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The seasonal climate niche predicts phenology and distribution of an ephemeral annual plant, *Mollugo verticillata*

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Summary

1.   Many short-lived species complete their life cycles during brief seasonal windows of favourable environmental conditions. Such species may persist in the face of climate warming by migration to track their seasonal climate niche in space and/or by phenological shifts to track favourable conditions in time within the year. To describe the seasonal climate niche of the short-lived annual *Mollugo verticillata* in California, we used data from herbarium specimens and historic climate records to estimate environmental conditions at the location, month and year of each collection.

2.   We used these data in a MaxEnt framework to construct a seasonal species distribution model (SDM) of the species' climate niche within the total climate space available across all seasons and locations in California. The model provides fine-scale spatial and temporal predictions of habitat suitability, predicting both where and when the species should be observed.

3.   We compared the predictions of the model to those from a conventional SDM based on mean annual climate data. Both models showed that *M. verticillata* is limited to warm environments within California. However, the seasonal SDM also predicted phenology by mapping climate suitability across the state for each month of the year. *Mollugo verticillata* is limited to warm months, and its seasonal climate niche shifts in space across California in the course of the year.

4.   We used the seasonal SDM to map the predicted future species distribution for each month of the year under three warming scenarios. The species is predicted to expand its range and occur earlier in the year in most locations; in the warmest locations, seasonal suitability is predicted to decline in the warmest months, which may result in bimodal phenology with a mid-summer gap.

5.   *Synthesis*. We developed a novel species distribution model using herbarium records and monthly weather data, which predicts not only where a short-lived species should be found but also when during the year it is predicted to occur in those areas. This model can be used to predict how climate change will affect the species distribution in space as well as seasonal phenology across the landscape.

Introduction

Predicting how species will respond to climate change requires that we identify the environmental factors that limit a species' distribution, how variation in those factors is distributed across the landscape and how those factors will change in the future. Species are already responding to climate change through a combination of geographic and phenological shifts (Inouye 2008; Wolkovich & Cleland 2014; Cavanaugh *et al*. 2015). These changes in distribution and phenology are occurring because species distributions track favourable conditions over space and time (Peterson *et al*. 2002; Lenoir & Svenning 2015). Thus, to accurately predict how species will respond to climate change, we need better knowledge of how species will respond to changes in environmental conditions in both space and time.

It is widely appreciated that climate change is altering seasonal temperatures, resulting in changes in phenology (White *et al*. 2009; Duputie *et al*. 2015). Thus, climate change is altering expression of phenological characters through changes in seasonal patterns (Cleland *et al*. 2012). Expression of phenological characters is a critical factor that determines where a species can live. Species range limits may result from the inability to express appropriate phenological characters under stressful conditions (Chuine & Beaubien 2001; Morin, Augspurger & Chuine 2007; Laube *et al*. 2015). Similarly, reductions in the duration of reproductive seasons may contribute to population decline and range shifts (Aldridge *et al*. 2011). Phenological responses to climate change are complicated because seasonal climate patterns and expression of phenological traits both vary across geographic space (Zhang, Tarpley & Sullivan 2007). Thus, climate change is not only altering seasonal rhythms but also the geographic patterns of seasonal variation.

Species can respond to changing climate by shifting their distribution in space and/or time (Fig. 1). Species that can migrate to more favourable areas and/or complete their life cycle during more favourable times of year are more likely to persist under rapid climate change (e.g.

Aitken *et al*. [2008](#); Willis *et al*. [2008](#)). Ultimately, predicting the response of species to climate change requires that we predict not only where more favourable conditions will exist but also when during the year favourable conditions will exist. The effects of climate change on phenology are expected to vary across space, as the timing of favourable periods for growth and/or reproduction shifts with latitude, elevation and other spatial gradients (Roots [1989](#); Karlsson, Jonsson & Jansson [2005](#)). Models that accurately predict the response of species' distributions to climate change will be enhanced if we can address both the geographic and temporal shift in seasonal climate niche.
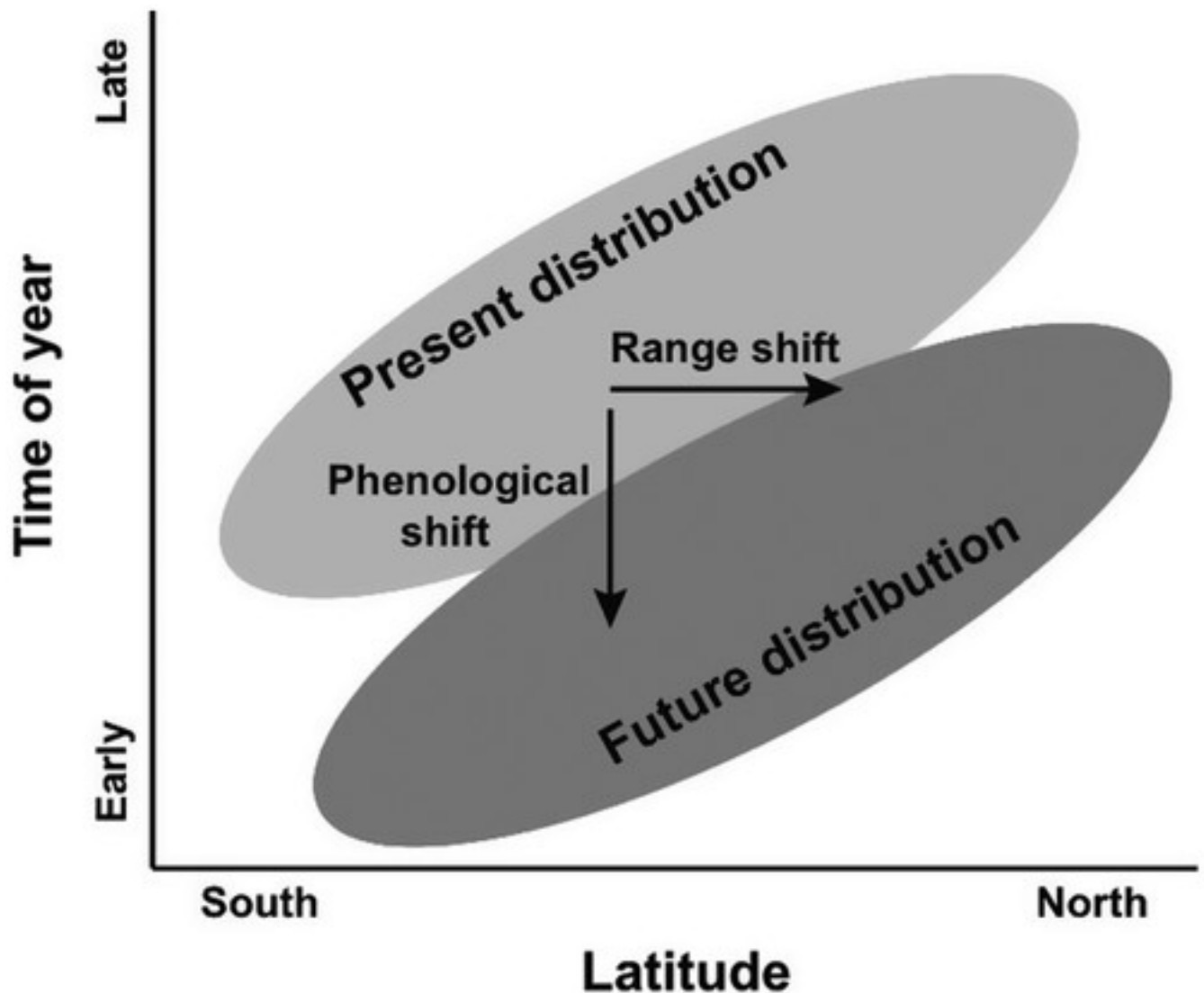

Figure 1
[Open in figure viewerPowerPoint](#)
Conceptual diagram of the relationship between spatial and temporal variation on suitability for a short-lived species, whose period of activity shifts from early in the season in warmer, southern latitudes to later in the season in cooler, northern locations. Under a warming climate, tracking of

suitable conditions can occur by phenological shifts to an earlier activity period and/or spatial shifts towards cooler locations, for activity at a given time of year.

