



# Modeling Current and Future Potential Distributions of Milkweeds and the Monarch Butterfly in Idaho

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Monarch butterflies (*Danaus plexippus*) are widespread in North America but have experienced large rangewide declines. Causes of recent declines likely involve multiple biotic and abiotic stressors including climate change and loss and degradation of native milkweed (*Asclepias* spp.), monarchs' obligate larval host plant. Recent broad-scale modeling efforts suggest milkweed and monarch distributions in the eastern United States will expand northward during summer months while fine-scale modeling of western population overwintering sites in California indicate shifts inland and upward in elevation. However, species' response to climate measures varies at sub-regional scales across its range and both the impacts of climate change and potential adaptation measures may be sensitive to the spatial scale of climate data used, particularly in areas of complex topography. Here, we develop fine-scale models of monarch breeding habitat and milkweed distributions in Idaho, an area at the northern extent of the monarch breeding range in North America and important in western overwintering population recruitment. Our models accurately predict current distributions for showy milkweed (*A. speciosa*), swamp milkweed (*A. incarnata*), and monarch with AUC (area under the receiver operating characteristic curve) = 0.899, 0.981, and 0.929, respectively. Topographic, geographic, edaphic, and climatic factors all play important roles in determining milkweed and, thus, monarch distributions. In particular, our results suggest that at sub-regional and fine-scales, non-climatic factors such as soil depth, distance to water, and elevation contribute significantly. We further assess changes in potential habitat across Idaho under mid-21st century climate change scenarios and potential management implications of these changing distributions. Models project slight decreases ( $-1,318 \text{ km}^2$ ) in potential suitable habitat for showy milkweed and significant increases ( $+5,830 \text{ km}^2$ ) for swamp milkweed. Projected amounts of suitable habitat for monarch are likely to remain roughly stable with expansion nearly equal to contraction under a moderate scenario and slightly greater when under the more severe scenario. Protected areas encompass 8% of current suitable habitat for showy milkweed, 11% for swamp milkweed, and 9% for monarch. Our study shows that suitable habitat for monarchs and/or milkweeds will likely continue to be found in managed areas traditionally seen as priority habitats in Idaho through mid-century.

**Keywords:** monarch, showy milkweed, swamp milkweed, climate change, species distribution model, Idaho, *Asclepias*, *Danaus plexippus*

## INTRODUCTION

Monarch butterflies (*Danaus plexippus plexippus*) are widespread in North America but appear to be experiencing large rangewide declines in both the eastern (Semmens et al., 2016; Agrawal and Inamine, 2018) and western populations (Jepsen et al., 2015; Schultz et al., 2017). Factors contributing to declines are increasingly understood and likely involve multiple biotic and abiotic stressors including climate change and loss and degradation of native milkweed (*Asclepias* spp.), monarchs' obligate larval host plant (Flockhart et al., 2015; Jepsen et al., 2015; Inamine et al., 2016; Thogmartin et al., 2017; Belsky and Joshi, 2018). Changes in climate patterns, in particular, may both favor and hinder species through complex, seasonal relationships. Monarchs, for example, appear to benefit from warm winters and warm, wet springs (Zipkin et al., 2012; Espeset et al., 2016; Thogmartin et al., 2017), while excessively hot, dry, cold, or wet conditions may be a detriment (Zalucki, 1982; York and Oberhauser, 2002; Zalucki and Rochester, 2004; Nail et al., 2015; James, 2016), but these relationships are region-specific (Zipkin et al., 2012; Flockhart et al., 2017). Similarly, warmer temperatures result in increased growth for some milkweed species while drought reduces their growth, survivorship, seed production and germination, and nutritional quality (Bowles et al., 1998; Woods et al., 2012; Couture et al., 2015). These patterns have led to suggestions that northern populations of both milkweed and monarchs may benefit from projected changes in climate (Couture et al., 2015) depending on if and how milkweed distributions change (Lemoine, 2015).

Species distribution models (SDMs) are increasingly used to assess the current "climate envelope" for species and project the potential effects of changes in those climate variables under different future scenarios (Porfirio et al., 2014). To date, broad-scale modeling efforts suggest milkweed and monarch distributions in the eastern United States (US) will expand northward during summer months (Batalden et al., 2007; Lemoine, 2015) while fine-scale modeling of western population overwintering sites in California indicate shifts upward in elevation and inland (Fisher et al., 2018). Such modeling efforts, however, are often limited due to a mismatch between the spatial resolution of climate data available (e.g., 1–30 km) and the scale relevant to the species of interest (e.g., 10–100 m), especially in areas of complex terrain (Randin et al., 2009; Austin and Van Niel, 2011; Suggitt et al., 2011; Franklin et al., 2013). In addition, several modeling efforts have shown that species' response to climate often varies across its range (e.g., Pearman et al., 2010; Hällfors et al., 2016; Ikeda et al., 2017; Nice et al., 2019). Given that monarchs are a widespread, highly migratory species, one may not expect significant variability in climate response across the species range, while milkweed may exhibit more local adaptability.

Currently at the northern extent of monarch breeding range, Idaho significantly contributes to recruitment of monarchs to the western population (Yang et al., 2016). Chosen as the Idaho state insect, yet classified as unprotected wildlife in the state, the monarch butterfly was recently designated as an Idaho Species of Greatest Conservation Need predominantly due to

significant rangewide declines and a lack of information on Idaho-specific status and trends [Idaho Department of Fish and Game (IDFG), 2017]. In particular, knowledge of monarch breeding locations, distribution, and movement patterns as well as potential impacts of climate change and other threats are limited in the region. Initial mapping of western milkweed and monarch observations (Xerces Society, 2014) and modeling work (Stevens and Frey, 2010; USFWS/Xerces Society, 2016) identified probable breeding habitat across seven western states, including Idaho. These and other studies suggested that monarchs in the intermountain states (Idaho, Utah, Nevada) are comparatively sparsely populated and may be constrained by low milkweed species diversity, semi-arid climates, and unsuitable temperature regimes associated with elevation or latitude (Pyle, 1999; Stevens and Frey, 2010). However, surveys by the Idaho Department of Fish and Game (IDFG) (Waterbury and Ruth, 2015) identified monarch breeding activity in a climatic region previously considered to be thermally unsuitable for monarch reproduction (Stevens and Frey, 2010). This finding suggests that other regions of Idaho, also previously deemed thermally constrained for monarch breeding, may currently support suitable natal habitat. Beginning in 2015, IDFG engaged in several efforts aimed at improving the knowledge base for monarchs including collaborating with Washington Department of Fish and Wildlife on a project to investigate monarch distributions and status in Idaho and Washington (Waterbury and Potter, 2018). Here, we employ data collected through these efforts to (1) develop fine-scale models of current milkweed and monarch butterfly distributions in Idaho using the most scale-relevant data available, (2) assess potential changes under mid-century climate change scenarios, and (3) assess potential management implications of these changing distributions.

## MATERIALS AND METHODS

### Milkweed and Monarch Observations

All known observations of monarch and milkweed in Idaho as of April 26, 2018, were compiled for this modeling effort. This included data from the Western Monarch and Milkweed Mapper Occurrence Database (museum and herbarium specimens, older survey efforts, and incidental observations) (Xerces Society, 2018), recently collected IDFG and College of Western Idaho survey data (summers 2016, 2017), and incidental observations recorded in iNaturalist and in the Idaho Fish and Wildlife Information System Species Diversity Database [Idaho Department of Fish and Game (IDFG), 2018]. We carefully evaluated all data for use in the distribution models to ensure spatial and temporal accuracy. As part of this evaluation, we determined sufficient data exist in Idaho to model distributions for monarch ( $n = 1603$ ) and two native milkweed species, showy milkweed (*A. speciosa*) ( $n = 5258$ ) and swamp milkweed (*A. incarnata*) ( $n = 313$ ). Other milkweed species documented but not modeled included narrow-leaf milkweed (*A. fascicularis*) ( $n = 94$ ), pallid milkweed (*A. cryptoceras*) ( $n = 84$ ), and spider milkweed (*A. asperula*) ( $n = 7$ ). All compiled data are available online [Idaho Department of Fish and Game (IDFG), 2018 data used for modeling can be requested from the lead author].

Compiled observation data such as these are prone to errors of observational certainty, spatial accuracy, and sampling bias both geographically (e.g., more samples in easily accessible areas) and environmentally (e.g., more samples at lower elevations). To maximize observational certainty, we used only observations classified as verified (e.g., specimen, DNA, or photograph) or trusted (e.g., documented by a biologist, researcher, or taxonomic expert). To maximize spatial accuracy, we limited our data set to those locations with  $\leq 100$  m accuracy. Even though the vast majority of our observations resulted from targeted inventory or survey efforts (93% of showy milkweed, 91% of swamp milkweed, and 88% of monarch observations), sampling bias was still an issue as data were highly clustered at fine scales in portions of the state. Species distribution models can be sensitive to such bias and several authors have suggested spatial filtering or subsampling of the presence data to account for it (Phillips et al., 2009; Veloz, 2009; Anderson and Raza, 2010; Kramer-Schadt et al., 2013; Radosavljevic and Anderson, 2013). The key to spatial filtering is to randomly subsample presence data with a minimum distance separating the sample points, thereby limiting spatial autocorrelation and reducing the environmental bias caused by uneven sampling. That minimum distance is somewhat arbitrary, however, and depends on the environmental conditions of the study area as well as the resolution of the data used for modeling. We reduced the locally dense sampling of monarch and milkweed by randomly subsampling the observations with a minimum distance of 270 m, which accounted for the coarsest spatial data resolution of the environmental variables and the sampling design of the majority of field surveys. These filtering procedures (trusted or verified,  $\leq 100$  m accuracy, and  $> 270$  m separation) resulted in a total of 1079 showy milkweed observations, 100 swamp milkweed observations, and 344 monarch observations available for use in our modeling efforts (Figure 1).

