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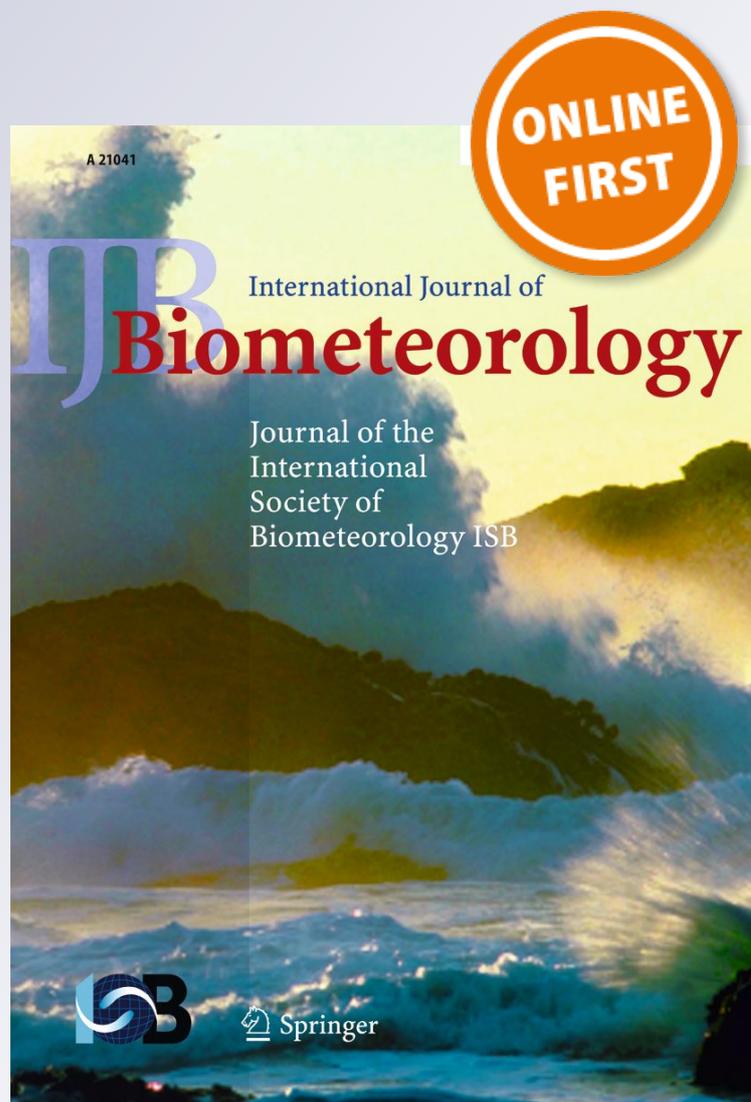
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# Comparing mechanistic and empirical approaches to modeling the thermal niche of almond

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**Abstract** Delineating locations that are thermally viable for cultivating high-value crops can help to guide land use planning, agronomics, and water management. Three modeling approaches were used to identify the potential distribution and key thermal constraints on almond cultivation across the southwestern United States (US), including two empirical species distribution models (SDMs)—one using commonly used bioclimatic variables (traditional SDM) and the other using more physiologically relevant climate variables (nontraditional SDM)—and a mechanistic model (MM) developed using published thermal limitations from field studies. While models showed comparable results over the majority of the domain, including over existing croplands with high almond density, the MM suggested the greatest potential for the geographic expansion of almond cultivation, with frost susceptibility and insufficient heat accumulation being the primary thermal constraints in the southwestern US. The traditional SDM over-predicted almond suitability in locations shown by the MM to be limited by frost, whereas the nontraditional SDM showed greater agreement with the MM in these locations, indicating that incorporating physiologically relevant variables in SDMs can improve predictions. Finally, opportunities for geographic expansion of almond cultivation under current climatic conditions in the region may be limited, suggesting that increasing production may rely on agronomical

advances and densifying current almond plantations in existing locations.

**Keywords** Agroclimatology · Species distribution modeling · Phenology · Almond

## Introduction

Climate plays an important role in shaping the geographic distribution and survival rates of organisms, both on natural and cultivated lands (Guisan and Zimmermann 2000; Leemans and Solomon, 1993). While adverse climate impacts can be mitigated to some extent in horticultural settings (e.g., irrigation), climate is an important factor in determining the geographic distribution of crops. This is particularly notable for perennial crops, which, unlike annuals, are subject to climate conditions year-round and whose decade-long life spans limit adaptation efforts such as fallowing (Lobell and Field 2011). Understanding the viability of cropping choices across a geographic region—from both an agricultural and economic perspective—is important for addressing food security challenges under both present-day conditions, as well as in the coming decades under climate change and increased global caloric demands (Lobell et al. 2008).

Modeling the potential geographic ranges of crops using biophysical environmental predictors can elucidate crop viability through space and time. However, agricultural research has typically used mechanistic models (MMs) that focus on modeling crop yield in a predefined geographic area rather than the potential geographic distribution of a crop. These models attempt to capture relationships between environmental cause and phenological effect, realized from agronomic studies (Dourado-Neto et al. 1998). Agricultural MMs vary in their specifics, though each use input data on weather, soils,

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and crop phenology to simulate crop production (Stöckle et al. 2003). However, the ability to use MMs may be limited by the availability of environmental input data, the capability to accurately parameterize the model, stationarity assumptions when extrapolating MMs in time and space, and computational expense (Challinor et al. 2009).

Though MMs that specifically model habitat suitability have been used to identify species range (Buckley et al. 2010), species distribution models (SDMs) are a more common method for estimating the geographic niche of an organism. SDMs are an empirical approach that have been used to determine the potential range of native species (Vetaas 2002), assess the possible advancement of invasive species (Jiménez-Valverde et al. 2011), and estimate the impact of climate change on species distributions (Pearson and Dawson 2003). SDMs utilize a sample of observed locations of a given species and co-located environmental data to model the species' potential geographic range. Despite their utility, there are a number of limitations and criticisms of SDMs. For example, SDMs overlook biotic interactions and species adaptation (McKenney et al. 2007; Guisan and Zimmermann 2000) and assume species-environment equilibrium, implying that species absence is purely a function of uninhabitability (Araújo and Pearson, 2005). Additionally, SDMs typically use climatological means and bioclimatic variables that may not be mechanistically related to biological viability and are unable to account for the impact of extremes on species prevalence (Woodward et al. 2004).

Whereas both modeling approaches have their merits and shortcomings, SDMs may be more suited to native species whose growing conditions are not managed. Still, some studies have utilized SDMs to address the impact of climate and climate change on managed crops, including some perennial species (Pocle et al. 2014). Further, while SDMs differ in their approach from MMs (i.e., correlative vs. process basis), previous work has shown that modeling frameworks can produce similar results in projecting both distribution and productivity in agricultural settings (Estes et al. 2013).