One common method of predicting the distribution of species in space is the use of ecological niche models or species distribution models (SDM). SDMs are widely employed for projecting the response of species to climate change, as a result of their relative ease of use and flexibility (Guisan & Zimmermann 2000; Elith & Leathwick 2009). These models utilize the relationship between the geographic distribution of species and variation in environmental factors to estimate the climatic niche of species and/or predict the distribution of species across the landscape. The models have been used to predict species' distributions in terrestrial and aquatic habitats, for both long- and short-lived species (Rouget & Richardson 2003; Skov *et al*. 2008; Porfirio *et al*. 2014). They can predict the limits of species' present-day distributions and the possible influence of climate change on species' distributions in the future (Barrows *et al*. 2008; Morin & Lechowicz 2008; Telleria, Fernandez-Lopez & Fandos 2016).

Species distribution model have not generally been used to examine the temporal component of species distributions. Most species germinate, flower, hibernate, etc. at specific times of the year, and the timing of these events will vary across a species' geographic range. Modelling these events therefore requires spatial and temporal climate layers, e.g. monthly or seasonal temperature and precipitation. The need for temporally fine-grained climate data is especially apparent when modelling the distribution of species that complete their life cycle in less than a year and thus only experience climate during the times of year they are active. Such species require fine-grained climate data to define their seasonal climate niche and model their response to climate change. Conventional SDM methods relate the presence of a species to integrated environmental factors, and differences in timing of individual species occurrences are not examined in relation to intra-annual changes in the environment. For example, temperature at a site is often characterized as maximum summer temperature averaged over a 30-year period. If a species is not biologically active in summer or if variation in growth results from environmental variation that occurs during other periods, conventional SDM methods may predict the correct distribution, but will not provide any insight into the mechanisms that limit the species' distribution. This is an area in which novel methods could expand the utility of SDMs, especially for short-lived species. Species distribution modelling is frequently criticized for ignoring biological and ecological reality (Araujo & Guisan 2006; Hawkins *et al*. 2007). Expanding the temporal resolution of the environmental data could lead to more realistic SDMs, and provide greater insight into the mechanisms that limit species' distributions.

Here we quantify the seasonal ecological niche of the annual plant *Mollugo verticillata* in California, combining dated occurrence records with climate data from the location, month and year of collection to create a spatiotemporal distribution model for this short-lived species. The approach that we introduce here should be generally applicable to other short-lived species, as well as modelling the spatial and temporal occurrence of other phenological events such as flowering time of trees, insect emergence or bird migrations. Using this approach, we ask: What factors determine the seasonal climatic niche of *M. verticillata*? How do these factors influence patterns of seasonal occurrence of this species across California? What changes in the seasonal phenology and spatial distribution of *M. verticillata* are likely to occur under future climate change scenarios?

Materials and methods

Mollugo verticillata (Molluginaceae) is a self-fertilizing, short-lived, annual with a large species range from South America to southern Canada. In North America it is found in warm climates, and in California it is found in many zones within the California Floristic Province (Baldwin *et al*. 2012). It is native to tropical America and possibly exotic in temperate North America (Klinkenberg 2015). Outside of California it is found along humid riverbanks, in agricultural fields and in deserts where there are summer monsoon rains (Kearney & Peebles 1964; J. Hereford, personal observation). Within California it is found in cool climates along the coast and warmer climates inland, generally associated with water sources. It is seldom found in the California deserts where the summer monsoons are not as strong as they are to the east. The species utilizes C2 photosynthesis, a type of C3-C4 intermediate mode (Sage, Sage & Kocacinar 2012). *Mollugo verticillata* grows fast and can set seed in c. 30 days from germination (J. Hereford, unpublished data). The short life span allows populations to grow and reproduce quickly during favourable conditions, and avoid unfavourable seasons, over a large geographic scale.

We quantified the seasonal climatic niche of *M. verticillata* in California by gathering collection records from the online Consortium of California Herbaria database (all associated with voucher specimens) and from Cal Flora, with one record taken from iNaturalist (a citizen science resource). There were a total of 216 records with reliable collection dates, 28 of which do not have voucher specimens available because they are not housed in herbaria. The years of collection varied from 1893 to 2012, with 76 collections occurring before 1970. Most collections were made in May through October, with only 16 collections made in the remaining months. We excluded collections made at reservoirs as these habitats are heavily influenced by human

activities. Excluding reservoirs resulted in a final sample of 176 collection records. For each collection, we noted the date (month and year) and location of the collection. These records and the short life cycle can be used to infer both seasonal and spatial variation in occurrences (Davis *et al*. 2015). Given the short life cycle of *M. verticillata*, and its relatively non-descript vegetative appearance, we assume that all the samples were collected in flower or post-flowering. Plants begin to bud within 10 days of germination when they are small with fewer than eight leaves (J. Hereford, unpublished data). Thus, any variation in life cycle timing will have little or no impact on our results. While germination may have occurred in the month prior to the collection date, we assume that any climatic variation between the two adjacent months will have negligible effects on our model.

The climate data were obtained from the Basin Characterization Model (BCM), which provides gridded climate layers derived from PRISM climate data (PRISM Climate group 2004), together with a landscape-scale water balance model (Flint & Flint 2012). This model provides fine-scaled maps (270 m) of the climate of California (Flint *et al*. 2013). The model has been run for every month from 1896 to the present, providing monthly data for each point on the grid at each month and year. We used the data from this model to obtain estimates of monthly climate variables at each collection location during the specific month and year that the collection of *M. verticillata* was recorded.

Given the biology of *M. verticillata*, we considered the following climate variables: actual evapotranspiration (AET, mm), potential evapotranspiration (PET, mm), climatic water deficit (CWD, mm), precipitation (PPT, mm), monthly minimum temperature (TMN, °C) and monthly maximum temperature (TMX, °C). The temperature and PPT variables are the minimum or maximum temperature for the month and monthly total PPT respectively. There were strong correlations between the temperature variables so we combined these into two derived variables for each month, TMEAN (average of TMX and TMN) and TDIFF (TMX − TMN), which were less strongly correlated with each other and better suited for model estimation. Maps of average TMEAN and PPT are shown in Fig. S1, Supporting Information. Water balance variables are interrelated because CWD for a given month is the difference between PET and AET (Flint *et al*. 2013). In addition, PPT and AET were highly correlated ($r > 0\cdot7$). Based on examination of these relationships, we selected AET to represent moisture availability in our model. In addition to climate variables, we obtained estimates of soil depth (m) from the base layer used in the BCM (see Flint *et al*. 2013), and calculated a day length map for California using the RAtmosphere library in R (https://cran.r-project.org/web/packages/RAtmosphere/RAtmosphere.pdf).

From these data, we constructed two SDMs for *M. verticillata*: a 'conventional model' based on spatial occurrences and long-term average climate data and a 'seasonal model' using our spatiotemporal data of climate in the specific month and year of observed occurrences. For the conventional SDM, we used four variables: 30-year average values (1981–2010) of the annual means for TMEAN and TDIFF, the cumulative sum for AET and soil depth for each collection location. For the seasonal model, we used five variables: monthly records for TMEAN, TDIFF and AET for the location, month and year of each occurrence, day length for the location and month of each collection and soil depth at the location. Day length was included as it is a potentially important determinant of seasonal timing of growth and reproduction in *M. verticillata* (J. Hereford, personal observation).