## Environmental Variables

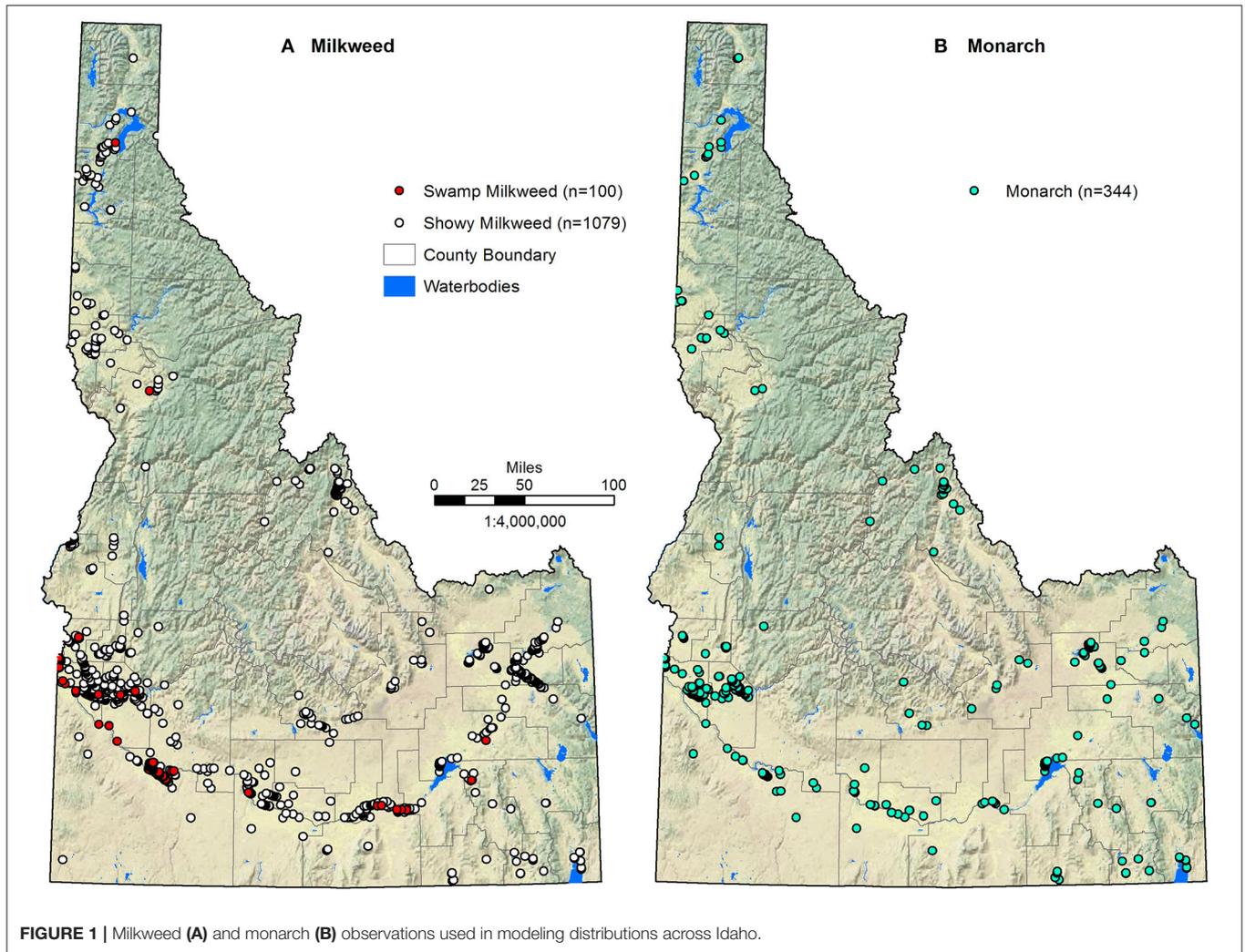
Previous modeling efforts have focused on a number of climatic, topographic, and edaphic environmental covariates at broader spatial extents (western US, eastern US) and resolutions (90 m–10 km cell sizes) (Batalden et al., 2007; Lemoine, 2015; Dilts et al., 2018). Learning from and building on these efforts, we compiled and/or developed finer-scale versions of these covariates (Table 1), striving to use data at scales most applicable to milkweed and monarch butterflies and to ensure variables represented ecophysiological processes known to influence plant growth either directly or as surrogates (Austin and Van Niel, 2011). Conducting all spatial analyses in ArcGIS 10.5.1 (ESRI, 2017), we ensured spatial data were in a common geographic coordinate system, spatial resolution (30 m), and extent (Idaho), and exported as ASCII files for input into R (3.5.0; R Core Team, 2018) and Maxent (Maxent 3.4.1; Phillips et al., 2006, 2017; Phillips and Dudík, 2008).

Topographic variables generally act as surrogates for factors influencing plant growth, but can also directly account for differences in local climate and be important in SDMs (Luoto and Heikkinen, 2008; Austin and Van Niel, 2011). We developed several topographic variables including elevation, slope, aspect, compound topographic index (CTI), roughness, and vector

ruggedness measure (VRM) from the National Elevation Data (30 m) (US Geological Survey, 2016b). The CTI, a steady-state wetness index, measures the catenary topographic position represented by both slope and catchment size and aims to model soil water content (Moore et al., 1993). Roughness, similar to the terrain ruggedness index (Riley et al., 1999), calculates the amount of elevation difference between a grid cell and its neighbors, essentially the variance of elevation within the neighborhood ( $8 \times 8$  cells in this analysis). The VRM, which measures terrain heterogeneity within a neighborhood ( $9 \times 9$  cells in this analysis), captures variability in both slope and aspect into a single measure (Sappington et al., 2007). We calculated CTI and roughness using Evans et al. (2014) and VRM using Sappington (2012), both freely available ArcGIS tools. All of these topographic variables, to varying degrees, were selected to reflect temperature, water and light resources that help determine plant distributions and may contribute to monarch habitats. For example, CTI and roughness may serve as proxies for local temperature patterns (e.g., cold air drainage, Dobrowski et al., 2009) while VRM, slope, and aspect act as surrogates for light or solar radiation.

Edaphic measures developed were characteristics known to either affect the availability of nutrients or exert direct physiological limitations, or both, on plants and included percent sand, percent silt, percent clay, pH, available water supply, calcium carbonate, cation-exchange capacity, organic matter, and depth to a restrictive layer. To focus on the most critical soil for plant establishment, we used a weighted average based on percent composition for aggregating across all soil map units in the top 0–25 cm for all variables except soil depth. These data were developed primarily from the Soil Survey Geographic database (SSURGO, USDA Natural Resource Conservation Service, 2016a), with missing areas filled in with the U.S. General Soils database (STATSGO2, USDA Natural Resource Conservation Service, 2016b), following the national standard methodology and tools used for similar products (e.g., gSSURGO) (USDA Natural Resource Conservation Service, 2016c).

Climatic variables used in previous efforts relied on temperature and precipitation at moderate ( $\sim 1$  km) spatial resolution (Hijmans et al., 2005; Daly et al., 2008; Wang et al., 2012). To better represent Idaho climate we used more recent temperature data developed at finer spatial resolution (250 m) for the Northern Rockies (Holden et al., 2015) in combination with precipitation data (originally 800 m, resampled to 250 m resolution using cubic convolution to match the temperature data) from the Parameterized Regression on Independent Slopes Model (PRISM, Version 14.1-20140502-1000) (PRISM Climate Group, 2012; Daly et al., 2015). Both of these datasets represent monthly 30-year normals covering the period 1981–2010, from which we calculated 19 bioclimatic variables following Nix (1986) and Hijmans et al. (2005). These bioclimatic variables have been used extensively in SDMs for decades (e.g., Elith et al., 2010, 2011; Anderson and Gonzalez, 2011; Stanton et al., 2011; Booth et al., 2014), as well as in previous monarch and milkweed modeling studies (e.g., Lemoine, 2015; Dilts et al., 2018), and



**FIGURE 1** | Milkweed (A) and monarch (B) observations used in modeling distributions across Idaho.

characterize climatic conditions best related to species physiology (O'Donnell and Ignizio, 2012; Booth et al., 2014).

To portray mid-century climate conditions we used projections from 20 Global Climate Models (GCM) participating in the Fifth Coupled Model Intercomparison Project that were statistically downscaled using the Multivariate Adaptive Constructed Analogs (MACA, Abatzoglou and Brown, 2012). Output from GCMs were downscaled using the historical training dataset of Abatzoglou (2013) to a 4-km spatial resolution. We calculated differences in monthly mean minimum temperature, maximum temperature, and accumulated precipitation between 1981-2010 and 2040-2069 for each of the 20 models given two emission scenarios, Representative Concentration Pathway [RCP] 4.5 and RCP 8.5. The latter, which we refer to herein as severe, assumes a business as usual emissions pathway whereas the former, referred to as moderate, assumes policies that lead to a plateau and eventual decline in emissions. While there is potential value in examining difference in the uncertainty in climate projections across models, we constrain our efforts on the 20-model mean change.

Differences between ensemble mean future and baseline monthly climate data at a 4-km spatial resolution were interpolated to the 250-m resolution of the observed data and superposed to these 250-m gridded observed data to provide an estimate of the projected climate fields. We then recalculated the 19 bioclimatic variables using these projected values.

