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SPATIAL REGRESSION METHODS CAPTURE PREDICTION UNCERTAINTY IN SPECIES

DISTRIBUTION MODEL PROJECTIONS THROUGH TIME

By

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Thesis

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Preface

This thesis is largely based on a manuscript entitled "Spatial regression methods capture prediction uncertainty in species distribution model projections through time", which was accepted for publication in April of 2012 in the journal *Global Ecology and Biogeography* with coauthors Solomon Z. Dobrowski, Andrew O. Finley, James H. Thorne, Michael K. Schwartz. With the exception of several paragraphs in the methods section written by A.O. Finley, the writing is mine. The main section of my thesis is based on this manuscript but with an expanded introduction and discussion, along with some reorganization. An appendix has been included which gives detailed information about modeling results for individual species.

Spatial regression methods capture prediction uncertainty in species distribution model projections through time

Chairperson: Solomon Dobrowski

Abstract

Species distribution models (SDMs) relate observed locations of a species to climate, and are used for projecting the fate of a species under climate change scenarios. To be useful in a decision-making context, the uncertainty associated with these projections must be known. However, the uncertainty associated with SDM projections is largely ignored, perhaps because many current methods have been shown to produce biased estimates.

Failure to account for spatial autocorrelation (SAC) of residual error explains much of this bias. Generalized linear mixed models (GLMM) have the ability to account for SAC through the inclusion of a spatially structured random intercept, interpreted to account for the effect of missing predictors. This framework promises a more realistic representation of parameter and prediction uncertainty.

My work assesses the ability of GLMMs and a conventional SDM approach, based on generalized linear models (GLM), to produce accurate projections and estimates of prediction uncertainty. Bayesian methods were used to fit models to historical (1928-1940) observations for 99 woody plant species in California, USA, and assessed using modern "temporally independent" validation data (2000-2005). A set of climatic water balance metrics were calculated to inform the models. GLMMs provided a closer fit to historic data, had fewer significant covariates, were better able to nearly eliminate spatial autocorrelation of residual error, and had larger credible intervals for projections than GLMs. The accuracy of projections was similar between methods but the GLMMs better quantified projection uncertainty. Additionally, the GLMMs produced more conservative estimates of species range size and range size change than the GLMs. I conclude that the GLMM error structure allows for a more realistic characterization of SDM uncertainty. This is critical for conservation applications that rely on robust assessments of projection uncertainty.

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Chapter 1: Introduction

Ecological forecasting has emerged as a research priority as scientists and policy-makers seek to anticipate the response of biota to rapid changes induced by changing climate and chemical cycles, exotic species, and resource depletion . Species distribution models (SDMs) are numerical models which relate observed locations of a species to spatially explicit climate and other environmental data, allowing the distribution of suitable habitat to be projected over time and space . SDM projections are increasingly used for conservation planning and climate adaptation applications such as assisted migration and identifying locations suitable for reserves . Informed decisions require knowledge of the uncertainties inherent in these projections , yet the uncertainty of SDM projections, although acknowledged to be large, is poorly understood and rarely considered in applications . Repeated calls have been made for estimates of uncertainty to be presented with results , and their absence has led some to question the utility of SDM projections for conservation planning . In this study I assess the ability of a spatial regression SDM method to provide useful estimates of projection uncertainty.

NICHE CONCEPT

The concept of a species' niche was introduced by Grinnell as the subset of habitat with environmental conditions which allow a species to survive and reproduce. Hutchinson cast the niche in environmental rather than geographic space, and made the distinction between the *realized* and *fundamental* niche. The fundamental niche of

Hutchinson is the set of resources required for a species to persist, while the realized niche is the portion of the fundamental niche the species is constrained to by biotic interactions such as mutualism or competitive exclusion. Further, observed species distributions are shaped by many other factors including dispersal limitations, legacy effects and metapopulation dynamics, and may contain non-viable "sink" populations falling outside of their fundamental niche . Figure 1 illustrates these concepts.

In predicting the response of plant species to climate change, we are primarily concerned with identifying areas in which abiotic conditions will become unsuitable (or new areas which become suitable) for a species, so it is arguably the fundamental niche we wish to characterize . Absent experimentation, the fundamental niche is unobservable , so our ability to characterize it depends on how well its captured by species observations, a topic which has been debated . The fidelity of the observed distribution will depend on the evolving interplay of biotic interactions, dispersal, and stochastic processes over the geographic domain of the fundamental niche .

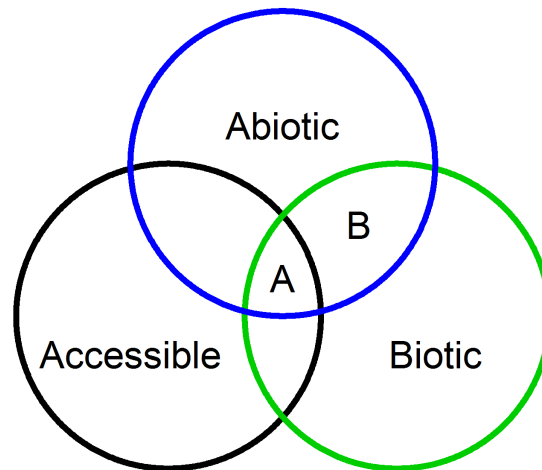


Figure 1: Illustration of the niche concept. The blue circle represents the set of abiotic conditions necessary for a hypothetical species to survive and reproduce, e.g. the fundamental niche. The area of overlap between the green and blue circles (A+B) is the subset of the fundamental niche to which the species is limited by biotic interactions, e.g. the realized niche. The black circle shows how the realized niche is further limited by accessibility, yielding the observed distribution of the species (A). Note that sink populations may be observed outside of area A. Adapted from Soberon and Nakamura (2009).

SPECIES DISTRIBUTION MODELS

As previously stated, a species distribution model is a numerical model relating environmental data to species distributions. Such models are also referred to as bioclimatic envelope models, ecological niche models, or resource selection functions, and can be used to model animal or plant distributions. SDMs can be divided into two major categories. Mechanistic SDMs are based on physiology of the species and are typically fit using detailed study of the organism in question, while correlative SDMs are

purely empirical and seek to identify the statistical relationship between observed species locations and environmental data. My work is concerned with the latter.

SDMs were first developed in the mid-1970's. Kessell used GIS technology to link abstract n-dimensional "artificial resource models" to geographic space. His early work was in Glacier National Park with a primary goal of providing decision support tools for fire ecologists and land managers. Hoffer and Strahler, working independently, developed similar techniques around the same time. SDM techniques and applications grew slowly through the 1980's, but their use expanded in the 1990's and has grown exponentially in the 2000's. Over 850 SDM papers were published between 2005 and 2010, compared to only 79 between 1999 and 2004 . The range of available SDM methodology has expanded coincident with their rise in popularity. Early methods were relatively simple, such as generalized linear models (GLMs) and bounding-box type methods. At the other extreme are more recently developed machine learning methods which use sophisticated algorithms to automatically fit a flexible response functions to a set of covariates.

In addition to their use in conservation planning, SDM applications include estimating individual species' ranges , predicting range expansion of invasive species , providing insight into the ecology and biology of organisms , and predicting changes in the size and spatial arrangement of species' available habitat under scenarios of environmental change .

SDM ASSUMPTIONS

Several important assumptions must be made in the application of SDMs. Statistically, most methods assume independent errors and that all relevant predictors are included in their correct functional form . These assumptions can be relaxed somewhat with methods which allow for spatial autocorrelation of errors .

Biologically, species are assumed to be at equilibrium with their environment and occurring throughout the environmental space defined by their fundamental niche . As previously noted, the latter assumption is questionable because of the complicated interplay between space and environment . When SDMs are used for extrapolation into new spatiotemporal domains, further assumptions apply. Essentially, one must assume that all limiting factors (biotic and abiotic) will be the same under the extrapolated conditions, and that phenotypic and evolutionary changes are negligible .

The degree to which limiting factors remain constant under changing conditions is subject to debate . Controlled experiments have shown strong shifts in species interactions under manipulated conditions for insects and grassland species , and have provided evidence that escape from natural enemies may be important in exotic species invasions . Natural experiments involving invasive species have provided evidence of rapid evolution within their invaded range , and have documented invasive species establishing populations in *biomes* not represented in their native range .