Conventional model

We used MaxEnt Phillips, Anderson & Schapire (2006) to construct the SDM, with sample data based on the 176 collections and background data for the model sampled from the corresponding 30-year mean climate rasters for hydrologic California (an area extending slightly beyond the political boundaries, see Flint *et al.* 2013). The SDM was used to project the suitabilities onto the climate of California to generate a predicted distribution. The model was set to include 20 000 background points, allowed for duplicate presence records from the same location during the same month and year, and included linear, quadratic and product features. Hinge features were not included. We ran an additional set of models excluding duplicate records. The difference in fit of the alternate models was evaluated based on area under the receiver operating characteristic curve (AUC) values, which measures the fit of the data to the predictions of the model based on the balance between false positives and false negatives for different suitability thresholds. The maximum value of AUC is 1. As there was only a slight difference in the results of the analyses (difference in AUC values <0·006), we present the analysis with duplicate records in order to utilize all the data. This model predicts where *M. verticillata* is expected to occur, but it does not predict the time of year that it is expected to be growing at specific locations. The distinction is important because populations could be dormant during 1 month and germinating and flowering during another month at that site.

Seasonal model

To characterize the spatial and temporal niche of *M. verticillata*, we compared the values of environmental variables at the sites in the month and year where *M. verticillata* was collected to corresponding values drawn from randomly selected points distributed across all months and years as background data. This procedure allowed comparison of the climate envelope

of *M. verticillata* to the total climate space within California to reveal how much of the available spatiotemporal climate envelope is occupied by *M. verticillata*. The background distribution of climate variables was constructed by randomly sampling 14 520 observations from the entire spatial domain of the BCM model across all individual months and years from 1896 to 2010. This dataset also included day length at the month and location for each occurrence and background point, and soil depth based on the location alone. The sampling was structured so that fewer samples were taken from earlier years to reflect the historical distribution of occurrence records, as specimens have been collected at higher frequency after the 1970s (see Wolf *et al*. 2016), resulting in 14 520 background points. The background data were sampled such that climate data from two random locations were sampled for every month of all years in the period from 1896 to 1920. Eight random points were sampled in months and years from 1920 to 1950, and eight in the years from 1951 to 1980. Finally, 22 points were randomly sampled in each month of each year in the period from 1981 to 2010. This sampling method resulted in a total of 14 520 background points. The sample size results from the 1:4:4:11 ratio of observations in the data from the four periods listed above. The number of random samples was doubled to arrive at 14 520 background points. In this way, any effects of climate change were similarly distributed in the sample and background dataset. We compared the distribution of environmental variables at the site during the time of collection for each herbarium record to the background distribution. For TMEAN and day length, we performed a convex hull analysis to visualize how these variables were distributed over the available climate space.

We constructed the seasonal SDM model, also using MaxEnt, based on the climate values for each specimen in the year and month of collection, against the background sampled across all months and years. After assembling the data following the procedures described above, the model algorithm is identical to the conventional and seasonal models. The seasonal model takes advantage of the 'samples with data' feature in MaxEnt allowing the occurrence and background datasets to be constructed first and read from a text file, rather than being sampled from climate rasters (Phillips, Anderson & Schapire 2006). We then mapped the predicted suitabilities from this model across seasons within California, based on average climate layers for each month. The monthly climate layers reflect average conditions, by month, from 1981 to 2010. These mapped suitabilities illustrate where across California we would generally expect to find *M. verticillata* in flower in each month; conversely, the sequence of monthly suitability values at a given site represents a prediction of seasonal phenology for that location.

We tested how well the seasonal model predicts phenology by comparing the maximum suitability across all months to the suitability during the month that herbarium collections were

made, from the year and at the location in which the collection occurred. We used a method based on delete‑one cross‑validation to test the model's predictions against the observed data. To perform the validation, we projected the seasonal SDM onto the climate maps for each month of the year for each observation in the data. From these projections we obtained a suitability score for each month at the site of each observation (12 scores per observed record). We compared the suitability score for the month that the observation was made to the maximum suitability at that site over the year, by subtracting the suitability in the observed month from the maximum suitability. We used delete‑one cross‑validation to test whether the predictions from the seasonal model are significantly accurate. To perform the cross‑validation, we removed a single observation from the dataset and recalculated the seasonal model with the remaining 175 observations. This model predicted the suitability score for each month of the year at the location of the record that was withheld from the dataset. This procedure was repeated sequentially for each observation, resulting in a vector of 12 suitability scores for each observation. We calculated the difference between each of these scores and the maximum score of that observation, and compared this difference to the difference between the maximum score and the score during the month that the observation collected. We tested whether the 95% confidence interval of the distribution of randomly obtained differences contained the observed median difference. This significance test was performed by randomly selecting a suitability score from the 12 possible scores for each site of collection and subtracting the score from the maximum suitability at that site for the year of collection. This was done for all collections and an overall median difference was calculated by subtracting the maximum suitability from the randomly obtained suitability. The procedure was repeated 1000 times to build a distribution of randomly generated median differences. We then determined if our observed value fell within that distribution to assess if the difference was significantly different from what would be expected by chance.

The seasonal SDM can be used in conjunction with projected future climate scenarios to predict how climate change will impact the seasonal distribution of *M. verticillata*. The projections were based on three future climate scenarios: GISS‑AOM‑A1B (Smith *et al*. [2000](#)), MIROC‑RCP6.0 and MIOC‑RCP8.5 (Meehl *et al*. [2007](#)). The first two represent intermediate degrees of climate change, while the latter is more severe. The difference between RCP6.0 and GISS‑AOM‑A1B arises because RCP6.0 is based on an updated model of global socioeconomic activity. All scenarios were projected onto average months for the years 2040–2069. We projected the seasonal SDM onto 30‑year average monthly climate layers from these future climate scenarios, as was done with the contemporary months, to explore predicted changes in seasonal distributions and phenology. These scenarios were chosen because they represent a range of

possible climate change scenarios. The RCP scenarios supersede the GISS-AOM-A1B scenario, but the latter is included for comparison with RCP6.0, to determine how sensitive the results are to alternate warming scenarios (Fig. S2).

Results

Conventional model

The conventional SDM provided a good fit of the species distribution to underlying climate layers (AUC = 0·881). Based on the permutation importance values, TMEAN contributed most to suitability, and AET was an important factor as well (Table 1). The model was not heavily influenced by soil depth. The conventional SDM reveals that warmer non-desert climates of the California Coast Ranges and Central Valley are expected to be most suitable for populations of *M. verticillata* (Fig. 2, Fig. S1). The hot desert, cool summer coastline and high elevation mountain climates are predicted to be unsuitable.

