate only	0.184	0.886	0.213

Note: Full models include climate as well as geophysical variables; climate-only models include the same climate variables but no geophysical variables.
Abbreviation: AUC, area under the curve.
[a]Projected.

TABLE 3 Covariates included in boosted regression tree models created using a combination of geophysical and climatic variables and climatic variables only for predicting relative probability of willow flycatcher presence at 18,780 locations across the greater Sierra Nevada region under historic climate conditions (1981–2010), and their relative influence on model performance.

Variable	Relative influence (%)
Full model	
Catchment area	11.83
Runoff	11.56
Meadow slope	7.85
Recharge	7.36
Climate water deficit	7.29
Minimum temperature	6.60
April snowpack	6.56
Clay total	6.54
Potential evapotranspiration	6.52
Maximum temperature	6.24
Actual evapotranspiration	6.23
Precipitation	4.98
Soil erodibility	4.16
Dominant rock type	3.23
Dominant soil type	3.00
Climate-only model	
April snowpack	14.75
Maximum temperature	13.24
Minimum temperature	12.14
Soil water recharge	11.79
Precipitation	11.10
Runoff	10.52
Actual evapotranspiration	10.29
Climate water deficit	9.05
Potential evapotranspiration	7.15

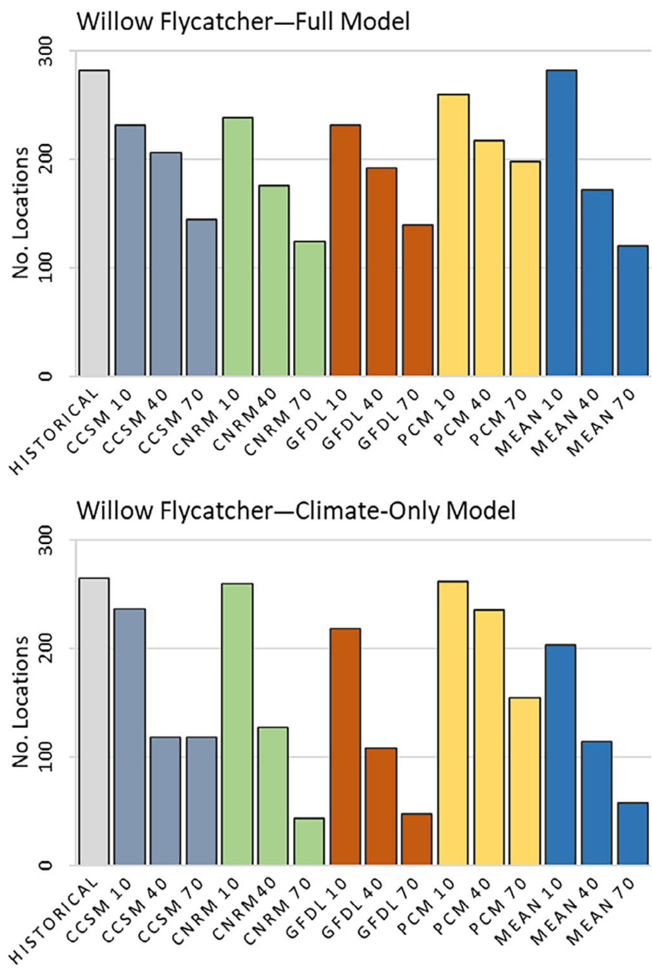

FIGURE 2 Number of locations in the greater Sierra Nevada region predicted by boosted regression tree models combining both geophysical and climatic variables (full model) and climatic variables only (climate-only model) to be favorable for willow flycatchers during four time intervals (1981–2010 [i.e., historical], 2010–2039, 2040–2069, and 2070–2099) under four different climate model projections (community climate system model [CCSM], French National Center for Meteorological Research [CNRM], geophysical fluid dynamics laboratory [GFDL], and parallel climate model [PCM]), and mean of the predicted values of these climate projections. Colors distinguish distinct climate models, as indicated.

In addition to a decrease in total favorable locations over time predicted by both BRT models, the mean elevation and mean latitude of locations identified to be favorable for willow flycatchers differed significantly between time intervals and climate models according to Tukey post hoc pairwise interaction tests (Table 4). The mean elevation of all sites projected to be favorable to willow flycatchers progressively increased between historical and projected climate conditions under all models, while the mean latitude decreased between historical and projected climate conditions (Figures 3 and 4). However, the increase in mean elevation and decline in latitude differed between the full SDM and climate-only SDM across all climate projections. The climate-only SDM model showed a more dramatic increase in elevation and a more gradual decrease in latitude (Figures 3 and 4). For both the full and climate-only SDM, Tukey post hoc pairwise interaction tests reveal a significant difference between predicted elevation and latitude of favorable meadows under historical conditions and meadows predicted to be favorable under climate conditions projected by the four combined climate models at each time interval (Table 4).

Meadows observed to be occupied by willow flycatchers after 2010 had a mean elevation of 1818 m (±27 m) and a mean latitude of 4,372,240 m (±7945 m; UTM Zone 10). In contrast, the mean elevation of

TABLE 4 Tukey pairwise interactions testing for differences in elevation and latitude of predicted willow flycatcher locations between historical observations and predicted climate scenarios across three time periods: 2010–2039 (“10”), 2040–2069 (“40”), and 2070–2099 (“70”).

