

ARTICLE

Climate Ecology

Ventenata dubia projected to expand in the western United States despite future novel conditions

Ty C. Nietupski¹ | John B. Kim²  | Claire M. Tortorelli³  |
Rebecca Lemons⁴ | Becky K. Kerns⁵ 

¹USDA Forest Service, Geospatial Technology and Applications Center, Fort Collins, Colorado, USA

²Western Wildland Environmental Threats Assessment Center, USDA Forest Service, Corvallis, Oregon, USA

³Department of Plant Sciences, University of California, Davis, Davis, California, USA

⁴Department of Forest Engineering, Resources and Management, Oregon State University, Corvallis, Oregon, USA

⁵Pacific Northwest Research Station, USDA Forest Service, Corvallis, Oregon, USA

Correspondence

Ty C. Nietupski
Email: ty.nietupski@usda.gov

Present addresses

Claire M. Tortorelli, Pacific Northwest Research Station, USDA Forest Service, Corvallis, Oregon, USA; and
Rebecca Lemons, USDA Forest Service, Klamath River Basin Landscape, Eureka, California, USA.

Funding information

Oak Ridge Institute for Science and Education (ORISE)

Handling Editor: Jennifer M. Fraterrigo

Abstract

Distributions of both native and invasive species are expected to shift under future climate. Species distribution models (SDMs) are often used to explore future habitats, but sources of uncertainty including novel climate conditions may reduce the reliability of future projections. We explore the potential spread of the invasive annual grass *ventenata* (*Ventenata dubia*) in the western United States under both current and future climate scenarios using boosted regression tree models and 30 global climate models (GCMs). We quantify novel climate conditions, prediction variability arising from both the SDMs and GCMs, and the agreement among GCMs. Results demonstrate that currently suitable habitat is concentrated inside the invaded range of the north-west, but substantial habitat exists outside the invaded range in the Southern Rockies and southwestern US mountains. Future suitability projections vary greatly among GCMs, but GCMs commonly projected decreased suitability in the invaded range and increased suitability along higher elevations of interior mountainous areas. Climate novelty did not appear to undermine the prediction reliability in many cases where the climate–species relationship was fully represented by the occurrence data. GCM-derived variability resulting from variation in future cool season precipitation and temperature seasonality was greatest in the Rocky Mountains. SDM-derived variability was higher in currently suitable habitat, and few GCMs projections agreed that these areas would contain future suitable habitat. However, while prediction variability was high, many GCM projections agreed that parts of the Rocky, Wasatch, and Uinta Mountains would contain highly suitable habitat in the future. As disturbances in the interior mountains occur in coming decades, reducing some natural barriers to invasion, land managers, and conservationists will need to monitor for *ventenata* in post-disturbance environments. Changes to invasion potential may not play out for several decades, but results related to current potential may have applications for early detection and rapid response planning.

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Published 2024. This article is a U.S. Government work and is in the public domain in the USA. *Ecosphere* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

KEYWORDS

boosted regression trees, climate change, ecological niche modeling, global climate model, invasive species, novel climate, species distribution modeling, uncertainty, *Ventennata dubia*

INTRODUCTION

Biological invasions are a leading cause of biodiversity loss and have significant impacts on socioeconomic systems worldwide (Bellard et al., 2016; Bradshaw et al., 2016; Crystal-Ornelas et al., 2021; Shackleton et al., 2019). The impact of invasions may become increasingly severe as a result of changing climate, with increased species translocations (Seebens et al., 2015, 2018; van Kleunen et al., 2015) and the reorganization of native biotic communities (Bartley et al., 2019; Lurgi et al., 2012). However, the success of invasive species varies by region and ecosystem (Sorte et al., 2013), thereby reducing the broadscale application of management strategies for some invasions. When coupled with the increasing cost of invasion management over time (Gaskin et al., 2021), management practices like early detection and rapid response will be essential in mitigating the negative impacts of invasive species. The success of these practices will rely on information that can adequately describe the influence of climate change on a species' invasion potential (Funk et al., 2020; Hulme, 2017).

Climate change is expected to impact the future distribution of many plant species (Root et al., 2003; Walther et al., 2002). Additionally, future wildfire activity is expected to increase due to changes in temperature and precipitation patterns (Abatzoglou & Williams, 2016; Liu et al., 2010). The combined effect of changes to these two drivers of species distribution may disproportionately impact grass invasions. Invasive grasses can develop a grass–fire cycle where grass invasion facilitates fire and fire facilitates grass invasion (Brooks et al., 2004; D'Antonio & Vitousek, 1992). As a result, understanding the potential future distribution of invasive grasses will be important to understanding potential synergistic impacts of changing climate and wildfire disturbances on native plant communities. For some species of invasive grass, climate change may result in habitat reductions (Gallagher et al., 2013), while habitat might shift or increase for others (Abatzoglou & Kolden, 2011; Bradley, 2009). Knowing where and when changes to habitat are expected may provide enough warning for managers to prevent the postfire proliferation of invasive grasses in newly vulnerable ecosystems.

Species distribution models (SDMs), also known as ecological niche models, have been used to predict potential invasion across broad geographic domains

(Elith et al., 2010; Gallien et al., 2010; Peterson, 2003; Srivastava et al., 2019; Thuiller et al., 2005). SDMs estimate the relationship between a species and its environment, which can then be used to identify regions in space or time where the environment is amenable for a species' habitation (Guisan & Thuiller, 2005). While SDMs have known limitations (Guillera-Arroita et al., 2015; Mainali et al., 2015; Srivastava et al., 2019), they can provide a reasonable assessment of the distribution of habitat or potential range shifts when the characteristics of the species, such as dispersal dynamics, species interactions, or physiological constraints, are not yet fully understood (Fordham et al., 2018). SDMs developed for invasive species can be used to prioritize areas for heightened management and prevention efforts, especially during the early stages of invasion, when management efforts may be more effective (Creutzburg et al., 2022).

The reliability of SDM predictions is affected by uncertainty, which can arise from several aspects of the modeling process in addition to the natural variability of systems (Gould et al., 2014). An important source of uncertainty comes from climate novelty (Elith et al., 2010), where new climate does not resemble previously observed climate. To date, research on SDM applications in novel climate conditions has suggested many modeling algorithms can produce unreliable predictions in novel climate conditions (Mahony et al., 2017; Owens et al., 2013). Therefore, it is commonly recommended to assess climate novelty when predicting habitat distributions to identify where model predictions may be unreliable (Feng et al., 2019; Sofaer et al., 2019). Uncertainty in climate suitability can also arise from the global climate models (GCMs) used to project future climate conditions (Gould et al., 2014). For instance, projections of future habitat for cheatgrass (*Bromus tectorum*) in the western United States showed up to a 135% difference in the future change of suitable habitat depending on the GCM used to project future climate (Bradley, 2009). However, it is uncommon for more than a few GCM projections to be used for species distribution modeling, which limits our understanding of the range and variability of future invasion potential. Therefore, explicit consideration of the differences and agreement among many GCM-based predictions may provide a more wholistic understanding of potential, future species distributions.

In this study, we use species distribution modeling to examine the current and future invasion potential of a

rapidly spreading Eurasian annual grass, *Ventenata dubia* (ventenata), across the western United States. Ventenata is particularly problematic because it has the potential to transform invaded areas into annual grasslands, resulting in significant economic and ecological losses. Much like other pervasive annual grasses in the western United States, for example, cheatgrass, it increases fuel loading and promotes fire in historically sparsely vegetated ecosystems (Tortorelli et al., 2023). Such altered fire regimes can result in the loss of important plant species (e.g., sagebrush) and wildlife habitat (D'Antonio & Vitousek, 1992; Tortorelli et al., 2020). While ventenata shares characteristics with other widely studied invasive annual grasses, it appears to occupy a unique niche and has heavily invaded areas previously resistant to other annual grasses (Applestein & Germino, 2021; Tortorelli et al., 2020, 2022a). Despite invading pastures, shrublands, grasslands, and dry forests, ventenata may still be in an early stage of invasion (Jones et al., 2018). The spread of ventenata into new landscapes and the potential climate change impacts to its future distribution are concerning given ventenata's dispersal ability, wide-ranging ecological tolerances, and capacity to cause ecological and economic losses (Prather & Steele, 2009). Understanding the potential for current and future invasion of ventenata could help managers prioritize areas for prevention and treatment while effectively utilizing limited resources.

Our study objectives are to: (1) develop an SDM that explains both current and future climatically suitable habitats; (2) examine ventenata's relationship with climate, and (3) explore the forms of uncertainty that may impact projections and our understanding of invasion potential. While an SDM of ventenata's current habitat has been developed for the western United States (Jarnevich et al., 2021), we employ a unique modeling approach and explore climate relationships and uncertainty in depth. In addition, this study provides the first assessment of future ventenata invasion potential.

MATERIALS AND METHODS

Study area

The study area is the western conterminous United States, all lands west of -104° longitude (3 million km^2 ; Figure 1). The climate varies widely across the study area and is Mediterranean in the coastal states, with mean annual precipitation exceeding 2000 mm year^{-1} in the coastal northwest. Drier climates dominate the south and much of the low-elevation interior. In the interior, significant summer rainfall is delivered by convective storms.

Summer rainfall is particularly important in the southern portion of the region, where the monsoon season brings up to 50% of the annual rainfall (Higgins et al., 1997). Nearly half (46%) of the western United States is covered by shrublands, the majority of which are spread between the Great Basin and the southwestern deserts (Figure 1; Dewitz, 2019). Forests, mostly in mountainous areas, cover 22% of the western United States and the remaining third is split between grassland or herbaceous cover (18%), agriculture (7%), development (3%), and wetlands (1%).

Species data

Ventenata occurrence data were drawn from observational and experimental studies and publicly available databases (Appendix S1: Table S1). Occurrence records were cleaned and compiled, resulting in 2083 observations spanning the years 1957–2018. Most records were found in the interior northwest but included all states with recorded occurrence in the USDA plants database (<https://plants.uds.gov>), except for Wyoming.

We minimized the potential impacts of sampling bias by spatially thinning the occurrence dataset using a 5 km minimum distance between occurrence points (Boria et al., 2014; Phillips et al., 2009), resulting in 563 observations. To retain information potentially lost during the thinning process, we created 100 different thinned datasets of occurrence for use in model development. We also weighted occurrence records based on an observation's proximity to the nearest major road (protocols detailed in Appendix S1: Section 1.2; Statistics Canada, 2015; U.S. Geological Survey, 2014) and the distance to the invasion origin.

Absence data were generated (i.e., pseudo-absence) to control for nonequilibrium distribution issues, as the species may still be expanding in extent or abundance in the invaded ranges (Thuiller et al., 2005). The generation of pseudo-absences can impact the generality and bias of SDMs (Srivastava et al., 2019). However, sampling bias in occurrence data has a greater impact to model bias and generality than the method of pseudo-absence generation (Kramer-Schadt et al., 2013; Stokland et al., 2011). We focused on methods to minimize bias in the occurrence data and implemented pseudo-absence generation methods that have been shown to improve SDMs, including limiting the proximity of pseudo-absences and restricting the total geographic extent of pseudo-absence generation. We applied two constraints to generate pseudo-absences. First, we defined the "invaded range" as a 50-km buffer of the convex hull around all occurrence points (Figure 1; Mainali et al., 2015). We (1) randomly generated 100 replicates of 10,000 pseudo-absences within

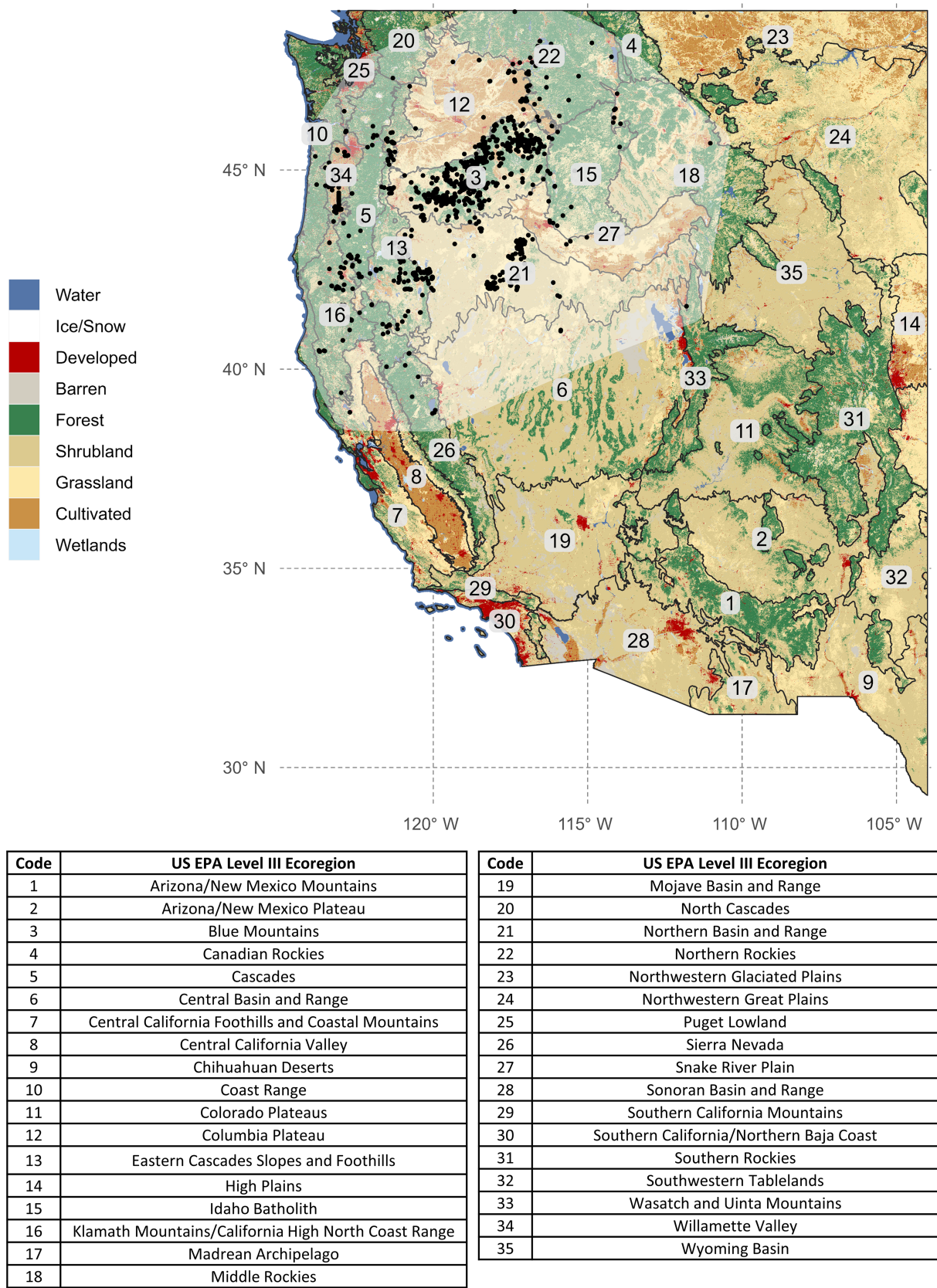


FIGURE 1 *Ventenata* (*Ventenata dubia*) occurrence and the diversity of vegetation, ecoregions, and land cover types in the western United States. The white shaded polygon shows *ventenata*’s invaded range (i.e., the minimum convex hull around occurrence points buffered by 50 km).