Other potentially informative landscape-related variables developed included distance to intermittent streams and distance to perennial streams and waterbodies based on the National Hydrography Data (US Geological Survey, 2017) (FCodes 46006 and 46003, respectively). We considered including land cover and percent natural land cover following Dilts et al. (2018), but instead chose to omit these variables because the spatial and thematic scale of the most current land cover data (US Geological Survey, 2016a) did not accurately reflect known milkweed occurrences. For example, >50% of both showy and swamp milkweed locations were mapped as developed, cultivated cropland, or open water, yet field surveys determined milkweed was rarely found in these types and instead preferred grasslands-herbaceous, emergent herbaceous wetlands, and deciduous

**TABLE 1** | Environmental variables used in monarch and milkweed distribution modeling in Idaho.

Variable	Code	Units	Source (resolution)	
Soils	Percent clay	Clay025	SSURGO and STATSGO2 (USDA Natural Resource Conservation Service, 2016a,b), weighted average of all mapunits in top 0–25 cm of soil for all but Dep2Res. (1:24,000–1:100,000)	
	Percent sand	Sand025		
	Percent silt	Silt025		
	pH	pH025		
	Available water supply	Aws025		
	Calcium Carbonate	CaCO3		
	Cation-exchange capacity	CEC7		
Topography	Organic matter	OM025	National Elevation Data (US Geological Survey, 2016b), Evans et al. (2014) [CTI, Rough8], Sappington et al. (2007) [VRM] (30 m)	
	Depth to restrictive layer	Dep2Res		
	Aspect	Asp		
	Slope	Slp		
	Elevation	Elev		
	Compound topographic index	CTI		
	Roughness (8 neighbor cells)	Rough8		
Climate	Vector ruggedness measure	VRM	Holden et al. (2015), PRISM Climate Group (2012), <i>dismo</i> package in R. (250, 800 m)	
	Mean annual temperature	Bio1		
	Mean diurnal range	Bio2		
	Isothermality (Bio2/Bio7 * 100)	Bio3		
	Temperature seasonality (standard deviation of monthly temperatures *100)	Bio4		
	Maximum temperature of warmest month	Bio5		
	Minimum temperature of coldest month	Bio6		
	Temperature annual range	Bio7		
	Mean temperature of the wettest quarter	Bio8		
	Mean temperature of the driest quarter	Bio9		
	Mean temperature of warmest quarter	Bio10		
	Mean temperature of coldest quarter	Bio11		
	Total annual precipitation	Bio12		
	Precipitation of wettest month	Bio13		
	Precipitation of driest month	Bio14		
	Precipitation seasonality (coefficient of variation of monthly precipitation)	Bio15		
	Precipitation of wettest quarter	Bio16		
	Precipitation of driest quarter	Bio17		
	Precipitation of warmest quarter	Bio18		
Precipitation of coldest quarter	Bio19			
Annual mean growing degree days	GDD	Number	Holden et al. (2015)	
Water	Distance to perennial water	D2Peren	Meters	National Hydrography Dataset (US Geological Survey, 2017) (1:24,000)

forests (Waterbury and Potter, 2018). In addition, even if found important, future projections of land cover were lacking. Finally, as monarch breeding habitat is generally found to be constrained by the occurrence of milkweed (Lemoine, 2015; Dilts et al., 2018), the outputs from the showy and swamp milkweed models were included with the previous covariates when modeling monarchs.

### Current/Future Habitat Suitability

We used maximum entropy methods (Maxent 3.4.1; Phillips et al., 2006, 2017; Phillips and Dudík, 2008) to model current potential habitat suitability for monarch, showy milkweed, and

swamp milkweed, as well as the potential habitat suitability for the mid-21st century. Given a set of environmental variables and presence-only species occurrences, Maxent identifies the correlations between each variable and the presence data, compares that with the range of environmental conditions available in the modeled region, and develops a continuous model of relative likelihood of suitable habitat across the study area based on environmental similarity to known occupied sites. We choose to use Maxent because it does not require absence data, it efficiently handles complex interactions, it has been shown to perform better than other approaches with similar data,

and it effectively transfers model projections to future conditions (Phillips et al., 2006; Elith et al., 2010, 2011). We supplied Maxent with occurrence data as described above, as well as background points consisting of 10,000 randomly generated pseudo-absences across Idaho that were >270 m apart, >270 m from presence locations, and outside of waterbodies.

Following recommended approaches (Elith et al., 2010, 2011; Anderson and Gonzalez, 2011; Merow et al., 2013; Radosavljevic and Anderson, 2013; Yackulic et al., 2013; Porfirio et al., 2014; Wright et al., 2015; Searcy and Shaffer, 2016; Morales et al., 2017), we developed current distribution models for monarch and milkweed using species-specific model parameters, particularly with regard to collinearity, regularization multiplier, and feature types. In Maxent, the feature types represent mathematical transformations of the covariates to allow complex relationships while the regularization multiplier imposes penalties to the model to help prevent overfitting (Elith et al., 2010, 2011; Merow et al., 2013). In an iterative approach, we optimized each model for feature types (linear, quadratic, product, threshold, hinge, and interactions) and regularization multiplier (values tested included 0.5, 1, 1.5, 2, 2.5, 3, 3.5, 4, 4.5, 5, 6, 7, 8, 9, 10, 12.5, 15, 17.5, and 20) using the *enmSdm* package (Smith, 2017) in R 3.5.0 (R Core Team, 2018) and selected the best performing combination based on sample size-corrected Akaike Information Criteria ( $AIC_c$ ) (Warren and Seifert, 2011; Wright et al., 2015). Beginning with a full model inclusive of all covariates ( $n = 37$ ), we implemented 10-fold cross-validation and jackknifing to measure importance of each variable to the resulting model. Variables were then ranked based on their permutation importance (Searcy and Shaffer, 2016) and removed if <1% contribution. Correlated variables (Pearson correlation >|0.70|) were also removed keeping the variable with the higher permutation importance. This process of model optimization, development, and variable ranking and removal was repeated until all variables had a minimum contribution of  $\geq 2\%$ . The final model for each species represented the average of 10 cross-validation replicates using the optimized parameters and most important variables in cloglog output format and was evaluated using AUC (area under the receiver operating characteristic curve). We then projected the final models for each species onto spatial data projected for the two mid-century climate scenarios.

We imported all mean model outputs into ArcGIS 10.5.1 (ESRI, 2017) and identified areas of suitable and unsuitable habitat based on the “balance training omission, predicted area and threshold value” threshold calculated by Maxent. This threshold uses weighting constants to provide a balance between over-fitting and over-estimating. For comparative purposes, we further binned the suitable habitat using an expert opinion-based threshold to identify marginal and optimal suitability for each species. The current and two future models for each species were then overlaid to calculate the proportion of suitable habitat projected to remain suitable in the future (persistence), the proportion of current suitable habitat projected to become unsuitable (contraction), and the proportion of future habitat projected in currently unsuitable areas (expansion). Lastly, we tabulated the areas of gain and loss for pertinent IDFG Wildlife Management Areas (WMA), US Fish and Wildlife Service

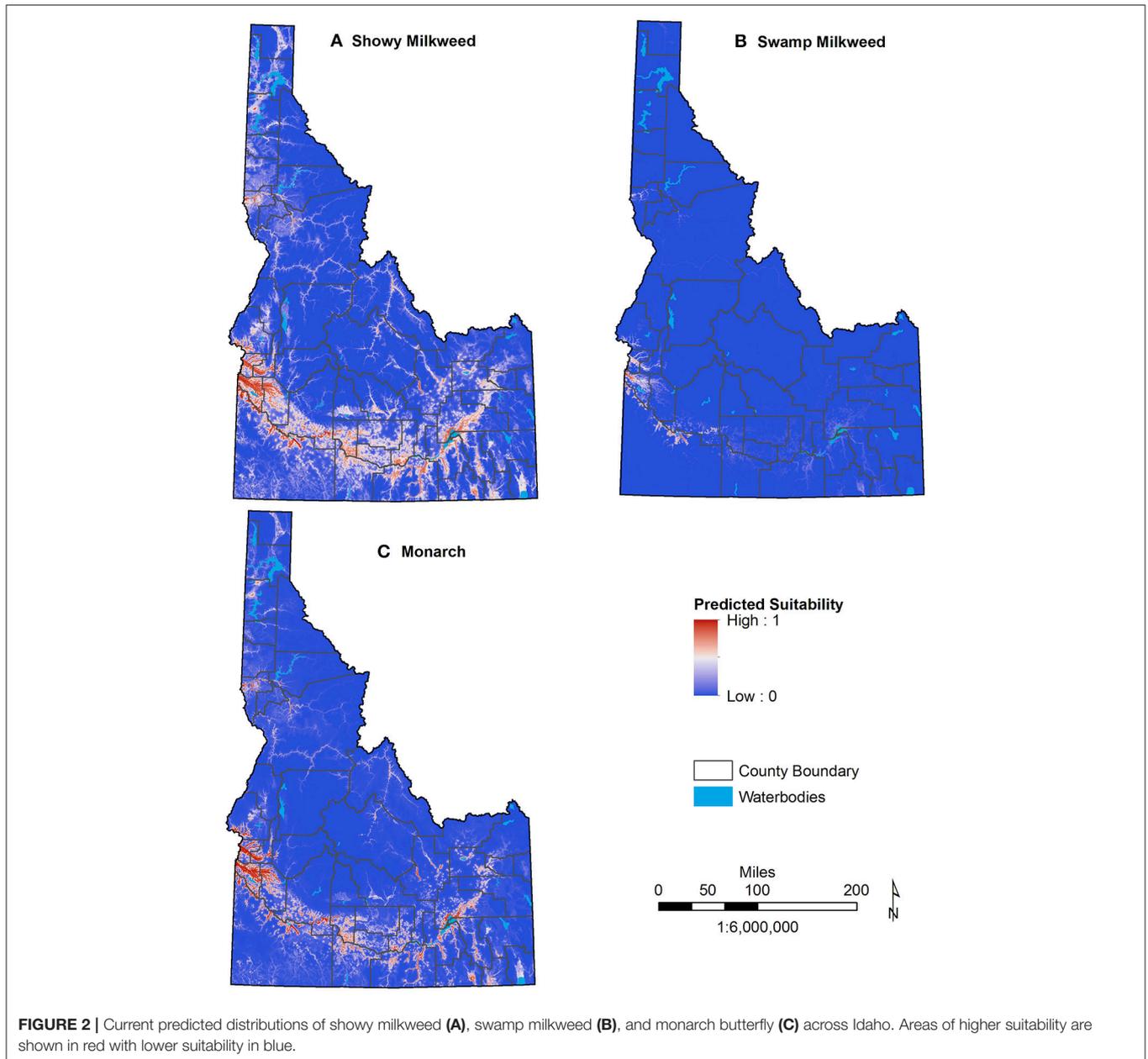
(USFWS) National Wildlife Refuges (NWR), and the US Forest Service (USFS) Curlew National Grassland (NG) to identify potential areas of concern.

Uncertainty is inherent in species distribution modeling simply due to limited knowledge of species-habitat relationships and correlative nature of the modeling process. Modeling potential effects of climate change introduces additional sources of potential variability given the range of estimates provided by each GCM. To assess how variability in projected changes might influence both the calculated bioclimatic variables as well as the modeling of suitable species habitat, we addressed potential uncertainty in two ways. First, we calculated the monthly standard deviation of projected changes in each climate measure (minimum temperature, maximum temperature, precipitation) to map variability among the 20 GCMs. This provided a simple way of evaluating potential influences on the bioclimatic variables. Second, we evaluated results of a Multivariate Environmental Similarity Surface analysis (Elith et al., 2010, 2011) to identify areas where novel conditions (i.e., conditions outside of the training range of the covariates) exist in model predictions and which variables were most limiting. In all cases, we assumed the species relationships with mapped covariates and correlations among covariates would remain consistent through time.