Interval	Difference	Lower	Upper	*p* Adj
Willow flycatcher full model: Elevation				
Historical–10	27	−117	171	0.964
40–Historical	−111	−46	267	0.266
70–Historical*	648	551	745	<0.00001
40–10	−84	−80	247	0.552
70–10*	621	513	729	<0.00001
70–40*	538	414	662	<0.00001
Willow flycatcher full model: Latitude				
Historical–10	20,222	−9334	49,779	0.294
40–Historical	3409	−28,698	35,516	0.993
70–Historical*	−148,730	−168,642	−128,818	<0.00001
40–10	−16,813	−50,330	16,703	0.57
70–10*	−168,953	−191,066	−146,839	<0.00001
70–40*	−152,139	−177,561	−126,717	<0.00001
Willow flycatcher climate-only model: Elevation				
Historical–10	−2802	−13,941	8337	0.917
40–Historical	−6191	−18,314	5931	0.555
70–Historical	−17,386	−31,509	−3262	0.009
40–10	−3389	−15,330	8551	0.885
70–10	−14,584	−28,551	−616	0.037
70–40	−11,194	−25,958	3569	0.208
Willow flycatcher climate-only model: Latitude				
Historical–10	−2802	−13,941	8337	0.917
40–Historical	−6191	−18,314	5931	0.555
70–Historical	−17,386	−31,509	−3262	0.009
40–10	−3389	−15,330	8551	0.885
70–10	−14,584	−28,551	−616	0.037
70–40	−11,194	−25,958	3569	0.208

Note: Results from two different models (climate only and full) are presented. Significant differences are indicated with an asterisk (*).

locations predicted to be favorable for willow flycatchers by the full SDM during the 2010–2039 interval was 1884 m (±22 m), and mean latitude was 4,365,863 m (±8055 m; Figure 3). The mean elevation of locations predicted to be favorable by the climate-only SDM during the 2010–2039 interval was 2057 m (±18 m), and mean latitude of meadows predicted to be favorable by the climate-only model during the 2010–2039 interval was 4,328,591 m (±5979 m; Figure 3). We found that the mean elevation and latitude during this interval were both significantly different between the predicted and observed locations in both SDMs, although the overall difference between predictions and observations in the full model was substantially smaller than that of the climate-only model (Table 4; Figure 3). The full and climate-only models differ only slightly in their predictions of favorable locations at the northern and southern peripheries of the overall range in the Sierra Nevada during the historical time interval (Figure 4). Future predictions made by the climate-only model show favorable locations to be more restricted to higher elevations compared with the full model.

Great gray owl

We identified 417 of the 18,780 meadows classified by the SNMMPC as occupied by territorial great gray owls during one or more years between 1971 and 2019 (Figure 1). The BRT model that incorporated both geophysical and climatic variables (Table 5) for predicting great gray owl presence within meadows in the greater Sierra Nevada region had an AUC of 0.978 when applied to the test data and an overall MCC of 0.796 (Table 2). The BRT model that used only climatic variables (Table 5) to predict great gray owl presence at randomly distributed points across the greater Sierra Nevada region had an AUC of 0.984 and an overall MCC of 0.832. In the full model, the percent of clay in the soil, annual precipitation, and potential evapotranspiration had the highest relative influence in explaining a location’s favorability for great gray owls, and combined these variables have a relative influence of 39.2% (Table 5). In total, geophysical variables had a relative influence of 27.6% on the full model predictions of the favorability of locations for great gray owls with climate variables having a relative influence of 72.4% (Table 5). For the climate-only model, annual precipitation, soil water recharge, and April snowpack had the greatest relative influence on the model, and combined, these variables accounted for 56.0% of the relative model influence.

The full BRT model that included both geophysical and climatic data predicted that, under conditions projected by three of the climate models (CNRM, GFDL, and PCM), the number of locations that reached the threshold values considered favorable (Table 2) for great gray owl will decline between the historic period and the three time intervals examined (Figure 5). The climate-only SDM predicted that, under conditions projected by all four climate models (CCSM, CNRM, GFDL, and PCM), the number of locations considered to be favorable will decline sharply by the 2070–2099 interval. Based on the mean of the relative probability of occurrence of the four climate model projections