TABLE 1 Climatic predictors explored for the species distribution modeling of *Venttena dubia*.

Code	Description	Units
bio1	Annual mean temperature	°C
bio2	Mean diurnal range	°C
bio3	Isothermality	°C
bio4	Temperature seasonality	°C
bio5	Maximum temperature of warmest month	°C
bio6	Minimum temperature of coldest month	°C
bio7	Temperature annual range	°C
bio8	Mean temperature of wettest quarter	°C
bio9	Mean temperature of driest quarter	°C
bio10	Mean temperature of warmest quarter	°C
bio11	Mean temperature of coldest quarter	°C
bio12	Annual precipitation	mm
bio13	Precipitation of wettest month	mm
bio14	Precipitation of driest month	mm
bio15	Precipitation seasonality	mm
bio16	Precipitation of wettest quarter	mm
bio17	Precipitation of driest quarter	mm
bio18	Precipitation of warmest quarter	mm
bio19	Precipitation of coldest quarter	mm
csppt	Cool season precipitation	mm
qacqppt	Precipitation of quarter after coldest quarter	mm
qacqtavg	Mean temperature of quarter after coldest quarter	°C
sospt	Precipitation of start of season quarter	mm
sostavg	Mean temperature of start of season quarter	°C

Note: Bioclimatic variables were calculated with the “dismo” package in R (Hijmans et al., 2021), and the last five variables were developed specifically for winter-annual grass species.

the invaded range, (Elith et al., 2010; Mainali et al., 2015) and (2) excluded areas within 5 km of any individual occurrence (Barbet-Massin et al., 2012). The pseudo-absences were combined with the thinned *venttena* occurrence points. Finally, we weighted individual observations to account for the sample-size imbalance between the number of occurrence points and pseudo-absence points, ensuring that the sum of pseudo-absence weights equaled the sum of occurrence weights (Barbet-Massin et al., 2012).

Environmental data

Current climate was represented with 30-year normals calculated based on water-year (October 1982–September 2012)

at 800-m resolution (PRISM LT71; PRISM, 2012). From these climate normals, we calculated 19 bioclimatic variables (Hijmans et al., 2021; Nix, 1986) to characterize extremes, annual trends, and seasonal trends in long-term climate that could limit physiological functions and, consequently, species distributions (Table 1). We calculated five additional variables that characterize the critical periods of the growing season to address physiological controls on annual grass distributions (Gardner et al., 2019). While fall climate can be important for *venttena*, germination requirements may not be met until winter or spring periods (Wallace et al., 2015). Therefore, we only included winter and spring in our definition of the “cool season.” To account for potential variation in the timing of seasons at the end of the century, we tested two different ways to define spring: (1) the quarter after the coldest quarter, and (2) the first quarter where the mean monthly temperature exceeds 5°C in all three months (Linderholm, 2006). In addition, we defined cool season precipitation as the total precipitation in both the coldest quarter and the quarter immediately following the coldest quarter. Metrics related to soils and topography were evaluated in the early phases of the model development but had negligible influence and were excluded from further consideration.

Future climate was represented by the NASA Earth Exchange Downscaled Climate Projections dataset (NEX-DCP30; Thrasher et al., 2013). We used climate projections from 30 GCMs for Representative Concentration Pathway 8.5 (RCP8.5; van Vuuren et al., 2011). Further details on these 30 GCMs are provided in Appendix S1: Table S2. Climate projection data were accessed through Google Earth Engine (Gorelick et al., 2017), where they were processed to climate normals for the end of the century (October 2069–September 2099). Previously described climatic variables were calculated for each GCM, resulting in gridded predictions of future climate at an 800-m resolution.

Predictor selection and model transferability

Within the current climate space, we identified highly correlated variables (Pearson correlation threshold of ± 0.85 ; Elith et al., 2010) and retained those with stronger ecological importance for *venttena* based on the literature and the winter-annual grass life cycle. To minimize impacts to model spatial and temporal transferability, we calculated the correlation structure difference between (1) the invaded range and the western United States and (2) the current and future climate scenarios in the western United States (Appendix S1: Figures S1–S4).

We checked for sign changes or differences that exceeded ± 0.5 . From the 24 variables under initial consideration, this process resulted in seven predictor variables: mean diurnal range, isothermality, temperature seasonality, mean temperature of the warmest quarter, mean temperature of the coldest quarter, precipitation seasonality, and cool season precipitation.

Model development and evaluation

We used an ensemble of boosted regression tree (BRT) models to model *ventenata*'s climatically suitable habitat. BRTs have been demonstrated as a flexible and performative method for species distribution modeling, allowing for the use of diverse data types, handling outliers, and incorporating interactions (Elith et al., 2008; Norberg et al., 2019). Each model in the ensemble used a unique combination of occurrence and pseudo-absence data from the 100 replicate datasets (species data).

To improve model performance and minimize the potential for overfitting, we performed a cross-validated complete grid search of plausible hyperparameter values for 20 of the 100 replicates. From the tuning results, we chose the hyperparameters with the greatest ratio of performance to model simplicity (bag fraction = 0.75, interaction depth = 5, minimum observations per node = 40, learning rate = 0.005, number of trees = 1500). We used the selected hyperparameters to perform model simplification where predictors were iteratively dropped from the model until the average change in deviance exceeded the original model SE (Elith et al., 2008). As a result of this process, isothermality was dropped from the model, leaving six final variables (Appendix S1: Table S2).

We evaluated model performance in terms of sensitivity, specificity, and the area under the receiver operating characteristic curve (AUC) with fivefold cross-validation of each of the 100 replicate datasets. For each BRT model, we summarize each evaluation statistic by the mean and SD across that BRT model's five cross-validation datasets. We report the ensemble's performance as the mean of the 100 BRT models' means and SDs for each statistic.

Climate suitability and relationships

We predicted climatic suitability across the western United States under current (PRISM) and future climate conditions (NEX-DCP30). We assessed the area of suitable habitat by grouping probability values into four classes. The high suitability class ($0.72 \leq p < 1$) was

determined from the threshold that maximized the kappa statistic (Freeman & Moisen, 2008). We then further divided the probability gradient below this threshold into three additional classes: unsuitable ($0 \leq p < 0.05$), low suitability ($0.05 \leq p < 0.36$), and moderate suitability ($0.36 \leq p < 0.72$). To identify differences between regions, we examined classes across the west within and outside the invaded range, and by US EPA Level III ecoregions (Omernik & Griffith, 2014).

To characterize relationship between *ventenata* and current climate, we examined partial dependence plots from the BRT models. To determine where and how climate conditions were influencing suitability, we quantified the effect size of each predictor on each prediction location with SHapley Additive exPlanations (SHAP values; Lundberg et al., 2019). As the calculation of SHAP values is computationally intensive, we calculated SHAP values for 10% of BRT models for both current and future climate scenarios. From these raw SHAP values, importance was determined by ranking the predictors by their absolute SHAP values.

Assessing uncertainty and reliability

We used prediction variability and climate novelty to assess how different types of uncertainty may impact the model prediction reliability. We quantified both SDM- (current and future) and GCM-derived prediction variability. Current SDM-derived prediction variability was calculated as the SD of the BRT 100 models' predictions. For future SDM-derived variability, the same process was followed for each GCM and then averaged across the 30 GCMs. GCM-derived prediction variability was calculated as the SD of suitability predictions from the 30 GCMs. To determine whether and where the ensemble may be extrapolating, we assessed climate novelty and the source of novelty (i.e., the climate predictor leading to novel conditions) using multivariate environmental suitability surfaces (MESS; Elith et al., 2010). Finally, to identify locations where future suitability is more certain, we summed the number of GCMs that predicted a location as highly suitable (i.e., "suitability agreement") and identified ecoregions within the western United States where predictions agreed that climate conditions could support *ventenata*.

All model development, prediction, and assessment were performed in R version 4.1 (R Core Team, 2020) using packages caret (Kuhn, 2022), dismo (Hijmans et al., 2021), gbm (Greenwell et al., 2020), raster (Hijmans, 2022a), spThin (Aiello-Lammens et al., 2015), terra (Hijmans, 2022b), and treeshap (Komisarczyk et al., 2022).

GCM case studies

To evaluate the bounds of potential future climate that may impact *ventenata*'s distribution, we chose to highlight the results from four GCMs (Figure 2). These four GCMs were selected by examining the change in climate by the end of the century under RCP8.5 with respect to the top two predictors (i.e., the two predictors with the greatest relative importance). RCP8.5 is a high-warming scenario (Riahi et al., 2011) and may project well to mid-century (Schwalm et al., 2020, but see Ritchie & Dowlatabadi, 2017). While less severe warming scenarios may be more likely (Hausfather & Peters, 2020), the four selected GCMs project lower changes to mean annual temperature in comparison with the other GCMs used in this study.

RESULTS

The BRT models demonstrated strong performance with an average cross-validated AUC of 0.85 ± 0.02 , sensitivity of 0.95 ± 0.01 , and specificity of 0.38 ± 0.06 (individual

replicate evaluation statistics are found in Appendix S1: Table S3). Climatic suitability was most strongly explained by cool season precipitation followed closely by temperature seasonality, which accounted for 55% of the relative influence (Figure 3A). Mean temperature in the coldest and warmest quarters accounted for an additional 31% of relative influence. Precipitation seasonality and mean diurnal range accounted for the remaining 14% of relative influence. The top four predictors all showed a roughly unimodal relationship with suitability (Figure 3B). Suitability decreased with increasing precipitation seasonality and had a multimodal relationship with mean diurnal range.

Current suitability and uncertainty

Substantial portions of the western United States were predicted to contain highly to moderately suitable habitat (Figure 4; Table 2), which occurred between 1000- and 2000-m elevation (interquartile range; average of 1200 m). Within *ventenata*'s invaded range (see Figure 1), 25% of the area was classified as highly or moderately suitable

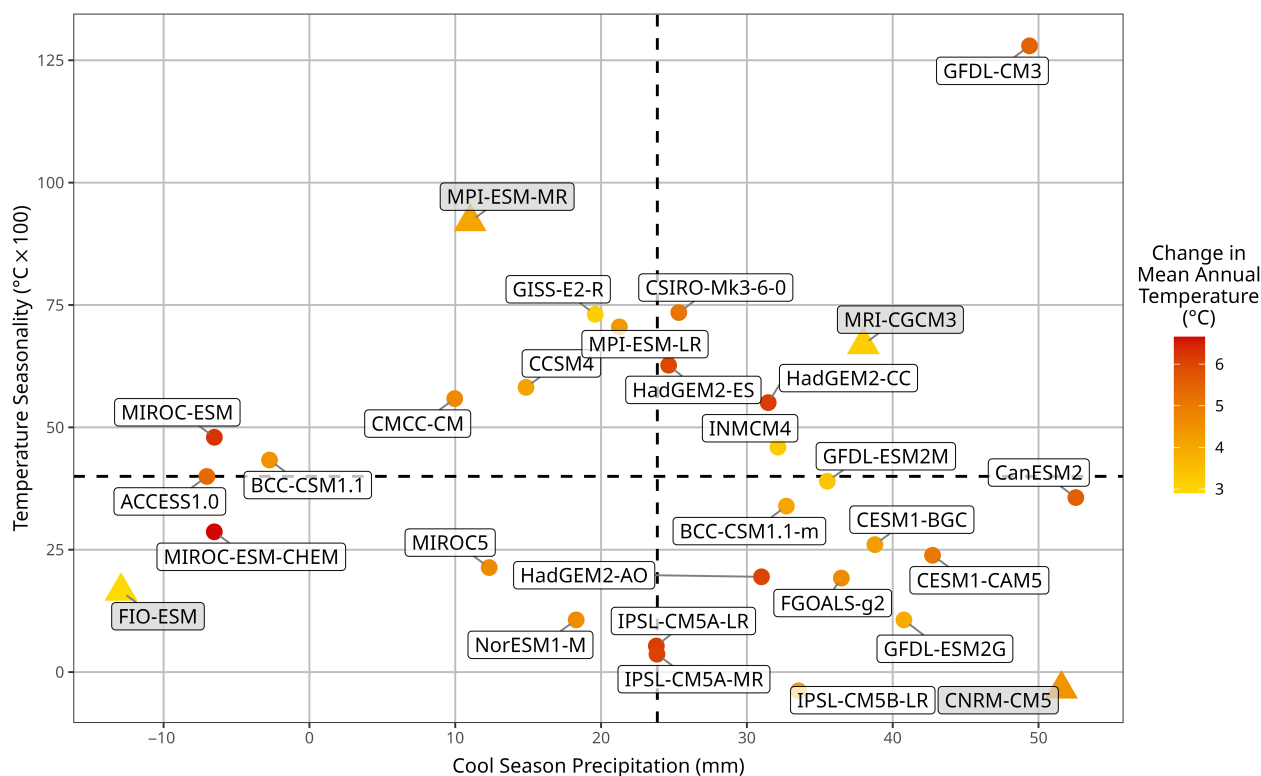


FIGURE 2 Projected change in temperature seasonality and cool season precipitation from 1982–2012 to 2069–2099 for 30 global climate models (GCMs). Temperature seasonality and cool season precipitation are the two most important *Ventenata dubia* habitat suitability predictors and are not highly correlated with projected mean annual temperature. The lower left quadrant represents climate most like current conditions and the upper right quadrant represents the greatest divergence in future climate. Gray label shading and triangles indicate the four GCM case studies.