Table 1. Important values of the climate variables in the conventional (a) and seasonal (b) species distribution models (SDM). The values show the contribution of each variable in the overall predictive power of the SDM

Model/factor	Permutation importance
(a) Conventional model	
Actual evapotranspiration (AET)	42·4
Mean temperature (TMEAN)	54·7
Monthly temperature range (TDIFF)	0·1
Soil depth	2·9
(b) Seasonal model	

Model/factor	Permutation importance
Actual evapotranspiration (AET)	3·0
Day length	6·7
Mean temperature (TMEAN)	78·7
Monthly temperature range (TDIFF)	1·7
Soil depth	9·9
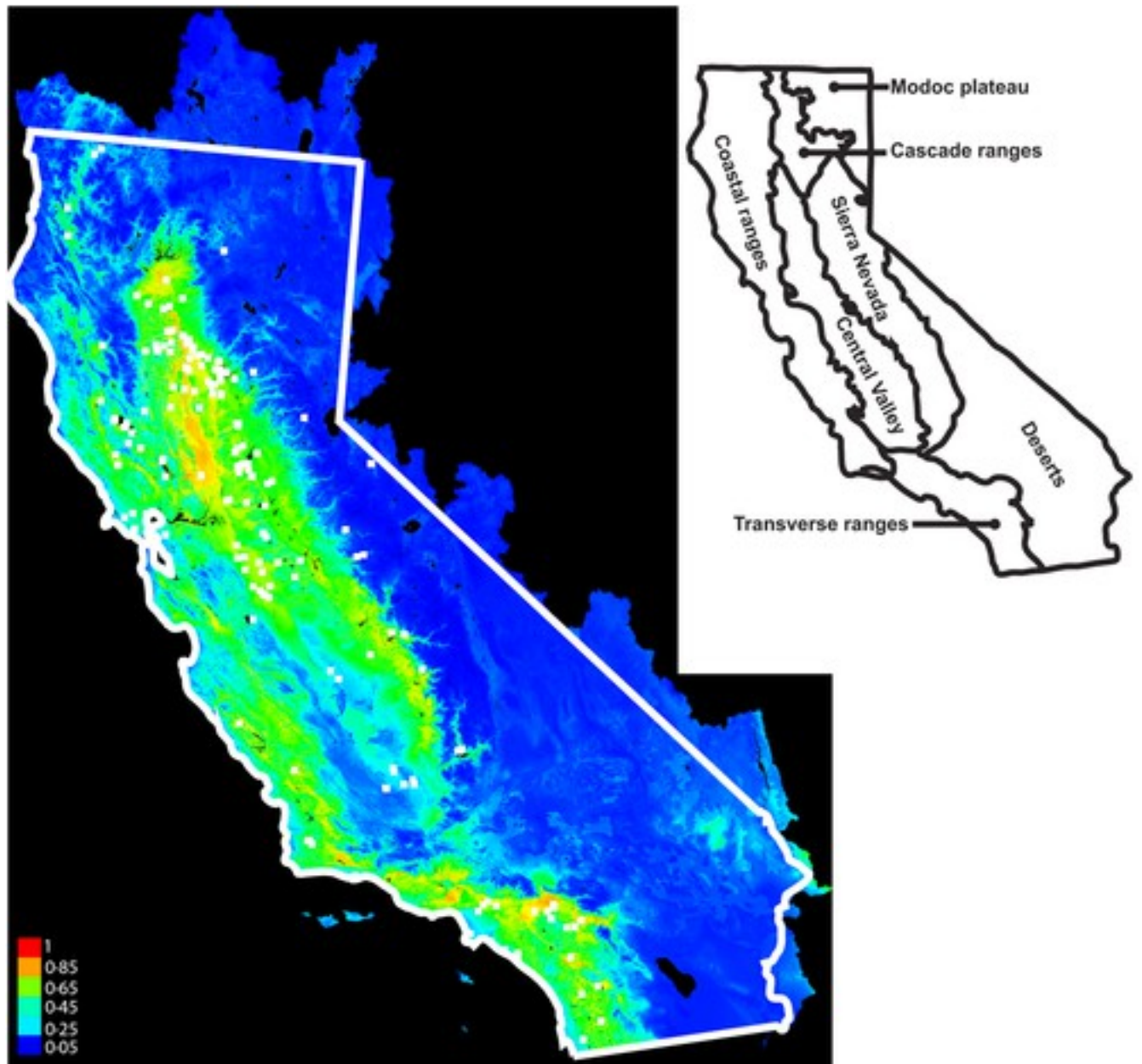
Figure 2
MaxEnt map of projected climatic suitability for *Mollugo verticillata*, under historical conditions used to parameterize the model, based on the conventional species distribution model. Square points show the locations of the actual observations. The inset shows the locations of specific regions within California. [Colour figure can be viewed at wileyonlinelibrary.com]

Seasonal model

For most seasonal variables, populations of *M. verticillata* occupy a narrower climate envelope than is available across space and time in California. The distributions suggest that *M. verticillata* requires relatively long days, warm temperatures and deeper soils (Fig. 3).