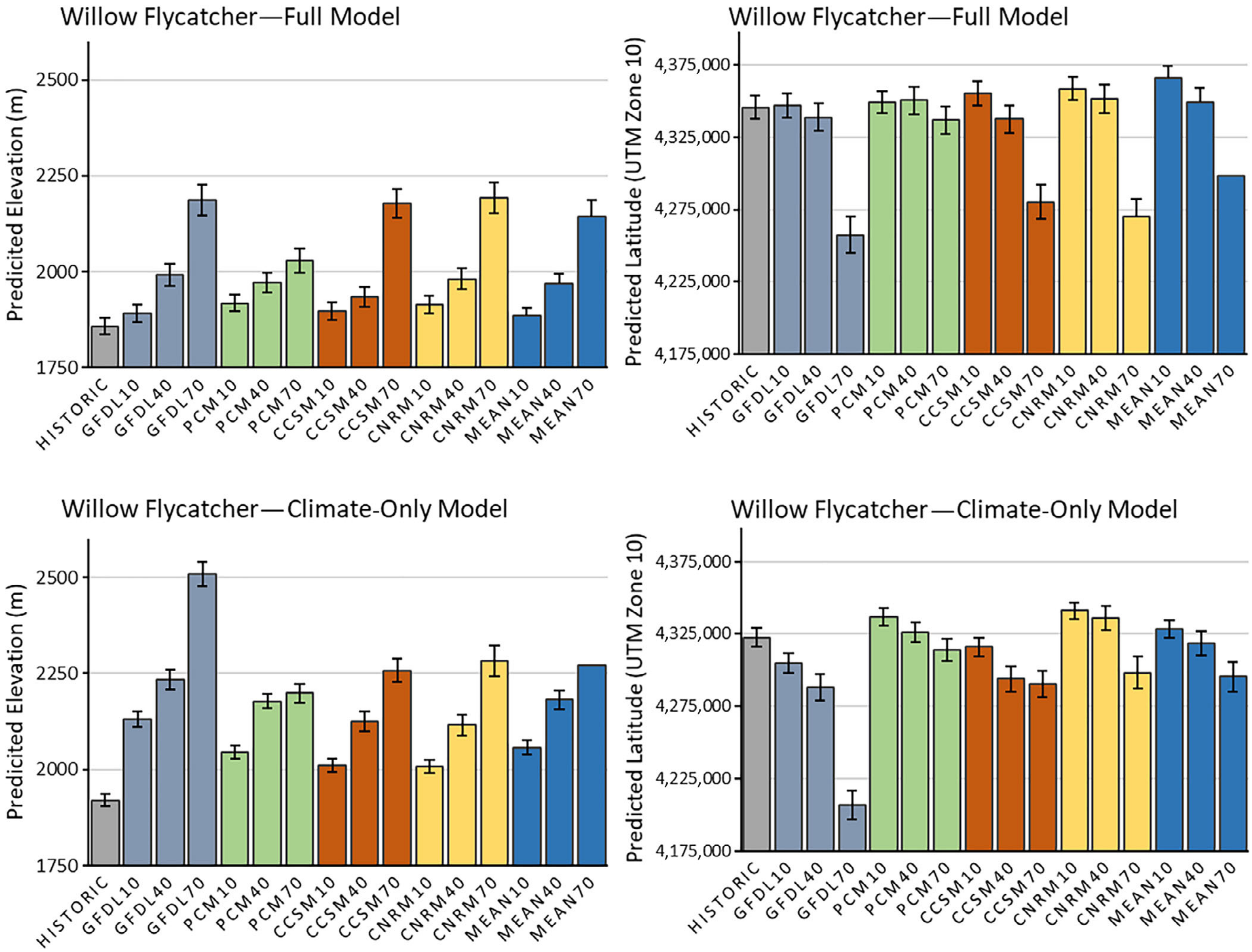

FIGURE 3 Mean elevation in meters (left) and mean latitude in meters (UTM Zone 10; right) of locations predicted to be favorable or highly favorable for willow flycatcher during four time intervals (1981–2010 [i.e., historical], 2010–2039, 2040–2069, and 2070–2099) under four different climate model projections (community climate system model [CCSM], French National Center for Meteorological Research [CNRM], geophysical fluid dynamics laboratory [GFDL], and parallel climate model [PCM]) and mean of the predicted values of these climate projections, based on boosted regression tree (BRT) models using both geophysical and climatic variables in Sierra Nevada meadows (top) and BRT models using only climatic variables at points randomly distributed across the greater Sierra Nevada region (bottom). Error bars show standard error.

combined, only two favorable meadows are predicted to remain, perhaps making extirpation likely. For both the full and climate-only BRT models, Tukey post hoc pairwise interaction tests reveal a significant difference between predicted elevation and latitude of favorable meadows under historical conditions and meadows predicted to be favorable under climate conditions projected from each of the four climate models and at each time interval (Table 6). Mean predicted elevation and latitude differed significantly between most climate models. In the case of the full model, mean predicted elevation, latitude, or both differed among all models.

The mean elevation of all locations predicted to be favorable to great gray owls by the full BRT model increased modestly between historical and projected climate conditions under all models with the exception of a sharp increase predicted by the CCSM 2070–2099 climate projection (Figures 6 and 7). The mean predicted latitude under the full model remained steady across all climate projections. (Figures 6 and 7). Under the climate-only model, the mean elevation of favorable meadows was predicted by all models to sharply increase, with the exception of the CCSM model which predicts elevation to remain steady, although this is likely due to the very small number of favorable meadows. The climate-only SDM also predicted a substantial progressive increase in the mean latitude of favorable meadows relative to historical conditions for all four climate models. The full and climate-only models differ only slightly in their predictions of favorable locations at the northern and southern peripheries of the overall range in the Sierra Nevada during the historical time interval (Figure 7). The full