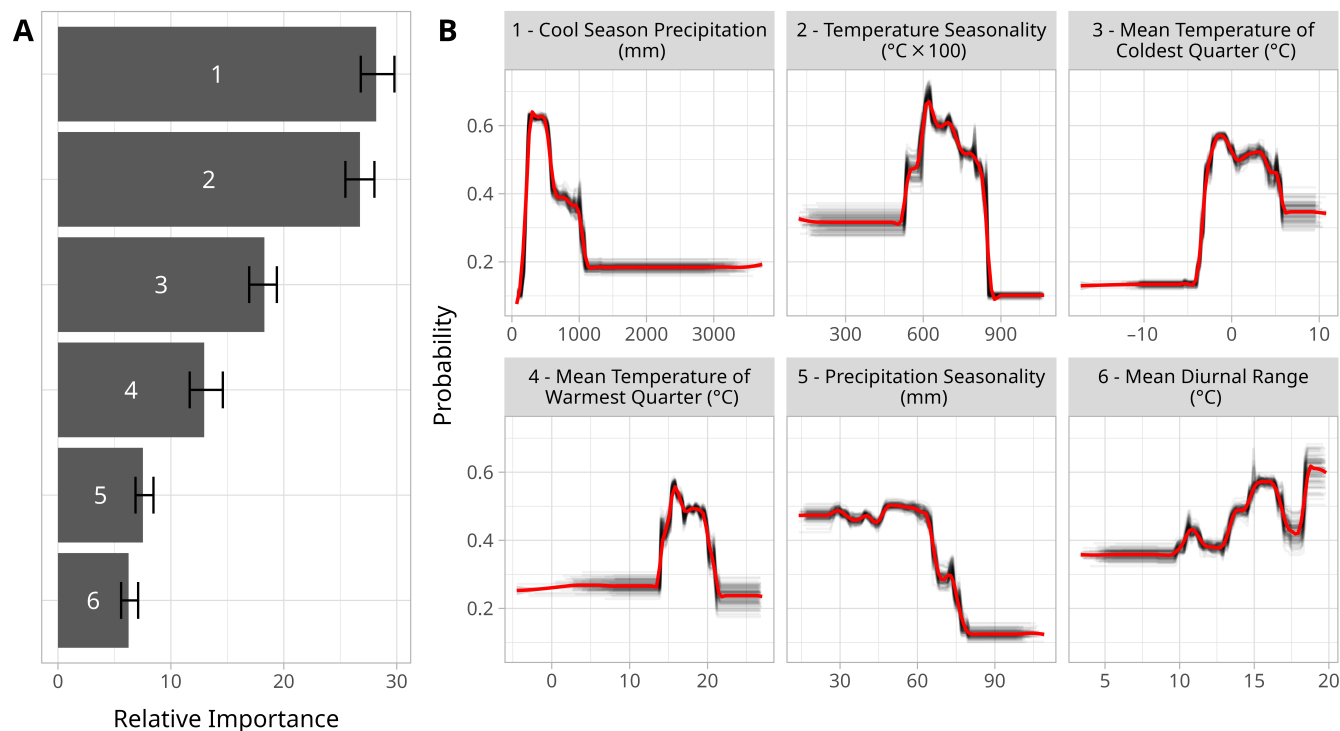


FIGURE 3 Partial dependence and relative importance of each climate predictor. (A) The bar width indicates the median relative importance of the model replicates while the error bars represent the 5th and 95th percentiles. (B) Black lines show the partial dependence for model replicates and the red line is a loess curve fit to highlight the general trend among replicates. Labels correspond with the numbers in the bar labels of panel A.

habitat. However, these classes cover less than 5% of the rest of the western United States. Most vulnerable ecoregions (i.e., with abundant highly and moderately suitable habitat) overlapped the invaded range. Vulnerable ecoregions outside of the invaded range include the Arizona/New Mexico Mountains (29,505 km²; 8% of total), Central Basin and Range (27,805 km²; 8% of total), and the Southern Rockies (17,095 km²; 5% of total). Habitat in these three ecoregions occurred at an average elevation of 2300 m. SDM replicates also had low prediction variability across the western United States (Figure 4; see Appendix S1: Section 4 for more information on SDM-derived uncertainty). Only areas with moderate suitability, such as portions of the Northern Basin and Range, had relatively high prediction variability (e.g., suitability 0.4 ± 0.2).

The importance map illustrates the dominant effect of cool season precipitation across much of the western United States (Figure 5). However, suitability in some regions was more strongly governed by other climate predictors, some of which were not ranked highly in the model-level assessment (Figure 3). For example, high precipitation seasonality (i.e., >80 mm) decreased suitability in much of the Central California Foothills and Coastal Mountains, Central California Valley, Sierra Nevada, and Klamath Mountains/California High North

Coast Range ecoregions. In other areas, low coldest quarter temperature (i.e., $<-6^{\circ}\text{C}$) decreased suitability along the higher elevation Rockies.

Future suitability and uncertainty

The distribution of climatically suitable habitat varied substantially by GCM (Figure 6). Projections of highly suitable habitat may decrease from 19% to 95% by the end of the century (Appendix S1: Table S7). Moderately suitable habitat was also frequently projected to decrease by GCMs, but some GCMs (FIO-ESM, INMCM4.0, IPSL-CM5B-LR, MIROC5, GFDL-ESM2G, CNRM-CM5, CESM1-CAM5, and CESM1-BGC) projected an increase in moderate suitability by as much as 39%. Relative to the others, these GCMs projected larger increases in cool season precipitation along with smaller increases in temperature seasonality and smaller changes in mean annual temperature (Figure 2). Compared with the current distribution, models driven by some GCMs projected a similar elevational range but higher average elevation (e.g., CNRM-CM5: avg. 2200 m and range 1700–2700 m; MPI-ESM-MR: avg. 1850 m and range 1400–2300 m), while other GCMs projected a narrower elevational range

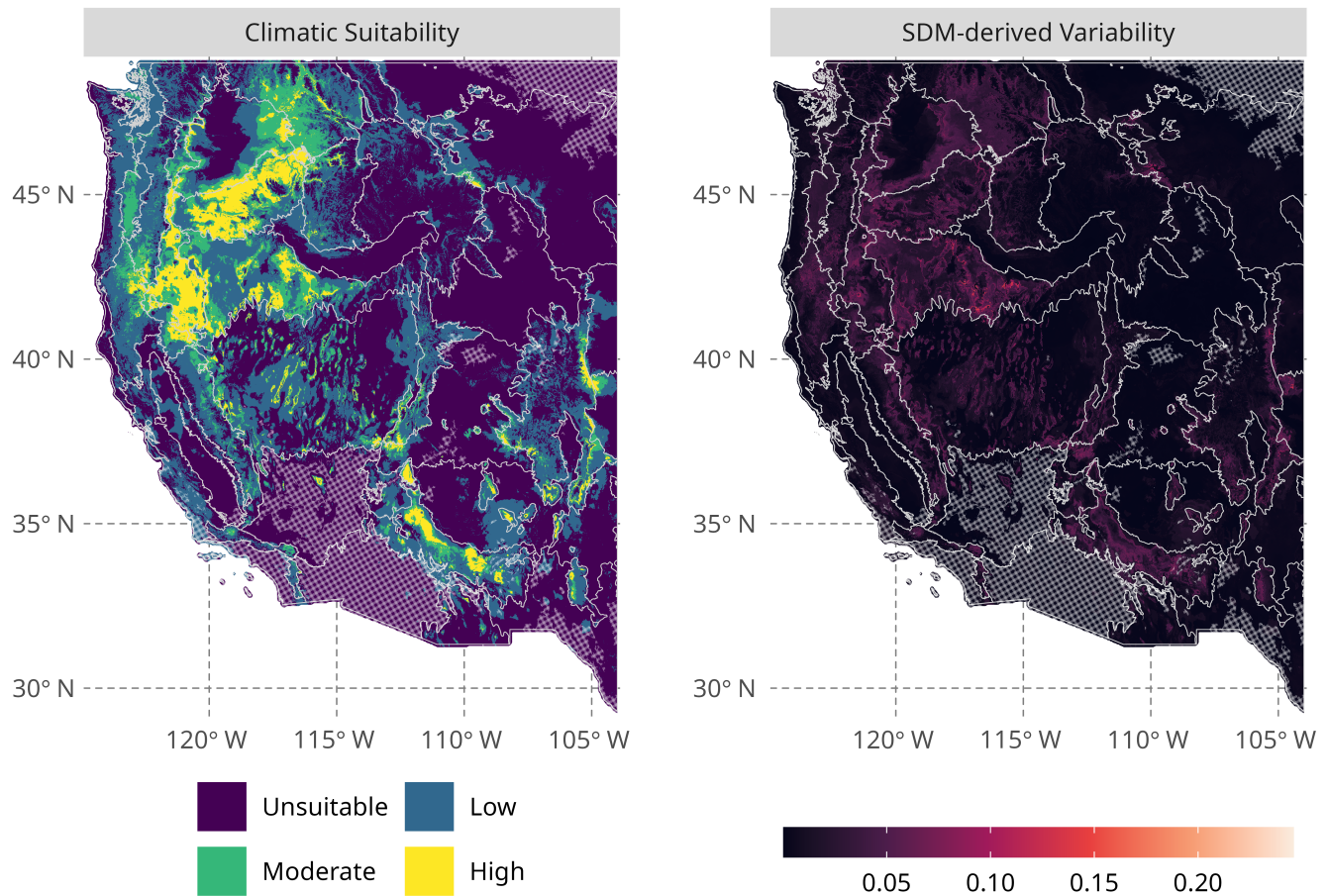


FIGURE 4 *Ventenata dubia* climatic suitability and species distribution model-derived prediction variability across the western United States under current climate (PRISM; 1982–2012). Areas with the white crosshatch pattern indicate climate novelty. SDM, species distribution model.

TABLE 2 Composition of suitability classes within and outside of the invaded range of *ventenata (Ventenata dubia)* under current climate conditions (PRISM; 1982–2012).

Climatic suitability class	Area inside invaded range (km ² × 1000)	Area outside invaded range (km ² × 1000)	Percentage of area inside invaded range	Percentage of area outside invaded range	Percentage of area in western United States
High	96.97	26.92	9.5	1.3	4.1
Moderate	170.73	60.61	16.7	3.0	7.6
Low	410.13	508.30	40.1	25.2	30.2
Unsuitable	345.17	1419.17	33.7	70.4	58.1

and increased average elevation (Appendix S1: Figure S8). At higher latitudes of the western United States, highly and moderately suitable habitats were projected to shift upward from 250 to 1250 m (GISS-E2-R and CanESM2), while these classes within the mid-latitudes shifted from −50 to 1250 m (MPI-ESM-MR and HadGEM2-ES) and low latitudes shifted from 200 to 850 m (GISS-E2-R and IPSL-CM5A-LR). Across GCMs, much of the suitable habitat expansion occurred in the Rockies and especially the Southern Rockies (e.g., NorESM1-M; Appendix S1:

Figure S6), but some GCMs projected increased suitability along the entire range (e.g., CNRM-CM5; Appendix S1: Figure S6).

Future projections also differed significantly between currently invaded and uninvaded ranges. Within the invaded range, highly suitable habitat contracted in all GCMs and moderately suitable habitat contracted in 26 out of the 30 GCMs. Outside of the invaded range, highly and moderately suitable habitat expanded in about 60% of GCMs and by as much as 160% and 124%,