SDM PREDICTORS

Choice of predictors is critical given that SDM methods typically assume all relevant predictors to be included. Ideally, an understanding of a species' physiology

and ecology will suggest a concise set of predictors known to limit its distribution, but in most SDM applications this is not the case. Rather, an assortment of available predictors are tested and a model is built interactively or using an automated model selection procedure. This can result in a set of predictors which may precisely describe the observed distribution, but lack predictive power in new spatiotemporal domains . For this reason, it has been recommended to use a reduced set of biologically meaningful predictors . Climatic water balance metrics are attractive in this regard because they provide a summary of concurrent energy and moisture availability (illustrated in Figure 2), reducing a large number of daily or monthly climate observations to a handful of annual summaries with a clear biological interpretation.

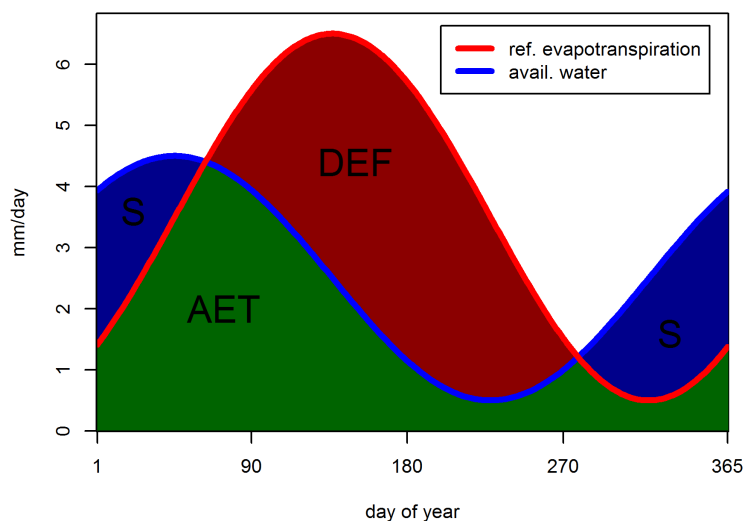


Figure 2: Illustration of climatic water balance metrics. Reference evapotranspiration (ET_0), shown as a red line, is a measure of the energy available at a site and is calculated using temperature, net solar radiation, humidity and wind. This is interpreted as how much evapotranspiration (e.g. growth) a reference crop (2" grass) would be capable of given unlimited moisture. The blue line shows available moisture, which integrates precipitation, soil moisture and snowmelt. Moisture availability constrains ET_0 to give actual evapotranspiration (AET; green). When moisture availability exceeds ET_0 it is considered surplus (S; blue), and when ET_0 exceeds moisture availability it is considered climatic water deficit (DEF; red).

UNCERTAINTY

Sources of uncertainty in SDM projections include species observations and covariates used to fit the SDM, choice of SDM method, specification of SDM model, parameter estimation within the chosen SDM, and covariates used in the projection of the SDM. Buisson *et al.* assessed the relative contribution of these sources and found that choice of SDM method introduced the greatest amount of uncertainty in range change projections of fish species. Other authors have noted similarly large variability

between methods in SDM projections . This has led to the use of “ensemble” methods, in which numerous models are fit using a range of methods and input data . Outcomes are averaged and those consistent between fitted models are deemed more reliable than those for which the models do not agree. A lack of consensus within an ensemble qualitatively suggests uncertainty, but the reasons that methods disagree are poorly understood .

Existing work

Several notable attempts have been made to quantify SDM prediction uncertainty. Buckland and Elston demonstrate a non-parametric bootstrapping approach in which numerous models are fit to permutations of the original data, resulting in maps indicating the proportion of iterations the species was predicted to be present. Hartley et al. present a Bayesian model averaging approach to estimating uncertainty. They fit a set of plausible models containing different covariates and calculate uncertainty by combining between-model and within-model variability. While these approaches provide a quantitative representation of uncertainty, they don't consider the bias induced by spatial autocorrelation of residual error (SAC) on model selection (e.g. Lennon, 2000) and are unable to account for uncertainty due to important covariates not considered. Other authors have presented maps of uncertainty using Bayesian spatial regression approaches , but I am unaware of previous attempts to validate estimates of projection uncertainty.

SPATIAL AUTOCORRELATION

Issues related to spatial autocorrelation (SAC) may partially explain inconsistency between methods in SDM projections. Positive SAC arises because observations close in geographic space are generally more similar than those further apart. When a model is unable to fully explain the spatial pattern of a species' distribution, residual errors will exhibit this property, violating a key assumption of the statistical methods underlying most SDM approaches. SAC of residual error has been shown to be very common in SDM applications and can easily be introduced if important covariates are missing or if a species exhibits spatial aggregation due to biotic factors. Most SDM methods are incapable of accounting for this type of error, since they consider only sampling variability (as in a coin toss) and its resultant effect on the precision of parameter estimates. Although SAC has been shown not to bias parameter estimates (at least for linear models e.g. , it has been shown to decrease their precision and lead to downwardly biased variance estimates and inflating tests of significance. The latter issue is especially problematic when such tests are used within automated model selection procedures, since this can lead to the inclusion of spurious covariates and a fit tailored to the training data . Nonparametric methods such as generalized additive models, maximum entropy or regression trees are not immune to this issue and may in fact be more vulnerable due to their ability to fit complex response functions. This overfitting of models may help explain the large degree of disagreement between SDM methods and has been hypothesized to reduce their transferability through space and time . Numerous methods have been proposed to correct for the adverse effects of spatial autocorrelation on SDMs . Generally, the focus of this research has been on methods to improve parameter estimates and tests of significance , and less on

assessing the transferability of these models and accurately estimating projection uncertainty.

METHODS TO ACCOUNT FOR SAC

Numerous methods have been developed to account for SAC when modeling binary response data. Autologistic methods include a weighted average of adjacent observations, referred to as an autocovariate, as an additional predictor. The weighing scheme is typically chosen arbitrarily. Spatial eigenvector mapping (SVM) methods construct a set of orthogonal "predictors" describing spatial patterns in the data, which are then selectively included as additional predictors. Generalized estimating equations (GEE) split the data into spatial clusters and model correlation within these clusters, which are considered spatially independent of each other. With the exception of autologistic regression, these methods have been shown to provide better controlled tests of parameter significance, but are poorly suited to prediction and fail to provide reasonable estimates of prediction uncertainty (Dormann et al. 2007).

GENERALIZED LINEAR MIXED MODELS

Generalized linear models (GLM) adapt linear regression methods to allow for different types of response data, such as the presence/absence data typically used in SDM applications. Generalized linear mixed models (GLMMs) extend GLMs to include random effects capable of accounting for additional sources of uncertainty. To account for SAC, this random effect can be specified as a spatially structured random intercept,

or spatial process term, interpreted as the effects of unobserved processes with spatial structure . The spatially-structured random intercept has intuitive appeal in that it is able to represent the greater confidence we feel in finding a species when closer to a known presence location. The variance-covariance parameters of the random intercept control the magnitude, range, and smoothness of its dependence in space, and are estimated during the model-fitting process. This avoids subjective modeling choices regarding the zone of spatial influence and allows its effect to be integrated into both parameter estimates and predictions. Spatial process GLMMs can be fit through the use of Bayesian hierarchical methods and Markov chain Monte Carlo (MCMC) techniques . Although computationally intensive, this methodology provides full access to the distributions of the model's parameters given the data, i.e., posterior distributions, and the posterior predictive distributions of the response variable at unobserved locations and/or times. Latimer et al. and Finley *et al.* have explored some of the utility of spatial process GLMMs (hereafter referred to as GLMMs) to model species distributions, but their projections have yet to be validated against independent data. If validation shows that GLMMs are able to account for the uncertainties in modeling species distributions through time, realistic mapping of uncertainty and statistical inference on predicted range changes should be possible.

OBJECTIVES

Estimates of projection uncertainty are essential if SDMs are to be useful for conservation planning, and GLMMs have the potential to accurately provide this information. My primary objective is to assess the ability of GLM and GLMM models to

characterize SDM projection uncertainty through time. To this goal I fit a both models to historical observations of 99 woody plant species from California, USA, and use contemporary data to assess the accuracy of projections and uncertainty estimates of these models.