This study compares the results of an MM and two SDMs for modeling the viability of cultivating *Prunus dulcis* (almond) across the southwestern United States (US) by exclusively considering thermal factors. Following Hijmans and Graham (2006), we consider the MM to be a more accurate representation of the potential distribution to which we compare two SDMs. One SDM is developed using a common approach for selecting thermal variables (Porfirio et al. 2014). The other SDM selects thermal variables that more directly relate to the physiological requirements for a species (Dilts et al. 2015; Zimmermann et al. 2009). Although other environmental factors such as precipitation and soils are commonly included in such models, we focus solely on temperature variables as virtually all commercially grown almonds in the US are irrigated (Lobell and Field 2011), and cultivated

systems may have the capacity to augment soils and biotic conditions that would otherwise be limiting (Yao et al. 2005). Although others have undertaken similar studies examining annual crops (Estes et al. 2013), this study is novel in that it considers a perennial cultivar subject to interannual climate variability.

Almonds are an important agricultural commodity and have a significant impact on regional water resources. California's Mediterranean climate is ideal for almond cultivation and enables the state to produce essentially all of the commercially grown US almond supply and more than 80% of the global supply, adding US\$11 billion in revenue to the California economy (Almond Board of California 2015). Likely as a result of the reported health benefits of almond consumption (Tan and Mattes 2013), global almond demand has increased; coupled with high profitability for growers, increased almond demand has led to a doubling of almond acreage in California since 1995 (US Department of Agriculture 2016). Despite the relatively high water demands of almonds, newer (since 2010) orchards have principally replaced annuals with larger water requirements, potentially reducing agricultural water needs (Howitt et al. 2015); however, the inability to fallow perennials and the increasing water demand of orchards as they age may offset these initial reductions.

The objective of this study is to address the ability of MMs and SDMs to model the potential geographic distribution of thermally suitable land for almond cultivation under present-day climatic conditions across the southwestern US. To this end, we endeavor to (1) identify key thermal controls on almond range across the region, (2) determine how well SDMs capture the thermal niche of almond as compared with the MM, (3) assess the value of incorporating physiologically relevant variables in SDMs, and (4) assess the potential for an expansion of thermally suitable land for almond cultivation across the southwestern US. Given the current increase in almond plantations and climatic water stress precipitated by drought in California (Williams et al. 2015), the geography of suitable almond habitat has implications for land use, agricultural water demands, and economics.

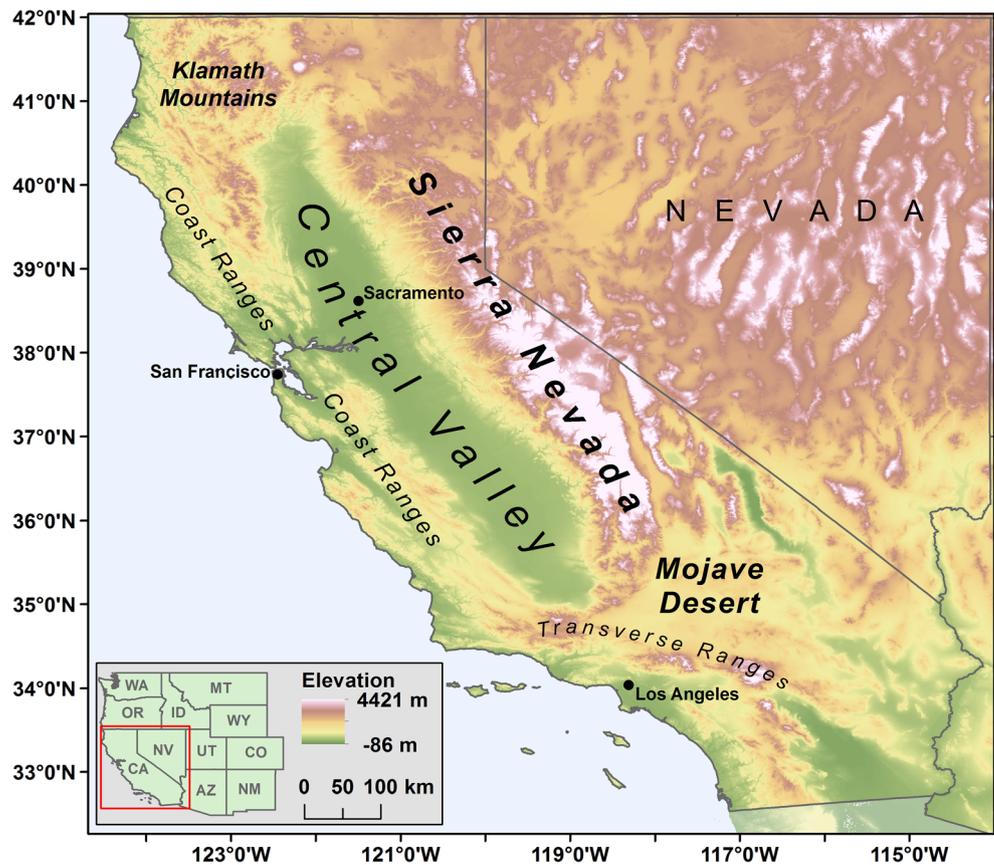
## Data and methods

### Data

#### *Climatological data*

Daily maximum and minimum temperature ( $T_{\max}$ ,  $T_{\min}$ ) for the period 1979–2014 for the southwestern US (32–42° N, 114–125° W (Fig. 1)) were acquired from the gridded surface meteorological dataset (METDATA) of Abatzoglou (2013). METDATA was created using two datasets: hourly data at

**Fig. 1** Overview of the study area, including names of prominent geographic features and cities



~12 km resolution from the North American Land Data Assimilation System Phase 2 (NLDAS-2, Mitchell et al. 2004) and monthly data at ~4 km resolution from the Parameter-Elevation Regressions on Independent Slopes Model (PRISM, Daly et al. 2008). The resulting 4 km resolution gridded daily dataset provides meteorological data at spatial and temporal scales suitable for both local- and landscape-scale ecological and agricultural modeling.

#### *Species presence data*

Almond location data were obtained from the 2015 US Department of Agriculture National Agriculture Statistics Service (USDA-NASS) Cropland Data Layer (CDL). While CDL almond location data is available dating back to 2007, 2015 provides the greatest extent of almond acreage due to the recent increase in cultivated almond cropland (Lobell and Field 2011). The CDL maps the location of more than 100 crop categories across the US at 30 m resolution based on spectral signatures from satellite imagery that have been classified using a manual training process (Boryan et al. 2011). Despite inherent limitations of satellite-derived proxies, the CDL provides the most current and the highest spatial resolution publicly

available data for crop occurrence. Only almond locations in California were used as occurrence data given that CDL data show that 99.97% of cultivated almond cropland in 2015 was in California. Nearly 5500 km<sup>2</sup> were classified as almond in the 2015 California CDL. An almond crop density map was generated by calculating the proportion of land classified as almond by the CDL at the 4-km resolution of the climate data.