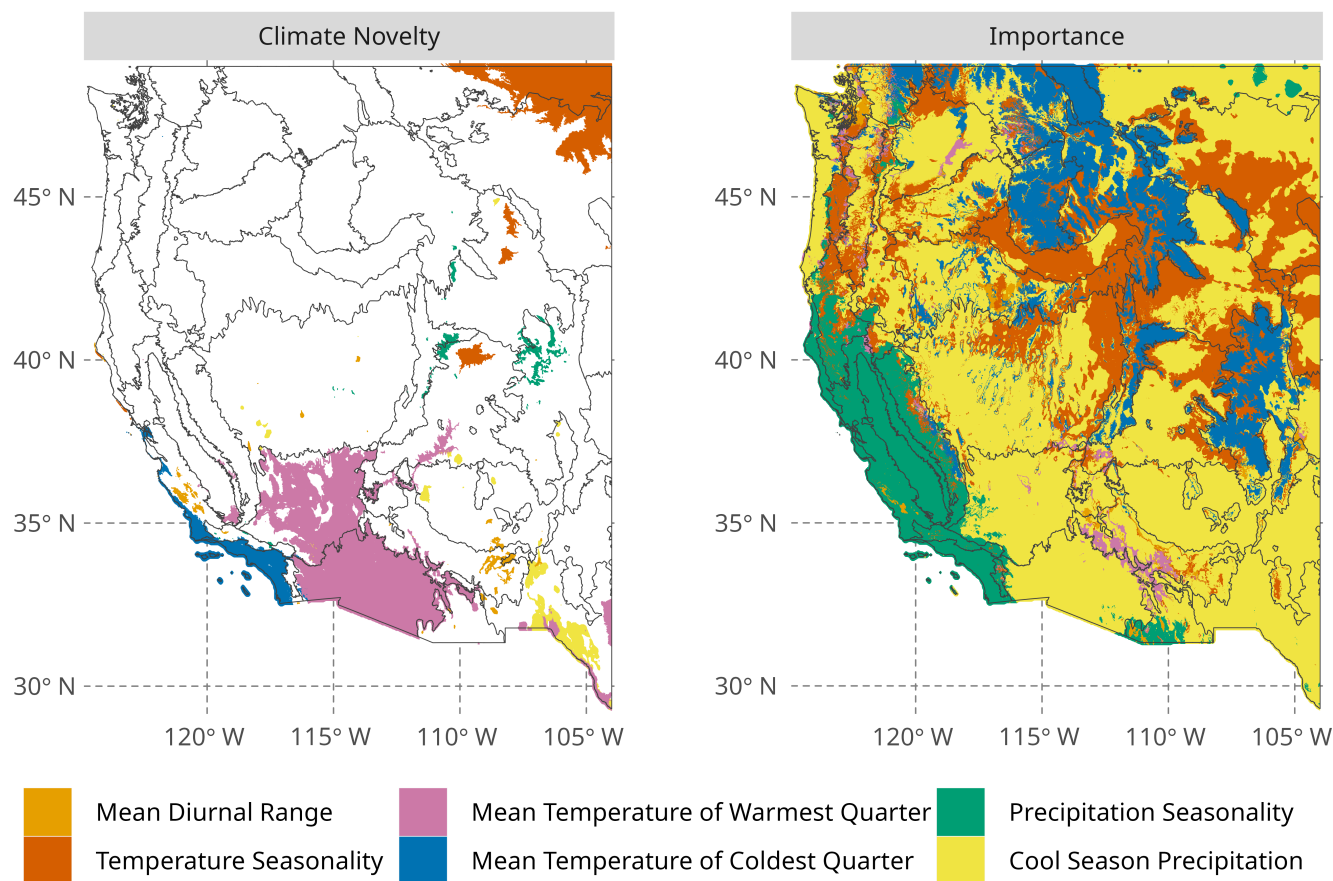


FIGURE 5 The source of climate novelty and predictor importance under current climate conditions (PRISM; 1982–2012). Climate novelty shows the location of climate conditions that were outside the observed range in the occurrence data. Importance shows the predictor with the greatest influence on the climate suitability. Under current climate conditions, most areas of novel climate were predicted to be unsuitable (Figure 4). Large contiguous areas of climate novelty in the Northwestern Plains and the Mojave and Sonoran deserts contributed to the low suitability for *Ventemata dubia*. However, low suitability was most influenced by low cool season precipitation in the Northwestern Plains. Therefore, while temperature seasonality was novel in the Northwestern Plains, the unsuitable classification is mostly related to cool season precipitation, suggesting that predictions may be reasonable. While the Mojave and Sonoran Deserts were novel in terms of warmest quarter temperatures, cool season precipitation, and coldest quarter temperatures, the observed *Ventemata*–climate relationship suggests that habitat suitability is low near the novel values. Therefore, the low suitability predicted in these areas may be reasonable. Not all locations of climate novelty coincided with low *Ventemata* suitability. Exceptions occurred in areas that were novel due to high diurnal range or low precipitation seasonality. In these cases, the *Ventemata*–climate relationship shows high suitability at the high or low extremes of the observed climate gradient (e.g., high suitability at 20°C diurnal range). The Arizona/New Mexico Mountains, Arizona/New Mexico Plateau, and Chihuahuan had diurnal range values (20 and 21°C), which increased the predicted suitability. When coupled with the relatively high species distribution model-derived variability, suitability predictions in these areas may be less reasonable.

respectively. GCMs that projected an increase in moderately suitable habitat outside of the invaded range generally projected an increase across the western United States. A few GCMs that did not predict an expansion across the west but did project an expansion outside the invaded range shared temperature seasonality and cool season precipitation characteristics with those that projected an expansion across the west. However, 7 out of 10 of these GCMs (e.g., CanESM2, FGOALS-g2, HadGEM2-AO, IPSL-CM5A-LR, IPSL-CM5A-MR, MIROC-ESM, MIROC-ESM-CHEM, NorESM1-M) had greater than average changes in mean annual temperature (Figure 2).

Variability from GCM projections was nearly an order of magnitude greater than that derived from the SDM (Figure 6). GCM-derived variation generally decreased with decreasing suitability (Table 3), and the greatest GCM-derived variation occurred along the Rockies, much of which has low current suitability. This variation arose from the interaction between cool season precipitation, temperature seasonality, and mean annual temperature. In contrast to the GCM-derived variability, SDM-derived variability was highest in areas predicted to be highly or moderately suitable under current climate. This pattern of high SDM-derived uncertainty

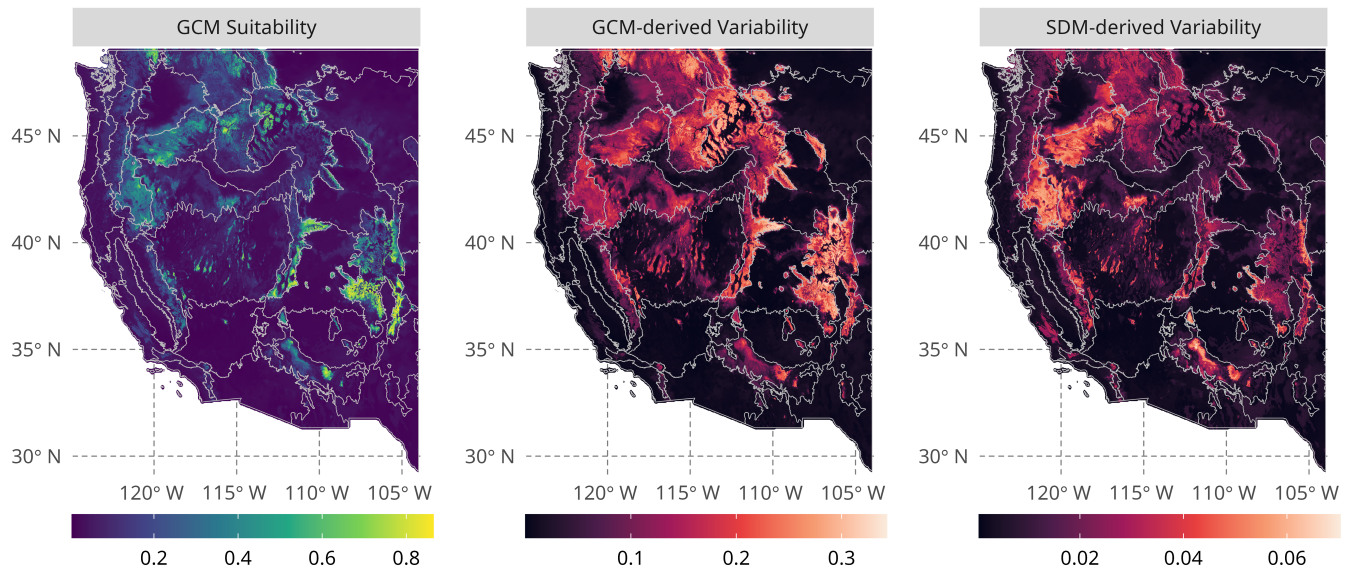


FIGURE 6 Summary of suitability projections from 30 global climate models (GCMs) for the end of the century (2060–2099) based on the RCP8.5 emissions pathway. GCM suitability (left) is the median suitability across the 30 suitability projections. GCM-derived variability (center) is the SD of suitability across the 30 suitability projections. Species distribution model-derived variability (right) is the SD of suitability from boosted regression tree replicates averaged across GCMs. SDM, species distribution model.

TABLE 3 Prediction variability for climatic suitability classes arising from global climate models (GCMs) and the species distribution model (SDM).

Climatic suitability class	GCM-derived variability			SDM-derived variability		
	Avg	Min	Max	Avg	Min	Max
High	0.206	0.038	0.341	0.023	0.011	0.049
Moderate	0.224	0.048	0.343	0.038	0.015	0.070
Low	0.104	0.002	0.338	0.018	0.004	0.067
Unsuitable	0.015	0.000	0.288	0.004	0.001	0.017

Note: Variability was summarized by the median prediction across GCMs for the end of the century (2069–2099) under RCP8.5 climate change scenario.

coincides with future projections of moderate suitability, indicating that suitability may become marginal in many currently suitable areas.

Under many of the GCM predictions, cool season precipitation remained the most important climate predictor of suitability at the end of the century (Figures 7 and 10C; Appendix S1: Figure S11). Nonetheless, temperature seasonality displaces cool season precipitation as the most important predictor in much of the Intermountain West. Additionally, precipitation seasonality became more important at higher latitudes to the west of the Sierra Nevada and Cascade ranges, as well as in some parts of the Mojave, Sonoran, and Chihuahuan Deserts.

Novel climate conditions were projected to increase across the west under the majority of the GCMs (Figure 8; Appendix S1: Figure S5), with some GCMs

(e.g., GFDL-CM3) projecting novel conditions for much of the western United States. Climate novelty was projected to mostly expand from the currently novel regions. For example, novelty from the warmest quarter temperatures may expand to the north from the Mojave and Sonoran Deserts. Other notable expansions occurred for coldest quarter temperatures along the Coast Range and mean diurnal range in the Arizona/New Mexico Plateau and Southwestern Tablelands.

Although *ventenata* habitat suitability varied across the study and across GCMs, some locations had high agreement across multiple GCMs (Figure 9). Agreement most frequently occurred within the Southern and Middle Rockies, Wasatch and Uinta Mountains, and Idaho Batholith ecoregions. When weighted by ecoregion area (i.e., agreement/unit area), the Canadian

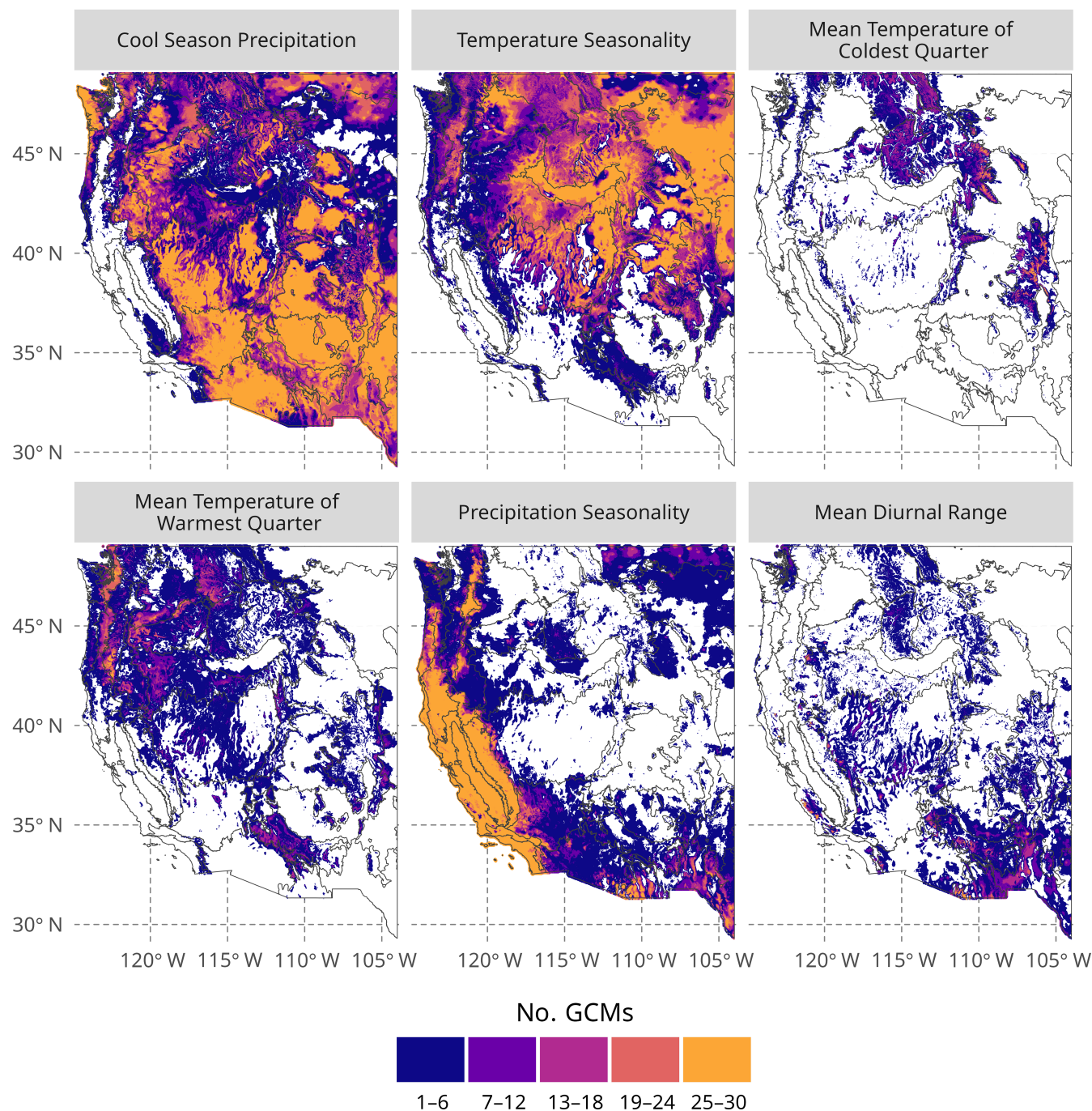


FIGURE 7 The number of global climate models (GCMs) that ranked each predictor as most important under RCP8.5 at the end of the century (2069–2099).

Rockies, Northern Rockies, North Cascades, Eastern Cascades Slopes and Foothills, and Blue Mountains ecoregions had moderate vulnerability to *ventenata*. The Arizona/New Mexico Mountains had somewhat low vulnerability, with GCM model agreement primarily occurring only in the highest elevations. Similarly, high elevations of the Central Basin and Range had somewhat high agreement, but these areas compose a relatively small proportion of the total ecoregion.