Chapter 2: Case Study

METHODS

Vegetation data

To train the models, I used presence and absence data for 99 species (table 1) from 13,746 vegetation plots collected as part of the USDA Forest Service's Vegetation Type Map Project (VTM) between 1928 and 1940 within the state of California, USA. Plot size was 800 m² in forests and 400 m² in other vegetation types. VTM plots were sampled in the mountainous regions of California (Fig. 3). For model validation data, I compiled a collection of 33,596 contemporary (2000-2005) vegetation plots with presence and absence data from a variety of sources (further detail provided in Dobrowski et al.). Plot size in the contemporary validation data ranged from 400m² to 800m² in size. Vegetation plots were aggregated to 10km by 10km grid cells and the count of presence observations within each cell, relative to the total number of observations in that cell, was considered the response. The spatial aggregation was performed to ease computational demands. Because not all species were sampled (e.g. looked for) at each vegetation plot, the total number of grid cells sampled varied by species. This yielded grid cell counts for species that ranged from 825 to 1302 for the historic data and 1334 to 1929 for the modern data. Historical prevalence values ranged from 2.4% to 39.6% at the grid cell level, while modern prevalence values ranged from 0.45% to 43.7%. The historic and modern samples overlapped in 320-715 grid cells depending on species.

Table 1: Plant species modeled

Species	Common name	Life-form	Endemicity	Physiognomy
<i>Abies concolor</i>	white fir	Tree	not endemic	evergreen
<i>Abies magnifica</i>	California red fir	Tree	not endemic	evergreen
<i>Acer macrophyllum</i>	bigleaf maple	Tree	not endemic	deciduous
<i>Adenostoma fasciculatum</i>	chamise	Shrub	not endemic	evergreen
<i>Aesculus californica</i>	California buckeye	Tree	endemic	deciduous
<i>Amelanchier alnifolia</i>	Saskatoon serviceberry	Shrub	not endemic	deciduous
<i>Artemisia californica</i>	coastal sagebrush	Shrub	not endemic	deciduous
<i>Arctostaphylos canescens</i>	hoary manzanita	Shrub	not endemic	evergreen
<i>Arctostaphylos glandulosa</i>	Eastwood's manzanita	Shrub	endemic	evergreen
<i>Arctostaphylos glauca</i>	bigberry manzanita	Shrub	not endemic	evergreen
<i>Arctostaphylos manzanita</i>	whiteleaf manzanita	Shrub	endemic	evergreen
<i>Arbutus menziesii</i>	Pacific madrone	Tree	not endemic	evergreen
<i>Arctostaphylos mewukka</i>	Indian manzanita	Shrub	endemic	evergreen
<i>Arctostaphylos nevadensis</i>	pinemat manzanita	Shrub	not endemic	evergreen
<i>Artemisia tridentata</i>	big sagebrush	Shrub	not endemic	evergreen
<i>Arctostaphylos viscida</i>	sticky whiteleaf manzanita	Shrub	not endemic	evergreen
<i>Baccharis pilularis</i>	coyotebrush	Shrub	not endemic	evergreen
<i>Calocedrus decurrens</i>	incense cedar	Tree	not endemic	evergreen
<i>Ceanothus cordulatus</i>	whitethorn ceanothus	Shrub	not endemic	evergreen
<i>Ceanothus crassifolius</i>	hoaryleaf ceanothus	Shrub	not endemic	evergreen
<i>Ceanothus cuneatus</i>	buckbrush	Shrub	not endemic	evergreen
<i>Ceanothus greggii</i>	desert ceanothus	Shrub	not endemic	evergreen
<i>Ceanothus integerrimus</i>	deerbrush	Shrub	not endemic	evergreen
<i>Ceanothus leucodermis</i>	chaparral whitethorn curl-leaf mountain	Shrub	endemic	evergreen
<i>Cercocarpus ledifolius</i>	mahogany	Shrub	not endemic	deciduous
<i>Ceanothus oliganthus</i>	hairy ceanothus	Shrub	endemic	evergreen
<i>Ceanothus prostratus</i>	squawcarpet	Shrub	not endemic	evergreen
<i>Ceanothus tomentosus</i>	woollyleaf ceanothus	Shrub	not endemic	evergreen
<i>Ceanothus velutinus</i>	snowbrush ceanothus	Shrub	not endemic	evergreen
<i>Chamaebatia foliolosa</i>	mountain misery	Shrub	endemic	evergreen
<i>Chrysolepis sempervirens</i>	bush chinquapin	Shrub	not endemic	evergreen
<i>Chrysothamnus viscidiflorus</i>	yellow rabbitbrush	Shrub	not endemic	evergreen
<i>Corylus cornuta</i>	beaked hazelnut	Shrub	not endemic	deciduous
<i>Cornus nuttallii</i>	Pacific dogwood	Shrub	not endemic	deciduous
<i>Dendromecon rigida</i>	tree poppy	Shrub	not endemic	evergreen
<i>Ephedra californica</i>	California jointfir	Shrub	not endemic	evergreen
<i>Ericameria arborescens</i>	goldenfleece	Shrub	endemic	unknown
<i>Eriodictyon californicum</i>	California yerba santa	Shrub	not endemic	evergreen

<i>Eriophyllum confertiflorum</i>	golden-yarrow	Shrub	not endemic	evergreen
<i>Eriodictyon crassifolium</i>	thickleaf yerba santa	Shrub	endemic	evergreen
<i>Eriogonum fasciculatum</i>	Eastern Mojave buckwheat	Shrub	not endemic	evergreen
<i>Ericameria linearifolia</i>	narrowleaf goldenbush	Shrub	not endemic	deciduous
<i>Eriogonum umbellatum</i>	sulphur-flower buckwheat	Shrub	not endemic	evergreen
<i>Fremontodendron californicum</i>	California flannelbush	Shrub	not endemic	evergreen
<i>Fraxinus dipetala</i>	California ash	Tree	endemic	deciduous
<i>Garrya fremontii</i>	bearbrush	Shrub	not endemic	evergreen
<i>Hazardia squarrosa</i>	sawtooth goldenbush	Shrub	not endemic	evergreen
<i>Heteromeles arbutifolia</i>	toyon	Shrub	endemic	evergreen
<i>Hesperoyucca whipplei</i>	chaparral yucca	Shrub	not endemic	evergreen
<i>Holodiscus discolor</i>	oceanspray	Shrub	not endemic	deciduous
<i>Juniperus californica</i>	California juniper	Tree	endemic	evergreen
<i>Juniperus occidentalis</i>	western juniper	Tree	not endemic	evergreen
<i>Lepechinia calycina</i>	woodbalm	Shrub	endemic	deciduous
<i>Lithocarpus densiflorus</i>	tanoak	Shrub	not endemic	evergreen
<i>Lotus scoparius</i>	common deerweed	Shrub	not endemic	deciduous
<i>Lonicera subspicata</i>	southern honeysuckle	Shrub	endemic	deciduous
<i>Malosma laurina</i>	laurel sumac	Shrub	endemic	evergreen
<i>Pinus albicaulis</i>	whitebark pine	Tree	not endemic	evergreen
<i>Pinus attenuata</i>	knobcone pine	Tree	not endemic	evergreen
<i>Pinus contorta</i>	lodgepole pine	Tree	not endemic	evergreen
<i>Pinus coulteri</i>	Coulter pine	Tree	not endemic	evergreen
<i>Pinus jeffreyi</i>	Jeffrey pine	Tree	not endemic	evergreen
<i>Pinus lambertiana</i>	sugar pine	Tree	not endemic	evergreen
<i>Pinus monticola</i>	western white pine	Tree	not endemic	evergreen
<i>Pickeringia montana</i>	Montana chaparral pea	Shrub	endemic	evergreen
<i>Pinus ponderosa</i>	ponderosa pine	Tree	not endemic	evergreen
<i>Pinus sabiniana</i>	California foothill pine	Tree	endemic	evergreen
<i>Prunus emarginata</i>	bitter cherry	Shrub	not endemic	deciduous
<i>Prunus ilicifolia</i>	hollyleaf cherry	Shrub	not endemic	deciduous
<i>Pseudotsuga menziesii</i>	Douglas-fir	Tree	not endemic	evergreen
<i>Purshia tridentata</i>	antelope bitterbrush	Shrub	not endemic	deciduous
<i>Quercus agrifolia</i>	California live oak	Tree	not endemic	evergreen
<i>Quercus berberidifolia</i>	scrub oak	Shrub	endemic	evergreen
<i>Quercus chrysolepis</i>	canyon live oak	Tree	not endemic	evergreen
<i>Quercus douglasii</i>	blue oak	Tree	endemic	deciduous
<i>Quercus durata</i>	leather oak	Shrub	endemic	evergreen
<i>Quercus garryana</i>	Oregon white oak	Tree	not endemic	deciduous
<i>Quercus kelloggii</i>	California black oak	Tree	not endemic	deciduous
<i>Quercus lobata</i>	California white oak	Tree	endemic	deciduous
<i>Quercus vacciniifolia</i>	huckleberry oak	Shrub	endemic	evergreen
<i>Quercus wislizeni</i>	interior live oak	Shrub	endemic	evergreen
<i>Rhamnus crocea</i>	redberry buckthorn	Shrub	not endemic	evergreen