#### **Almond phenology**

Almond phenology is a complex, multi-year cycle wherein the bud development of the subsequent year's crop coincides with the development of the current year's crop, vegetative bud development, the differentiation to reproductive buds, the development of almond flowers, and the maturation of almond nuts (Covert 2011). We simplified almond phenology and focused on four stages of reproductive development based on the availability and consistency of information from agronomic literature: endodormancy, ecodormancy, flower development, and hull split.

Endodormancy is a period during which almonds trees are dormant and flower buds are prevented from emerging to prevent cold damage. Chill begins to accumulate during

**Table 1** Phenological thresholds used in the MM and their sources

Stage	Model threshold	Published range	Source
Cold hardiness	-25 °C		Janick and Moore (1996)
Chill portions	23	23–30	Covert (2011)
GDD base temperature	4.5 °C		Rattigan and Hill (1986)
1% bloom GDD	176 (80% of 50% bloom GDD)		RAVT, University of California (1996–2006)
1% bloom frost	-15 °C (undefined damage %)	-15 to -20 °C	Janick and Moore (1996)
50% bloom GDD	220	220–370	Covert (2011)
50% bloom frost	-5.6 °C (20% damage)	-6.5 to -3 °C (up to 50% damage)	Model threshold: Snyder and Melo-Abreu (2005) Published range: Snyder and Melo-Abreu (2005), Janick and Moore (1996)
100% bloom GDD	300	300–500	Janick and Moore (1996)
100% bloom frost	-3.9 °C (20% damage)	-5.6 to -2.2 °C (up to 75% damage)	Model threshold: Snyder and Melo-Abreu (2005) Published Range: Snyder and Melo-Abreu (2005), Janick and Moore (1996)
1% hull-split GDD	2219	~1900–2550	Based on Connell et al. (2010)
1% hull-split frost	-2.8 °C (19% damage)	-2.8 - -0.5 °C (up to 50% damage)	Model threshold: Snyder and Melo-Abreu (2005) Published range: Snyder and Melo-Abreu (2005), Janick and Moore (1996)
100% hull-split GDD	2750	~2390–3100	Based on Connell et al. (2010)
100% hull-split Frost	-2.8 °C (19% damage)	-2.8 to -0.5	Model threshold: Snyder and Melo-Abreu (2005) Published range: Snyder and Melo-Abreu (2005), Janick and Moore (1996)
Harvest GDD	3032	~2760–3530	Based on Connell et al. (2010)

endodormancy (Covert 2011), and the completion of chill accumulation signals the beginning of ecodormancy, a period during which internal physiology no longer limits growth. Growth remains limited by environmental conditions during ecodormancy. The accumulation of heat (e.g., growing degree days (GDD)) during ecodormancy allows for floral buds begin to emerge. Ecodormancy ends when approximately 50% of the flowers have bloomed, and flower development continues until sufficient cumulative GDD allows the crop to reach 100% bloom. Fruit development continues during the months after bloom as GDD continue to accumulate (Covert 2011). Hull split is the final stage of fruit development, occurring when the hull separates from the shell. While growers may alter water and pest management practices at the onset of hull split, continued GDD accumulation is needed to advance the tree from the start of hull split to maturity, when 100% of the tree's hulls have split. Although harvest can occur once 100% of the hulls have split, additional GDD is often accumulated between 100% hull split and harvest, given the logistical influences on harvest timing (UCIPM 2016).

## Mechanistic model

### *Thresholds for almond development*

The MM was conceptualized as a biophysical approach to delineating the thermal niche for perennial crops. The MM considers the thermal requirements for almond reproductive development compiled from published literature, which are based on field observations and growth chamber experiments (Table 1). We applied conservative thresholds for crop suitability when a range of values was identified in the literature and used values for the nonpareil cultivar when a range of values was provided for different cultivars as it is the most widespread almond varietal grown in California. For example, while published data offer a wide range of temperatures that could result in varying levels of frost damage during flower development, we used frost temperature thresholds that result in ~20% damage (Snyder and Melo-Abreu 2005). GDD values for 1% bloom were not established in the literature and were calculated using phenology data from the Regional Almond Variety Trials (RAVT; University of California 1996–2006); cumulative GDD at 1% bloom was found to be 80% of

that at 50% bloom. Similarly, GDD for hull split and harvest were calculated using phenology data from Connell et al. (2010). When accounting for GDD in crop phenology, we used low GDD thresholds during flowering stages to best assess frost risk in early bloom, whereas we used the average of the published GDD ranges during later stages of development (i.e., nut and harvest stages). The MM focuses solely on the thermal requirements for almond development and assumes that water needs can be met throughout development. This assumption also eliminates a need to account for heat stress, which is physiologically a function of water stress due to increased evaporative demand coupled with limited water supply rather than a direct response to ambient air temperature (David Doll, personal communication).

The MM accounts both for the conditions necessary for growth, as well as the conditions that would halt the growth cycle or result in crop damage, including cold hardiness, chilling requirements, heat accumulation requirements, and frost damage during ecodormancy, flowering, and nut development (Connell et al. 2010; Janick and Moore 1996; Rattigan and Hill 1986). The MM examines a total of 13 thermal requirements throughout crop development each year. A year is considered to be unviable for almond cultivation if any of the thermal requirements are not met. Details of these thermal requirements are highlighted as follows:

#### 1. Cold hardiness

Cold hardiness temperature thresholds, defined by the annual coldest daily minimum temperature ( $T_{N_n}$ ), provide constraints on the potential geographic range of both natural and cultivated species, and have a direct link to the thermal viability of species (Parker and Abatzoglou 2016). We employed an absolute cold hardiness threshold temperature of  $-25$  °C (Janick and Moore 1996) to define suitable locations for over winter survival and assessed over winter survival on an annual basis.

#### 2. Chill accumulation

We utilized the Dynamic Model (Fishman et al. 1987) for calculating chill portions (CP) as it has been shown to be a more accurate approach for calculating chill accumulation (Luedeling and Brown 2011). CP were calculated from the equations provided in Luedeling et al. (2009b) after temporally disaggregated daily data to hourly data using a modified sine curve model (Linvill 1990). We calculate cumulative CP between November 1 and March 31, covering the common period for chill accumulation for almonds (Covert 2011).

#### 3. Growing degree days

Heat accumulation is a key driver of crop development and is commonly used to estimate crop phenology (e.g., timing of

maturation). Heat accumulation is commonly measured as GDD above a crop-specific base temperature threshold ( $T_{base}$ ). Following McMaster and Wilhelm (1997), we define GDD as:

$$GDD = \begin{cases} \frac{T_{max} + T_{min}}{2} - T_{base}, & \frac{T_{max} + T_{min}}{2} > T_{base} \\ 0, & \frac{T_{max} + T_{min}}{2} \leq T_{base} \end{cases}$$

where  $T_{base} = 4.5$  °C (Rattigan and Hill 1986).