The convex hull of TMEAN and day length shows that when days are short during cooler months, populations of *M. verticillata* are restricted to relatively warm areas (Fig. 3). These distributions illustrate the data and patterns captured in the seasonal SDM.
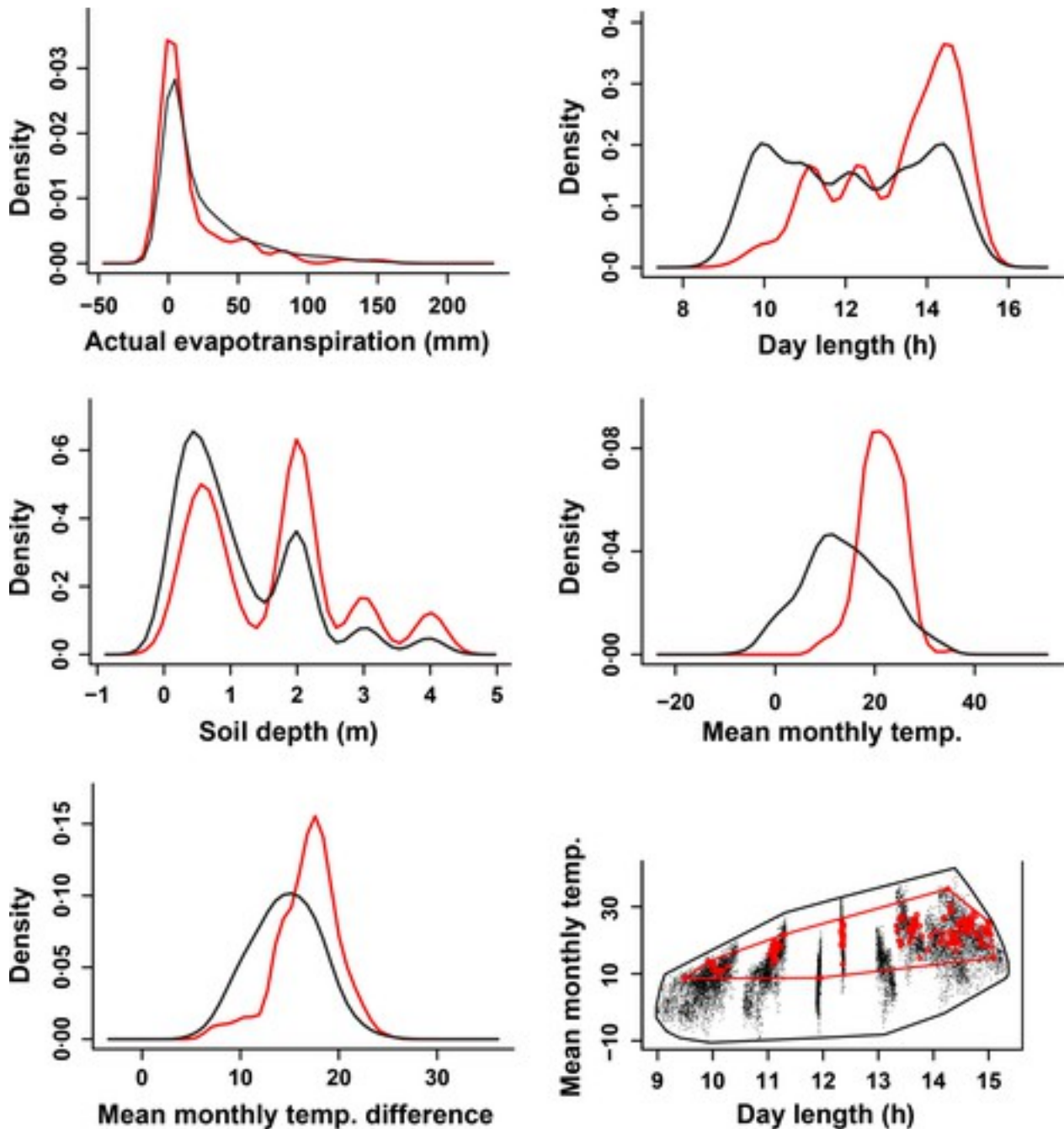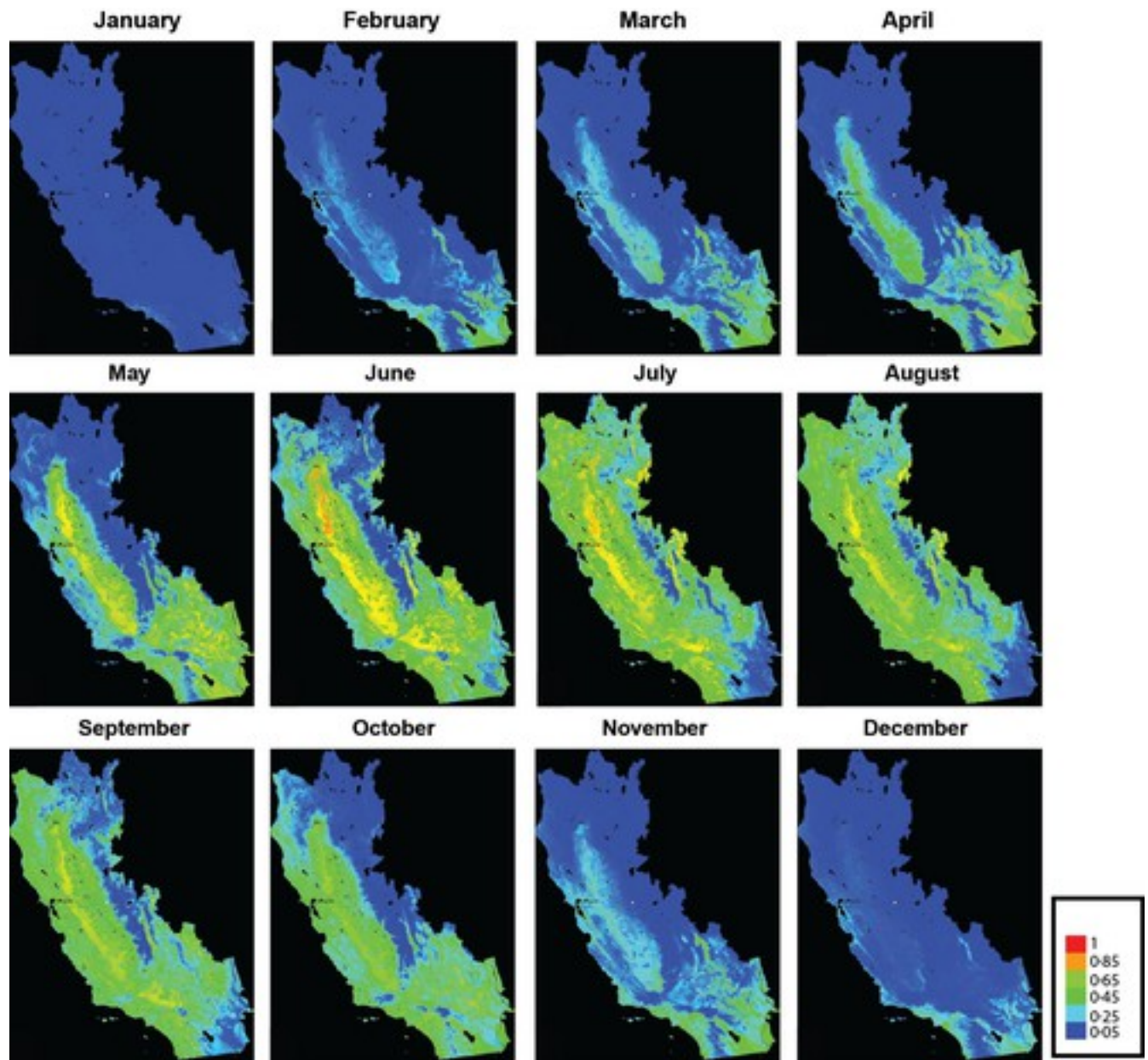

Figure 3
Density plots of environmental variables used in the seasonal species distribution model for both the sample and background data. Sample data are records of actual collection, and background is randomly selected data points from climate records generated by the BCM (see text).

Background points are in black and sample data in red. The lower right-hand corner shows a convex hull analysis of the relationship between mean monthly temperature and day length. [Colour figure can be viewed at wileyonlinelibrary.com]

The seasonal SDM captures the shifting geographic distribution of climatic suitability through the year. The AUC for this model was 0·854, only slightly lower than the conventional model. Similar to the conventional SDM, TMEAN was the major determinant of suitability (Table 1). To quantify the seasonal change in the geographic distribution of suitability through the year, this model was projected onto mean climate layers for each month. The results show dramatic seasonal changes in suitability for *M. verticillata* (Fig. 4). During cooler/shorter day length months, *M. verticillata* is not expected to grow in California, but as the climate warms, suitability becomes more widespread, with increases in the southern deserts and the Central Valley. In late spring, suitability continues to increase in the Central Valley and in the north, while it decreases dramatically during the summer in the southern deserts. During spring and autumn months, the model predicts that *M. verticillata* should be encountered in some desert and Great Basin areas. The conventional model predicts that this region is highly unsuitable (Fig. 3). However, the seasonal model also predicts suitable environments for *M. verticillata* in summer months in coastal and mountain regions – where it does occur despite low suitability predictions from the conventional model. The seasonal model also predicts that *M. verticillata* will be very common in the Central Valley, but should not be present in the Modoc Plateau and northern Sierra Nevada mountains. This pattern is the same as the pattern in the conventional SDM (Fig. 2).
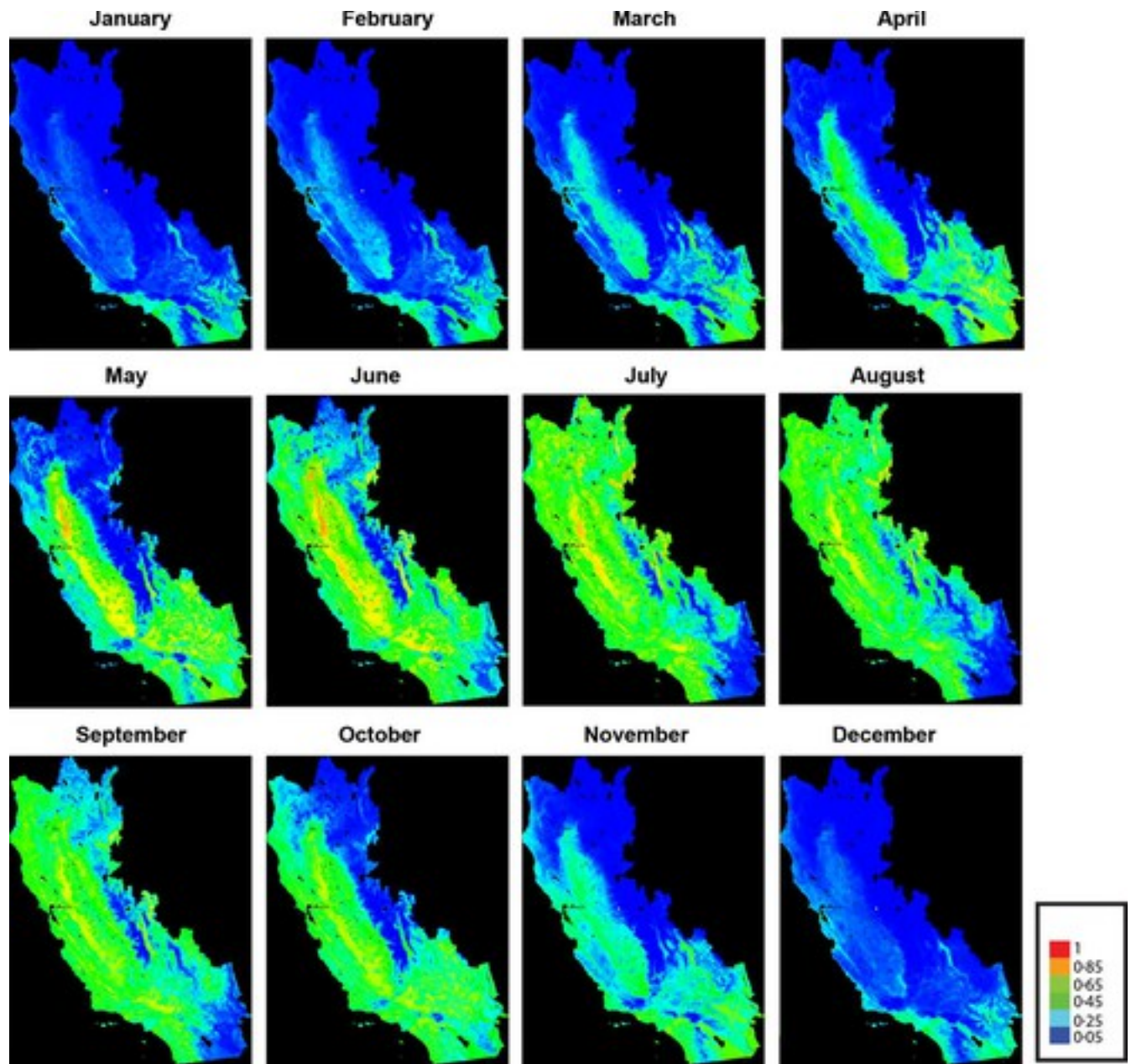
Figure 4
Projections of the seasonal model on historical climate conditions, for 30-year averages of monthly climate (1981–2010). Warmer colours indicate greater suitability. [Colour figure can be viewed at wileyonlinelibrary.com]