Rhamnus ilicifolia	hollyleaf redberry	Shrub	not endemic	evergreen
Rhus integrifolia	lemonade sumac	Shrub	not endemic	evergreen
Rhus ovata	sugar sumac	Shrub	not endemic	evergreen
Rhus trilobata	skunkbush sumac	Shrub	not endemic	deciduous
Ribes californicum	hillside gooseberry	Shrub	endemic	deciduous
Ribes cereum	wax currant	Shrub	not endemic	deciduous
Ribes malvaceum	chaparral currant	Shrub	endemic	deciduous
Ribes roezlii	Sierra gooseberry	Shrub	endemic	deciduous
Rubus ursinus	California blackberry	Shrub	not endemic	evergreen
Salvia apiana	white sage	Shrub	not endemic	evergreen
Salvia leucophylla	San Luis purple sage	Shrub	endemic	evergreen
Salvia mellifera	black sage	Shrub	not endemic	evergreen
Symphoricarpos albus	common snowberry	Shrub	not endemic	deciduous
Symphoricarpos mollis	creeping snowberry	Shrub	not endemic	deciduous
Toxicodendron diversilobum	Pacific poison oak	Shrub	not endemic	deciduous
Tsuga mertensiana	mountain hemlock	Tree	not endemic	evergreen
Umbellularia californica	California laurel	Tree	not endemic	evergreen

Because microclimate can vary greatly within a 10km grid cell, the course resolution of the climate data could affect results. To test the effect of grid cell size, I fit a series of models to data at finer resolutions (4km, 1km, 270m). Due to computational constraints I simulated GLMM fits using GLMs which included the spatial random intercept of the initial 10km GLMM fit as an offset. Since the effective range of this term was constrained to be greater than 20km, its spatial pattern should not change at finer resolutions, although its magnitude could vary if the relative importance of covariates changes.

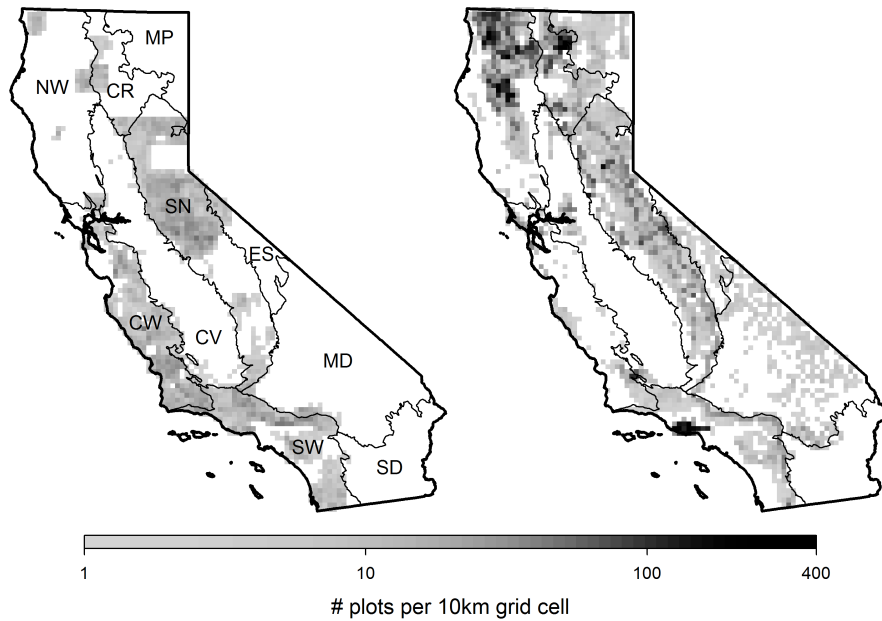


Figure 3: Distribution of vegetation sampling plot density (# plots per 100km²) for historic (left) and modern (right) periods. Text codes in the left panel are abbreviations for the ecoregions of California as defined by Hickman (1993); CR = Cascade Ranges, CV= Central Valley, CW= Central Western, ES = East of Sierras, MD = Mojave Desert, MP = Modoc Plateau, NW = Northwestern, SD = Sonora Desert, SN = Sierra Nevada, SW = Southwestern.

Climate data

A set of climate data and water balance metrics were obtained for the study area . These were based on climate data from Parameter-elevation Regression on Independent Slopes Model (PRISM) at 4km resolution, downscaled to 270m using a statistical downscaling method. The PRISM dataset interpolates meteorological station data using a model which incorporates expert knowledge of climatic factors such as rain

shadows, coastal effects, temperature inversions and elevation (Daly *et al.*, 2008). Hydrologic processes were accounted for using the Basin Characteristic Model .

All metrics were averaged over 30-year periods; 1911-1940 for the historic period and 1971-2000 for the modern period. For modeling purposes I selected a subset of commonly used and biologically relevant climate metrics including AET, CWD, mean temperature of coldest month, mean temperature of warmest month, and annual snowfall (table 2). I removed predictors in the historic training data with linear correlation coefficients greater 0.85. I chose this threshold because the primary impact of collinearity is to increase variance of coefficient estimates an effect that should affect both candidate models equally. The data were aggregated to courser resolutions using a simple average.

Over the study period, mean temperatures increased by approximately 1.0° C across the state while precipitation increased by 20-80mm in the northern mountains resulting in spatially variable trends in climatic water balance .

Table 2: climate covariates used for modeling

Covariate	Units
Actual Evapotranspiration (AET)	mm/yr
Climatic Water Deficit (CWD)	mm/yr
Mean temperature of coldest month	C
Mean temperature of hottest month	C
Annual snowfall	mm/yr

Modeling techniques

For each species I fit GLMs and GLMMs to the full historic dataset assuming a binomial distribution for the response variable and a logistic link function. I follow Latimer et al. in using the count of presence observations per grid cell as my response, weighted by the number of vegetation plots per grid cell. Predictions from these models reflect estimated probability of occurrence for a species within each cell, equivalent to predicted prevalence. I used quadratic functions of all 5 covariates to allow for non-linear relationships between the covariates and response variables. Interactions were not included.

For the spatial models, an exponential spatial correlation function was assumed. I used a spatial predictive process model to reduce the costly computations involved in estimating the spatial process. Models were fit within a Bayesian framework using MCMC techniques. Computations were performed in R (2.10.1; R Development Core Team, 2011) using the spGLM routine in the spBayes package. Each model required several days to complete the MCMC sampling on a quad-core server (Intel Xeon E5440 2.83Ghz).

Spatial Process GLMM Specification and Priors

The response variable $y(s_i)$ was the number of vegetation plots that contain the species of interest within the i^{th} 10km grid cell at location s_i . Given the total number of vegetation plots within the grid cell, $N(s_i)$, I assumed $y(s_i)$ followed a binomial distribution. For the i^{th} location, the distribution of $y(s_i)$ was taken to be:

$$\pi(y(s_i) | \eta(s_i)) \sim \text{Binomial}(N(s_i), p(\eta(s_i))),$$

where $p(\eta(s_i)) = \exp(\eta(s_i)) / (1 + \exp(\eta(s_i)))$ is the probability of species presence,

and $\eta(s_i) = x(s_i)' \beta + w(s_i)$,

where $x(s_i)$ is a vector comprising an intercept and location-specific climate covariates, β is a vector of regression coefficients, and $w(s_i)$ is the spatial random effect.

The output of the models is an estimate of the probability of occurrence, $p(\eta(s_i))$, for individual samples within a grid cell, which is equivalent to predicted prevalence; I will use these two terms interchangeably throughout this manuscript. The random effect, $w(s)$, was specified as a Gaussian process with a mean of zero with a covariance function between locations s_i and s_j defined as:

$$C(s_i, s_j) = \sigma^2 \cdot \exp(-\varphi \cdot \|s_i - s_j\|)$$

where σ^2 defines the variance, and

φ is the spatial decay parameter.