## RESULTS

Maxent accurately predicted current distributions for showy milkweed, swamp milkweed, and monarch with AUC = 0.899, 0.981, and 0.929, respectively (**Figure 2**). The best-fit models based on  $AIC_c$  for all three species employed linear, quadratic, and product features, with a regularization multiplier of 0.5 for showy milkweed and monarch and a regularization multiplier of 2.0 for swamp milkweed.

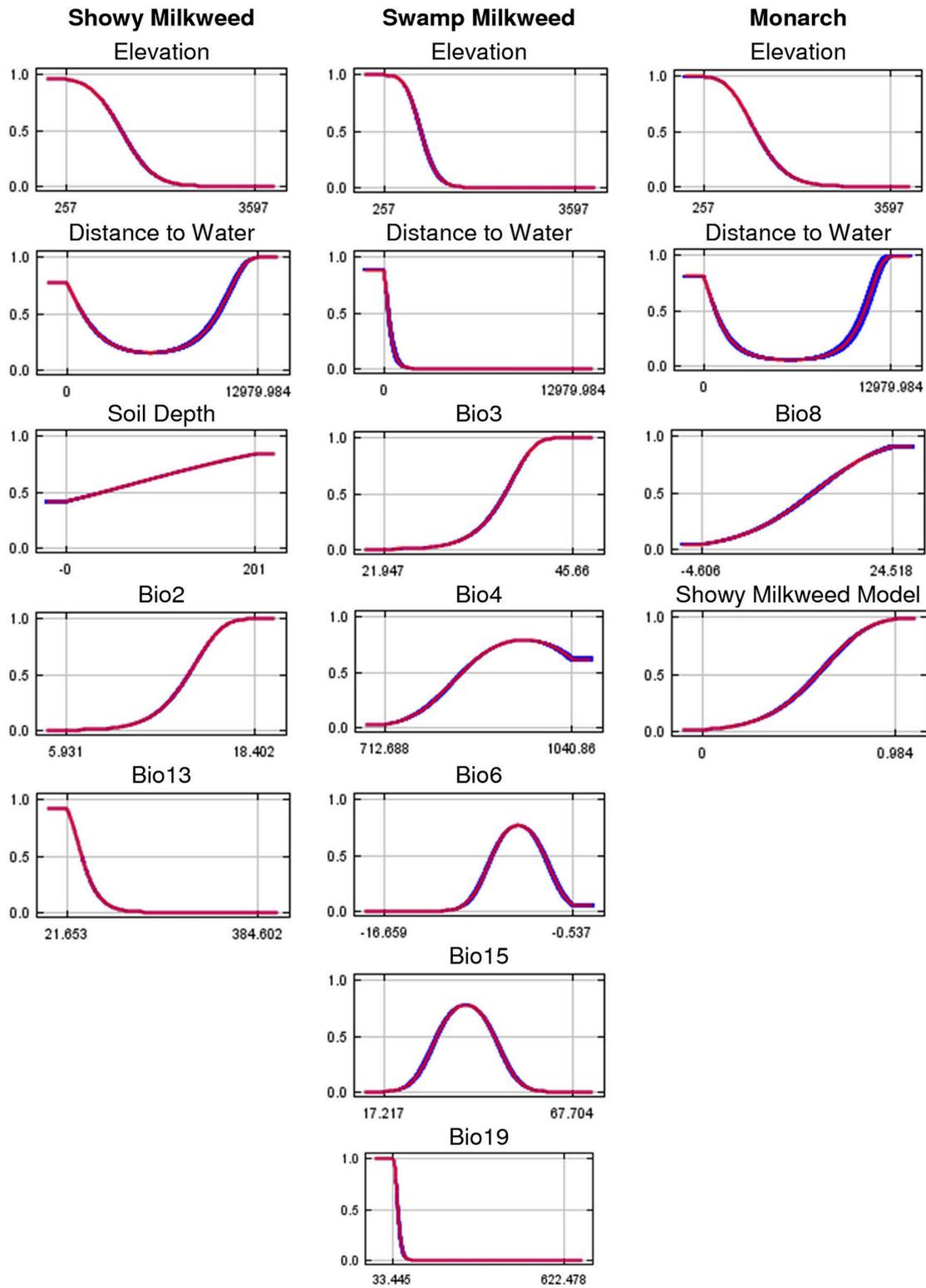
Suitable habitats for all three species were predominantly characterized as low in elevation ( $\leq 1,300$  m) and near perennial water ( $\leq 1,000$  m), particularly swamp milkweed. In addition, showy milkweed habitat occurred in areas of deeper soils ( $\geq 30$  cm), lower precipitation (i.e., wettest month was relatively dry at  $\leq 50$  mm), and higher diurnal temperature range ( $\geq 14^\circ\text{C}$ ) (**Figure 3; Table 2**). Jackknife tests for showy milkweed indicated that mean diurnal temperature range had the most useful information by itself and elevation appeared to have the most information that was not present in other variables. Similarly, suitable swamp milkweed habitat was also characterized by areas with moderate monthly and annual temperature variability (isothermality  $\geq 33\%$ , temperature seasonality  $\geq 7.75^\circ\text{C}$ ), moderate minimum winter temperatures ( $-1$  to  $-9^\circ\text{C}$ ), low winter precipitation ( $\leq 75$  mm), and moderate annual precipitation variability (seasonality 26–52%). Jackknife tests for swamp milkweed indicated that precipitation of the coldest quarter had the most useful information by itself and distance to perennial streams appeared to have the most information that was not present in other variables. Monarch habitat was predominantly a function of modeled showy milkweed habitat (probability  $\geq 0.53$ ) but also depended on



warmer average temperatures ( $\geq 10^{\circ}\text{C}$ ) during the wettest part of the year. Jackknife tests for monarch indicated that the modeled prediction of showy milkweed had the most useful information by itself as well as appeared to have the most information that was not present in other variables.

Because selection of specific model thresholds is somewhat arbitrary and biologically meaningful thresholds can be difficult to determine, reporting a range of threshold values, or none at all, is often recommended (Liu et al., 2005; Merow et al., 2013). Although we considered several thresholds calculated by Maxent in the interpretation of habitat suitability (Table 3), the “Balance training omission, predicted area and threshold value area” threshold best reflected expert knowledge of known

habitats across the state and captured 75% of monarch and showy milkweed occurrences and 88% of swamp milkweed occurrences. Thus, we defined suitable habitat for showy milkweed, swamp milkweed, and monarch using the threshold values of 0.4704, 0.1415, and 0.399, respectively. For all three species, we used an expert-opinion-based threshold of 0.7 to separate marginal and optimal habitat. Using these threshold values, models for present day conditions predicted 15,836 km<sup>2</sup> of Idaho (7.4%) as suitable showy milkweed habitat with 36.0% (5,701 km<sup>2</sup>) of that as optimal, 3,125 km<sup>2</sup> (1.5%) of Idaho as suitable swamp milkweed habitat with 8.8% (275 km<sup>2</sup>) as optimal, and 11,521 km<sup>2</sup> (5.4%) of Idaho as suitable monarch habitat with 44.6% (5,143 km<sup>2</sup>) as optimal. Suitable habitats for all three species



**FIGURE 3** | Response curves for the most important variables in the final showy milkweed, swamp milkweed, and monarch predicted current distribution models. Curves represent a model created using only that variable, and reflect the dependence of predicted suitability on the selected variable and on correlations between the selected variable and other variables. The mean response of 10 replicate runs is in red and the mean  $\pm$  1 standard deviation is in blue. Y-axis values are predicted probability of suitable conditions, as given by cloglog output format. See **Table 1** for variable abbreviations.

occur primarily along the Snake River and tributaries in south Idaho, with smaller amounts of habitat in the Pend Oreille, Coeur d'Alene, and Clearwater River valleys of north Idaho and the Salmon River of east-central Idaho (Figure 4). Nearly all (>98%) predicted suitable habitat for monarchs and swamp milkweed is encompassed by that predicted as suitable habitat for showy milkweed. Similarly, predicted suitable monarch habitat includes 98% of swamp milkweed distribution, but only 72% of showy milkweed distribution.

Mid-century projections suggested relatively small (<8.5% of current habitat) changes in the cumulative area of suitable habitat statewide for showy milkweed and monarch under either the moderate or more severe emission scenario (Figure 4; Table S1). Models projected contraction of showy milkweed

suitable habitat (1,259 and 1,349 km<sup>2</sup> for moderate and severe scenarios, respectively), with minor expansion (29 and 31 km<sup>2</sup>) into previously unsuitable areas, predominantly due to increased precipitation in the wettest month. For monarch, projected expansion (543 and 859 km<sup>2</sup>) was roughly similar to contraction (558 and 573 km<sup>2</sup>) and largely due to changes in the showy milkweed model as well as increased temperature of the wettest quarter. Conversely, projections for swamp milkweed showed considerable expansion (3,444 and 5,830 km<sup>2</sup>) with only minor contraction (1 km<sup>2</sup> under moderate and 0 km<sup>2</sup> under severe), a result of increased temperature seasonality, minimum temperature of the coldest month, and precipitation in the coldest quarter.

At a local scale, however, areas of expansion and contraction appear more substantial. This expansion and contraction is particularly apparent with projected increases of swamp milkweed into southeast Idaho, and contraction of both showy milkweed and monarch habitat in portions of north and south-central Idaho (Figure 5). Projected changes for selected managed areas are also important (Figure 6; Table S2). For example, 14 WMAs, four NWRs, and the Curlew NG are all projected to gain suitable habitat for swamp milkweed, including >10 km<sup>2</sup> gains in Curlew NG, Minidoka NWR, and Mud Lake WMA. Conversely, while persistence of showy milkweed remains high, expansion of suitable habitat for the species is minor in extent (<0.2 km<sup>2</sup>) and limited to only two WMAs (CJ Strike and Craig Mountain). In fact, 20 of the 30 managed areas assessed are projected to lose suitable showy milkweed habitat, although all projected losses are <4.5 km<sup>2</sup>. Monarch projections are more variable with 12 areas projected to experience habitat expansion (0.1–15.2 km<sup>2</sup>), 7 to experience habitat contraction (0.1–1.4 km<sup>2</sup>), and two to experience both expansion and contraction. Overall, five managed areas in northern Idaho are projected to experience a cumulative loss of monarch and/or showy milkweed habitat by mid-century under a severe emission scenario (Figure 6).