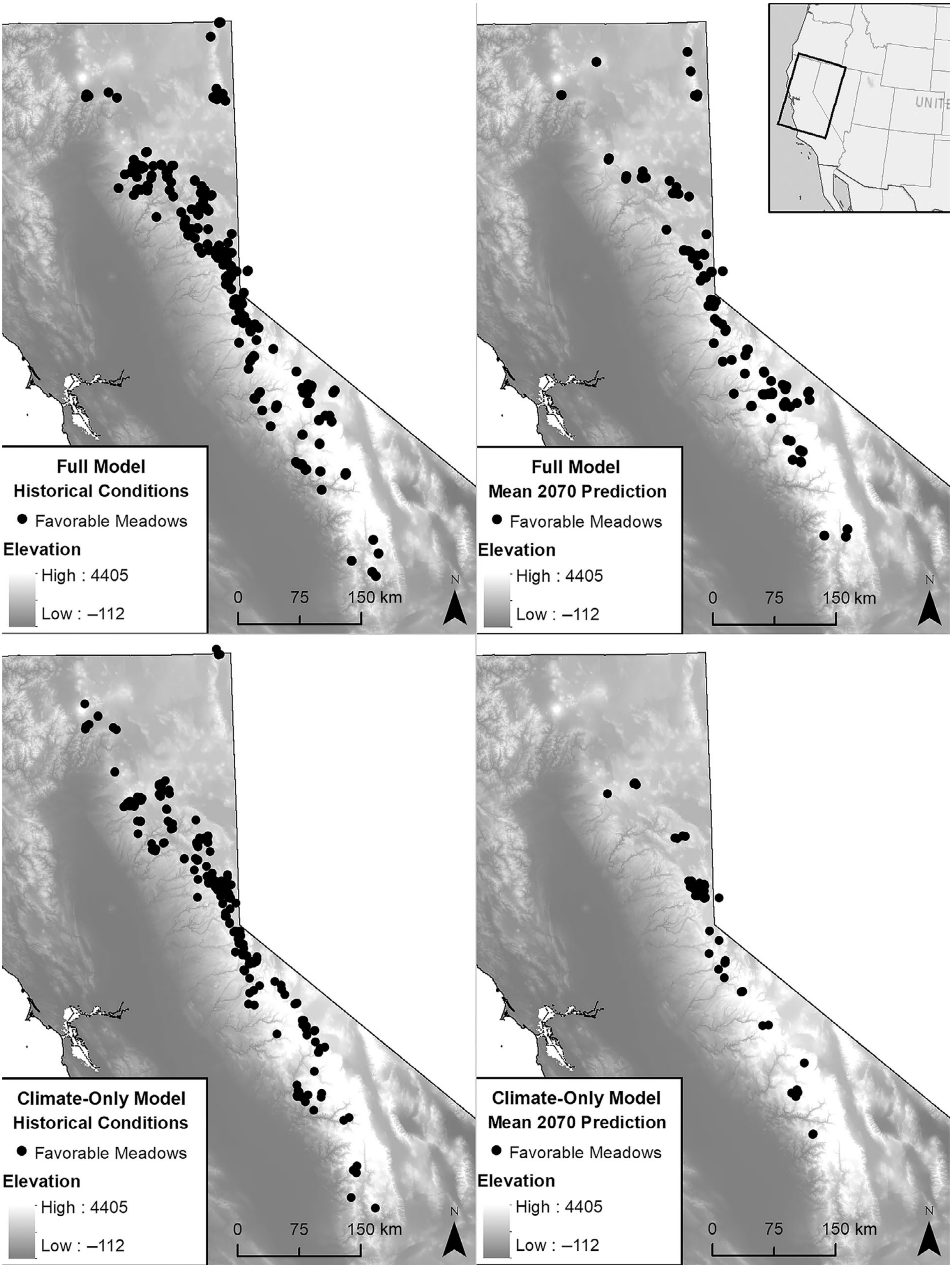

FIGURE 4 Locations predicted by boosted regression tree models that include either geophysical and climatic variables combined (top) or climatic variables alone (bottom) to be favorable for willow flycatchers under historical climate conditions and the mean of the predicted values of four climate models (community climate system model, French National Center for Meteorological Research, geophysical fluid dynamics laboratory, and parallel climate model) during the 2070–2099 interval.

TABLE 5 Covariates included in boosted regression tree models created using a combination of geophysical and climatic variables, and climatic variables only for predicting relative probability of great gray owl presence at 18,780 locations across the greater Sierra Nevada region under historic climate conditions (1981–2010), and their relative influence on model performance.

Variable	Relative influence (%)
Full model	
Clay total	16.93
Precipitation	11.97
Potential evapotranspiration	10.34
Minimum temperature	9.88
Actual evapotranspiration	7.72
Maximum temperature	7.64
Soil water recharge	7.46
April snowpack	5.97
Runoff	4.41
Dominant soil type	3.91
Climate water deficit	3.59
Soil erodibility	3.45
Catchment area	3.22
Slope	2.46
Dominant rock type	1.05
Climate-only model	
Precipitation	23.51
Soil water recharge	19.64
April snowpack	12.82
Minimum temperature	11.81
Actual evapotranspiration	8.93
Runoff	6.95
Potential evapotranspiration	6.38
Maximum temperature	6.21
Climate water deficit	3.73

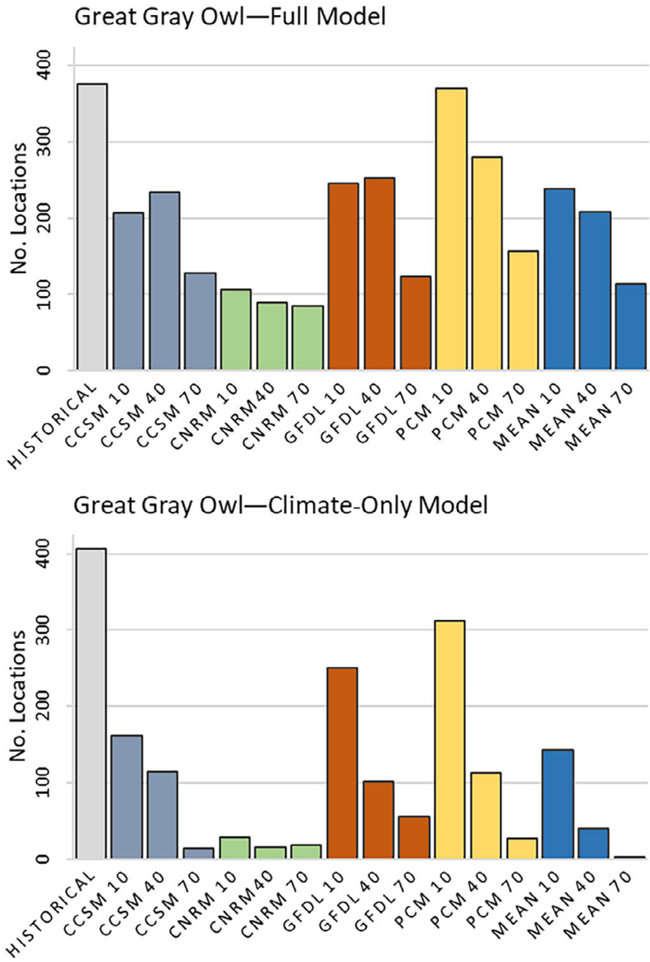

FIGURE 5 Number of locations in the greater Sierra Nevada region predicted by boosted regression tree models combining both geophysical and climatic variables and climatic variables only to be favorable or highly favorable for great gray owls during four time intervals (1981–2010 [i.e., historical], 2010–2039, 2040–2069, and 2070–2099) under four different climate model projections (community climate system model [CCSM], French National Center for Meteorological Research [CNRM], geophysical fluid dynamics laboratory [GFDL], and parallel climate model [PCM]) and mean of the predicted values of these climate projections.