Prior distributions on the remaining parameters complete the hierarchical model. The vector of regression effects β was assigned an uninformative multivariate Gaussian prior, while the latent variance component σ^2 was assigned an uninformative inverse gamma prior with shape and scale parameters of 2 and 1 respectively. The spatial decay parameter, φ , was assigned a uniform prior with support between effective ranges (the range at which the magnitude of correlation decays to 5% of its maximum value, calculated approximately as $3/\varphi$) of 20 and 600km, based on the average nearest neighbor distance between knots and half the span of the study area

respectively. Point locations for the spatial process were defined as the centroid of the plot locations within a given grid cell. I also fit the corresponding GLMs with $\eta(s_i) = x(s_i)' \beta$.

Fitting of Models

Models were fit within a Bayesian framework using an adaptive Metropolis within Gibbs sampler . All covariates were standardized prior to modeling to avoid collinearity with the intercept and thus speed model convergence. Quadratic functions of each covariate were included to allow for non-linear responses. GLM models were also fit within the Bayesian framework to facilitate comparison between methods.

In the fitting of GLMMs, I ran 3 independent chains in parallel to convergence using an iterative approach. Individual chains were initiated using randomized starting values. An initial set of 25000 iterations was assessed for convergence over the last 50% of iterations using two criteria. First, I used the Multivariate Potential Scale Reduction Factor (MPSRF) diagnostic of Brooks and Gelman to assess mixing of the three chains. MPSRF values close to one indicate good mixing of the chains. I used a upper threshold of 1.3 to determine convergence. Trace plots indicated that in some cases, the spatial process parameters followed a trend despite good mixing of the chains as indicated by the MPSRF statistic. To check for such trends, I fit linear mixed effects models to each of the spatial process parameters, with slope and intercept as fixed effects and slope by chain as a random effect. The chains were thinned to every 50th observation to reduce autocorrelation. If MPSRF or either trend test ($\alpha=0.05$) indicated a lack of convergence, I resumed the chains for an additional 10000 iterations and repeated the tests for

convergence using the last 50% of amended chains. This process was repeated until convergence was achieved, requiring a total of 35000 to 75000 iterations. Upon convergence, samples were extracted from the last 50% of each chain and were systematically thinned to a total of 3000 samples for further analysis.

Spatial Predictive Process GLMs

The space varying intercept term, i.e., a spatial random effect, in the GLMM captures residual spatial dependence and is modeled using a zero centered spatial Gaussian process, see, e.g., Diggle and Ribeiro . This random effect follows a multivariate normal distribution, with a n -by- n variance-covariance matrix that represents the spatial covariance among the n locations where species occurrence was recorded. Estimation of the model's parameters requires that the inverse and determinant of this n -by- n be evaluated within each MCMC iteration. The computational expense of these inversions is proportional to n^3 , making it difficult to fit such models to large datasets (> 1000 observations) using current computational technology. The spatial predictive process model introduced by Banerjee et al. (provides an approximation to the "parent process" or the process estimated over the n observed locations. Following the notation in Banerjee et al. (2008), the spatial random effect, $w(s)$, where s is the geographic coordinates of an observation, is modeled over a reduced set of locations, referred to as knots. Instead of inverting the n -by- n spatial variance-covariance matrix, the inversion is performed on a smaller matrix representing the spatial association among the knots, saving computationally expense. Then the value of $w(s)$ at the n observed locations is predicted using an optimal estimator. The

original predictive process specified in Banerjee et al. induces a bias in the variance parameter estimates. A modified predictive process which adjusts for this bias was specified by Finley et al. and used in the current analysis.

For the current analysis, the predictive process was based on 300 knot locations, selected using k-means clustering on the historic data locations. Such knot designs have been shown to produce results comparable to other, more sophisticated, designs, see, e.g., Guhaniyogi et al. . Here, the most critical element of the knot design is that the domain is adequately covered and the distance between knots is sufficiently short to allow the spatial random effects decay parameter to be estimated. For my knot design, the median distance from each historic data point to the nearest knot location was 7.5 km and the median nearest-neighbor distance between knots was 17.0 km. The estimated spatial decay parameter had a median effective range of 160 km, which suggests the chosen knot intensity was sufficient.

GLMM Predictions

Predictions over the entire study area were made using the spPredict function in the spBayes library, which combines posterior fixed effects and kriging interpolations of the random intercept. I used historic climate data to make predictions in the historic period, and modern climate data to make projections to the modern period. Modern projections were made using models fit to the historic data, and the spatial random intercept from this fit was included in these projections. Projections were made by pooling 1000 posterior observations from each chain. Median values from pooled

projections were used for accuracy assessment, and quantiles were used to construct credible intervals for assessment of prediction variability.

Model assessment

Candidate models, i.e., GLM and GLMM, were assessed using resubstituted historic training data (the same data used to train the model; internal validation) and "temporally independent" data from the contemporary period (independent validation). For independent validation, parameter estimates from models fit to the historic data were used to make projections with the `spPredict` function in the `spBayes` library and modern climate data. The spatially-varying random intercept was included in GLMM projections. For internal validation, comparisons of model fit were made using the Deviance Information Criterion (DIC;), which is a measure of prediction accuracy with a penalty, pD , for model complexity interpreted as the effective number of parameters. Although DIC has been criticized for a variety of theoretical and applied shortcomings (see, e.g., the discussion supplement for), there are few alternative fit criteria suitable for hierarchical models and its use for broad comparisons is reasonable. As a measure of predictive accuracy for both internal and independent validation, I used AUC (area under the receiver operating curve; Fielding & Bell, 1997), an index ranging from 0.5 to 1.0, which measures the ability of a model to discriminate between presence and absence observations. A ROC plot is constructed by plotting sensitivity values (correctly predicted presences) against 1-specificity (absent when predicted present) over a full range of threshold values, and AUC is calculated as the area under this curve. A larger AUC values indicates better ability to separate observed presences from observed

absences. AUC is considered advantageous because it gives a single measure of accuracy not dependent on a single threshold. Although AUC has been criticized because it doesn't consider the goodness of fit of predictions (only their ranking) and required reducing the data to presence or absence within each grid cell, it remains useful for comparisons between candidate models for the same species.

To directly assess prediction uncertainty I estimated coverage rates of 90% credible intervals for probability of occurrence, derived from posterior predictive distributions for sampled grid cells. Coverage rates were calculated as the proportion of observed prevalence values fell within their respective 90% credible intervals. Because a logistic link function can never return a value of zero or one, I considered intervals including 0.001 to include zero, and intervals including .999 to include one.

Testing the effect of grain size

To test the effect of grid cell size, I fit a series of models to data at finer resolutions (4km, 1km, 270m). The GLM models were fit using the standard iterative optimization routine rather than Bayesian. Due to computational constraints I simulated GLMM fits using GLMs which included the spatial random intercept of the initial 10km GLMM fit as an offset, which is identical to including it as a predictor with a coefficient fixed at 1. Since the effective range of this term was constrained to be greater than 20km, its spatial pattern should not change at finer resolutions, although its magnitude could vary if its importance relative to the covariates changes. I calculated GLMM prediction variance as the linear combination of variance of the random intercept and variance of its GLM fit, ignoring potential covariance between

these terms. Prediction intervals were calculated using Gaussian quantiles of prediction standard error transformed by the logit link function. Accuracy for internal and independent validation was assessed using methods identical to the 10km analysis, which required reducing multiple observations within a grid cell to single presence and absence. Coverage rates were calculated as described in the previous section.

Assessment of Residual Autocorrelation

To assess spatial dependency I used Moran's I test on deviance residuals in 12 discrete distance classes. The classes used, in km, were: 0-15; 15-30; 30-45; 45-60; 60-75; 75-90; 90-120; 120-150; 150-200; 200-250; 250-300; and 300-600. Deviance residuals were calculated as:

$$\begin{aligned}
 z_i &= \text{sgn} \cdot \sqrt{2 \cdot (y_i \cdot \ln(y_i - n_i \cdot \hat{p}_i) + (n_i - y_i) \cdot \ln((n_i - y_i)/(n_i \cdot (1 - \hat{p}_i))))} & 0 < y_i < n_i \\
 &= -1 \cdot \sqrt{2 \cdot n_i \cdot |\ln(1 - \hat{p}_i)|} & y_i = 0 \\
 &= \sqrt{2 \cdot n_i \cdot |\ln(1 - \hat{p}_i)|} & y_i = n_i
 \end{aligned}$$

where y_i is the observed number of presences in grid cell i , n_i is the number of observations, \hat{p}_i is the estimated probability of occurrence, and sgn is 1 if $y_i \geq n_i \cdot \hat{p}_i$ and -1 otherwise.