Although previous work has suggested that growing degree hours (GDH) may provide a more accurate measure of heat accumulation than GDD, differences in accuracy vary between species and location, and the temporal disaggregation of daily data to hourly data to estimate GDH can contribute to uncertainty (Roltsch et al. 1999). We hereafter used GDD as a proxy for heat accumulation as GDD have successfully predicted development rates in several *prunus* species, including almond (Zavalloni et al. 2006), and are a more common means of computing heat accumulation when daily summarized weather data are available. Bloom timing from our model using GDD compared favorably with field study data from the RAVT, with modeled bloom occurring within  $\pm 6$  days of observed bloom timing on average, with the modeled bloom timing typically occurring earlier than observed, consistent with the conservative nature of selected GDD phenology thresholds. Similarly, nut development rates compared favorably with field study data from Connell et al. (2010), which showed a nonpareil nut maturation date 23–25 days after the onset of hull split; our model showed a mean nut maturation date of 24 days after the onset of hull split in locations with  $>1\%$  almond density. The MM uses GDD to both assess crop maturation as well as track crop phenology in order to assess other thermal requirements, namely frost damage. Specifically, the MM uses GDD accumulation beginning 1 November in order to determine whether sufficient heat accumulates—irrespective of sufficient chill accumulation—for reaching phenology stages of 1, 50, and 100% bloom, 1 and 100% hull split, and harvest. Separately, the MM uses GDD accumulation beginning at the onset of ecodormancy in order to track the timing of almond maturity, which is used to determine frost susceptibility.

#### 4. Frost damage

Crops are susceptible to frost damage throughout their reproductive cycle, with damage-causing temperature thresholds ( $T_{frost}$ ) rising throughout the progression of crop development. The MM assesses frost damage for ecodormancy through harvest and defines frost-induced development failure when a development stage has at least 1 day where  $T_{min} < T_{frost}$ . Frost damage was calculated for each phenological stage from 1% bloom to 100% hull split. GDD was used

to determine the timing of transition between each stage, and each frost damage assessment was for the period ending with the given stage. For example, frost damage for 1% bloom occurs only if  $T_{\min} < T_{\text{frost}}$  for any day between the end of endodormancy and the date on which the 1% bloom GDD threshold is met. Frost damage for individual phenostages was only calculated for regions and years where sufficient CP and GDD were met. In subsequent results, we report the fraction of years during which frost damage occurred of the years in which it was calculated.

### Modeling almond development

The MM (Online Resource 1) used the thresholds outlined in Table 1 to model the thermal requirements for almond development for each year (1 November–31 October) over the 35-year period (November 1979–October 2014). The MM provides for the opportunity for failed development at each growth stage and year, which is treated as a binary variable. However, the true impact to crop yield—or viability—varies across development stage. For example, failure to meet the frost damage threshold values used in the MM results in 20% crop damage, while failure to meet the CP and GDD accumulation threshold values may result in reduced crop quality and yield (Luedeling et al. 2009a), and deficiency in meeting cold hardiness requirements results in tree mortality (Janick and Moore 1996). The MM treats failure during any development stage as an unviable year for almond cultivation without explicitly modeling crop yield. By considering each year independently, this approach may better account for the influences of interannual climate variability on almond cultivation and can be used to assess the percent of years with

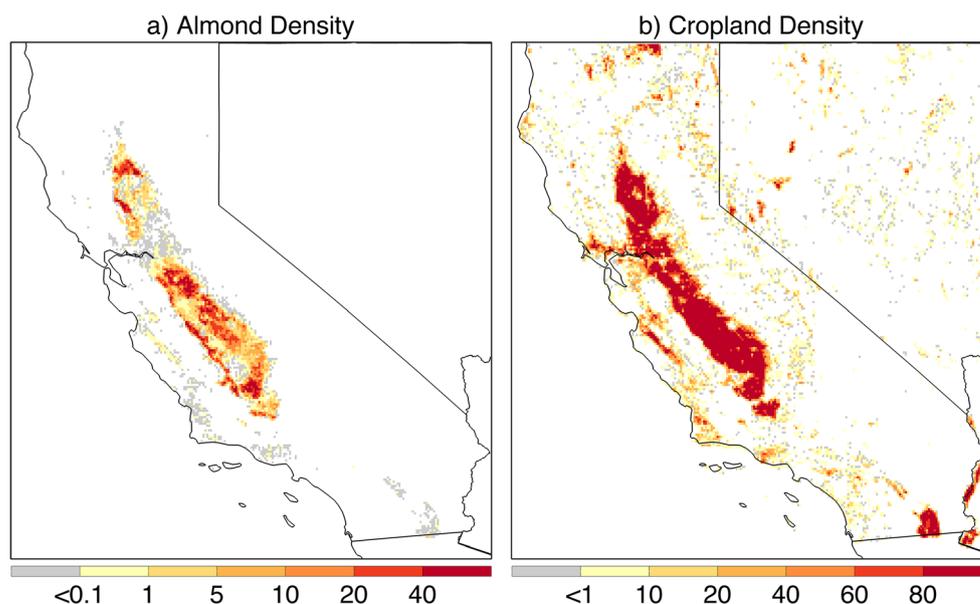
suitable conditions. Additionally, the MM highlights the specific thermal attributes that limit consistent crop development across geographic regions.

### Species distribution model

While multiple empirical methods for SDM exist, we used a maximum entropy method (MaxEnt, version 3.3.3; Phillips et al. 2006). Although Phillips et al. (2006) highlight some of the limitations of presence-only species distribution modeling and the MaxEnt method specifically, work by Aguirre-Gutiérrez (2013) showed that MaxEnt performs well relative to other empirical species distribution modeling methods.

The statistical mechanics of the MaxEnt solution are detailed in Elith et al. (2011). Briefly, MaxEnt utilizes geolocated species presence data in concert with environmental data (e.g., climate, soils) to quantify the species' environmental niche as defined by the probability of species occurrence. MaxEnt randomly selects locations from a predefined geographic domain where species presence is unknown. Referred to as background points, the spatial scope of these locations can influence MaxEnt output and performance (Elith et al. 2011). It has been recommended that background points be chosen only from locations accessible to the species of interest (Merow et al. 2013). Consequently, we limited the geographic domain of the training data to 4-km grid cells where >10% of the cell is classed as cropland by the 30-m resolution USGS Land Cover Institute's MODIS-based Global Land Cover Climatology (henceforth, cropland) (Broxton et al. 2014) (Fig. 2a). Experiments confirmed that these restrictions on background point locations improved model function.