Analyses of variability among GCMs and uncertainty in the SDMs suggest areas where these projections should be interpreted with caution. For showy milkweed, analyses indicated few areas with novel conditions under a severe emission scenario with only a few limiting variables in localized areas (Figure 7). For swamp milkweed, novel conditions are much more apparent,

**TABLE 2 |** Most important variables based on percent permutation importance for the final monarch and milkweed models.

Variable	Showy milkweed	Swamp milkweed	Monarch
Elevation	36.9**	37.0	3.4
Distance to perennial streams	12.1	20.9**	5.9
Soil depth	5.5		
Bio2—Mean diurnal range	16.6*		
Bio3—Isothermality		16.8	
Bio4—Temperature seasonality		14.6	
Bio6—Minimum temperature of coldest month		4.9	
Bio8—Mean temperature of the wettest quarter			4.9
Bio13—Precipitation of wettest month	28.9		
Bio15—Precipitation seasonality (coefficient of variation)		3.2	
Bio19—Precipitation of coldest quarter		2.7*	
Showy milkweed (modeled prediction)			85.8*, **

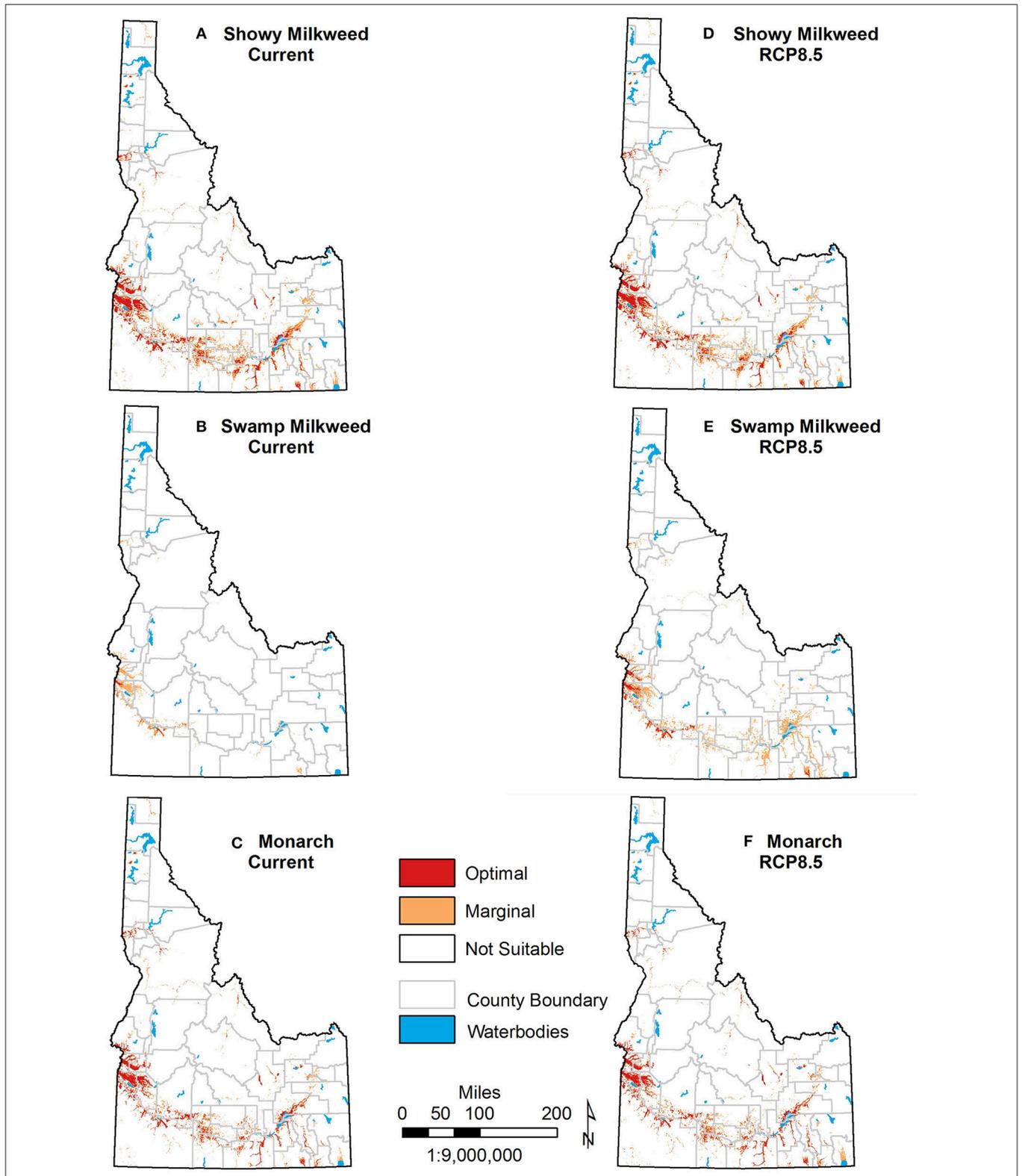
\*Variable with highest gain when used in isolation (i.e., appears to have the most useful information by itself).

\*\*Variable that decreases the gain the most when omitted (i.e., appear to have the most useful information not present in other variables).

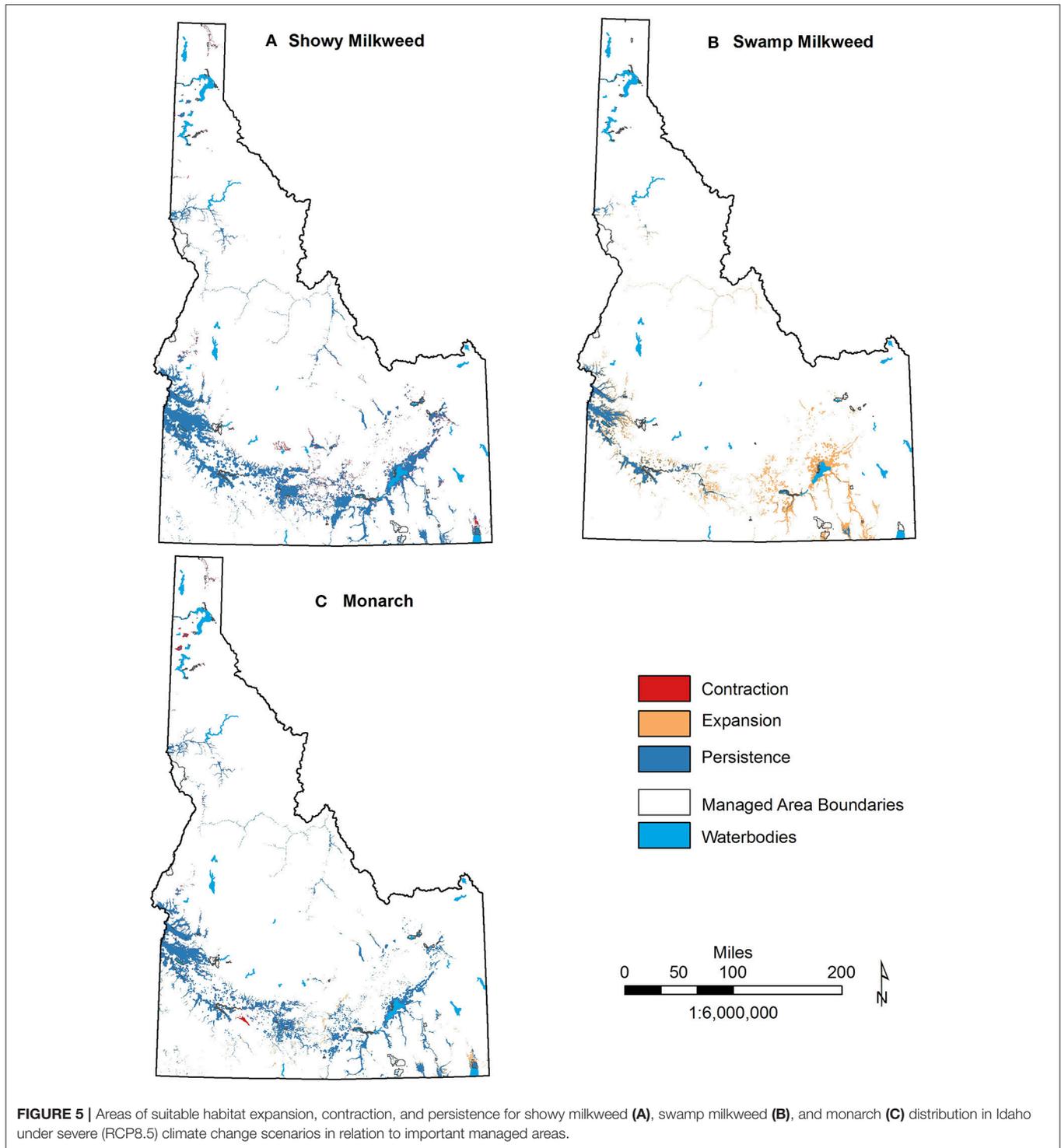
**TABLE 3 |** Maxent modeled and expert opinion-based thresholds used in aiding interpretation of habitat suitability.

Source	Threshold	Showy milkweed	Swamp milkweed	Monarch
Maxent	Prevalence	0.1653	0.0148	0.0911
	Minimum training presence	0.0006	0.0001	0.009
	10 percentile training presence	0.2440	0.1211	0.0944
	Equal training sensitivity and specificity	0.3692	0.0473	0.1509
	Maximum training sensitivity plus specificity	0.2433	0.0462	0.1784
	Balance training omission, predicted area and threshold value area	<b>0.4704</b>	<b>0.1415</b>	<b>0.3990</b>
	Equate entropy of thresholded and original distributions	0.1748	0.0987	0.1111
Experts	Fixed value	0.7	0.7	0.7

Threshold values used to differentiate suitable and unsuitable habitat are highlighted in bold.