The formula for Moran's I is:

$$I = \left(\frac{n}{S} \right) \cdot \left[\frac{\sum_i \sum_j (y_i - \bar{y}) \cdot (y_j - \bar{y}) \cdot w_{ij}}{\sum_i (y_i - \bar{y})^2} \right]$$

where n is the sample size, y_i and y_j are the i^{th} and j^{th} deviance residuals respectively, S is the number of observations within a distance class, and w_{ij} is a weight which is assigned 1 for observations within a distance class and 0 otherwise. Global significance was assessed using the minimum p-value of these tests after adjustment for multiple comparisons using the method of Holm. Range of significant autocorrelation was estimated as the upper limit of the furthest significant bin for which all lesser bins were also significant. Magnitude of autocorrelation was measured using the value of the Moran's I statistic in the first distance class, which included only adjacent grid cells.

Range size estimates

I estimated range size as the cumulative area of cells for which the posterior predicted probability of occurrence was above a threshold value. The threshold value was chosen to minimize the difference between sensitivity (proportion of presence observations correctly predicted) and specificity (proportion of absence observations correctly predicted) for the historic data used to fit the models. This threshold was calculated individually for each model and species. I tested the statistical significance of range size change by subtracting the posterior distributions of range size estimates for the two time periods to generate a posterior for range size change; if the 90% credible interval for this distribution excluded 0, the change was deemed significant.

In addition to estimating overall changes in range size, I identified where significant changes to the species ranges were predicted to occur. For each grid cell I compared the posterior predictive distributions in the historic period to those for the modern period (see figure 9). From the historic posterior I calculated the probability of

observing a value as extreme or more extreme than the median projected value for the modern period.

Displaying uncertainty

In order to graphically depict uncertainty in the predictions, I adapted the methods of Hengl et al. . Median predictions for each grid cell were displayed using a color ramp and degree of uncertainty (width of a 90% credible interval) was shown by increasing the whiteness of these colors.

RESULTS

Internal Validation

Internal validation showed significant differences between model fits (Table 3 and Fig. 4). Median DIC scores dropped by 454.6 for GLMMs compared to GLMs, despite a median increase in model complexity of $p_D = 87.5$, suggesting a considerable improvement in fit for GLMMs over GLMs. AUC scores for GLMs had a median value of 0.88, indicating good discrimination between presence and absence observations (Swets 1988). GLMMs yielded a median AUC score of 0.98, indicating near-perfect discrimination between presence and absence observations. Coverage rates for GLMMs had a median value of 0.91, very close to their nominal value of 0.90, while those for GLMs had a median value of 0.46, implying overconfident predictions from the latter.

The posterior distributions of regression coefficients differed greatly between GLMMs and GLMs. Standard errors of GLMM coefficients were, on average, 2.17 times

greater than that of GLM coefficients. GLMMs had fewer significant coefficients; of the 5 covariates examined, the mean number that were significant as either 1st or 2nd order (90% credible interval not including 0) was 4.5 for GLMs, and 3.0 for GLMMs. There were no strong patterns with regard to which covariates were found to be significant. GLM estimates generally fell within the 90% GLMM credible interval (70.4% of all parameter estimates).

The Moran statistics and range of autocorrelation given in Table 3 show that GLMMs nearly eliminated spatial autocorrelation of residual error (although 3 of the 99 species still showed significant dependence with adjacent grid cells), while all GLMs exhibited significant autocorrelation of residual error with a median range of 45km.

Table 3: Summary of median fit statistics on historic data (internal validation) for models fit for 99 plant species. Coverage is proportion of times a 90% credible interval for probability of occurrence contained the observed prevalence value. Range refers to the range of significant spatial autocorrelation found in binned Morans I tests. p_D is a measure of model complexity, interpreted as the effective number of parameters in each model. DIC is the Deviance Information Criterion, lower values indicate better fit. Different letters indicate significant difference based on a matched-pairs t-test between models, adjusted for multiple comparisons following the method of Holm (1979).

	AUC	coverage	range (km)	Morans I	p_D	DIC
GLM	0.88a	0.46a	45a	0.28a	10.7	2012
GLMM	0.98B	0.91b	0b	-0.02b	98.2	1557

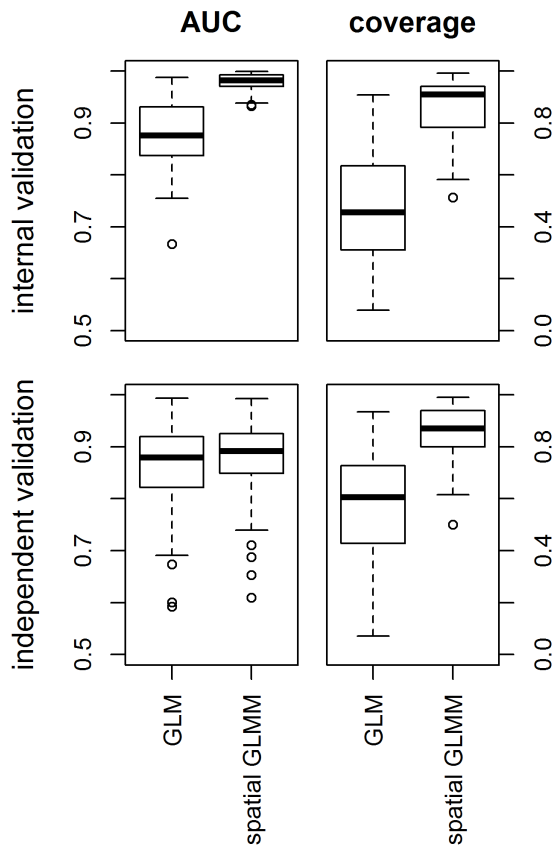


Figure 4: Fit statistics under internal (historic data) and independent (modern data) validation. Coverage rates, shown in the right column, are the proportion of times a 90% prediction interval captured observed prevalence.

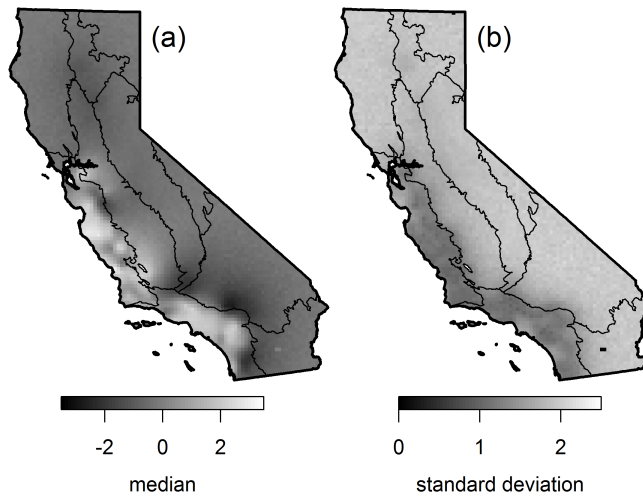


Figure 5: : (a) Median fitted value of the GLMM spatial random intercept for *Salvia mellifera* (Black Sage). This can be interpreted as a latent covariate representing unobserved processes with spatial structure. Higher values indicate greater suitability than predicted by the climatic covariates included in the model. Note that the random intercept is not logit-transformed, so its values are not restricted to 0-1. (b) Standard deviation of spatial term. This is the amount of variability added to predictions by the spatial process term.