Our test of the phenology patterns predicted by the seasonal model for individual locations demonstrated that the model predicts phenology significantly better than would be expected by chance. The mean estimated difference between the maximum suitability at a site during the specific year of collection and the predicted suitability during the month of the actual observation was 0·08. The randomly generated 99% confidence interval of differences between maximum

and observed suitability scores was 0·14–0·31, so the observed values fall well outside this confidence interval.

We projected the seasonal model onto predicted average future monthly climates of California. These future projections predict different conditions for *M. verticillata* than in contemporary climates. The major difference is that the future layers suggest greater suitability over much of the state for longer periods during the year (Fig. 5). There are exceptions; some areas in the southern Central Valley are expected to become less hospitable in midsummer with a resurgence of suitability in fall. To quantify the change in estimated suitability in the future versus the contemporary climate, we subtracted the suitability at each recorded location in the contemporary climate from the suitability in the RCP6.0 scenario. This comparison confirms the qualitative patterns in Figs. 4 and 5. Suitability is expected to increase in the cooler months overall, but is expected to decrease at many locations in the warmer months, resulting in little overall change in suitability in summer months (Fig. 6a). The same patterns result from the GISS-AOM-A1B scenario (Fig. S2). July suitability is predicted to decline in warmer locations and increase in cooler locations, resulting in a significant negative regression of contemporary summer temperatures on the difference in suitability (Fig. 6c, b = −0·01, $P < 0·0001$). In contrast, the relationship is positive in January and cooler months, suggesting that increases in suitability are associated with warmer sites during those months (Fig. 6b, b = 0·03, $P < 0·0001$).