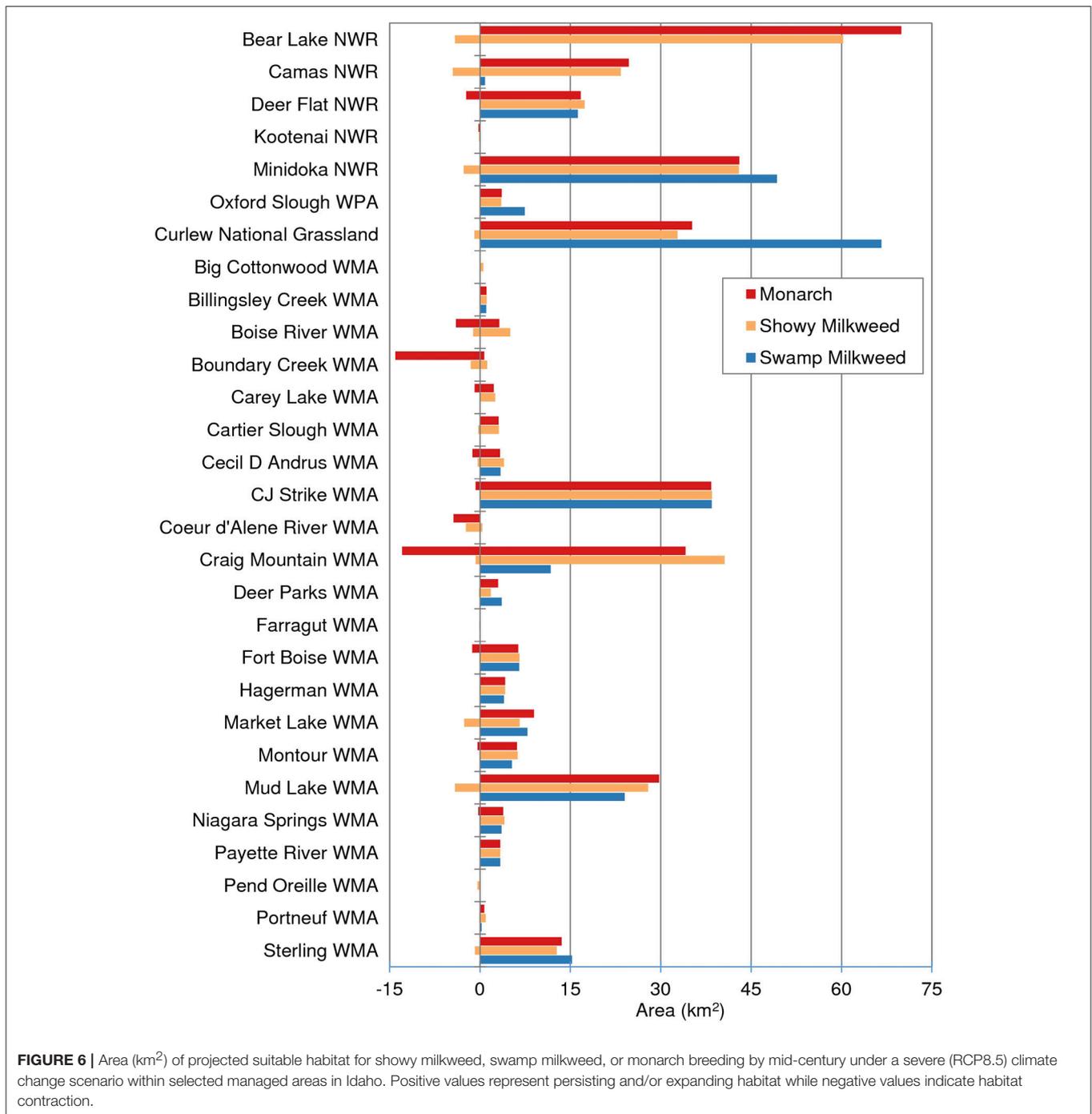


**FIGURE 4 |** Current and future predicted distributions of showy milkweed (A,D), swamp milkweed (B,E), and monarch (C,F) across Idaho. Future distributions represent 20 global climate model average ensemble projections under severe (RCP 8.5) climate change scenarios. Separation of non-suitable habitat with marginal habitat is based on the “Balance training omission, predicted area and threshold value area” threshold, and separation with optimal habitat is based on an expert-derived threshold.



particularly in the valley bottoms of northcentral Idaho and a few localized areas in south Idaho due, predominantly, to the influence of minimum temperature of the coldest month (particularly in north Idaho), temperature seasonality and precipitation seasonality. For monarchs, novel conditions are evident in the southwest and a few areas in northcentral,

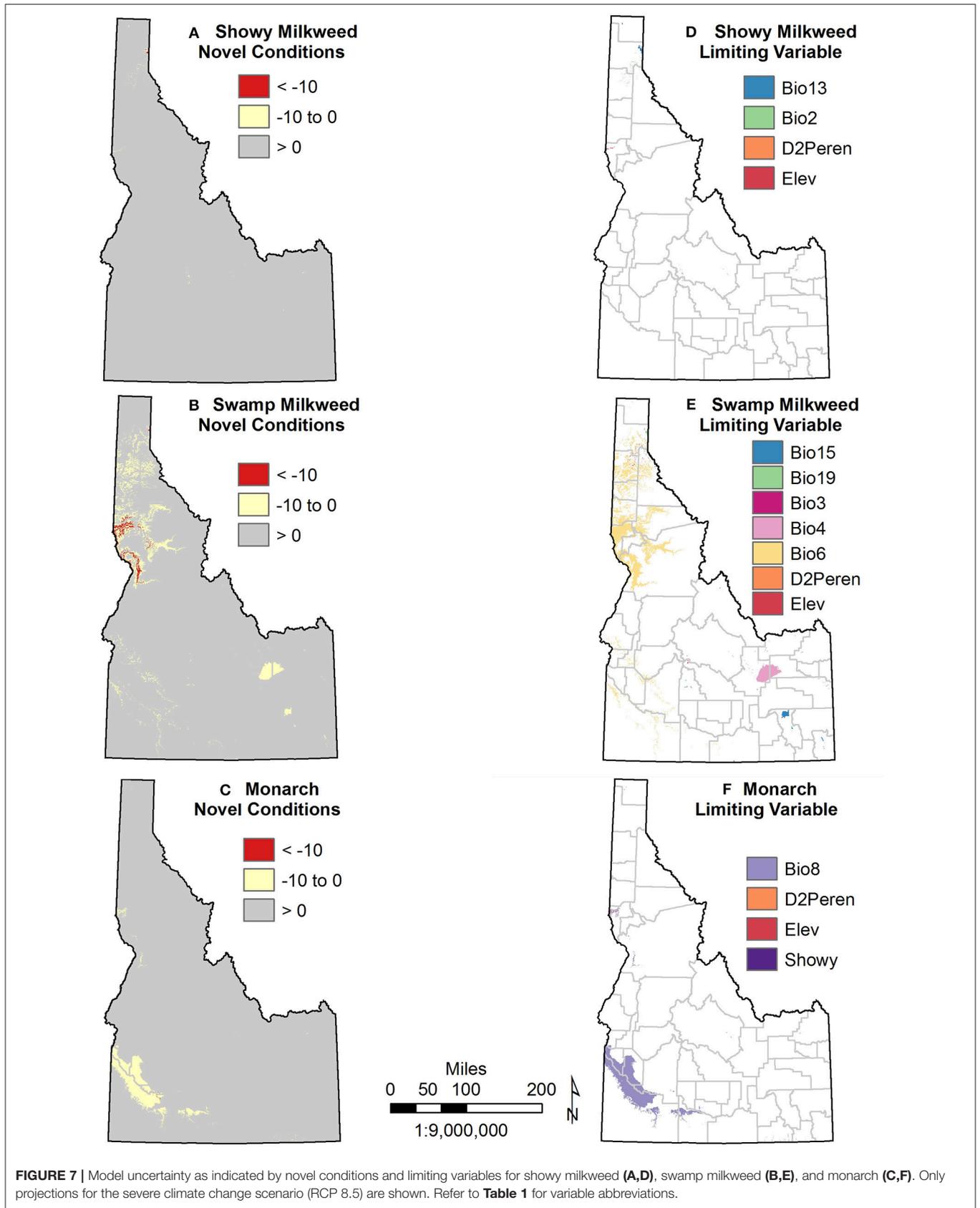
primarily limited by mean temperature of the wettest quarter. In addition, monthly standard deviation of the projected changes in each of the core climate variables (minimum temperature, maximum temperature, precipitation) indicated both seasonal and spatial variability among the 20 GCMs (Figures S1–S3). For both minimum and maximum temperature, variability among



the GCMs is greatest in early spring (Feb-April) in south-central and southeast Idaho, regardless of emission scenario. For precipitation, variability among the models is greatest during the summer months (July-Sept) in southwest Idaho, which also has the lowest precipitation during this time. Given the seasonality of the variability among GCMs, the bioclimatic variables most likely affected include mean diurnal range, isothermality, temperature seasonality, and precipitation seasonality. Thus, SDMs using these variables may over- or under-predict possible changes in suitable habitats.

## DISCUSSION

Use of SDMs to depict current and potential future species distributions under changing climates is becoming commonplace, however local adaptation can result in significant variability in climate responses across a species range (Pearman et al., 2010; Hällfors et al., 2016; Ikeda et al., 2017; Nice et al., 2019). Our results indicated variability in milkweed response to projected climates in Idaho with the amount of showy milkweed suitable habitat decreased slightly statewide while swamp



milkweed potential habitat doubled under a moderate emission scenario and nearly tripled under a more severe emission scenario. Projected amounts of suitable habitat for monarch in Idaho are likely to remain roughly stable with expansion nearly equal to contraction under a moderate scenario and slightly greater when under the more severe scenario. As such, our assessment of potential changes in monarch and milkweed distributions at a finer scale and in the northern portion of the range represents important contributions to the long-term conservation and management of the species.

Overall, our models of current distributions of milkweed and monarch habitats are similar to other broad-scale modeling efforts (Lemoine, 2015; Dilts et al., 2018) in that monarch distribution was largely a function of milkweed occurrence with relatively minimal influence of climate variables, although spring temperatures were positively related in our case as in Espeset et al. (2016). While monarchs are not in Idaho during the wettest time of year (spring), the combination of warm/wet conditions likely facilitates milkweed habitat, and thus suitability of monarch habitat. Milkweed distributions in Idaho were influenced by variables emphasizing annual and seasonal variability in temperature and precipitation as opposed to the more broad-scale efforts (Lemoine, 2015; Espeset et al., 2016; Dilts et al., 2018) that highlighted mean and maximum variables (e.g., mean annual temperature). Perhaps more importantly, our results suggest that at a more local/state scale, non-climatic factors such as soil depth, distance to water, and elevation play important roles in determining milkweed and monarch distributions. Although these factors (soil, water, elevation) are likely not independent of climate, but rather interact with climate to create suitable conditions.