**Fig. 2** Almond (a) and cropland (b) locations and their relative densities on a 4-km grid



**Table 2** Climatological variables used in the traditional and nontraditional SDMs

Traditional SDM variables	Nontraditional SDM variables
Average annual temperature ( $T_{\text{ann}}$ )	Average annual growing degree days (GDD)
Average annual diurnal range ( $T_{\text{diurnal}}$ )	Average annual freeze-free days (FFD)
Average annual temperature range ( $T_{\text{range}}$ )	Average frost probability during bloom (FP)
Average minimum temperature of the coldest month ( $T_{\text{N}_{\text{month}}}$ )	Average annual coldest minimum temperature ( $T_{\text{N}_n}$ )
Average maximum temperature of the warmest month ( $T_{\text{X}_{\text{month}}}$ )	Average annual warmest maximum temperature ( $T_{\text{X}_n}$ )
Average temperature of the coldest quarter ( $T_{\text{DJF}}$ )	Average minimum temperature of the coldest quarter ( $T_{\text{N}_{\text{DJF}}}$ )
Average temperature of the warmest quarter ( $T_{\text{JJA}}$ )	Average maximum temperature of the warmest quarter ( $T_{\text{X}_{\text{JJA}}}$ )

Previous SDM studies have utilized combinations of bioclimate variables—typically climate normals—as environmental data in modeling species habitat (McKenney et al. 2007). We considered two sets of climate variables (Table 2). One set, hereafter referred to as traditional, was based on variables common in SDM literature and the BioClim dataset (Hijmans et al. 2005), calculated using the 1979–2014 climatologies from METDATA. The second set of climate variables, hereafter referred to as nontraditional, was based on 1979–2014 averages of the variables used in the MM. We define frost probability (FP) as the percent of years that experienced with  $T_{\text{min}} < T_{\text{frost}}$  between the end of ecodormancy and 1% hull split, during which time frost damage concern among growers is highest. Finally, to avoid over-fitting the model and ostensibly utilize the more suitable locations for almond cultivation in our presence data, presence locations were restricted to 4 km cells with >1% almond density (Fig. 2b). While the model was trained over the cropland background, the model was projected over the full domain.

Following Phillips and Dudík (2008), we utilized MaxEnt's default settings, detailed in Merow et al. (2013), with the exception of the model features wherein we restricted MaxEnt to linear and quadratic features to produce models that are more easily interpreted and provide a better reflection of general species-environment relationships (Syfert et al. 2013). Using a random subsample of 20%, we completed 100 replicated runs for both the traditional and nontraditional models. We used the area under curve (AUC) from the receiver operating curve (ROC) as a measure of model performance. The maximum AUC is defined as:

$$\text{AUC} = 1 - \frac{\alpha}{2}$$

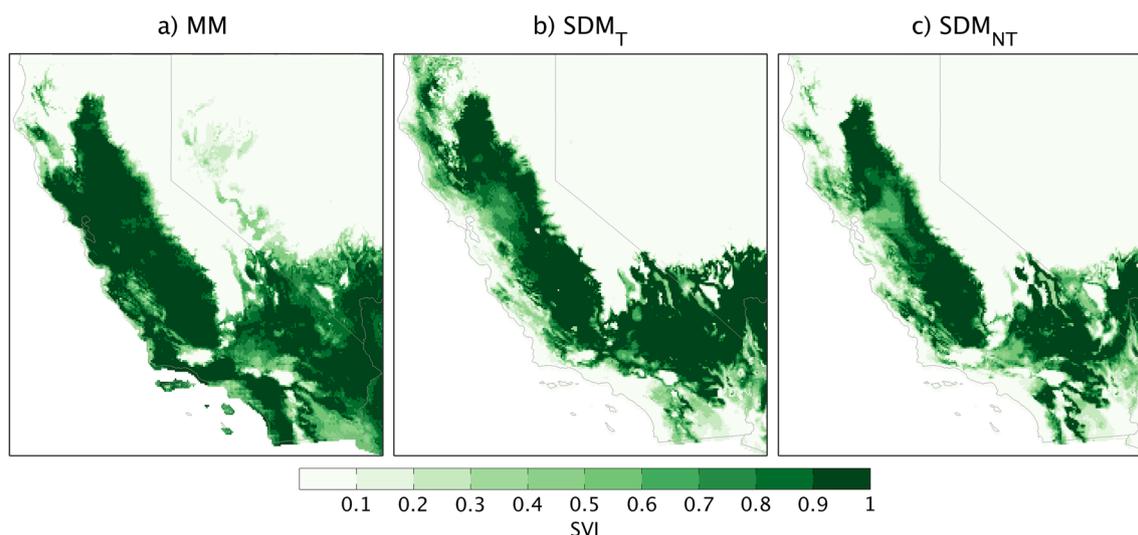
where  $\alpha$  is the fraction of pixels covered by or containing the species (Aguirre-Gutiérrez 2013; Phillips et al. 2006). Unlike many ecological applications where  $\alpha$  is unknown, here the

fraction of background pixels (cropland >10%) with almond density >1% is 0.35, making the maximum AUC for our models 0.83.

The MaxEnt training process tracks the contribution of environmental variables to model fit and provides a measure of variable importance as the percent contribution of each variable. MaxEnt's logistic output provides an estimate of the probability of occurrence of a species at a location, which we use as a measure of the thermal suitability of that location. Finally, to facilitate a more direct comparison with the results of the MM, we normalized MaxEnt output by dividing the logistic output by the median value over almond occurrence locations with >1% density and capping values at 1. We refer to this value as the species viability index (SVI) and compare this with the ratio of suitable years to total years for almond cultivation as simulated by the MM.

### Caveats

Although we consider the MM to be a more accurate representation of the potential distribution (Hijmans and Graham 2006), neither the MM nor the SDMs provide definitive predictions of where almonds can be successfully cultivated. First, the models do not differentiate between those locations where the physical and legal infrastructure for irrigation exists and where it does not. Secondly, the models do not differentiate between regions with and without competing land use, suitable soils, or topography conducive to cultivation. Thirdly, errors in parameterization in the MM could lead to poor accuracy in prediction (Buckley et al. 2010). For example, our conservative estimates of temperature and GDD thresholds may under-predict suitability in some locations, and published frost damage thresholds are primarily meant to serve as guidelines rather than definitive measures of critical temperature (Snyder and Melo-Abreu 2005). Finally, biotic interactions between the species, pests, pollinators, and climate are not explicitly considered but are likely important for almond cultivation (Polce et al. 2014).



**Fig. 3** Species viability index (SVI) for the (a) mechanistic model (MM), (b) traditional species distribution model ( $SDM_T$ ), and (c) nontraditional species distribution model ( $SDM_{NT}$ )

## Results

### Mechanistic model

The MM showed the highest SVI values over California's Central Valley, Central Coast and the deserts of southeastern California, southern Nevada, and western Arizona (Fig. 3a). Approximately one third of the domain had high suitability (SVI >0.8); whereas, ~57% of the domain had low suitability (SVI <0.5). The MM showed strong agreement for subdomain locations with >1% almond density; 99.6% of these locations had high suitability for almond cultivation, indicating that the model performs well compared with independent records of species presence.