SDM projects that during the 2070–2099 interval, favorable locations for great gray owls will remain roughly within their historical core area. The prediction for the 2070–2099 time interval made by the climate-only model, however, shows almost total loss of favorable locations, with the remaining two favorable locations centered much further north than the historical core area.

DISCUSSION

Both climate-only and full SDMs had strong predictive performance when identifying favorable habitat under historical conditions for both willow flycatchers and great gray owls. However, predictions of the amount, elevation, and latitude of future favorable habitat diverged among models, especially in the case of great gray owls. These differences raise questions as to when and how to use SDMs for making conservation decisions and what information is needed to create a reliable model.

For willow flycatchers, the full model performed slightly better than the climate-only model (AUC difference 0.02; MCC difference 0.121), as we expected, but both still showed what would typically be considered relatively good predictive performance. The MCC was able to reveal the differences in these models more effectively than the AUC. The predicted decline in favorable habitat and the predicted shift toward higher elevation are

TABLE 6 Tukey pairwise interactions testing for differences in elevation and latitude of predicted great gray owl locations between historical observations and predicted climate scenarios across three time periods: 2010–2039 ("10"), 2040–2069 ("40"), and 2070–2099 ("70").

Interval	Difference	Lower	Upper	p Adj
Great gray owl full model: Elevation				
Historical–10	80	11	148	0.015
40–Historical*	129	57	200	<0.00001
70–Historical*	206	118	294	<0.00001
40–10	49	−29	127	0.372
70–10*	127	33	221	0.003
70–40	78	−18	174	0.16
Great gray owl full model: Latitude				
Historical–10	1842	−7082	10,766	0.951
40–Historical	14,793	−381	29,967	0.059
70–Historical*	80,778	16,639	144,918	0.007
40–10	12,951	−3458	29,360	0.177
70–10*	78,937	14,494	143,379	0.009
70–40	65,985	385	131,586	0.048
Great gray owl climate-only model: Elevation				
Historical–10*	169	93	245	<0.00001
40–Historical*	358	228	488	<0.00001
70–Historical	348	−201	897	0.36
40–10*	189	48	329	0.003
70–10	179	−373	730	0.838
70–40	−10	−571	551	1
Great gray owl climate-only model: Latitude				
Historical–10	3174	−5716	12,064	0.794
40–Historical	13,898	−1252	29,048	0.085
70–Historical*	80,789	15,987	145,592	0.008
40–10	10,724	−5628	27,076	0.33
70–10*	77,616	12,522	142,710	0.012
70–40	66,892	652	133,132	0.047

Note: Results from two different models (climate only and full) are presented. Significant differences are indicated with an asterisk (*).

consistent in direction between the full and climate-only models, although not in degree. This was consistent across all climate projections made by each of the four climate models examined. Overall, these predictions are also consistent with SDMs created at a continent-wide scale for willow flycatchers as a whole and align with recently documented range contractions (Langham et al., 2015; Mathewson et al., 2012).

However, when tested against recent observations within the projected 2010–2039 climate conditions, model performance dropped substantially. These SDMs are unlikely to capture the full extent of range contractions for willow flycatchers, which are facing threats both on and off their breeding grounds (Paxton et al., 2017). Furthermore, willow flycatchers have relatively short dispersal distances in the Sierra Nevada (mean = 5.5 km; Mathewson et al., 2012) and rarely colonize new meadows (Schofield et al., 2018), likely posing challenges for tracking climate change (Huang et al., 2020; Santini et al., 2016; Zhang et al., 2020). Additionally, monitoring since the 1970s has shown a consistent range contraction northward in the Sierra Nevada rather than to higher elevations, with total loss of birds at most historic breeding sites in the Southern Sierra, Nevada. Even if the southern Sierra Nevada provides the most favorable habitat in the future, a source population from which to colonize new sites is thus lacking in that portion of the range (Mathewson et al., 2012; Siegel et al., 2008).

The best predictor of meadow favorability for willow flycatchers within the full model was overall catchment area, consistent with studies showing willow flycatchers are most successful in large meadow systems that can support multiple territorial pairs and hold water throughout the full growth season (Bombay, Morrison, et al., 2003; Mathewson et al., 2012; Schofield et al., 2018). The climate-only model predicts favorable willow flycatcher habitat to shift to significantly higher elevations, but it is unable to account for the fact that meadows in the region tend to be larger and more abundant at middle elevations. While willow flycatcher distribution can be limited by heat tolerance (Ruegg et al., 2018), the breeding range of the species overall extends well into the deserts of the American Southwest (Sedgwick, 2000), where temperatures already exceed those projected to occur in the current range of the Sierra Nevada willow flycatcher by the end of the century. For these reasons, we believe that predictions from the full model are likely more reliable than predictions from the climate-only model.