GCM case studies

The four selected GCMs illustrate individual model output across a range of climate conditions (Figure 10; Appendix S1: Figure S10). FIO-ESM simulates a future climate that is the most like present-day conditions and shows little change in suitability resulting from mild increases in temperature seasonality and cool season precipitation. Increases in temperature seasonality under

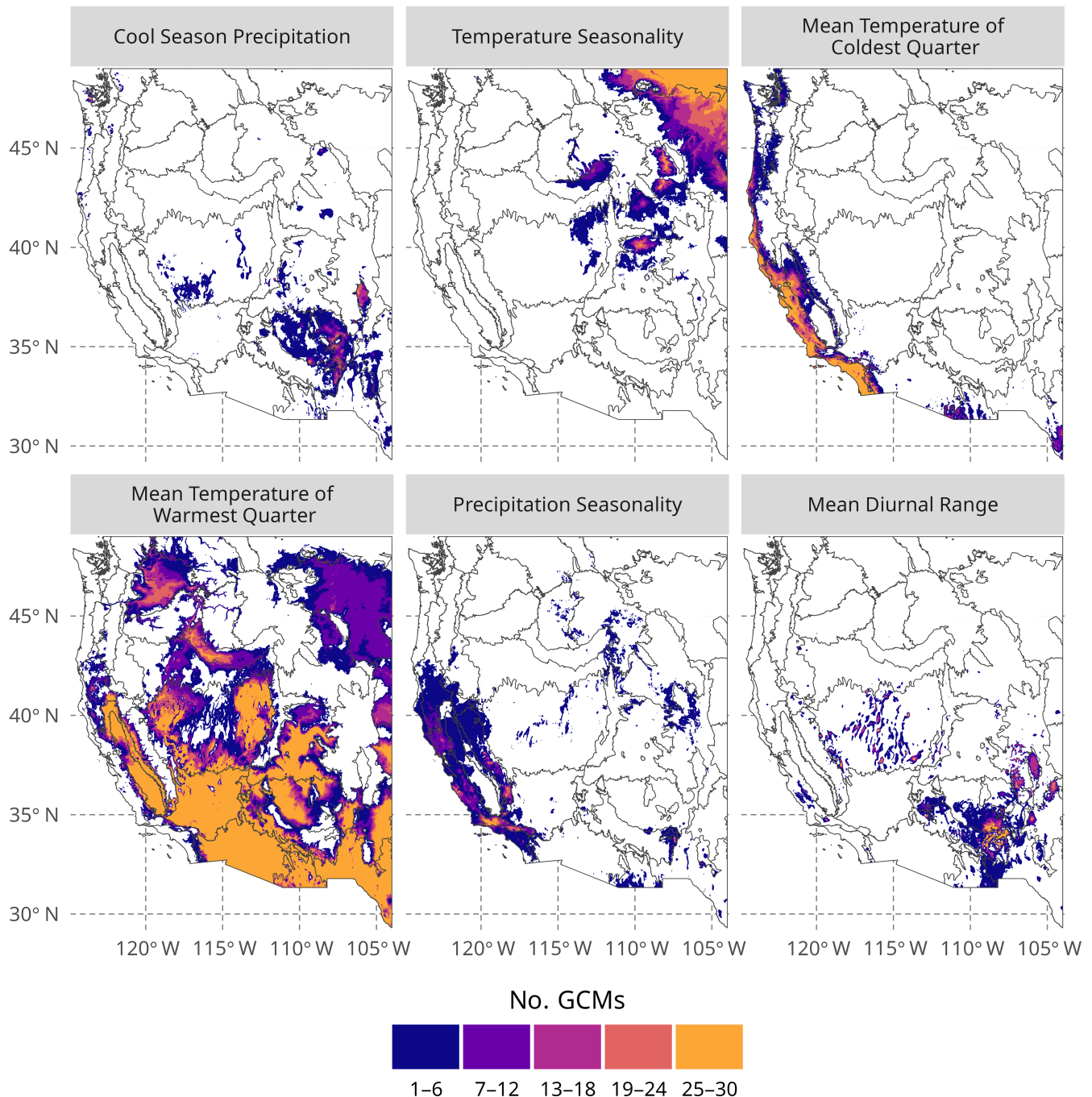


FIGURE 8 The number of global climate models (GCMs) with novel future climate conditions under RCP8.5 for the end of the century (2069–2099).

MPI-ESM-MR resulted in a large suitability decrease both inside and outside of the invaded range. As expected, the other two GCMs showed more moderate changes in suitability within the invaded range and variable changes outside. At higher latitudes, increased cool season precipitation increased the proportion of suitable habitat across the elevation gradient (e.g., CNRM-CM5) and increased temperature seasonality tended to decrease the proportion of suitable habitat across the

elevation gradient (e.g., MRI-CGCM3). In the most extreme example (MPI-ESM-LR), very little suitable habitat remained at mid- and high latitudes by the end of the century. However, at lower latitudes, variation in the change of temperature seasonality and cool season precipitation between GCMs did not impact the proportion of moderately and highly suitable habitat per elevation class, which either remained similar or increased in the future (i.e., bottom row of Figure 10).

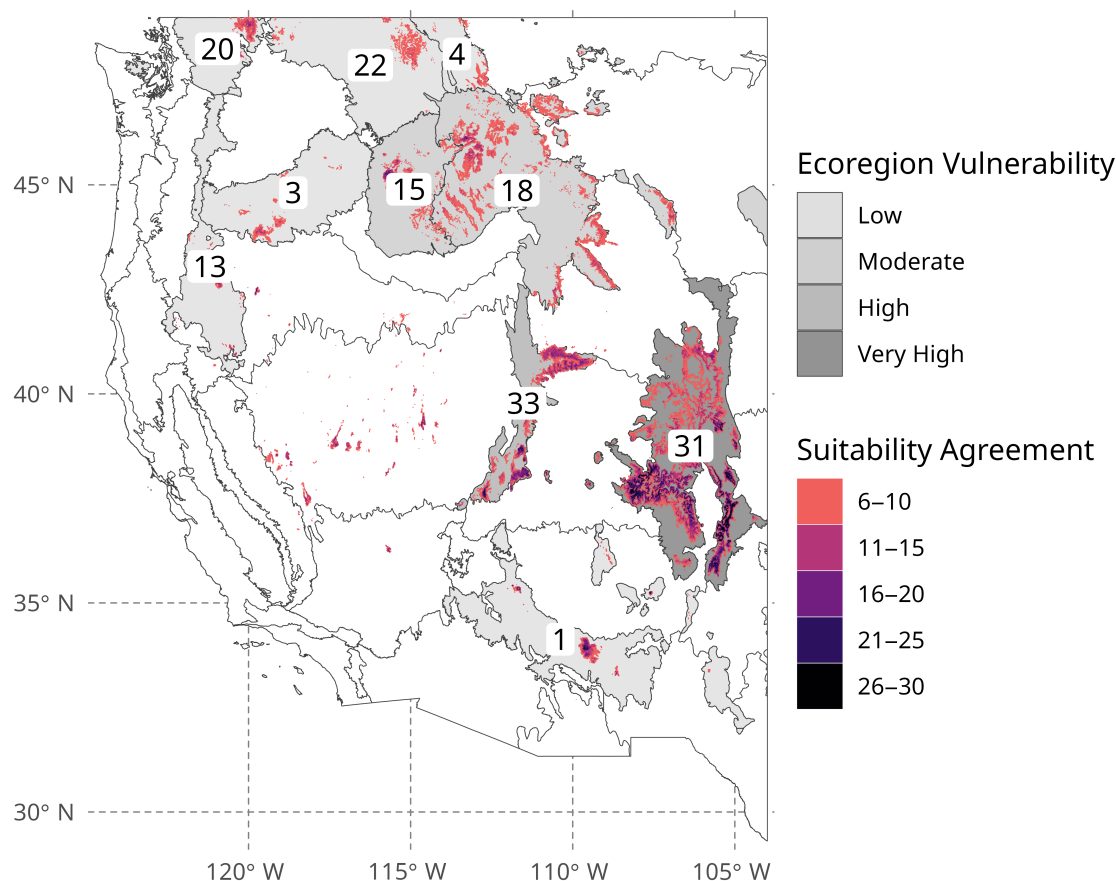


FIGURE 9 Agreement between global climate models (GCMs) of future climatically suitable habitat for *ventenata* (*Ventenata dubia*) in the western United States. Suitability agreement is the count of GCMs for which the location was predicted to be highly suitable at the end of the century (2069–2099). US EPA level III ecoregions in gray shading indicate greater vulnerability to invasion as determined by the area weighted sum of suitability agreement. Numeric codes correspond with the ecoregion names listed in the table in Figure 1. Ecoregions with low vulnerability include 1, 3, 4, 13, 20, and 22; 15 and 18 are moderate; 33 is high and 31 is very high.

DISCUSSION

Climate change will influence the distribution and composition of many plant communities and favor some non-native species over natives. We found that projected future climate may lead to substantial changes in the distribution of *ventenata*'s climatic habitat under a high-warming climate scenario (RCP8.5; Riahi et al., 2011), with suitable habitat shifting toward the mountainous regions of the west, especially toward the Rocky Mountains. However, predictions of future habitat varied greatly among GCMs, highlighting the uncertainty in future invasion potential. While projections of future habitat were variable, some areas within the west were projected to be suitable by as many as 25–30 of the GCMs. Uncertainty in current and future invasion potential can be compounded by novel climate conditions, which may mean that predictions in these areas are unreliable (Elith et al., 2010). However, based on the observed *ventenata*–climate relationship, we found that most novel

climate conditions were far beyond the threshold at which climate conditions became unsuitable, indicating that predictions in these areas may be reasonable.

Under both the current and future climate scenarios, areas with higher cool season precipitation supported suitable *ventenata* habitat. Cool season moisture coincides with the growth cycle of *ventenata* and is critically important for winter-annual grass species (Bradley, 2009; Pilliod et al., 2017; Prev y & Seastedt, 2015). Within the native range of many winter-annual grasses, the balance of annual and perennial species abundance follows a precipitation seasonality gradient, where annuals are favored by cool season precipitation and higher seasonality (Clary, 2008). Our results coincide with previous research in this regard with one exception: locations in California that have extreme precipitation seasonality have decreased habitat suitability. This observed effect of precipitation seasonality in California may be a proxy for competitive exclusion from other non-native annual grass species because California's Mediterranean climate is suitable for

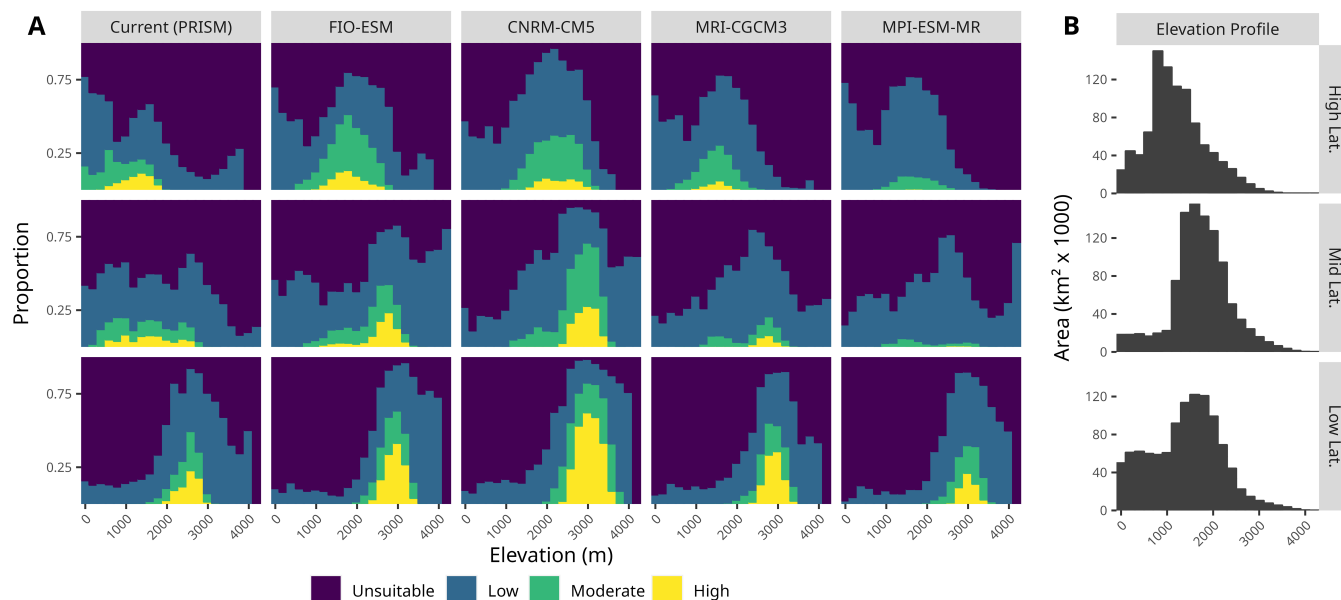


FIGURE 10 The distribution of climatic suitability in the western United States by elevation and latitude under current (PRISM; 1982–2012) and future (2069–2099) climate conditions, based on four selected global climate models. (A) The proportion of each elevation class occupied by each suitability class, and (B) the area of each elevation class. The rows represent three latitude classes (29.3–38.2°, 38.2–43.6°, and 43.6–49.1°, respectively). FIO-ESM has future climate the most similar to current climate. CNRM-CM5 has future climate the most favorable to *Venttena dubia* expansion, driven primarily by increasing cool season precipitation. MRI-CGCM3 is an intermediate case featuring increasing cool season precipitation and increasing temperature seasonality. MPI-ESM-MR has future climate the least favorable for *venttena* expansion, characterized by increasing temperature seasonality.

and heavily invaded by numerous annual grasses (HilleRisLambers et al., 2010; Jackson, 1985).

While cool season precipitation was the most important predictor under current climate, future suitability was driven as much, if not more, by temperature seasonality. We found that high temperature seasonality decreased habitat suitability, a finding that has also been reported for other non-native annual grasses in North America (Bowen & Stevens, 2020). *Venttena*'s life cycle tends to start (Noone et al., 2013) and end later (Pavek et al., 2011) than other co-occurring invasive annual grasses, which may expose *venttena* to more extreme cold or heat spells during important phases of its growth and reproduction. Additionally, if there is a rapid transition from extreme cold to hot temperatures, the duration in which soil temperature and moisture requirements meet *venttena*'s needs may not last long enough for *venttena* to complete a life cycle or produce viable seeds. Future increases in temperature seasonality have also been projected to drive the future grass–shrub dominance in dryland ecosystems where shrubs are expected to be favored over perennial grasses (Gremer et al., 2018). Therefore, while the abundance and distribution of precipitation over the year will be important moving forward, the variation in temperature over the year may

have a greater impact on the habitat suitability for certain species and functional groups.