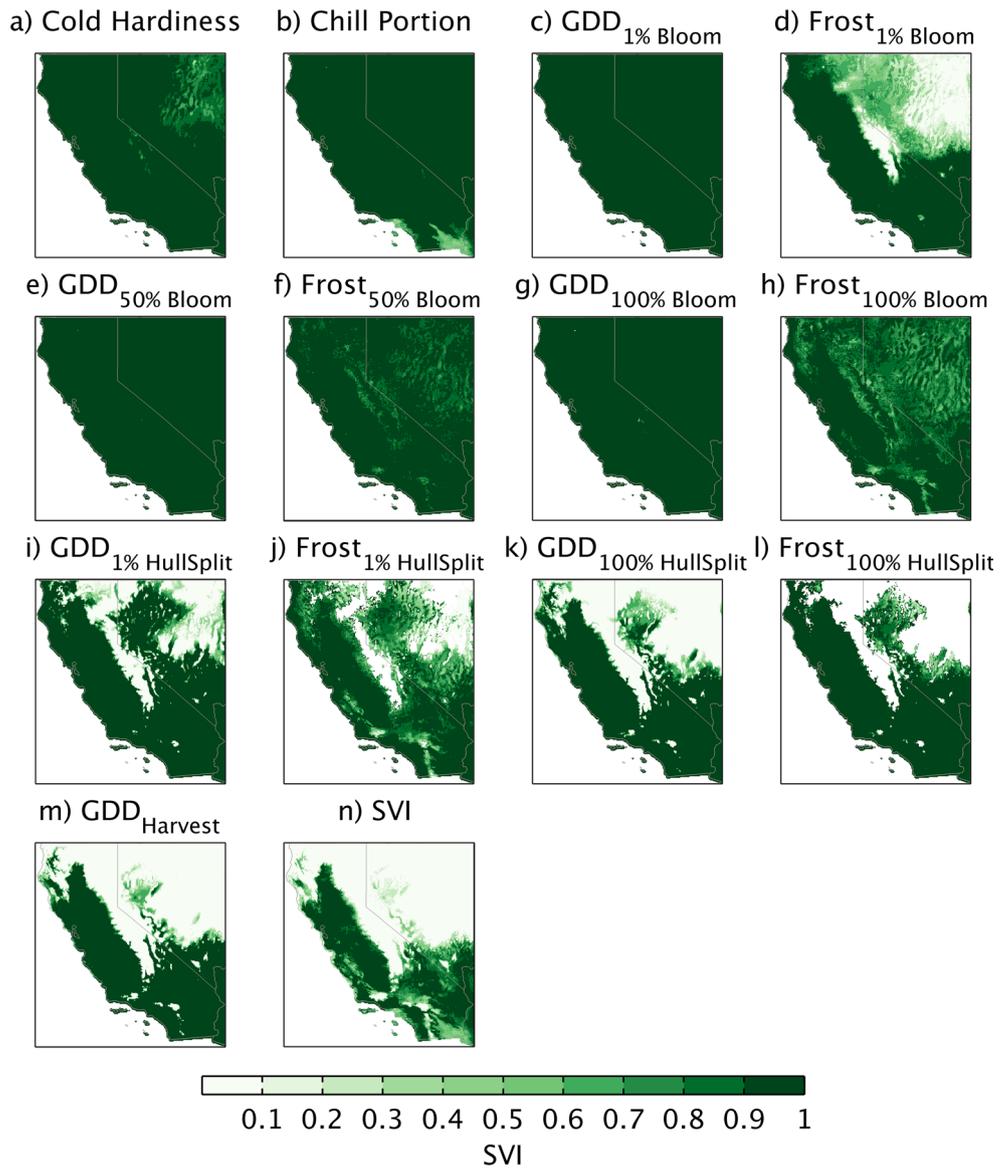
The fraction of years with suitable thermal conditions for each development stage of the MM is shown in Fig. 4. This figure elucidates the limiting thermal variables for almond cultivation across space and over the almond phenological cycle. While the majority (>96%) of the domain had sufficiently warm  $TN_n$  (suitability in >80% of years), portions of southern California failed to consistently meet CP requirements, a key limiting factor to almond cultivation. Frost damage and GDD accumulation were the primary limiting factors to suitability over higher elevation regions of California and Nevada. Although model results show diminished frost risk during later development stages, nearly one third of the domain experienced development failure due to frost between the onset of heat accumulation and 1% bloom in a majority of years. Further, ~40% of the domain lacks sufficient GDD accumulation to reach maturation and would not be viable in a majority of years even if frost were not a risk.

### Species distribution models

The traditional (nontraditional) SDM had an average AUC value of 0.744 (0.741). AUC results for both models were stable across the 100 replicated runs, with standard deviations <0.01. The AUC value of 0.74 would equal a normalized AUC of 0.89 given that the maximum AUC for our models was 0.83, and thus indicates that the models performed well over the training data. The traditional and nontraditional SDMs showed 25 and 18% of the domain to have high suitability (SVI >0.8) for almond cultivation, respectively (Fig. 3b, c). The traditional SDM showed highest SVI values over the northern and southern portions of the Central Valley, the Mojave Desert, southern Nevada, and northwestern California. By comparison, the extent of high suitability in the nontraditional SDM was reduced in the Sacramento-San Joaquin Delta to the south of the City of Sacramento, in the Mojave Desert, and in southern Nevada, and the model showed little or no suitability in northwestern California.

MaxEnt results showed that  $TN_{month}$  and  $TX_{month}$  provided the highest percent contribution to model gain for the traditional model, while FP and  $TN_{DJF}$  contributed the most to model gain for the nontraditional model (Table 3). Figure 5 shows response curves for these variables, illustrating their respective impact on almond suitability independent of other model variables. Response curves for the Traditional model showed an optimum in  $TN_{month}$  near 2 °C, with Gaussian-shaped decline for values to -4 and +7 °C. Similarly, the variable response curve for  $TX_{month}$  was Gaussian shaped, with an optimum near 37 °C. Nontraditional SVI exhibited a unimodal response to  $TN_{DJF}$  with an optimum near ~2.5 °C, while the

**Fig. 4** Mechanistic model SVIs for each development stage. SVIs for cold hardiness, chill portion, and GDD accumulation are calculated independently. SVIs for frost damage require the determination of the start and end dates of the development stage and so cannot be calculated independently. Consequently, SVIs for frost damage reflect the fraction of years in which CP and GDD requirements were met and frost did not occur



response curve for FP showed an optimum at 0 with declines at higher values of FP.

**Model comparison**

We compared the three modeling approaches by mapping the difference in SVI across the domain (Fig. 6). Average model differences were minimal (<0.1) for areas with current almond density >1%. Both SDMs generally under-predicted SVI relative to the MM west of the Central Valley, with the largest differences near the San Francisco Bay area, the Salinas Valley, the Central Coast, and in the Transverse Ranges north of the Los Angeles Basin. Conversely, the traditional SDM predicts higher SVI than the MM for the Sierra foothills, the Klamath Mountains of northwestern California, and the periphery of the Mojave Desert. The traditional SDM had higher suitability ( $SVI_{TRADITIONAL} - SVI_{MM} > 0.1$ ) for ~15% of the

domain. However, of the locations where the traditional SDM showed high suitability and the MM did not (~6% of the domain), 37% incurred frost damage between 50% bloom and 1% hull split in at least 20% of years. By comparison, the nontraditional model showed less area (<3% of the domain) with high suitability ( $SVI > 0.8$ ) where the MM did not also have high suitability.