The primary resources of light, heat, water, and nutrients constrain species distributions at topo- and meso-scales (Mackey and Lindenmayer, 2001). As such, several studies have indicated inclusion of edaphic variables is important when modeling plant distributions (Bertrand et al., 2012; Beauregard and de Blois, 2014; Diekman et al., 2015; Velazco et al., 2017) and we found a positive relationship between soil depth and showy milkweed habitat. Surprisingly, soil variables were not significant in the model for swamp milkweed, a species adapted for moist soils (Woodson, 1954) and typically found in marsh and saturated meadow habitats in the state (Waterbury and Potter, 2018). Distance to perennial water, however, was significant for all three species distributions but particularly swamp milkweed. Dilts et al. (2018) also found swamp milkweed dependent on proximity to perennial water and it may be that this factor overrides other explanatory soil variables important for the species (e.g., hydric soils). This general relationship of milkweeds with water may also help explain the use of riparian corridors as typical migratory paths for western monarchs (Pyle, 1999; Dingle et al., 2005; Morris et al., 2015). Future modeling efforts that go beyond the typical bioclimatic variables might effectively couple soils with climate. For example, a simple water balance model that considers soil water holding capacity, precipitation, and potential evapotranspiration that captures the joint seasonality of energy and moisture (e.g., Abatzoglou et al., 2018) might more concisely synthesize climatic and edaphic factors important for habitat.

Our results support the inclusion of elevation as a necessary predictor for species distributions (Luoto and Heikkinen, 2008; Randin et al., 2009; Oke and Thompson, 2015), potentially due to reflecting environmental conditions not properly portrayed by climate data (Körner, 2007; Oke and Thompson, 2015), the bioclimatic factors used in this study, or other topographic variables (e.g., slope, aspect, CTI). Correlations of elevation with climate and biophysical variables may vary over space and time (Phillips et al., 2006) and we chose to follow a process of variable selection that allowed for expert input while maximizing variable importance in the SDMs and minimizing correlations. As such, we identified only five climate variables that were significantly correlated with, but of less importance in the SDMs, and thus excluded by elevation. Interestingly, these excluded variables reflected mean and maximum temperature characteristics identified as important in broad-scale models (Lemoine, 2015; Espeset et al., 2016; Dilts et al., 2018) but suggested as less relevant to butterfly distributions (Filz et al., 2013). The importance of elevation in our models suggests the included bioclimatic variables may still be inadequately capturing physical processes related to moisture and/or energetics of milkweed habitat either due to missing variables (e.g., downward shortwave radiation) or mismatches of scale. Ultimately, local fine-scale variability in topographic, climatic, and edaphic characteristics can result in extreme differences in growing conditions for plants (Austin and Van Niel, 2011; Lembrechts et al., 2018). In addition, the effects of climate change may be elevationally dependent (Nice et al., 2019), although that effect is not well-represented through our current approach using a statistically downscaled model ensemble. It remains unknown on how synoptic and land-surface factors will modify the occurrence and strength of cold air drainages and other elevation-dependent changes in climate in future climate (Daly et al., 2010; Pepin et al., 2015). Advances in understanding how climate change will manifest itself at these finer spatial scales may help improve estimates of changes in impacts.

To date, the rather substantial projected broad-scale northward expansions of showy milkweed and swamp milkweed as well as monarch breeding distributions (Batalden et al., 2007; Lemoine, 2015) are driven chiefly by increasing temperatures. Our results suggest that northward expansion might not be the case in Idaho. While we did project expansions of suitable swamp milkweed habitat, expansions were predominantly in the east and southeastern portions of the state. Conversely, showy milkweed expansions and contractions were minimal, but concentrated such that many of the managed areas in the northern portion of Idaho were projected to experience greater habitat losses than gains. Similarly, projected expansion of monarch distribution occurred mainly in the southeast with contractions in the north. These estimates reflect the spatial patterns of observed and projected increases in winter and spring temperature and precipitation across Idaho (Abatzoglou et al., 2014; Klos et al., 2015; Rupp and Abatzoglou, 2017). Our models indicated species expansion in areas with moderately increasing precipitation coupled with warming temperatures (i.e., southeast) but contraction in some areas, particularly in north Idaho, that may become too wet during spring to

provide suitable habitat. Given future climate projections of progressively hotter, drier summers and warmer, wetter winters as well as the highly variable topography and amount of natural landscapes available in Idaho, one might hypothesize substantial expansion of showy milkweed suitable habitat due to upslope range shifts. While the iterative variable inclusion process works well modeling current distributions, it can be an important source of uncertainty for future predictions (Braunisch et al., 2013). Our models suggest current habitat suitability for all three species declines with increasing elevation. Given that elevation remains constant under future climate conditions, the future model projections are thus limited to lower elevations reducing the ability of higher elevation areas to potentially be modeled as expanded habitat under future scenarios. Development of a climate-only model, or inclusion of the elevation-correlated temperature variables mentioned above, may have resulted in just such changes in suitable habitat. However, projecting the effects of climate change on species in topographically diverse areas is complex. Climate-only models may not reflect realistic patterns as local topography can result in steep, fine-scale temperature gradients (e.g., insolation or cool-air pooling) (Daly et al., 2010; Holden et al., 2015) that can moderate the effects of rising temperatures by creating microclimates and refugia that enable species persistence (Luoto and Heikkinen, 2008; Austin and Van Niel, 2011; Suggitt et al., 2011; Lembrechts et al., 2018). In addition, variation in edaphic measures and habitat can also alter microclimates and refugia (Suggitt et al., 2011; Bertrand et al., 2012; Beauregard and de Blois, 2014). In fact, the presence of suitable microclimates due to substantial variability in these characteristics may be a key factor in the persistence of both milkweeds and monarch butterflies in Idaho.

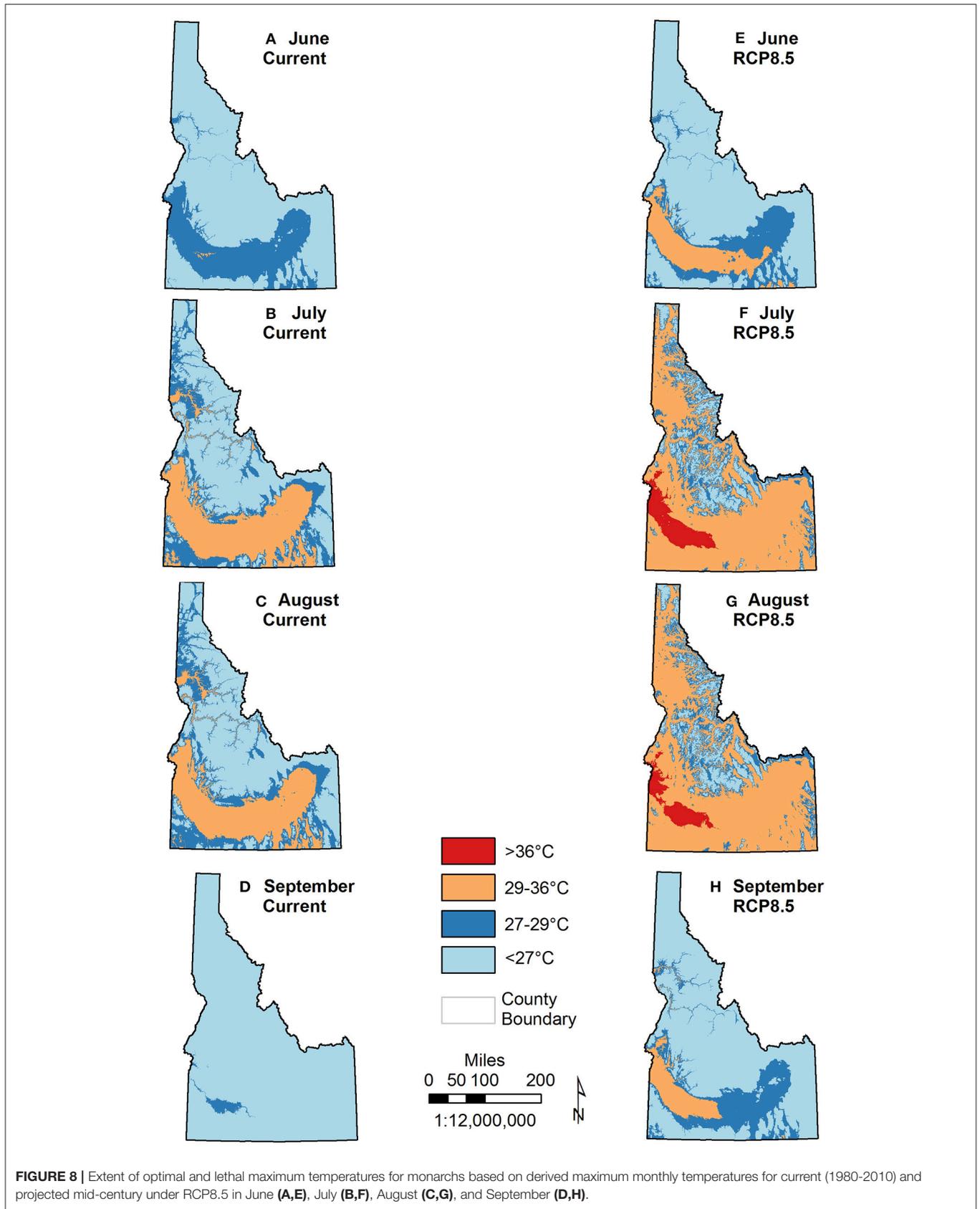
In the absence of climate refugia, known physiological constraints of monarchs may further alter the extent of breeding distribution in Idaho beyond our model results. Monarchs typically arrive in Idaho in June, breed through August, then depart mid-August/mid-September (Waterbury and Potter 2018). Currently, maximum monthly temperatures during these months are generally within the optimal (27–29°C) or sub-lethal (30–36°C) range for monarch survival identified in laboratory studies (Zalucki, 1982; York and Oberhauser, 2002; Zalucki and Rochester, 2004; Nail et al., 2015) (Figure 8). Under a severe emission scenario, however, maximum temperatures are projected to increase substantially between June and September with areas in the optimal and sub-lethal range expanding greatly and a portion of current habitat in the southwest exceeding 36°C (maximum 38.7°C). While limited exposure to high temperatures (36–38°C) is not detrimental to monarchs, extended exposure is lethal to immature stages (York and Oberhauser, 2002; Nail et al., 2015; James, 2016). Following a similar spatial pattern, minimum temperatures are also projected to increase such that the amount of area above the lower temperature threshold for larval development ( $\geq 11^\circ\text{C}$ , Zalucki, 1982) also expands substantially from June–September. Spatially extensive warming on the shoulder months of June and September may result in earlier and/or later breeding over broader areas of Idaho, potentially resulting in additional breeding generations (Batalden et al., 2007), but lethal

temperature limits in the southwest may result in increased mortality in important managed areas such as Payette River WMA, Montour WMA, Fort Boise WMA, CJ Strike WMA, and Deer Flat NWR. In addition, increases in the frequency and duration of extreme temperatures may result in earlier senescence and/or reduced nutritional quality of important milkweed and other nectaring plants. Given climate variability, there will likely be years in which summer temperatures are above and below averages reported here. These model projections underscore the need to investigate western monarch population vital rates across all life stages (i.e., survival, individual growth, reproduction, recruitment) to better predict monarch response to changing climates and weather (Schultz et al., 2017; Belsky and Joshi, 2018).