In contrast, for great gray owls, the climate-only model performed nearly identically to the full model when applied to historical conditions (AUC difference of <0.01; MCC difference of 0.04). Despite the full and climate-only models for great gray owl having similar predictive performance under historical conditions, when applied to future climate conditions, predictions of the range and extent of favorable habitat differed substantially. The full model predicts the availability of favorable habitat to decline, but for favorable meadows to remain within the species' current core area in the Sierra Nevada, which roughly coincides with the western half of YNP and adjacent areas outside the park (Bull & Duncan, 2020; Mendelsohn et al., 2020), while the climate-only model predicts a nearly complete loss of

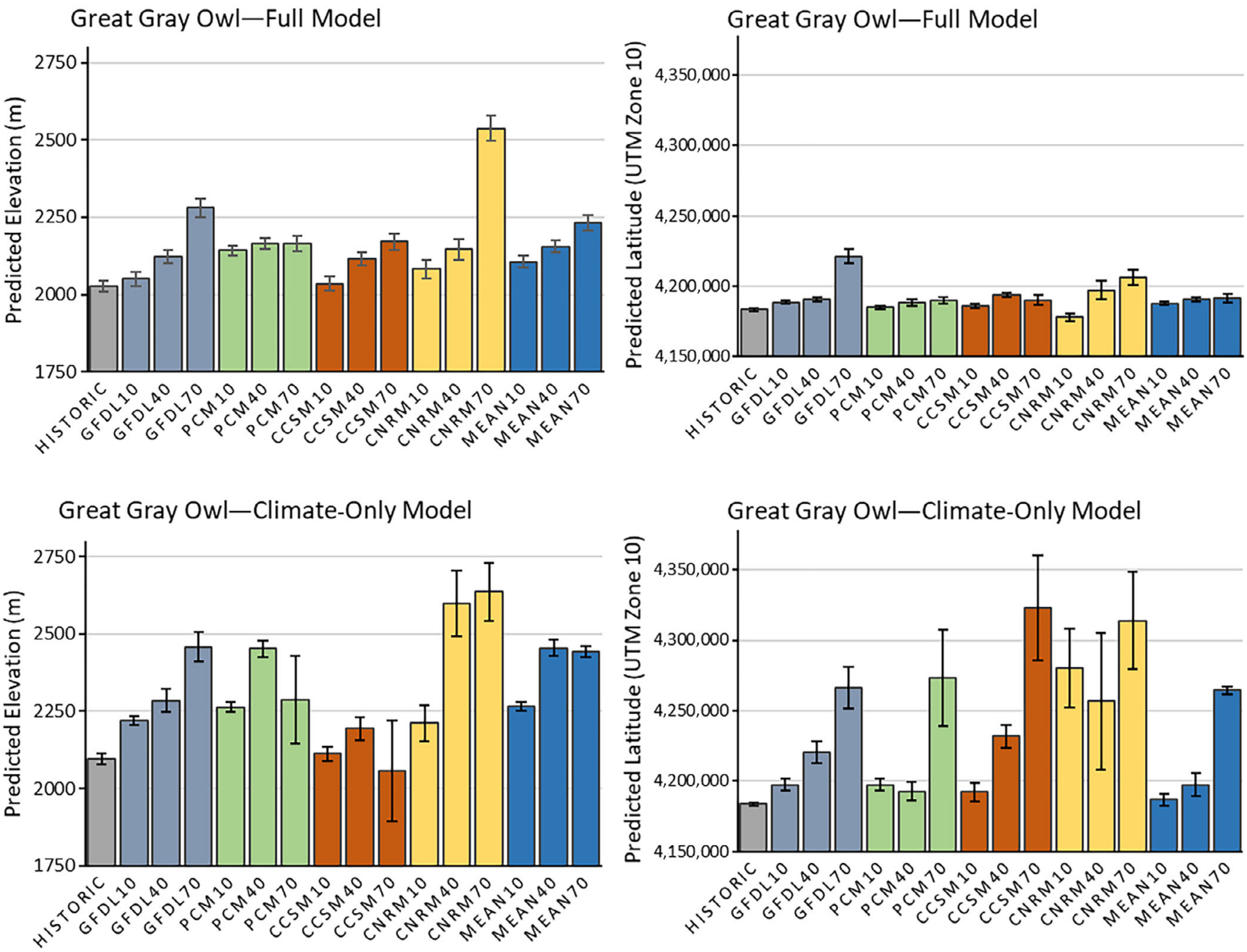

FIGURE 6 Mean elevation in meters (left) and mean latitude in meters (UTM Zone 10; right) of locations predicted to be favorable or highly favorable for great gray owl during four time intervals (1981–2010 [i.e., historical], 2010–2039, 2040–2069, and 2070–2099) under four different climate model projections (community climate system model [CCSM], French National Center for Meteorological Research [CNRM], geophysical fluid dynamics laboratory [GFDL], and parallel climate model [PCM]) and mean of the predicted values of these climate projections using boosted regression tree (BRT) models created using both geophysical and climatic variables in Sierra Nevada meadows (top) and using BRT models created using only climatic variables at points randomly distributed across the greater Sierra Nevada region (bottom). Error bars show standard error.

favorable habitat. The full model also predicts that the overall elevation and latitude of favorable locations will remain relatively steady, with favorable habitat remaining centered on the historic core of the species' range in the region, whereas the climate-only model predicted significant changes in favorable locations. Determining if either BRT model can be considered reliable and deciding which model is more likely to provide useful predictions of future habitat favorability is challenging and requires considering the natural history of this population of great gray owls.

Predictions from other SDMs that suggest the great gray owl's range will contract substantially at a continent-wide scale, with habitat disappearing entirely from the southern portions of its range (Langham et al., 2015), may indicate the reliability of our BRT model showing similar trends, especially because our climate-only model has a nominally higher AUC. However, other studies have observed that range shifts predicted by models including geophysical variables are generally less dramatic than those predicted by models only considering climate (Champion & Coleman, 2021).