Secondly, we assessed the mean SVI simulated by each model over croplands binned by almond density (Fig. 7). Across all almond densities, the MM showed a higher mean SVI than the SDMs. As almond density increases, differences between the MM and SDMs generally decrease, with all models showing very high mean suitability ( $SVI > 0.9$ ) for croplands with almond densities >0.5%. All models showed low average suitability over croplands where almonds are not currently cultivated. However, over croplands without current almond cultivation, high suitability ( $SVI > 0.8$ ) was found in

**Table 3** The relative contribution for each variable in the traditional and nontraditional species distribution models (SDM)

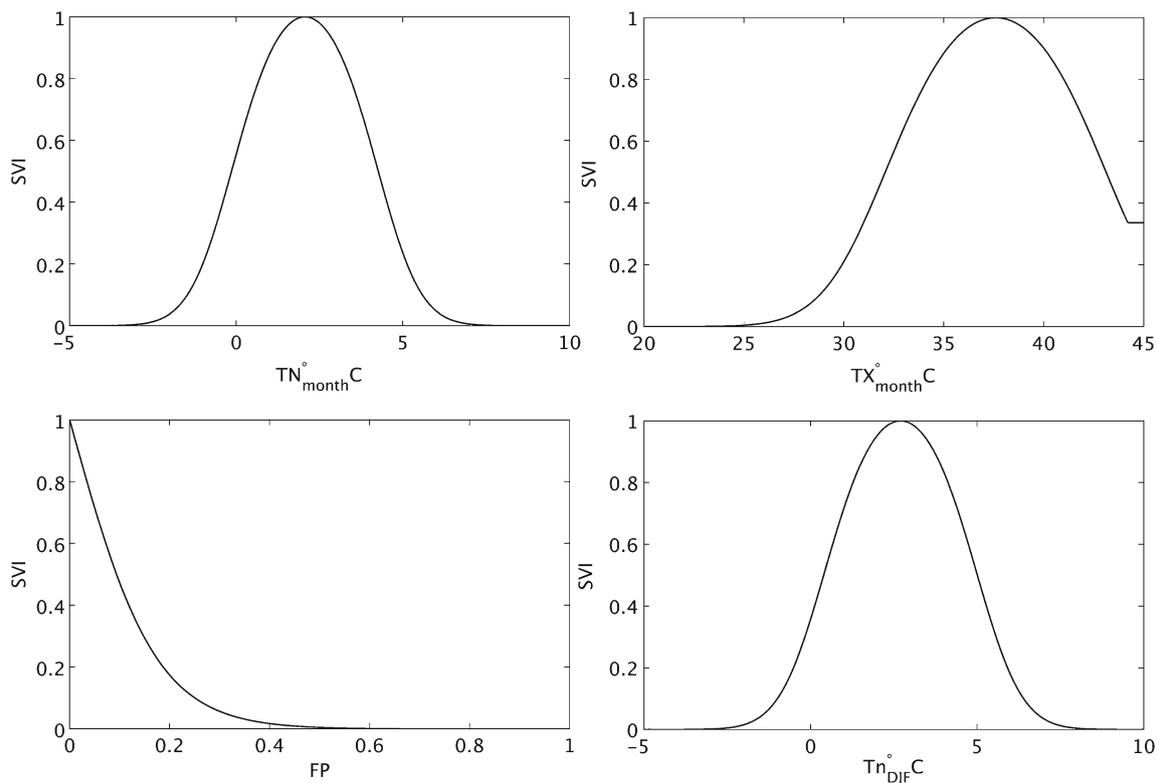
Variable	Percent contribution
Traditional SDM	
$TN_{\text{month}}$	63.3
$TX_{\text{month}}$	23.9
$T_{\text{diurnal}}$	10.6
$T_{\text{DJF}}$	1.7
$T_{\text{ann}}$	0.4
$T_{\text{range}}$	0.1
$T_{\text{JJA}}$	0.1
Nontraditional SDM	
FP	42.2
$TN_{\text{DJF}}$	30.1
$TX_x$	10.8
$TX_{\text{JJA}}$	7.3
FFD	4.8
GDD	4.7
$TN_n$	0

border, while the SDMs show high suitability areas scattered throughout the Central Valley and the Sierra Foothills east of Sacramento (Online Resource 2).

### Discussion

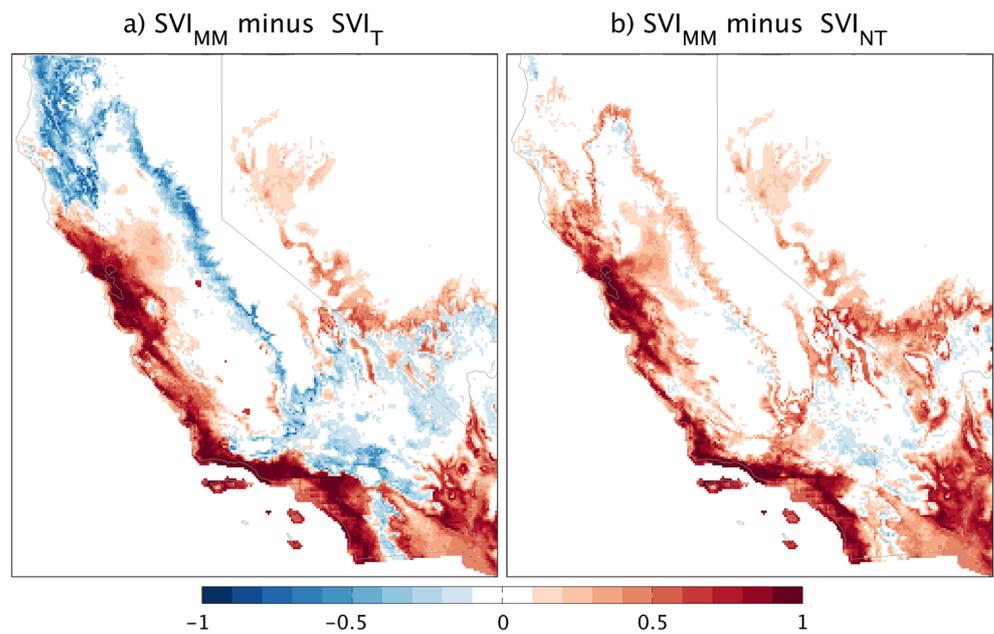
The MM showed frost during ecodormancy was a primary thermal constraint to almond cultivation over the broadest spatial extent of the domain, supporting previous research showing frost damage between bud swell and 50% bloom to be a key limiting factor in almond cultivation around the world (Miranda et al. 2005). Further, while the MM primarily highlights higher elevation regions as being most susceptible to frost, some reduction in SVI in lower elevation valleys, at scales finer than the 4-km resolution of our meteorological data, may occur as a function of localized cold air drainage (Dobrowski et al. 2009). However, it should be noted that because the MM accounts for crop failure when  $T_{\text{min}} < T_{\text{frost}}$ , some locations with moderate or low SVI may have higher suitability using less conservative thresholds for  $T_{\text{frost}}$ , if willing to accept the risk of associated yield declines with frost damage, or if using frost protection measures. Further, later blooming cultivars may mitigate frost damage risk; consequently, the development of late-blooming cultivars is a principal goal in almond breeding (Sorkheh et al. 2009).