Unsurprisingly, current predictions indicate that the largest area of high and moderate suitability is found within the invaded range. And while the percentage of suitable habitat in the remaining western United States is relatively small, the total area of highly and moderately suitable habitat is nearly equivalent. Given adequate time, transport, and climate conditions, this could mean a doubling of the total invaded area within the western United States. Invasive plant species commonly have a lag phase of 20 or more years after their introduction before they rapidly spread to new locations (Aikio et al., 2010). While *venttena* has been present in the Pacific Northwest for several decades, expansion has only recently increased in this region (Wallace et al., 2015). Another invasive annual grass, cheatgrass, rapidly expanded to its invaded range over about 40 years after being present in the United States for several decades prior (Novak & Mack, 2001). Therefore, *venttena* may only be at the beginning stages of a rapid expansion across the west.

The spatial patterns of current habitat generally aligned with those of another recently produced SDM for *venttena* (Jarnevich et al., 2021). However, our

models predicted substantial suitable habitat in the Arizona/New Mexico Mountains but did not predict much suitable habitat in the Wyoming Basin and Northwestern Great Plains. Predictions from the Jarnevich et al. (2021) study contrast with our predictions in these ecoregions. Unlike Jarnevich et al. (2021), we included cool season precipitation and temperature seasonality in our model. Cool season precipitation in the Arizona/New Mexico Mountains increased suitability while temperature seasonality decreased suitability in the Wyoming Basin and Northwestern Great Plains. Nevertheless, our habitat predictions did overlap with those of Jarnevich et al. (2021) in parts of the Wyoming Basin and Northwestern Great Plains and other nearby ecoregions.

Employing a combination of existing and recently developed methods allowed for a clearer understanding of uncertainty and the locations vulnerable to current and future invasion. Model projections based on the 30 GCMs generally agreed that suitability within many currently suitable areas would decrease, similar to results reported for other invasive grasses (Bradley, 2009; Gallagher et al., 2013). Many currently suitable areas are predicted to transition from high or moderate suitability to moderate or low suitability. In addition, future SDM-derived variability is relatively high in many of the same locations, indicating that habitat may become marginal in the future (Gould et al., 2014).

Across the western United States, all future suitability projections resulted in a decrease in the total amount of highly suitable habitat (Appendix S1: Table S6). However, suitability agreement suggested that ecoregions including the Southern Rockies, Middle Rockies, Wasatch and Uinta Mountains, and Idaho Batholith would contain substantial amounts of highly suitable habitat (Figure 9). These same ecoregions and much of the Rocky Mountains also had the greatest GCM-derived uncertainty (Figure 6). In these regions, GCMs consistently projected that there would be an increase in coldest quarter temperatures, which increased the suitability for *ventenata*. This increase in winter temperatures could lead to more precipitation falling as rain and a lengthening of the growing season, which has been shown to increase the habitat suitability for other invasive annual grass species (Concilio et al., 2013). Within the Middle Rockies and Idaho Batholith ecoregions, many of the GCMs also projected large increases in temperature seasonality, which somewhat dampened the impact of more favorable coldest quarter temperatures. However, for the Southern Rockies and Wasatch and Uinta Mountains ecoregions, GCMs projected that temperature seasonality would not increase as much, which led to a more frequent prediction of highly suitable habitat. The Southern Rockies and Wasatch and Uinta

Mountains ecoregions also have considerable habitat under current climate, so climate may be expected to remain suitable now and in the coming decades.

Our results support the close examination and interpretation of model predictions through the lens of climate novelty. Projections of habitat suitability across space and time can lead to model transferability issues arising from altered species–environment relationships in prediction domains and extrapolation of models in novel climatic space (Mainali et al., 2015; Qiao et al., 2019). In our study, climate novelty did not commonly reduce the reliability of model predictions. This contrasts with some reported assumptions about model extrapolation outside the observed environmental range (Gallagher et al., 2013; Owens et al., 2013). Owens et al. (2013) found that relationships fit by several modeling algorithms produced unrealistic responses that suggested high probability at the margins of the observed environmental range. As a result, unrealistic predictions occurred when these models were applied outside the observed environmental range.

The relationship between *ventenata* and most of the climate predictors was nearly unimodal (Figure 3), suggesting that the SDM may have reasonably captured the upper and lower suitability thresholds for *ventenata*. Consequently, many of the novel climate locations across the western United States fell outside the observed range of suitable conditions. For example, warmest quarter temperatures in the Mojave and Sonoran Deserts were novel but also far outside the observed climate relationship. However, not all climate variables had a unimodal relationship. Two of our predictors had relationships where probability was high at the margins of the observed environmental range, resulting in extrapolation when climate conditions were novel. One example of this extrapolation occurred from the influence of diurnal range in the Arizona/New Mexico Mountains, Arizona/New Mexico Plateau, and Chihuahuan Deserts, where predictions should be cautiously interpreted. In addition to examining the fitted species–environment relationship, it was also useful to determine the contribution of individual climate predictors to suitability using a recently developed method based on SHAP values. SHAP values in the Mojave and Sonoran Deserts indicated that the influence of cool season precipitation and temperature seasonality was four times the influence of the warmest quarter temperatures (Appendix S1: Figure S12). Therefore, climate novelty from warmest quarter temperatures in this region did not substantially contribute to the resulting suitability and may not signal unreliable predictions.

Much of the current moderate and highly suitable habitat outside the invaded range occurs at higher

elevations. This result is unsurprising given that the invaded range falls within the top half of the western United States' latitudinal gradient. *Ventenata* already invades higher elevations within its invaded range than other problematic annual grass species, including dry pine and mixed-conifer forests (Tortorelli et al., 2020). At lower latitudes, we found that suitable habitat was frequently projected in areas where dense conifer forests (i.e., areas with high canopy cover) would likely prevent *ventenata* establishment or confine populations to forest openings. Therefore, while the proportion of suitable habitat in ecoregions like the Arizona/New Mexico Mountains, Central Basin and Range, and the Southern Rockies may be relatively high, the actual area where this species could invade within these ecoregions may be much smaller.

Future suitable habitat generally increased in elevation within a given latitudinal band, consistent with reports for many plant species (Lenoir et al., 2008). However, in contrast to the lowest latitudinal band where the proportion of each elevation class was maintained or increased, the mid- and high latitudinal bands saw decreases in the area and proportion of elevation classes with suitable habitat with increasing temperature seasonality (Figure 10). This pattern suggests that if temperature seasonality increases, there may be a southward latitudinal shift of moderately or highly suitable habitat. However, suitability reductions in the northern latitudes may be tempered if cool season precipitation increases along with temperature seasonality. Historically, many species have been projected to shift both up in elevation and northward in latitude (Hickling et al., 2006; Pauchard et al., 2016). Our models partially confirm this effect, where increasing coldest quarter temperatures increased suitability at northern latitudes and decreased suitability at southern latitudes. However, as with other results from this analysis, increasing temperature seasonality trumped this effect, causing decreased suitability at northern latitudes.

We acknowledge several caveats in our modeling approach. While we used the finest resolution gridded datasets (800 m) available for both current and future conditions, the resolution may be problematic in complex or high-relief terrain. We also note that there are other nonclimate-related barriers to plant invasion that should be considered, particularly at local scales. Metrics related to soils and topography were evaluated in the early phases of our model development but had negligible influence and were excluded from further consideration. However, soils and topography may be important for invasion success at finer scales. Biotic interactions, such as competition and propagule pressure, also influence invasion dynamics. Mature native perennial grasses, especially those with

similar growth forms and phenology, can be highly effective competitors with some invasive annual grasses such as cheatgrass (Chambers et al., 2007), although one study suggests *ventenata* does not strongly interact with neighboring herbaceous species (Tortorelli et al., 2022b). While biotic relationships may be important to consider at local scales, macroclimate imposes the most control on species distributions at broad scale, and species niche relations also appear conserved at broad scales (Fraterrigo et al., 2014; Sexton et al., 2009; Soberón & Nakamura, 2009). Therefore, our models should be used as an initial coarse filter related to climate habitat only, with consideration of other processes at finer scales.

A key caveat of forests' resistance to *ventenata* invasion is that higher elevation forests of the western United States have experienced increasing insect outbreaks (Jenkins et al., 2014; Saab et al., 2014) and wildfires (Alizadeh et al., 2021) but are not regenerating (Pettit et al., 2019; Rodman, Veblen, Battaglia, et al., 2020; Rodman, Veblen, Chapman, et al., 2020), increasing vulnerability to invasion. In some cases, western wildfires are also producing larger, contiguous high-severity patches (Stephens et al., 2014). Stevens and Latimer (2015) found that climate conditions, disturbance, and propagule pressure were the main factors limiting plant invasion within higher elevation forests. Coldest quarter temperatures are the main limiting factor for *ventenata* suitability along much of the Rocky Mountains, and most GCMs projected that coldest quarter temperatures would decrease in the future, increasing suitability. When combined with expected future disturbance conditions, the only limitation to the spread of *ventenata* in these areas may be propagule pressure.

CONCLUSIONS

The invasion of *ventenata* in recent decades, its potential to degrade previously invasion-resistant plant communities, and the potential effect of grass invasion on fire behavior suggest that management of this species in the invaded range may be a priority both now and into the future. Our models suggest that while the climatic suitability of the invaded range will likely decrease in the future, suitable conditions for *ventenata* will persist. However, the trend in decreasing habitat suitability in much of the currently suitable range may provide opportunities for increased management efficacy (Gallagher et al., 2013). Areas of high future suitability will tend to move toward the east, throughout the Rockies, Wasatch, and Unita Mountains, and up in elevation. Given the present trend toward more fire in higher elevation forests

and the reduction in canopy cover resulting from insect outbreaks, these mountain ranges may be highly susceptible to future ventenata invasion.

ACKNOWLEDGMENTS

This research was supported by an appointment to the United States Forest Service Research Participation Program administered by the Oak Ridge Institute for Science and Education (ORISE) through an interagency agreement (contract number DE-SC0014664) between the U.S. Department of Energy (DOE) and the U.S. Department of Agriculture (USDA). All opinions expressed in this paper are the authors and do not necessarily reflect the policies and views of the USDA, DOE, or ORISE. The authors like to thank Michelle Day and Bridgett Naylor for their assistance with preparation of the ventenata occurrence data. The authors would also like to thank Lila Leatherman and Jeff Hollenbeck for their work on early versions of this analysis.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Species data and novel code (Nietupski et al., 2024) are available from Figshare: <https://doi.org/10.6084/m9.figshare.24615732.v2>. Climate data (Thrasher et al., 2013) are available from <https://registry.opendata.aws/nasanex/>.

ORCID

John B. Kim  <https://orcid.org/0000-0002-3720-7916>

Claire M. Tortorelli  <https://orcid.org/0000-0001-9493-9817>

Becky K. Kerns  <https://orcid.org/0000-0003-4613-2191>

REFERENCES

- Abatzoglou, J. T., and C. A. Kolden. 2011. "Climate Change in Western US Deserts: Potential for Increased Wildfire and Invasive Annual Grasses." *Rangeland Ecology & Management* 64: 471–78. <https://doi.org/10.2111/REM-D-09-00151.1>.
- Abatzoglou, J. T., and A. P. Williams. 2016. "Impact of Anthropogenic Climate Change on Wildfire across Western US Forests." *Proceedings of the National Academy of Sciences of the United States of America* 113: 11770–75. <https://doi.org/10.1073/pnas.1607171113>.
- Aiello-Lammens, M. E., R. A. Boria, A. Radosavljevic, B. Vilela, and R. P. Anderson. 2015. "spThin: An R Package for Spatial Thinning of Species Occurrence Records for Use in Ecological Niche Models." *Ecography* 38: 541–45.
- Aikio, S., R. P. Duncan, and P. E. Hulme. 2010. "Lag-Phases in Alien Plant Invasions: Separating the Facts from the Artefacts." *Oikos* 119: 370–78. <https://doi.org/10.1111/j.1600-0706.2009.17963.x>.
- Alizadeh, M. R., J. T. Abatzoglou, C. H. Luce, J. F. Adamowski, A. Farid, and M. Sadegh. 2021. "Warming Enabled Upslope Advance in Western US Forest Fires." *Proceedings of the National Academy of Sciences of the United States of America* 118: e2009717118. <https://doi.org/10.1073/pnas.2009717118>.
- Appelstein, C., and M. J. Germino. 2021. "Patterns of Post-Fire Invasion of Semiarid Shrub-Steppe Reveals a Diversity of Invasion Niches within an Exotic Annual Grass Community." *Biological Invasions* 24: 741–759. <https://doi.org/10.1007/s10530-021-02669-3>.
- Barbet-Massin, M., F. Jiguet, C. H. Albert, and W. Thuiller. 2012. "Selecting Pseudo-Absences for Species Distribution Models: How, Where and How Many?" *Methods in Ecology and Evolution* 3: 327–338. <https://doi.org/10.1111/j.2041-210X.2011.00172.x>.
- Bartley, T. J., K. S. McCann, C. Bieg, K. Cazelles, M. Granados, M. M. Guzzo, A. S. MacDougall, T. D. Tunney, and B. C. McMeans. 2019. "Food Web Rewiring in a Changing World." *Nature Ecology & Evolution* 3: 345–354. <https://doi.org/10.1038/s41559-018-0772-3>.
- Bellard, C., B. Leroy, W. Thuiller, J. F. Rysman, and F. Courchamp. 2016. "Major Drivers of Invasion Risks throughout the World." *Ecosphere* 7: 1–14. <https://doi.org/10.1002/ecs2.1241>.
- Boria, R. A., L. E. Olson, S. M. Goodman, and R. P. Anderson. 2014. "Spatial Filtering to Reduce Sampling Bias Can Improve the Performance of Ecological Niche Models." *Ecological Modelling* 275: 73–77. <https://doi.org/10.1016/j.ecolmodel.2013.12.012>.
- Bowen, A. K. M., and M. H. H. Stevens. 2020. "Temperature, Topography, Soil Characteristics, and NDVI Drive Habitat Preferences of a Shade-Tolerant Invasive Grass." *Ecology and Evolution* 10: 10785–97. <https://doi.org/10.1002/ece3.6735>.
- Bradley, B. A. 2009. "Regional Analysis of the Impacts of Climate Change on Cheatgrass Invasion Shows Potential Risk and Opportunity." *Global Change Biology* 15: 196–208. <https://doi.org/10.1111/j.1365-2486.2008.01709.x>.
- Bradshaw, C. J. A., B. Leroy, C. Bellard, D. Roiz, C. Albert, A. Fournier, M. Barbet-Massin, J. M. Salles, F. Simard, and F. Courchamp. 2016. "Massive Yet Grossly Underestimated Global Costs of Invasive Insects." *Nature Communications* 7(1): 12986. <https://doi.org/10.1038/ncomms12986>.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. "Effects of Invasive Alien Plants on Fire Regimes." *BioScience* 54: 677–688. [https://doi.org/10.1641/0006-3568\(2004\)054\[0677:eoiapo\]2.0.co;2](https://doi.org/10.1641/0006-3568(2004)054[0677:eoiapo]2.0.co;2).
- Chambers, J. C., B. A. Roundy, R. B. Blank, S. E. Meyer, and A. Whittaker. 2007. "What Makes Great Basin Sagebrush Ecosystems Invasible by *Bromus tectorum*?" *Ecological Monographs* 77: 117–145. <https://doi.org/10.1890/05-1991>.
- Clary, J. 2008. "Rainfall Seasonality Determines Annual/Perennial Grass Balance in Vegetation of Mediterranean Iberian." *Plant Ecology* 195: 13–20.
- Concilio, A. L., M. E. Loik, and J. Belnap. 2013. "Global Change Effects on *Bromus tectorum* L. (Poaceae) at Its High-Elevation Range Margin." *Global Change Biology* 19: 161–172. <https://doi.org/10.1111/gcb.12032>.
- Creutzburg, M. K., A. C. Olsen, M. A. Anthony, J. D. Maestas, J. B. Cupples, N. R. Vora, and B. W. Allred. 2022. "A Geographic Strategy for Cross-Jurisdictional, Proactive Management of Invasive Annual Grasses in Oregon." *Rangelands* 1–8: 173–180. <https://doi.org/10.1016/j.rala.2021.12.007>.