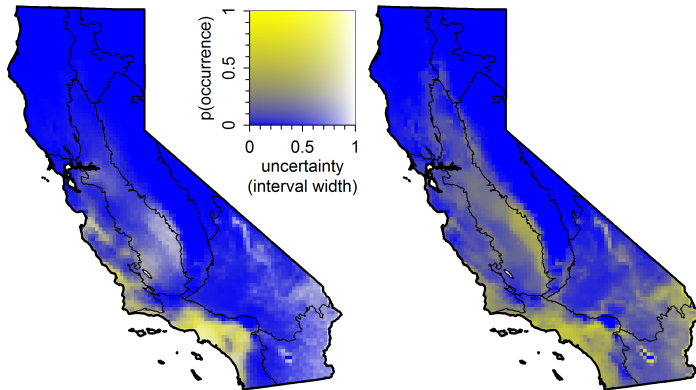


Figure 6: : Example of fitted models for black sage (*Salvia mellifera*). The left panel shows predicted probability of occurrence from the spatial GLMM model. Color indicates the prediction while the degree of whiteness indicates width of a 90% credible interval. The right panel shows the same for the non-spatial GLM model.

Independent validation

Validation with modern data yielded lower mean accuracy statistics than internal validation for both GLM and GLMMs (Table 2 and Fig. 4). AUC values were slightly higher for GLMMs compared to GLMs. Coverage rates for GLMMs showed only a slight drop (compared to internal validation), remaining very close to their nominal value of 0.90 (Table 4), while those for GLMs improved but remained poor. Restricting the independent validation to those grid cells that had been sampled historically (roughly 50% of historic grid cells were resampled) had little effect on accuracy statistics but caused a slight drop in coverage rates for both candidate models, while restricting validation to cells not sampled historically had also little effect on AUC but caused a slight increase in coverage rates for both candidate models (results not shown) as was previously demonstrated in

Table 4: Summary of median fit statistics on the modern data (independent validation) for models fit for 99 plant species. Coverage is proportion of times a 90% credible interval for p(occurrence) contained the observed prevalence value. Letters indicate significant differences in matched-pairs t-tests, adjusted for multiple comparisons following the method of Holm (1979).

	AUC	coverage
GLM	0.88a	0.61a
GLMM	0.89b	0.87b

Effect of scale

Reducing the grain size of the analysis from 10km to 4km, 1km and 270m had little effect on GLM results, but GLMMs showed a drop in both accuracy and coverage rates when going to smaller grain size (figures 7 and 8).

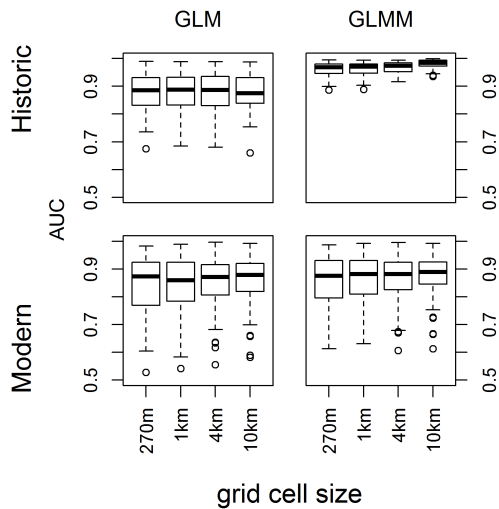


Figure 7: Effect of grain size on accuracy statistics.

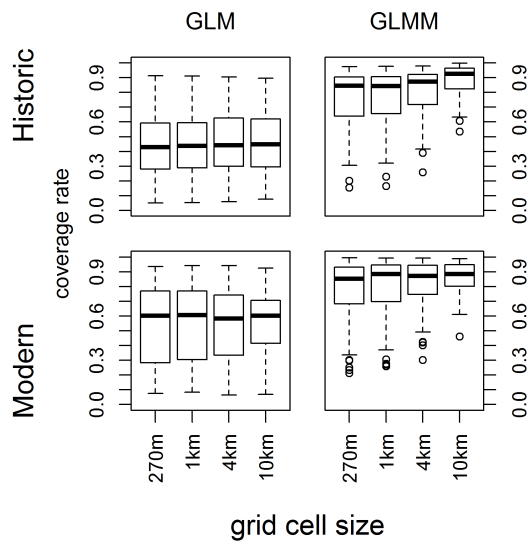


Figure 8: Effect of grain size on coverage rates

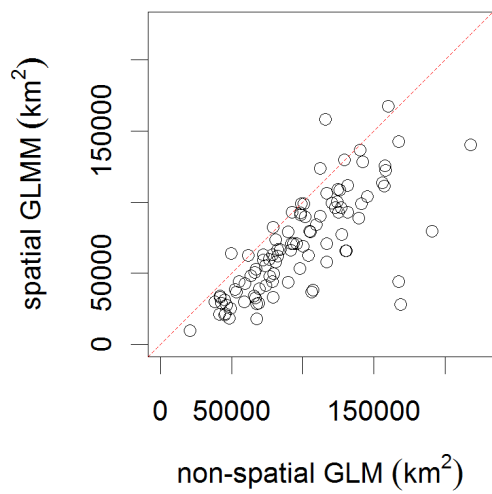


Figure 9: Range size estimates in square kilometers for the modern period by method. Red dashed line is 1:1.

Range size estimates and predicted changes

Mean range size estimates were correlated between time periods (Pearson correlation coefficient $r = 0.94$ GLM, $r = 0.99$ GLMM) and candidate models ($r = 0.65$ historic, $r = 0.68$ modern). Range size estimates varied by model with GLM estimates averaging ~70% larger than GLMM estimates for both time periods (Fig. 7). Interval widths for estimated range size averaged 48.4% of range size for GLMMs vs. 25.0% for GLMs. Estimated changes in range size were also highly correlated between candidate models ($r = 0.77$), but GLMM estimates predicted, on average, 50% smaller changes in range size. Figure 8 shows estimates of percent range size change by model, highlighting estimated changes that were significant ($\alpha = 0.10$). It is notable that the two models predicted similar numbers of significant changes, but in many cases failed to agree on which species were facing these changes. Figure 9 shows an example of the spatial distribution of predicted changes in probability of occurrence for *Salvia mellifera*.

DISCUSSION

Performance under internal vs. independent validation

GLMMs consistently outperformed GLMs under internal evaluation, but performed similarly when confronted with independent data. Under internal validation, the flexibility of the spatially structured random intercept allowed it to capture spatial patterns not accounted for by the climate covariates. These patterns were smooth in space, as evidenced by the spatial autocorrelation of GLM errors and the ability of GLMMs to account for these errors. The similar performance of the candidate models under independent validation was surprising. This is apparently due to a lack of

temporal persistence, for most species, of the latent effects captured by the spatial random intercept. In effect, many of the species' observed distributions shifted in ways which could not be explained by the climate covariates. There are several ways in which this result can be interpreted. It could be attributable to a climate effect not captured by the covariates, or it could be the result of biotic interactions, population dynamics, disturbance, or land use change occurring within a broader envelope of environmental tolerance than is estimated by the GLM models. Spatial mis-match of the samples from each time period can be ruled out since the result holds when the validation data is subset to previously sample grid cells.

From a Bayesian perspective, the spatial random intercept can be viewed as an informative prior for projections into new temporal domains – drawing the projections back toward the historic ranges when information in the covariates is lacking. If the latent effects represented by the spatial random intercept are expected to change over time, it may be desirable to specify a temporally dynamic residual spatial process, allowing the influence of the spatial random intercept to evolve over space and time, see, e.g., Finley et al. . To my knowledge, this methodology has not been applied to SDM projections.

Projection Uncertainty

Although the spatial random intercept did not markedly improve the projection accuracy of GLMMs, its ability to account for variability not explained by covariates yielded improved estimates of uncertainty. Including such estimates alongside mean

projections gives a 'map of ignorance' as called for by Rocchini et al. (2011), highlighting areas where knowledge is lacking and could be improved with additional sampling effort or the inclusion of additional covariates. For instance, for *Salvia mellifera*, a historically calibrated GLM projection showed high probability of occurrence in the coastal regions of Southern California, the southern reaches of the Central Valley, and eastern portion of the Mojave desert (Fig. 6). These projections are flawed as the species does not currently occur in the latter two regions of the state. In contrast, the influence of the spatial random intercept term in the GLMM projection (Fig. 5) is readily apparent as the latter two regions of the state show lower probability of occurrence and more importantly, higher levels of uncertainty in projections to these regions (Fig. 5). In addition to improving the projections, the spatial random intercept term can provide biogeographical insights into latent covariates that can better explain the species distribution. In this case, the unobserved spatial process may be frequent disturbance from fire in the coastal sage and chaparral communities in which this species is found. *Salvia mellifera* has facultative fire adapted reproductive traits and although I cannot definitively prove that the spatial intercept is actually characterizing this latent process, this interpretation is consistent with the disturbance regime of the region and the autecology of the species.