Figure 5
Projections of the seasonal species distribution model on future climate conditions, for 30-year monthly averages (2040–2069). Warmer colours indicate greater suitability. These projections were made under a model of the RCP6.0 scenario. [Colour figure can be viewed at wileyonlinelibrary.com]
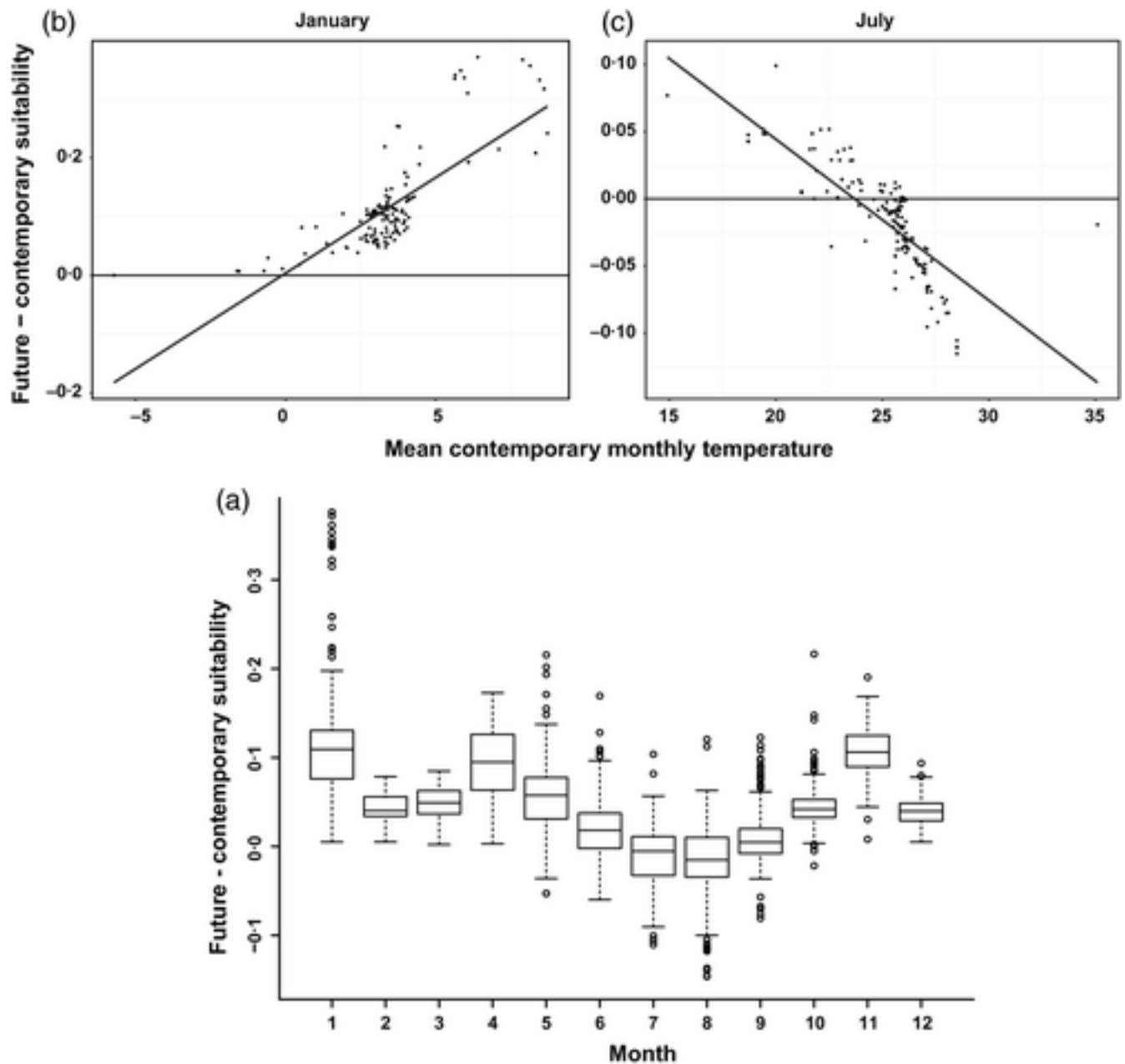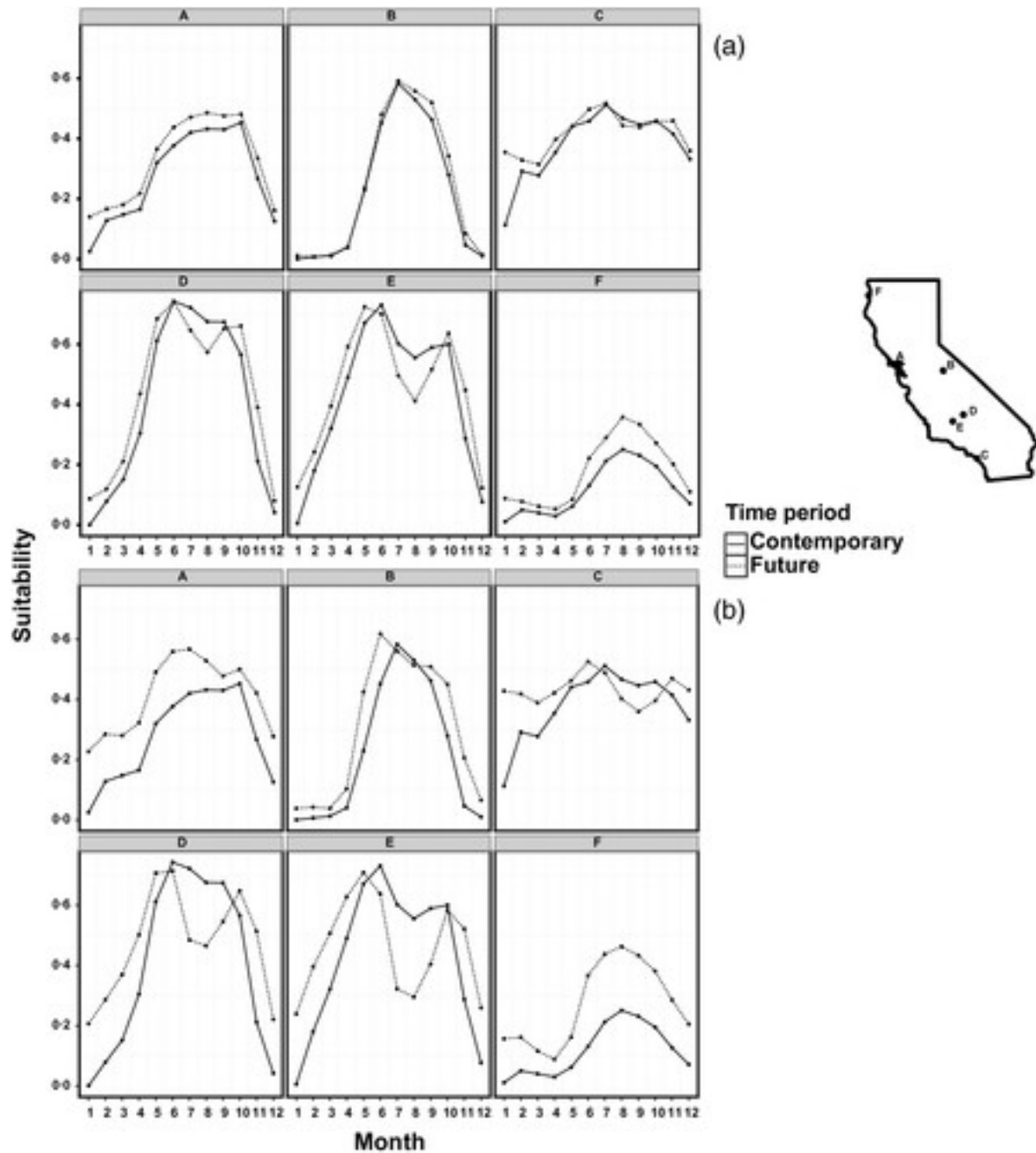
Figure 6

Box plot of the contemporary suitability subtracted from future suitability for all observations in the dataset across all months (a). Scatter plots above show the same difference in suitability for all observations in the dataset versus temperature in the contemporary climate for both January and July (b and c), the two months that were most different. The horizontal line indicates zero difference in suitability and the trend line is the regression slope of temperature in the contemporary climate on the difference in suitability. The future suitability values are calculated assuming the RCP6.0 scenario.

When comparing the change in suitability of specific sites throughout the year, it is clear that the future climates are generally predicted to be more suitable for *M. verticillata* in cooler sites in

California, and that the seasonal timing of peak suitability is often predicted to shift. This pattern is illustrated when comparing the seasonal change in suitability at six representative sites across California (Fig. 7). The sites chosen for this analysis are locations of collected samples of *M. verticillata* distributed across the region. Two northern coastal sites (A and F) show an overall increase in the magnitude and duration of high suitability in future relative to the past. In the remaining sites, the month of peak suitability is predicted to shift, at least under the more severe climate scenario (Fig. 7b). In sites D and E, a pattern of bimodal suitability is predicted, with suitability declining in summer and rebounding in fall (Fig. 7).

Figure 7

Comparisons of contemporary and predicted future suitability at six sites, where *Mollugo verticillata* has been recorded for each month. Suitability values were calculated from projections of the seasonal model on contemporary and future climates. (a) Assumes a future under the RCP6.0 scenario, and (b) assumes a future under the RCP8.5 scenario.

Discussion

For short-lived organisms, seasonal conditions during the time of the year when they are active may be critical for determining when and where a species may occur. Conventional SDM approaches based on annual averages may thus fail to capture the realized climate niche for short-lived species or for ephemeral life-history stages in longer lived species. To address this issue, we created a seasonal SDM based on monthly climate records from the location, month and year of each reported occurrence of the short-lived, annual species *M. verticillata* in California. This model allowed us to map the species' seasonal climate niche not only in space but also in time at monthly intervals over the course of a year. The model also made it possible to explore spatial and temporal shifts in the seasonal climate niche under a scenario of climate change. Thus, we could simultaneously predict potential shifts in geographic range and seasonal phenology in response to climate change.

Comparing results of the seasonal SDM with the conventional SDM provides complementary insights into the factors limiting the distribution of *M. verticillata* in California. Both SDMs suggest that *M. verticillata* requires warm temperatures. In both models, TMEAN (annual for the conventional model, and in the month of occurrence for the seasonal model) was the most important environmental predictor (Table 1). However, the two SDMs differ in other dimensions. In the conventional model, mean annual AET was nearly as important as mean annual temperature for determining climate suitability. While we do not have direct measures of vegetative cover or the effect of competing woody and herbaceous vegetation, mean annual AET provides an indirect measure of these effects. High AET environments include cooler and wetter areas near the Pacific coast (Flint *et al.* 2013). In California, *M. verticillata* is commonly found along the shores of drying lakes and streams. Species in these zones tend to be poor competitors that avoid competition (Wilson & Keddy 1986; Gaudet & Keddy 1995). This result suggests that *M. verticillata* prefers open sites that other species cannot exploit at that time of year. In contrast, in the seasonal model mean temperature in the month of occurrence was by far the strongest predictor; the species occurred in months and sites with the mean temperatures between 15 and 35 °C, but not in cooler or warmer seasonal environments. Mean AET in the observed month was much less important, probably because most collections were made at places and during periods when AET was near zero (Fig. 2). The seasonal model also revealed that *M. verticillata* is more likely to occur when days are long and potentially in sites with deeper soils, though the spatial resolution of soils data may not be sufficient to reflect *in situ* ecological requirements in this regard (Fig. 3).