- Crystal-Ornelas, R., E. J. Hudgins, R. N. Cuthbert, P. J. Haubrock, J. Fantle-Lepczyk, E. Angulo, A. M. Kramer, et al. 2021. "Economic Costs of Biological Invasions within North America." *NeoBiota* 67: 485–510. <https://doi.org/10.3897/neobiota.67.58038>.
- D'Antonio, C., and P. Vitousek. 1992. "Biological Invasions by Exotic Grasses, the Grass/Fire Cycle, and Global Change." *Annual Review of Ecology and Systematics* 23: 63–87. <https://doi.org/10.1146/annurev.es.23.110192.000431>.
- Dewitz, J. 2019. "National Land Cover Database (NLCD) 2016 Products: U.S. Geological Survey Data Release." <https://doi.org/10.5066/P96HHBIE>.
- Elith, J., M. Kearney, and S. Phillips. 2010. "The Art of Modelling Range-Shifting Species." *Methods in Ecology and Evolution* 1: 330–342. <https://doi.org/10.1111/j.2041-210x.2010.00036.x>.
- Elith, J., J. R. Leathwick, and T. Hastie. 2008. "A Working Guide to Boosted Regression Trees." *The Journal of Animal Ecology* 77: 802–813. <https://doi.org/10.1111/j.1365-2656.2008.01390.x>.
- Feng, X., D. S. Park, C. Walker, A. T. Peterson, C. Merow, and M. Papeş. 2019. "A Checklist for Maximizing Reproducibility of Ecological Niche Models." *Nature Ecology & Evolution* 3: 1382–95. <https://doi.org/10.1038/s41559-019-0972-5>.
- Fordham, D. A., C. Bertelsmeier, B. W. Brook, R. Early, D. Neto, S. C. Brown, S. Ollier, et al. 2018. "How Complex Should Models Be? Comparing Correlative and Mechanistic Range Dynamics Models." *Global Change Biology* 24: 1357–70. <https://doi.org/10.1111/gcb.13935>.
- Fraterrigo, J. M., S. Wagner, and R. J. Warren. 2014. "Local-Scale Biotic Interactions Embedded in Macroscale Climate Drivers Suggest Eltonian Noise Hypothesis Distribution Patterns for an Invasive Grass." *Ecology Letters* 17: 1447–54.
- Freeman, E. A., and G. G. Moisen. 2008. "A Comparison of the Performance of Threshold Criteria for Binary Classification in Terms of Predicted Prevalence and Kappa." *Ecological Modelling* 217: 48–58. <https://doi.org/10.1016/j.ecolmodel.2008.05.015>.
- Funk, J. L., I. M. Parker, V. Matzek, S. L. Flory, E. T. Aschehoug, C. M. D'Antonio, W. Dawson, D. M. Thomson, and J. Valliere. 2020. "Keys to Enhancing the Value of Invasion Ecology Research for Management." *Biological Invasions* 22: 2431–45. <https://doi.org/10.1007/s10530-020-02267-9>.
- Gallagher, R. V., D. Englert Duursma, J. O'Donnell, P. D. Wilson, P. O. Downey, L. Hughes, and M. R. Leishman. 2013. "The Grass May Not Always Be Greener: Projected Reductions in Climatic Suitability for Exotic Grasses under Future Climates in Australia." *Biological Invasions* 15: 961–975. <https://doi.org/10.1007/s10530-012-0342-6>.
- Gallien, L., T. Münkemüller, C. H. Albert, I. Boulangeat, and W. Thuiller. 2010. "Predicting Potential Distributions of Invasive Species: Where to Go from Here?" *Diversity and Distributions* 16: 331–342. <https://doi.org/10.1111/j.1472-4642.2010.00652.x>.
- Gardner, A. S., I. M. D. Maclean, and K. J. Gaston. 2019. "Climatic Predictors of Species Distributions Neglect Biophysically Meaningful Variables." *Diversity and Distributions* 25: 1318–33. <https://doi.org/10.1111/ddi.12939>.
- Gaskin, J. F., E. Espeland, C. D. Johnson, D. L. Larson, J. M. Mangold, R. A. McGee, C. Milner, et al. 2021. "Managing Invasive Plants on Great Plains Grasslands: A Discussion of Current Challenges." *Rangeland Ecology & Management* 78: 235–249. <https://doi.org/10.1016/j.rama.2020.04.003>.
- Gorelick, N., M. Hancher, M. Dixon, S. Ilyushchenko, D. Thau, and R. Moore. 2017. "Google Earth Engine: Planetary-Scale Geospatial Analysis for Everyone." *Remote Sensing of Environment* 202: 18–27. <https://doi.org/10.1016/j.rse.2017.06.031>.
- Gould, S. F., N. J. Beeton, R. M. B. Harris, M. F. Hutchinson, A. M. Lechner, L. L. Porfirio, and B. G. Mackey. 2014. "A Tool for Simulating and Communicating Uncertainty when Modelling Species Distributions under Future Climates." *Ecology and Evolution* 4: 4798–4811. <https://doi.org/10.1002/ece3.1319>.
- Greenwell, B., B. Boehmke, J. Cunningham, and G. Developers. 2020. "gbm: Generalized Boosted Regression Models." <https://cran.r-project.org/web/packages/gbm/>.
- Gremer, J. R., C. Andrews, J. R. Norris, L. P. Thomas, S. M. Munson, M. C. Duniway, and J. B. Bradford. 2018. "Increasing Temperature Seasonality May Overwhelm Shifts in Soil Moisture to Favor Shrub over Grass Dominance in Colorado Plateau Drylands." *Oecologia* 188: 1195–1207. <https://doi.org/10.1007/s00442-018-4282-4>.
- Guillera-Aroita, G., J. J. Lahoz-Monfort, J. Elith, A. Gordon, H. Kujala, P. E. Lentini, M. A. McCarthy, R. Tingley, and B. A. Wintle. 2015. "Is my Species Distribution Model Fit for Purpose? Matching Data and Models to Applications." *Global Ecology and Biogeography* 24: 276–292. <https://doi.org/10.1111/geb.12268>.
- Guisan, A., and W. Thuiller. 2005. "Predicting Species Distribution: Offering More than Simple Habitat Models." *Ecology Letters* 8: 993–1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>.
- Hausfather, Z., and G. P. Peters. 2020. "Emissions – The 'Business as Usual' Story Is Misleading." *Nature* 577: 618–620. <https://doi.org/10.1038/d41586-020-00177-3>.
- Hickling, R., D. B. Roy, J. K. Hill, R. Fox, and C. D. Thomas. 2006. "The Distributions of a Wide Range of Taxonomic Groups Are Expanding Polewards." *Global Change Biology* 12: 450–55. <https://doi.org/10.1111/j.1365-2486.2006.01116.x>.
- Higgins, R. W., Y. Yao, and X. L. Wang. 1997. "Influence of the North American Monsoon System on the U.S. Summer Precipitation Regime." *Journal of Climate* 10: 2600–2622. [https://doi.org/10.1175/1520-0442\(1997\)010<2600:IOTNAM>2.0.CO;2](https://doi.org/10.1175/1520-0442(1997)010<2600:IOTNAM>2.0.CO;2).
- Hijmans, R. 2022a. "raster: Geographic Data Analysis and Modeling." <https://cran.r-project.org/web/packages/raster/>.
- Hijmans, R. 2022b. "terra: Spatial Data Analysis." <https://cran.r-project.org/web/packages/terra/>.
- Hijmans, R. J., S. Phillips, J. Leathwick, and J. Elith. 2021. "Package 'dismo.'" <https://cran.r-project.org/web/packages/dismo/>.
- HilleRisLambers, J., S. G. Yelenik, B. P. Colman, and J. M. Levine. 2010. "California Annual Grass Invaders: The Drivers or Passengers of Change?" *Journal of Ecology* 98: 1147–56. <https://doi.org/10.1111/j.1365-2745.2010.01706.x>.
- Hulme, P. E. 2017. "Climate Change and Biological Invasions: Evidence, Expectations, and Response Options." *Biological Reviews* 92: 1297–1313. <https://doi.org/10.1111/brv.12282>.
- Jackson, L. E. 1985. "Ecological Origins of California's Mediterranean Grasses." *Journal of Biogeography* 12: 349–361.
- Jarnevich, C. S., H. R. Sofaer, and P. Engelstad. 2021. "Modelling Presence Versus Abundance for Invasive Species Risk