42, 10, and 11% for the MM, traditional SDM, and nontraditional SDM, respectively. The MM shows these locations to be predominantly in the greater Sacramento and San Francisco Bay Areas, and along the California-Arizona



**Fig. 5** Environmental variable response curves for the traditional (*top*) and nontraditional (*bottom*) species distribution models

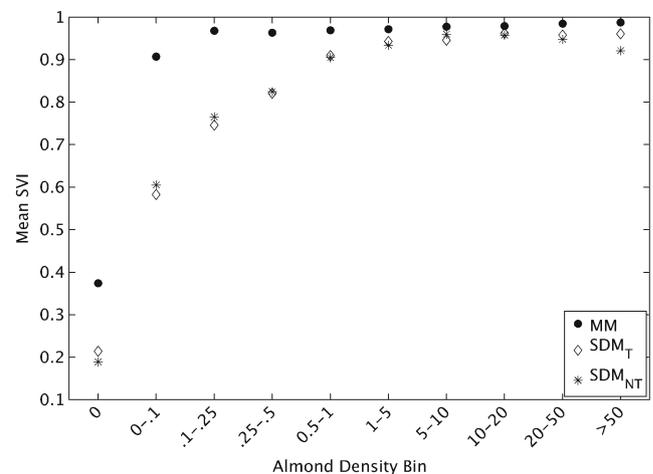
**Fig. 6** SVI differences between the mechanistic model and the (a) traditional ( $SDM_T$ ) and (b) nontraditional ( $SDM_{NT}$ ) species distribution models. *Red hues* indicate that the species distribution model under-predicted SVI relative to the mechanistic model, while *blue hues* indicate that the species distribution model over-predicted SVI relative to the mechanistic model. In order to highlight areas of more significant model disagreement, differences in SVI of  $\pm 0.1$  are masked with *white*



Like MMs, SDMs can provide insight into the potential distribution of perennial agriculture such as almonds. In a previous work in ecology, agroecology, and ecological modeling (Estes et al. 2013; Hijmans and Graham 2006), SDMs have been shown to produce broadly comparable spatial predictions with MMs (Estes et al. 2013). Our results show that the MM, though designed to produce a conservative model of almond suitability, projects a larger extent of highly suitable lands than do the SDMs, and the most significant differences between the models existed for locations where the current species is absent. These differences are likely a function of the correlative approach used by MaxEnt, which is better able to predict suitability in locations most similar to current almond locations; consequently, the SDMs appoint or restrict suitability as a function of the training data rather than true environmental limitations driven by physiology (Hijmans and Graham 2006). Further, the statistical output provided by MaxEnt (e.g., variable contribution and variable response curves) are also driven by the correlative modeling approach and may not reflect the true importance of – or physiological response to – the bioclimatic variables incorporated in the model. Though Estes et al. (2013) found SDMs to be a superior approach for modeling maize distribution compared with a MM given that SDMs provide comparable results and require less effort, as a perennial crop, almonds must survive on decadal rather than annual timescales and are thus subject to climate variability that is not captured well by SDMs. Although SDM results may be improved by using physiologically relevant variables such as in the nontraditional SDM employed in this study, MMs are not limited by the biases implicit in a correlative approach and are more capable of accounting for climate variability. Still, that the SDMs

projected a more conservative spatial extent of suitability may indicate a weakness in the strictly thermal approach of the MM.

Although attempts were made to address some aspects of climate variability through the use of nontraditional variables (e.g., frost probability) in one SDM, similar to previous findings (Dilts et al. 2015; Estes et al. 2013), the use of nontraditional variables did not significantly improve model performance as measured by AUC; however, disparities in SVI between the SDMs were evident in regions at risk for frost. The traditional SDM over-predicted suitability in locations shown by the MM to be limited by frost, indicating that the model does not capture the processes responsible for restricting species viability in these regions (Zimmerman et al. 2009). The more conservative geographic range of almond cultivation simulated by the



**Fig. 7** Mean SVI values, binned by almond density, for croplands

nontraditional model, and the relative absence of high suitability in locations shown by the MM to be limited by frost, indicate that these variables may be preferred over their traditional counterparts. Further, the use of nontraditional variables provides insight to crop suitability that is more directly related to agricultural productivity (Hatfield et al. 2014), may be of greater interest to almond growers and others in the agricultural industry (Crane et al. 2010), and may inform changes in crop distribution in response to climatic changes (Dilts et al. 2015).

Results from all three models show areas of high suitability outside of the current extent of almond cropland, suggesting potential for expanding almond plantations across the Southwest; however, the spatial patterns of potential expansion highlight a number of caveats. High suitability for almond cultivation is modeled for much of the Mojave Desert; however, our models do not account for water availability (e.g., precipitation or the physical and legal infrastructure required for irrigation), thus widespread expansion into such regions is likely to be limited as almond orchards require year-round watering (Johnson and Cody 2015). Additionally, our results do not account for nonclimatic restrictions to almond cultivation, such as current land use and socio-economic factors. Many of the high suitability locations outside of the Central Valley occur on Federal- or State-owned lands and therefore are not available for commercial expansion of almonds. Further, there may be limited opportunity for expansion on existing croplands where almonds are not currently present. For example, while existing croplands to the north of San Francisco (i.e., in Napa Valley) show high suitability for almond cultivation, these locations are currently cultivated with wine grapes and a variety of other high-value crops that are unlikely to be replaced by almond plantations. Finally, we do not account for any sociological or economic considerations that influence growers' management decisions, including grower risk tolerance and cost of cultivation versus profitability (Rougoor et al. 1998).

Though the high species viability simulated by models over the Central Valley elucidates the geographic hotspot for almond cultivation, divergence in model agreement on potential geographic expansion over existing cultivated lands may give pause to continued expansion of almond orchards in the southwestern US. While increasing almond density in areas already successfully growing the crop may provide a means to increase production, challenges may arise given the potential limitations (climatic, physical, legal, and political) in providing sufficient water for the crop's high water demand. Consequently, although our model results suggest that the geographic expansion of almond in the Southwest may be limited under current climate conditions, both mechanistic and empirical distribution models may be useful in projecting the potential suitability of almond cultivation under future climate. However, given the limitations of the correlative approach of SDMs, we suggest that using an MM is preferable

when biophysical limits are known, and that MMs are further advantageous when seeking to understand the physiological mechanisms driving distribution, and/or when assessing opportunities for translocation (Kearney and Porter 2009).

Finally, whereas our results suggest the geographic range is primarily limited by frost risk and insufficient heat accumulation under current climate, the impact of warming temperatures may impact winter chill requirements, and water limitations may become a larger issue across the southwestern US (Luedeling et al. 2009a, b; Averyt et al. 2013). Such prospective changes make it increasingly important to understand the geographic potential for cultivating high-value crops beyond their current range, and the strengths and limitations of the modeling techniques used to delineate a cultivar's fundamental niche.

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