The conventional and seasonal SDMs had similar explanatory ability, as indicated by similar AUC values. However, the seasonal model further allows mapping climate suitability month-by-

month to predict seasonal phenology of occurrence across California. Maps of suitability values predicted by each model reveal similar core areas of high climate suitability in the Central Valley and coastal mountains. The contrasts between these maps also reveal interesting insights. The conventional SDM predicts that *M. verticillata* should be rare at the coast and in the Sierra foothills, contrary to observations of occurrences in these areas (Fig. 2). In contrast, the seasonal SDM predicts periods of high suitability in these areas during warm summer months. In these regions, mean annual temperatures are relatively low, but a suitable climate niche still exists during a few warm months, which can be detected by the seasonal SDM to explain observed occurrences.

The conventional SDM also predicts that *M. verticillata* should be rare in the hot deserts. In contrast, the seasonal SDM predicts short periods of suitability in desert habitats in spring. It is difficult to verify the accuracy of these predictions; there are relatively few observations of *M. verticillata* in these habitats and most do not have reliable collection dates so could not be used in our modelling. However, the paucity of desert observations suggests that an additional factor may be needed for the seasonal SDM to predict the observed distribution more accurately. That factor is probably the limitation of germination by soil moisture. Although the temperature range is suitable in California desert habitats in March to May, rainfall is rare during these periods. Few California desert plants germinate during these months (Went 1948; Juhren, Went & Phillips 1956). While C2 photosynthesis provides *M. verticillata* drought tolerance (Sage, Sage & Kocacinar 2012), seeds still require an influx of moisture to germinate and survive. By the time summer monsoon rains arrive, the deserts are too hot for *M. verticillata*, although the C4 relative, *M. cerviana* is found in these regions and is able to rapidly germinate and grow on a limited influx of water in summer. Moving west towards the Arizona deserts, *M. verticillata* becomes common again as a greater proportion of the total rainfall occurs in the summer (J. Hereford, personal observation, Kearney & Peebles 1964). In California's Mediterranean-type climate, the warm seasonal temperature conditions for *M. verticillata* occur during months of little or no PPT. Consequently, in California, the species is found primarily near the drying banks of lakes, streams or reservoirs. These habitats provide plenty of moisture for seed germination without the need for immediate input of rain. The rarity of these habitats in the California desert may limit the range of *M. verticillata* in this region.

When the seasonal SDM is projected onto the mean future monthly climates, the results suggest that in the future, suitability will peak earlier in the year (or not change) across most of California, with some exceptions. This pattern is in agreement with the general observations of changing patterns of phenology with climate change, in which phenological events are occurring

earlier in many locations, but the pattern is not uniform across space (Richardson *et al*. 2013; Ault *et al*. 2015), or plant functional groups (Calinger, Queenborough & Curtis 2013). In addition, the effects of warming may not be uniform across seasons. Hart *et al*. (2014) showed that while increases in annual temperature accelerated flowering in 36 *Rhododendron* species, increased temperature in fall delayed flowering. When comparing the projections of the seasonal model for contemporary and future climates, the emerging pattern is that *M. verticillata* will grow over a larger area for longer periods of time in the future. The seasonal model suggests that *M. verticillata* will expand its range to the north in the summer. In the context of the conceptual diagram (Fig. 1), there will be a northward geographic shift accompanied by a phenological shift to earlier germination and flowering. When examining the patterns of the seasonal change in suitability, some locations show a general increase in suitability over all months, while others show a pattern of decreasing suitability in summer months (Fig. 7). In sites with hot summers, July suitability is predicted to decline, whereas in cooler sites, it is predicted to increase (Fig. 6a). Examining specific sites illustrates this pattern. Near location A, there is presently only a short period during late summer and early fall where *M. verticillata* is projected to grow. For 2 years (2013 and 2014), no plants at this location germinated before mid-July (J. Hereford, personal observation). Projection of the SDM on the future climate predicts that plants will germinate in May or June at that site in the future (Fig. 7a). The pattern of decreasing suitability in summer is most pronounced for location E, the warmest location. At site E, suitability drops in mid-summer under contemporary climates, and this drop is predicted to become more pronounced in the future. At site D, there is no predicted drop in suitability in summer in the contemporary climate, but the model predicts that in the future summer will be less hospitable. Other studies have shown similar patterns associated with midsummer drought. The increase in midsummer temperatures associated with climate change is decreasing the frequency of midsummer flowering in many species (Aldridge *et al*. 2011; Wolkovich *et al*. 2013).

While our focus has been on the benefits of the seasonal SDM approach in modelling the distribution of short-lived species, it should be noted that we are modelling one life stage of a species that spends most of its life as a seed. In this way, our modelling framework is general to examine specific life stages of a wide range of species, such as bud break, flowering or fruit set in plants, emergence time in insects and arrival times in migratory species. Potentially, this would make it possible to apply the model to predict factors that limit the distribution of long-lived species. Range limits are often caused by the inability of species to complete phenological transitions such as seed set before the environment becomes inhospitable (Chuine 2010). The seasonal SDM framework can be utilized in models of long-lived species by modelling specific

phenological stages or events. For example, if the presence of flowering or the onset of budburst is modelled for a tree species, the distribution and duration of the suitability of these life stages can predict limits of the distribution of the species. For these applications, it may be necessary to develop cumulative climate layers capturing degree day accumulation, chilling hours or similar measures up to the month or day of observation, rather than the monthly records as appropriate for the short-lived species considered here. Process-based phenological models can also model the processes that limit the growth and reproduction of species and predict causes of species range limits (Morin, Augspurger & Chuine 2007), but these models require extensive data for accurate parameterization. The seasonal SDM approach can complement those methods, taking advantage of available historical records to model seasonal and geographic distributions without detailed biological understanding of phenological mechanisms. Although similar seasonal frameworks have been employed in fisheries (e.g. Martins *et al*. 2015), and to a limited extent in conservation (Hamazaki 2002; Nielsen *et al*. 2003), this approach needs to be expanded to other fields in ecology to understand how seasonal variation interacts with geographic variation to limit species ranges.

Incorporating seasonality yielded greater insight into the factors that constrain the distribution of *M. verticillata* than conventional SDM methods alone because it shows how the seasonal change in climate is associated with seasonal changes in suitability. This relationship potentially illustrates the mechanisms that limit the species distribution in time and space. In this way, the seasonal niche is a generalized niche concept that defines the spatiotemporal envelope of the species' distribution. We were able to develop the seasonal SDM framework because we had access to monthly weather data distributed over a small geographic scale in California. The seasonal SDM showed that climate change is expected to expand the distribution of *M. verticillata* by increasing the length of the growing season in most places, and by expanding the geographic range of suitable sites within California. The seasonal SDM suggested testable mechanistic hypotheses to explain the constraints on the species' distribution. For example, it is expected that plants in lower central valley sites like the location shown in Fig. 7e, would have lower fitness in summer than in spring or fall. This seasonal framework is broadly applicable, and may be useful for managing threatened species in the face of climate change. If we can predict when and where species are most likely to grow and reproduce, we can more accurately predict constraints on their current distribution and their response to climate change.

Authors' contribution

The questions addressed in this manuscript and the analyses conducted were conceived by D.A., J.H. and J.S. All authors contributed equally to the writing of the manuscript. The seasonal MaxEnt analysis was designed by D.A. and the validation was designed by J.H. All analyses were performed by J.H.

Data accessibility

Specimen location, climate data and background climate data located on from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.0s9j3 (Hereford, Schmitt & Ackerly 2017).