- Assessment." *Diversity and Distributions* 27: 2454–64. <https://doi.org/10.1111/ddi.13414>.
- Jenkins, M. J., E. G. Hebertson, and A. Steven Munson. 2014. "Spruce Beetle Biology, Ecology and Management in the Rocky Mountains: An Addendum to Spruce Beetle in the Rockies." *Forests* 5: 21–71. <https://doi.org/10.3390/f5010021>.
- Jones, L. C., N. Norton, and T. S. Prather. 2018. "Indicators of *Venttenata* (*Venttenata dubia*) Invasion in Sagebrush Steppe Rangelands." *Invasive Plant Science and Management* 11: 1–9. <https://doi.org/10.1017/inp.2018.7>.
- Komisarczyk, K., P. Kozminski, S. Maksymiuk, and P. Biecek. 2022. "treesap: Fast SHAP Values Computation for Tree Ensemble Models." <https://cran.r-project.org/web/packages/treesap/>.
- Kramer-Schadt, S., J. Niedballa, J. D. Pilgrim, B. Schröder, J. Lindenborn, V. Reinfelder, M. Stillfried, et al. 2013. "The Importance of Correcting for Sampling Bias in MaxEnt Species Distribution Models." *Diversity and Distributions* 19: 1366–79. <https://doi.org/10.1111/ddi.12096>.
- Kuhn, M. 2022. "caret: Classification and Regression Training." <https://cran.r-project.org/web/packages/caret/>.
- Lenoir, J., J. C. Gégout, P. A. Marquet, P. De Ruffray, and H. Brisse. 2008. "A Significant Upward Shift in Plant Species Optimum Elevation during the 20th Century." *Science* 320: 1768–71. <https://doi.org/10.1126/science.1156831>.
- Linderholm, H. W. 2006. "Growing Season Changes in the Last Century." *Agricultural and Forest Meteorology* 137: 1–14.
- Liu, Y., J. Stanturf, and S. Goodrick. 2010. "Trends in Global Wildfire Potential in a Changing Climate." *Forest Ecology and Management* 259: 685–697. <https://doi.org/10.1016/j.foreco.2009.09.002>.
- Lundberg, S. M., G. G. Erion, and S. Lee. 2019. "Consistent Individualized Feature Attribution for Tree Ensembles." arXiv: 1802.03888.
- Lurgi, M., B. C. López, and J. M. Montoya. 2012. "Novel Communities from Climate Change." *Philosophical Transactions of the Royal Society B: Biological Sciences* 367: 2913–22. <https://doi.org/10.1098/rstb.2012.0238>.
- Mahony, C. R., A. J. Cannon, T. Wang, and S. N. Aitken. 2017. "A Closer Look at Novel Climates: New Methods and Insights at Continental to Landscape Scales." *Global Change Biology* 23: 3934–55. <https://doi.org/10.1111/gcb.13645>.
- Mainali, K. P., D. L. Warren, K. Dhileepan, A. McConnachie, L. Strathie, G. Hassan, D. Karki, B. B. Shrestha, and C. Parmesan. 2015. "Projecting Future Expansion of Invasive Species: Comparing and Improving Methodologies for Species Distribution Modeling." *Global Change Biology* 21: 4464–80. <https://doi.org/10.1111/gcb.13038>.
- Nietupski, T. C., J. Kim, C. Tortorelli, R. Lemons, and B. Kerns. 2024. "An Exploration of Current and Future Niche-Based Invasion Projections and Uncertainty for an Invasive Grass in the Western US." Dataset and Code. Figshare. <https://doi.org/10.6084/m9.figshare.24615732.v2>.
- Nix, H. A. 1986. "A Biogeographic Analysis of Australian Elapid Snakes." In *Atlas of Elapid Snakes of Australia*, edited by R. Longmore, 4–15. Canberra: Australian Government Publishing Service.
- Noone, M. D., J. S. Kagan, and E. Nielsen. 2013. *Western Juniper (Juniperus occidentalis) and Invasive Annual Grass Mapping in Eastern Oregon*. Portland, OR: Institute for Natural Resources, Portland State University 57 pp.
- Norberg, A., N. Abrego, F. G. Blanchet, F. R. Adler, B. J. Anderson, J. Anttila, M. B. Araújo, et al. 2019. "A Comprehensive Evaluation of Predictive Performance of 33 Species Distribution Models at Species and Community Levels." *Ecological Monographs* 89: 1–24. <https://doi.org/10.1002/ecm.1370>.
- Novak, S. J., and R. N. Mack. 2001. "Tracing Plant Introduction and Spread: Genetic Evidence from *Bromus tectorum* (Cheatgrass)." *BioScience* 51: 114–122. [https://doi.org/10.1641/0006-3568\(2001\)051\[0114:TPIASG\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0114:TPIASG]2.0.CO;2).
- Omernik, J. M., and G. E. Griffith. 2014. "Ecoregions of the Conterminous United States: Evolution of a Hierarchical Spatial Framework." *Environmental Management* 54: 1249–66. <https://doi.org/10.1007/s00267-014-0364-1>.
- Owens, H. L., L. P. Campbell, L. L. Dornak, E. E. Saupe, N. Barve, J. Soberón, K. Ingenloff, et al. 2013. "Constraints on Interpretation of Ecological Niche Models by Limited Environmental Ranges on Calibration Areas." *Ecological Modelling* 263: 10–18. <https://doi.org/10.1016/j.ecolmodel.2013.04.011>.
- Pauchard, A., A. Milbau, A. Albiñ, J. Alexander, T. Burgess, C. Daehler, G. Englund, et al. 2016. "Non-native and Native Organisms Moving into High Elevation and High Latitude Ecosystems in an Era of Climate Change: New Challenges for Ecology and Conservation." *Biological Invasions* 18: 345–353. <https://doi.org/10.1007/s10530-015-1025-x>.
- Pavek, P., J. Wallace, and T. Prather. 2011. *Venttenata Biology and Distribution in the Pacific Northwest*. Las Cruces, NM: Western Society of Weed Science 107 pp.
- Peterson, A. T. 2003. "Predicting the Geography of Species' Invasions Via Ecological Niche Modeling." *Quarterly Review of Biology* 78: 419–433. <https://doi.org/10.1086/378926>.
- Pettit, J. M., J. I. Burton, R. J. DeRose, J. N. Long, and S. L. Voelker. 2019. "Epidemic Spruce Beetle Outbreak Changes Drivers of Engelmann Spruce Regeneration." *Ecosphere* 10: e02912. <https://doi.org/10.1002/ecs2.2912>.
- Phillips, S. J., M. Dudík, J. Elith, C. H. Graham, A. Lehmann, J. Leathwick, and S. Ferrier. 2009. "Sample Selection Bias and Presence-Only Distribution Models: Implications for Background and Pseudo-Absence Data." *Ecological Applications* 19: 181–197. <https://doi.org/10.1890/07-2153.1>.
- Pilliod, D. S., J. L. Welty, and R. S. Arkle. 2017. "Refining the Cheatgrass–Fire Cycle in the Great Basin: Precipitation Timing and Fine Fuel Composition Predict Wildfire Trends." *Ecology and Evolution* 7: 8126–51. <https://doi.org/10.1002/ece3.3414>.
- Prather, T. S., and V. Steele. 2009. "Venttenata Control Strategies Found for Forage Producers."
- Prevéy, J. S., and T. R. Seastedt. 2015. "Effects of Precipitation Change and Neighboring Plants on Population Dynamics of *Bromus tectorum*." *Oecologia* 179: 765–775. <https://doi.org/10.1007/s00442-015-3398-z>.
- PRISM. 2012. "PRISM Climate Group [www Document]." Oregon State University. <http://prism.oregonstate.edu>.
- Qiao, H., X. Feng, L. E. Escobar, A. T. Peterson, J. Soberón, G. Zhu, and M. Papeş. 2019. "An Evaluation of Transferability of Ecological Niche Models." *Ecography* 42: 521–534. <https://doi.org/10.1111/ecog.03986>.

- R Core Team. 2020. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Riahi, K., S. Rao, V. Krey, C. Cho, V. Chirkov, G. Fischer, G. Kindermann, N. Nakicenovic, and P. Rafaj. 2011. "RCP8.5 – A Scenario of Comparatively High Greenhouse Gas Emissions." *Climatic Change* 109: 33–57. <https://doi.org/10.1007/s10584-011-0149-y>.
- Ritchie, J., and H. Dowlatabadi. 2017. "Why Do Climate Change Scenarios Return to Coal?" *Energy* 140: 1276–91. <https://doi.org/10.1016/j.energy.2017.08.083>.
- Rodman, K. C., T. T. Veblen, M. A. Battaglia, M. E. Chambers, P. J. Fornwalt, Z. A. Holden, T. E. Kolb, J. R. Ouzts, and M. T. Rother. 2020. "A Changing Climate Is Snuffing Out Post-Fire Recovery in Montane Forests." *Global Ecology and Biogeography* 29: 2039–51. <https://doi.org/10.1111/geb.13174>.
- Rodman, K. C., T. T. Veblen, T. B. Chapman, M. T. Rother, A. P. Wion, and M. D. Redmond. 2020. "Limitations to Recovery Following Wildfire in Dry Forests of Southern Colorado and Northern New Mexico, USA." *Ecological Applications* 30: 1–20. <https://doi.org/10.1002/eap.2001>.
- Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. "Fingerprints of Global Warming on Wild Animals and Plants." *Nature* 421: 54–57. <https://doi.org/10.1038/nature01309.1>.
- Saab, V. A., Q. S. Latif, M. M. Rowland, T. N. Johnson, A. D. Chalfoun, S. W. Buskirk, J. E. Heyward, and M. A. Dresser. 2014. "Ecological Consequences of Mountain Pine Beetle Outbreaks for Wildlife in Western North American Forests." *Forest Science* 60: 539–559. <https://doi.org/10.5849/forsci.13-022>.
- Schwalm, C. R., S. Glendon, and P. B. Duffy. 2020. "RCP8.5 Track Cumulative CO₂ Emissions." *Proceedings of the National Academy of Sciences of the United States of America* 117: 19656–57. <https://doi.org/10.1073/pnas.2007117117>.
- Seebens, H., T. M. Blackburn, E. E. Dyer, P. Genovesi, P. E. Hulme, J. M. Jeschke, S. Pagad, et al. 2018. "Global Rise in Emerging Alien Species Results from Increased Accessibility of New Source Pools." *Proceedings of the National Academy of Sciences of the United States of America* 115: E2264–E2273. <https://doi.org/10.1073/pnas.1719429115>.
- Seebens, H., F. Essl, W. Dawson, N. Fuentes, D. Moser, J. Pergl, P. Pyšek, et al. 2015. "Global Trade Will Accelerate Plant Invasions in Emerging Economies under Climate Change." *Global Change Biology* 21: 4128–40. <https://doi.org/10.1111/gcb.13021>.
- Sexton, J. P., P. J. McIntyre, A. L. Angert, and K. J. Rice. 2009. "Evolution and Ecology of Species Range Limits." *Annual Review of Ecology, Evolution, and Systematics* 40: 415–436. <https://doi.org/10.1146/annurev.ecolsys.110308.120317>.
- Shackleton, R. T., B. M. H. Larson, A. Novoa, D. M. Richardson, and C. A. Kull. 2019. "The Human and Social Dimensions of Invasion Science and Management." *Journal of Environmental Management* 229: 1–9. <https://doi.org/10.1016/j.jenvman.2018.08.041>.
- Soberón, J., and M. Nakamura. 2009. "Niches and Distributional Areas: Concepts, Methods, and Assumptions." *Proceedings of the National Academy of Sciences of the United States of America* 106: 19644–50. <https://doi.org/10.1073/pnas.0901637106>.
- Sofaer, H. R., C. S. Jarnevich, I. S. Pearse, R. L. Smyth, S. Auer, G. L. Cook, T. C. Edwards, et al. 2019. "Development and Delivery of Species Distribution Models to Inform Decision-Making." *BioScience* 69: 544–557. <https://doi.org/10.1093/biosci/biz045>.
- Sorte, C. J. B., I. Ibáñez, D. M. Blumenthal, N. A. Molinari, L. P. Miller, E. D. Grosholz, J. M. Diez, et al. 2013. "Poised to Prosper? A Cross-System Comparison of Climate Change Effects on Native and Non-Native Species Performance." *Ecology Letters* 16: 261–270. <https://doi.org/10.1111/ele.12017>.
- Srivastava, V., V. Lafond, and V. C. Griess. 2019. "Species Distribution Models (SDM): Applications, Benefits and Challenges in Invasive Species Management." *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources* 14: 1–13. <https://doi.org/10.1079/PAVSNNR201914020>.
- Statistics Canada. 2015. "National Road Network." Statistics Canada. <https://open.canada.ca/data/en/dataset/3d282116-e556-400c-9306-ca1a3cada77f>.
- Stephens, S. L., N. Burrows, A. Buyantuyev, R. W. Gray, R. E. Keane, R. Kubian, S. Liu, et al. 2014. "Temperate and Boreal Forest Mega-Fires: Characteristics and Challenges." *Frontiers in Ecology and the Environment* 12: 115–122. <https://doi.org/10.1890/120332>.
- Stevens, J. T., and A. M. Latimer. 2015. "Snowpack, Fire, and Forest Disturbance: Interactions Affect Montane Invasions by Non-Native Shrubs." *Global Change Biology* 21: 2379–93. <https://doi.org/10.1111/gcb.12824>.
- Stokland, J. N., R. Halvorsen, and B. Støa. 2011. "Species Distribution Modelling-Effect of Design and Sample Size of Pseudo-Absence Observations." *Ecological Modelling* 222: 1800–1809. <https://doi.org/10.1016/j.ecolmodel.2011.02.025>.
- Thrasher, B., J. Xiong, W. Wang, F. Melton, A. Michaelis, and R. Nemani. 2013. "Downscaled Climate Projections Suitable for Resource Management. Eos." *Transactions of the American Geophysical Union* 94: 321. <https://registry.opendata.aws/nasanex/-23>.
- Thuiller, W., D. M. Richardson, P. Pyssek, G. F. Midgley, G. O. Hughes, and M. Rouget. 2005. "Niche-Based Modelling as a Tool for Predicting the Risk of Alien Plant Invasions at a Global Scale." *Global Change Biology* 11: 2234–50. <https://doi.org/10.1111/j.1365-2486.2005.001018.x>.
- Tortorelli, C. M., B. K. Kerns, and M. A. Krawchuk. 2022a. "Community Invasion Resistance Is Influenced by Interactions between Plant Traits and Site Productivity." *Ecology* 103(7): e3697.
- Tortorelli, C. M., B. K. Kerns, and M. A. Krawchuk. 2022b. "The Invasive Annual Grass *Ventennata dubia* Is Insensitive to Experimental Removal of above-Ground Resident Biomass across a Productivity Gradient." *Biological Invasions* 24: 2961–71. <https://doi.org/10.1007/s10530-022-02823-5>.
- Tortorelli, C. M., J. B. Kim, N. M. Vaillant, K. Riley, A. Dye, T. C. Nietupski, K. C. Vogler, et al. 2023. "Feeding the Fire: Annual Grass Invasion Facilitates Modeled Fire Spread across Inland Northwest Forest-Mosaic Landscapes." *Ecosphere* 14(2): e4413.
- Tortorelli, C. M., M. A. Krawchuk, and B. K. Kerns. 2020. "Expanding the Invasion Footprint: *Ventennata dubia* and Relationships to Wildfire, Environment, and Plant

- Communities in the Blue Mountains of the Inland Northwest, USA." *Applied Vegetation Science* 1–13: 562–574. <https://doi.org/10.1111/avsc.12511>.
- U.S. Geological Survey. 2014. "USGS Small-Scale Dataset – 1: 1,000,000-Scale Major Roads of the United States 201403 Shapefile." U.S. Geological Survey. <https://www.sciencebase.gov/catalog/item/581d052be4b08da350d524ce>.
- van Kleunen, M., W. Dawson, F. Essl, J. Pergl, M. Winter, E. Weber, H. Kreft, et al. 2015. "Global Exchange and Accumulation of Non-Native Plants." *Nature* 525: 100–103. <https://doi.org/10.1038/nature14910>.
- van Vuuren, D. P., J. Edmonds, M. Kainuma, K. Riahi, A. Thomson, K. Hibbard, G. C. Hurtt, et al. 2011. "The Representative Concentration Pathways: An Overview." *Climatic Change* 109: 5–31. <https://doi.org/10.1007/s10584-011-0148-z>.
- Wallace, J. M., P. L. S. Pavsek, and T. S. Prather. 2015. "Ecological Characteristics of *Ventemata dubia* in the Intermountain Pacific Northwest." *Invasive Plant Science and Management* 8: 57–71. <https://doi.org/10.1614/IPSM-D-14-00034.1>.
- Walther, G., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. "Ecological Response to Recent Climate Change." *Nature* 416: 389–395. <https://doi.org/10.1038/416389a>.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Nietupski, Ty C., John B. Kim, Claire M. Tortorelli, Rebecca Lemons, and Becky K. Kerns. 2024. "*Ventemata Dubia* Projected to Expand in the Western United States Despite Future Novel Conditions." *Ecosphere* 15(9): e4979. <https://doi.org/10.1002/ecs2.4979>