Additionally, generalizations made from a range-wide model implicitly assume that Sierra Nevada great gray owls face the same physiological and ecological constraints as all other populations, which is untrue (Hull et al., 2014; Mendelsohn et al., 2020). Species traits have been postulated to play a substantial role in range shifts

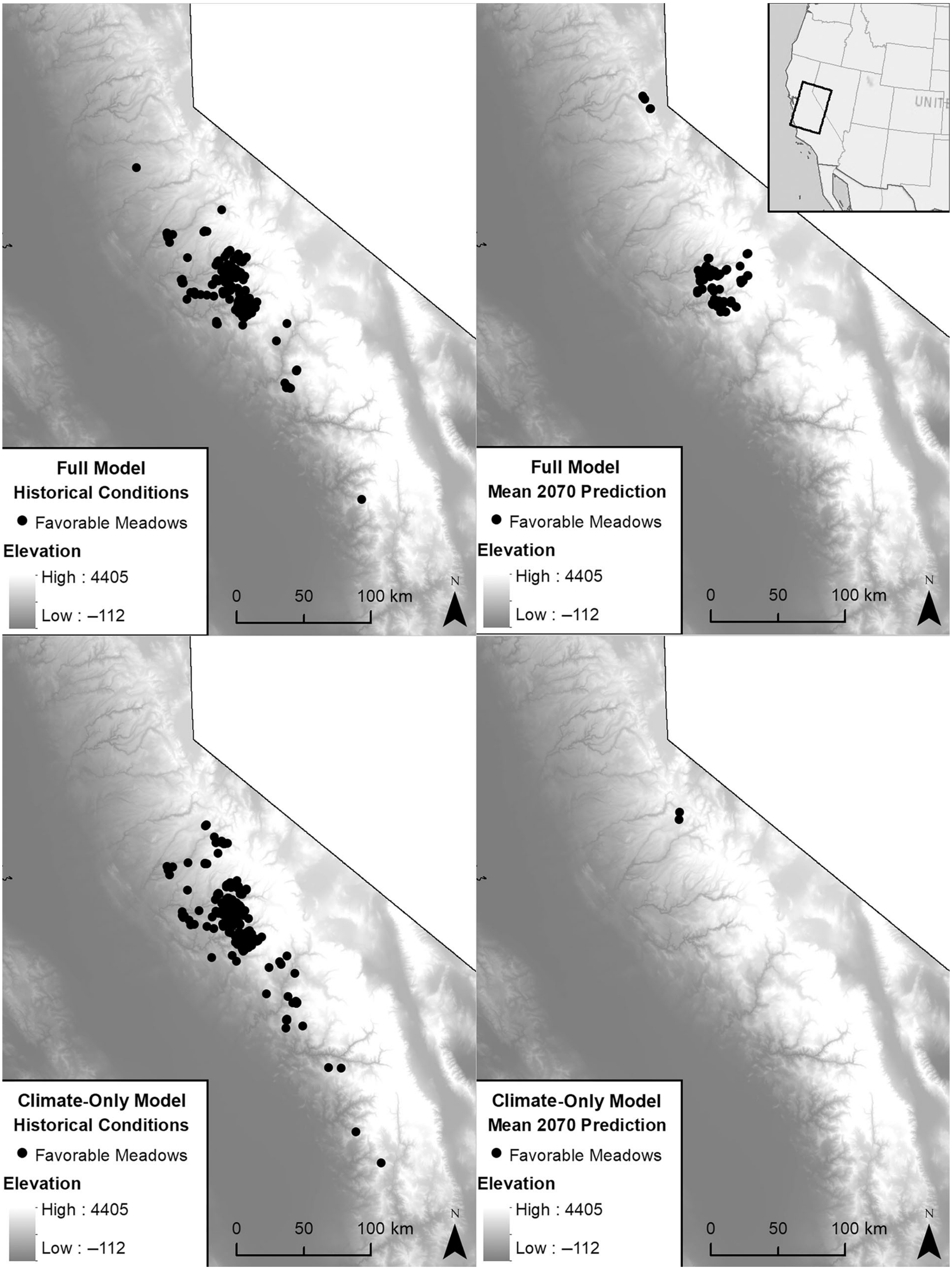

FIGURE 7 Locations predicted by boosted regression tree models that include either geophysical and climatic variables combined (top) or climatic variables alone (bottom) to be favorable for great gray owls under historical climate conditions and the mean of relative predicted values of four climate models (community climate system model, French National Center for Meteorological Research, geophysical fluid dynamics laboratory, and parallel climate model) during the 2070–2099 interval.

(MacLean & Beissinger, 2017). Although this is not universally observed, some studies found that species traits account for up to 60% of predicted range shifts with the inclusion of physiological traits in SDMs, moderating the predicted effects of climate change (Alofs et al., 2014; Brommer, 2008; Gamliel et al., 2020; MacLean & Beissinger, 2017). The traits unique to specific subspecies or subpopulations, if sufficiently distinct, could also influence range shifts in some cases. For example, while great gray owls elsewhere in the species' range have been shown to be prone to heat stress at temperatures over 20°C, in the Sierra Nevada great gray owls are known to breed in areas that regularly exceed those temperatures (Wu et al., 2016). Furthermore, although great gray owls are adapted to hunting in deep snow across most of their range (Bull & Duncan, 2020), the snowpack in the more Mediterranean climate of the Sierra Nevada tends to be denser due to repeated warming and cooling events and can preclude hunting in some locations during part of the year, which the owls respond to by migrating downslope to snow-free areas during the winter months when necessary (Jepsen et al., 2011). Just as behavioral plasticity can mitigate the effects of climate change for some species (Beever et al., 2017), differing adaptations among ecologically distinct subpopulations of a single species may also help some species cope with the effects of climate change.