## Management Implications and Caveats

Mapped classes of suitable, marginal, and optimal habitats showcase how relatively small and fragmented suitable areas are for monarch and milkweed in Idaho, which appears to be the case in on-the-ground surveys (Waterbury and Potter, 2018). Even so, our study shows that suitable habitat for monarch and/or milkweeds will likely continue to be found in managed areas traditionally seen as priority habitats through mid-century. For example, Waterbury and Potter (2018) documented major monarch eclosure events at Bear Lake NWR, CJ Strike WMA, Sterling WMA, and Fort Boise WMA in recent years. Extensive areas of suitable habitats are projected to persist in all four of these managed areas, with sizeable habitat expansions ( $>4\text{ km}^2$ ) in Bear Lake NWR. Additional managed areas with substantial expansions include Camas NWR, Minidoka NWR, Curlew NG, and Mud Lake WMA. Even though total amount of suitable habitat statewide is not projected to drastically diminish, geographic patterns in habitat contractions suggest that five areas in northern Idaho (Kootenai NWR, Boundary Creek WMA, CDA River WMA, Farragut WMA, and Pend Oreille WMA) may lose nearly all suitable habitat. Based on our results, protected areas currently encompass 8, 11, and 9% of suitable habitat for showy milkweed, swamp milkweed, and monarch, respectively, with 2.4% of showy milkweed habitat and 2.9% of swamp milkweed and monarch habitat protected under the IDFG, USFWS, and USFS managed areas we assessed. Under the most severe climate change scenario, this percentage increases for all three species to 2.5, 3.0, and 3.2%, respectively. These managed areas, however, represent a relatively small proportion of current and future suitable milkweed and monarch habitats in Idaho, indicating sizeable potential to engage private landowners and industry in expanding habitat protection, enhancement, and restoration to benefit monarchs and other pollinators in Idaho.

Currently, distribution of showy milkweed encompasses virtually all suitable swamp milkweed habitat. This relationship is seen in the field as well with swamp milkweed generally co-occurring with showy milkweed in Idaho. These areas of co-occurrence tend to have the highest monarch productivity due to extended phenology with showy milkweed early and swamp milkweed later (Waterbury and Potter, 2018). If swamp milkweed expands, but showy milkweed does not, these areas may experience reduced early-season monarch productivity but, conversely, increased later-season monarch productivity. Greater



availability of later-blooming swamp milkweed may also aid the migratory generation, both locally-produced and those stopping by from points further north. Although our results suggest broad-scale overlap of milkweed and monarch occurrence, at finer scales, presence of milkweed is not synonymous with presence of monarchs. Breeding monarchs likely select for a range of variables beyond what we could model to maximize reproductive fitness. Such resource selection studies are lacking but urgently needed for the western monarch population. Further inventory is also needed to assess potential climate adaptability and habitat relationships of monarchs with other native milkweeds (narrow-leaved, pallid, and spider) in Idaho. In addition, monitoring that incorporates areas of potential habitat expansion would ensure changes in distribution are documented and not just assumed a population loss due to declining numbers in specific areas.

Even though we employed best modeling practices recommended in the literature (Elith et al., 2010, 2011; Anderson and Gonzalez, 2011; Merow et al., 2013; Radosavljevic and Anderson, 2013; Yackulic et al., 2013; Porfirio et al., 2014; Wright et al., 2015; Searcy and Shaffer, 2016; Morales et al., 2017), our models and analyses are still subject to several caveats based on ecological and mathematical assumptions inherent in SDMs developed with Maxent and violation of these assumptions can affect model inferences to varying degrees (Phillips et al., 2006, 2017; Wiens et al., 2009; Merow et al., 2013; Yackulic et al., 2013). Key to Maxent, both sampling probability and detection probability are assumed constant across space. Although we attempted to account for multiple sources of uncertainty in our compiled occurrence data, including sampling bias, this key assumption may not be met. Similarly, detection probabilities for milkweed and monarch butterflies are unknown but, given both species are generally conspicuous on the landscape, we assumed detection probability was constant. Our choice of background extent and threshold values to determine suitable/non-suitable habitat likely also influenced model results, thus there may be more or less habitat available than we are suggesting. The true distribution of monarchs and milkweeds in Idaho is likely beyond the resolution our models provide, both spatially and thematically. We used the finest spatial data available (250 m climate, 30 m all others), yet even this resolution likely averaged over micro-environments important in the establishment of milkweed and/or the breeding of monarchs, as well as potential refugia.

Fundamental to SDMs, the species is assumed to be in equilibrium with its environment and its occurrence data representative of suitable habitat. In addition, SDMs are correlative in nature and, while selected model covariates are assumed to adequately reflect determinants of species distributions at relevant temporal and spatial scales, derived relationships may be due to other correlated variables not assessed. We modeled milkweed and monarch distributions based on the assumption that abiotic factors (light, heat, water, nutrients; Mackey and Lindenmayer, 2001) primarily controlled occurrence. However, other variables important in determining milkweed and monarch distributions may be lacking such as land cover or disturbance (Suggitt et al., 2011; Diltz et al., 2018) or light/solar radiation (Austin and Van Niel,

2011). Biotic interactions, genetic responses and geographic barriers limiting dispersal and/or colonization likely also dictate species distributions to some degree (Wiens et al., 2009). SDMs are also assumed to be spatially and temporally transferable. Projecting through time assumes the relationships among monarch, milkweeds, and their environs will remain consistent and that the correlation among this suite of variables will also remain consistent. In other words, we are assuming the species and their environment, as well as multiple components of that environment, will not become decoupled from each other (Walther, 2010). Furthermore, we still know little about monarch and milkweed direct relationships with climate and potential abiotic and biotic interactions (e.g., soils, parasites, monarch vital rates) at local scales, as well as species adaptive capacity (Dawson et al., 2011; Beever et al., 2016), both of which are likely to influence current and future distributions.

Lastly, uncertainty in the climate projections can be due to emission scenario, model structure, or natural climate variability (Hawkins and Sutton, 2011; Woldemeskel et al., 2016). We used a multi-model mean of 20 MACA downscaled GCMs because it performs well in areas of complex terrain (Abatzoglou and Brown, 2012). However, this does limit the SDMs to bulk-30 year averages and does not account for climate variability and extremes at finer temporal scales that may affect milkweeds and/or monarchs themselves, although assessments of SDMs and semi-process based models show similar performance (Parker and Abatzoglou, 2017). Both emission scenarios we assessed represent realistic scenarios of future conditions. Focusing on mid-century, as opposed to end-of-century, projections limited the extent of uncertainty as well in that there is an average of only about 1°C difference in temperature change between scenarios by the mid-century (Rupp and Abatzoglou, 2017). However, neither emission scenario takes into consideration potential cascading and/or interacting effects such as non-native plant invasions, changes in land use (e.g., extent of agricultural or urbanization), and changes in water usage. For instance, areas predicted to persist or expand under our two emission scenarios (i.e., Snake River Plain) are expected to favor cool-season species of exotic invasives such as cheatgrass (*Bromus tectorum*) (Smith et al., 2006; Bradley, 2009). Interactions between climate change and cheatgrass proliferation may combine to increase invasion risk to native rangeland and grassland ecosystems, thereby increasing fine fuels and risk of frequent and/or large-scale wildfires (Whisenant, 1990; D'Antonio and Vitousek, 1992). Likewise, changes in waterbody extent, distribution and water usage may play an important role in agriculture-intensive areas within an irrigation landscape (high water demand and diminishing aquifer), such as in areas of the Snake River Basin predicted as expansion for swamp milkweed. Because we limited our study extent to Idaho, future model projections may also not capture the full range of environments milkweed and monarch inhabit in other areas. In other words, areas and covariate values identified as “novel” in our analyses are only novel for Idaho and may not be in other areas.

Even with these caveats, our models accurately predict current and project future distributions of milkweed and monarchs

and provide a means for assessing potential changes in habitat and distributions, identifying priority areas for conservation, and directing future research and monitoring efforts. While broad-scale modeling efforts provide a baseline understanding of species-habitat relationships and distribution, and can help guide finer-scale sampling efforts (such as our use of earlier versions of Dilts et al. (2018), or adoption of sampling schemes that collect presence/absence data), they fail to consider the potential for intraspecific variability in climate relationships and potential for local refugia. Understanding this variability is key in knowing just how vulnerable a species may be in a given area, as well as identifying the most appropriate adaptive management. Even state-level analyses, as ours, are likely to overlook more regional or local level variability in species responses (Pearman et al., 2010; Hällfors et al., 2016; Ikeda et al., 2017; Nice et al., 2019) and we recommend additional efforts to identify regions of smaller extents where climate responses of monarchs and milkweed are likely to be more homogeneous.

## AUTHOR CONTRIBUTIONS

LS and BW contributed conception and design of the study and funding acquisition. JA developed climate scenarios. LS

conducted analysis and wrote the first draft of the manuscript. BW and JA wrote sections of the manuscript. All authors contributed to manuscript revision and read and approved the submitted version.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2019.00168/full#supplementary-material>

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**Conflict of Interest Statement:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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