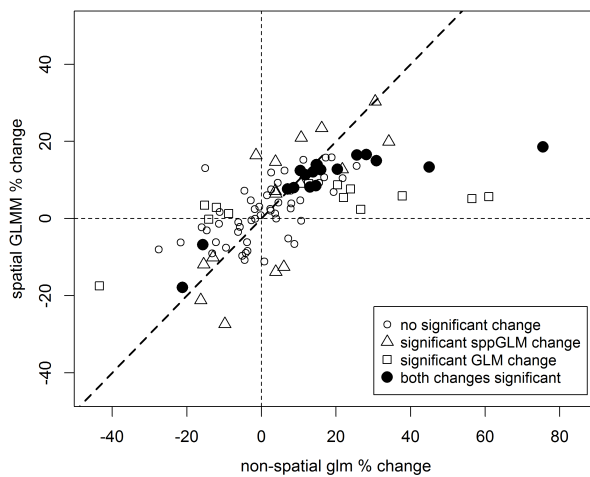


Figure 10: : Estimates of percent change in range size over the 75-year study period for all species. Percent change is relative to mean estimated range size for the historic period. Estimated change for GLM models is shown along the x-axis, while change for spatial GLMM models is shown on the y-axis. The thick dashed line is 1:1. Spatial GLMMs generally predict smaller changes in range size, and the significance of changes varies between methods.

Conservation applications

Conservation applications of SDMs such as reserve design and assisted migration of species represent costly management actions involving complex decisions for which the consequences of mistakes are high. An entire science was long ago developed around decision making in the face of uncertainty, yet standard SDM methods are ill equipped to provide the needed information. The independently validated estimates of uncertainty I have presented have utility in this context, allowing alternatives to be assessed with regard to the confidence of projections. The results I present for *Salvia mellifera* provide a relevant hypothetical example (Fig. 6). If there were concerns over habitat loss for this species, circa 1935, then GLM results suggest the southern Central Valley and Sierra Nevada ecoregion as plausible translocation sites

for assisted migration planning. However, the GLMM projection suggests that the suitability of these regions is far from certain, providing useful information to a hypothetical conservation planner.

SDMs are also used to project loss of habitat and subsequent extinction risk . Estimates of habitat loss (or gain) are driven by the shape of response curves for individual covariates, making them sensitive to model specification. In this context, spatial regression methods such as GLMMs offer a distinct advantage in that they have been shown to give more precise parameter estimates and are less likely to identify spurious covariates as significant in the presence of spatial autocorrelation . The latter issue can be especially problematic when automated model selection techniques are used in conjunction with non-spatial SDM methods, a situation common in SDM applications. In my analysis, GLMMs yielded more conservative estimates than GLMs of range size and range size change through time. This was likely due to the ability of the spatial random intercept to correctly identify areas of known absence not predicted by climate alone. Additionally, predicting a contraction or expansion of suitable habitat may be of limited use for conservation planning without regard to spatial context. I demonstrate that the posterior distributions of model projections can be used to distinguish between areas where habitat loss (or gain) is more certain compared to areas where change is less certain (Fig. 9). This type of analysis is valuable because changes occurring in areas where we have very little confidence in our original estimates should be of less concern than changes occurring in areas known to contain the focal species.

Caveats

Numerous criticisms could be made of my methods. Weaknesses include the coarse resolution of the study, missing predictors, and misspecification of models. I used GLMs for comparison, yet studies have shown more sophisticated methods such as generalized additive models, Random Forest, and Boosted Regression Trees to produce better fitted models (e.g.. Although such methods offer many advantages, little focus has been given to their estimates of projection uncertainty, and their accuracy under spatially (Randin et al. 2006) and temporally (Dobrowski et al. 2011) independent validation has been questioned. The other weaknesses noted above should affect both candidate models equally, although the advantage of GLMMs would disappear under conditions in which a model is correctly specified and all relevant predictors included, conditions rarely encountered in practice . Finally, one might look to other approaches to assess candidate models' predictive ability, see e.g., Gneiting and Raftery for a discussion of proper scoring rules.

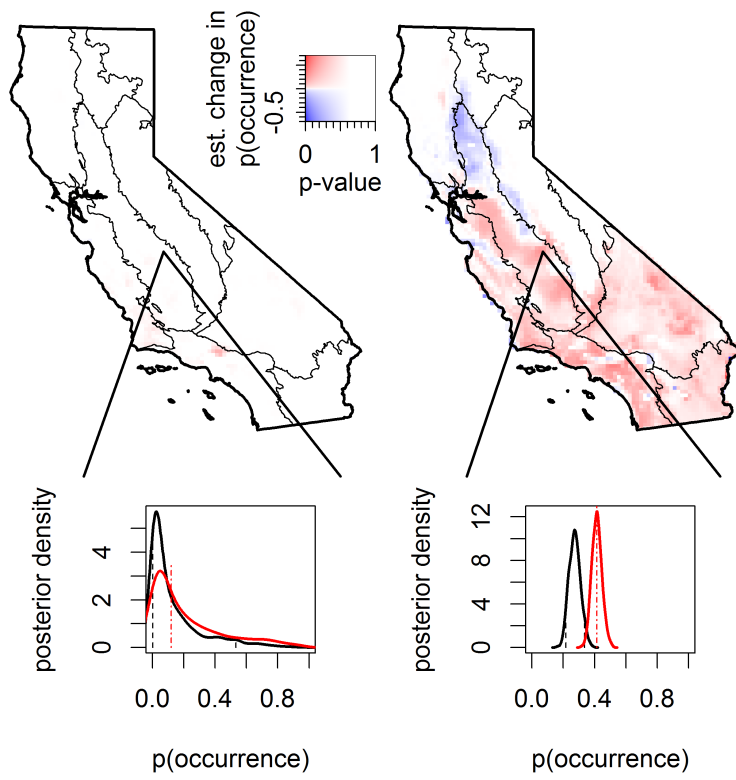


Figure 11: : Estimated change in probability of occurrence over 75 years for *Salvia mellifera*. The left panel shows the spatial GLMM estimates while the right panel shows non-spatial GLM estimates. Color ramp indicates magnitude of predicted change while degree of saturation conveys the result of a statistical test for per-pixel change in suitability over time, with darker colors indicating areas where significant change in habitat suitability. Inset plots show, for a single grid cell extracted from the central valley region, posterior distributions of predicted probability of occurrence for the two time periods and both methods. The black lines show the posterior distribution for the historic period while the red lines show the posterior for the forecast of the historic model to the modern period. Vertical black lines show the 90% prediction intervals for the historic period, while the vertical red lines show the median value for the modern period. The width of the 90% prediction interval is analogous to that used to convey uncertainty in figure 6. Cases in which the modern median fell outside the 90% prediction interval for the historic period are considered significant at the 10% level. For the highlighted grid cell, the spatial GLMM did not predict a significant change while the non-spatial GLM did.

Chapter 3: Conclusions and future research

I found that spatial regression models, although they produced similar levels of projection accuracy under independent validation, gave improved estimates of uncertainty over non-spatial methods fit to the same data. The ability of GLMMs to account for residual SAC and hence provide valid estimates of uncertainty suggests they are more suitable for drawing inference about SDM parameters and subsequent predictions. The degree of uncertainty was high in the fitted models, but their output provides valuable insight into the nature of this uncertainty and suggests ways it might be reduced. GLMM methods produced more conservative estimates of range size and range size change, and although we cannot definitely say these are more accurate than those derived from conventional methods, the statistical validity of GLMMs favors their

estimates. Useful projections of species' distributions into the future require an honest assessment of projection uncertainty. GLMMs with a spatially structured random intercept offer a clear improvement over commonly used methods.

Future work should focus on several issues. I have shown that GLMMs offer accurate and useful estimates of projection uncertainty, but each model required several days to fit. Improvements to their computational efficiency would increase their practicality. In the SDM literature projection uncertainty has been frequently discussed, but little thought has been given to how these estimates should be presented and used in conservation planning applications. I have provided some ideas on these topics, but others could certainly provide additional useful insight. Finally, my analysis revealed strong spatial patterning in species distributions which could not be explained by the climate covariates considered. It would be very interesting to investigate additional factors which may be able to explain these patterns, and factors such as land use change which may explain the shifts these distributions showed over time.

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