Great gray owls have historically occupied only a small portion of the Sierra Nevada. It seems unlikely that this restricted range represents the full spectrum of climatic conditions tolerable to the Sierra Nevada population, especially considering that this area is not contiguous with the rest of the species' range, and that more northerly and higher elevation portions of the Sierra Nevada itself have historically been unoccupied. The narrow range of climate conditions associated with great gray owl occupancy in the Sierra Nevada may therefore be incidental to its restricted range in the region, with meadow characteristics or other habitat factors playing the constraining role.

We might have expected that because great gray owls occur throughout the Boreal region and are typically associated with cold temperatures and deep snowpack, those two variables would be most important when predicting the range of Sierra Nevada great gray owls. However, the variables most important in the full model were clay composition and precipitation. These variables combined are likely to alter the composition and structure of meadow vegetation more than the climate conditions directly experienced by the owls themselves. Perhaps this indicates that the limiting factors for great gray owls in the Sierra Nevada are not physiological constraints on the owls themselves, but the needs of their preferred prey. Indeed, trophic interactions have been shown to impact range shifts and can affect the utility SDMs (Moullec et al., 2022). Previous studies have suggested that prey availability is more important to great gray owls than specific structural characteristics within their habitat (Bull et al., 1989; Kalinowski et al., 2014). Rodent species favored by great gray owls in the Sierra Nevada include pocket gophers (*Thomomys* sp.) and voles (*Microtus* sp.), both of which can occur across a broad gradient of climate conditions (Wu et al., 2016). The full BRT model's prediction that favorable great gray owl habitat will persist through 2099 within the population's core area in the Sierra Nevada, assuming it is not lost or degraded through other means, therefore makes sense even given increasing temperatures throughout the region. This is consistent with the apparent stability of great gray owl numbers in the Sierra Nevada throughout the past several decades (Wu et al., 2016).

Although the full model's predictions for future great gray owl habitat availability in the Sierra Nevada are relatively optimistic, both our full model and climate-only models nevertheless predict declines in the number of highly favorable meadows for great gray owls, which may indicate a decline in the quality of available great gray owl habitat that could result in population decreases even if owls remain distributed across their historical breeding range. The results of the full BRT model also suggest that great gray owls are likely to remain confined to their historical core area in the region, where their limited distribution may make them especially vulnerable to wildfire, exurban development, or other disturbance. Land use changes are known to amplify the effects of climate change on species distribution (Guo et al., 2018; Zhang et al., 2020). It is also possible that neither model is a reliable forecast of available habitat for this species in the future, so land managers should not take it for granted that Sierra Nevada great gray owls will maintain stable populations in the face of climate change.

The difference in predicted outcomes for willow flycatcher versus great gray owl habitat distribution highlights the importance of identifying a broad range of environmental factors that mediate the presence of individual species. Although SDMs can be a powerful tool for predicting shifts in habitat availability for species in a changing climate, different models that are equally effective at predicting currently favorable habitat may not be equally effective, or effective at all, at predicting future outcomes. Other studies have also found that SDMs can be misleading when predicting distributional changes in response to climate change (Sofaer et al., 2018), and the inclusion of additional biological variables in SDMs typically results in more robust models that yield different predictions from simpler models (Morley et al., 2018; Petitpierre et al., 2017; Santini et al., 2021). Our study reinforces these ideas but highlights that the reliability of

SDMs likely differs depending on the species under consideration. Just as creating conservation priorities for any given species based on broad generalizations across numerous taxa is likely to be ineffective, our results suggest that making range-wide generalizations that assume the ecological needs of a species are homogenous across the extent of its range may be a source of inaccurate predictions of future species distribution. Although the predictions made by the full model for willow flycatchers potentially represent a valid projection of where favorable habitat will be distributed in the future, diverging projections among competing models and lingering concerns about unmodeled drivers of distribution that may be important make our great gray owl models appear less informative. Although SDMs may be useful in understanding possible changes in habitat favorability at a broad scale and for predicting overall trends, they appear to be limited in their utility for making highly specific predictions. Care should be taken when trying to apply similar models to other systems.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Datasets utilized for this research are as follows: Publicly available species observation data were accessed from eBird (2021; https://ebird.org/home) and the California Natural Diversity Database (CNDDB; California Department of Fish and Wildlife, 2016; https://wildlife.ca.gov/Data/CNDDB/Maps-and-Data). We queried both databases for all observations that occurred between 15 June and 15 July, and we used only those records that contained specific evidence of breeding activity. We also used unpublished observations from S. Stock and unpublished observations compiled by Wu et al. (2016). All meadow occupancy data from all data sources can be found compiled in Schofield et al. (2022; https://doi.org/10.5061/dryad.1zcrjdfvw). Data regarding specific meadow locations and characteristics were accessed from the Sierra Nevada Multi-source Meadow Polygon Compilation v2 (UC Davis, 2017; https://meadows.sf.ucdavis.edu/resources/326). Soils data used were from the *State Soil Geographic* (*STATSGO2*) *database for California* (Soil Survey Staff, 2020; http://websoilsurvey.nrcs.usda.gov) and accessed from Data Basin (https://databasin.org/datasets/1ff4328039f948529c33e7e71bb9b5fc/). Historical and projected climate data used were 30-year summaries derived from the California Basin Characterization Model 2014 (Flint & Flint, 2017; https://ca.water.usgs.gov/projects/reg_hydro/basin-characterization-model.html) and accessed from the California Climate Commons.

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