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Utility of temporally-biased invasive species distribution models in the detection of Euwallacea sp. nr. fornicatus in California

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### UNIVERSITY OF CALIFORNIA

Los Angeles

Utility of temporally-biased invasive species distribution models in the detection of

Euwallacea sp. nr. fornicatus in California

A thesis submitted in partial satisfaction

of the requirements for the degree Master of Arts

in Geography

by

Monica Dimson

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#### ABSTRACT OF THE THESIS

Utility of temporally-biased invasive species distribution models in the detection of *Euwallacea* sp. nr. *fornicatus* in California

by

Monica Dimson

Master of Arts in Geography University of California, Los Angeles, 2017 Professor Thomas Welch Gillespie, Chair

Species distribution models (SDMs) are valuable risk assessment tools in the management of invasive species, for which early detection and containment are critical. Few studies have evaluated the utility of invasive SDMs trained on temporally-biased presence data. While the abundance and range of occurrence records may increase with time after invasion, management objectives become more difficult to achieve as a destructive species nears establishment. This research assesses the relative predictive ability of models for the invasive shot hole borer (Coleoptera: Curculionidae: Scolytinae: *Euwallacea* sp. nr. *fornicatus*), which was first detected in Southern California in 2003. A series of 100-meter resolution models were developed in Maxent, selected for its ability to produce reliable models with relatively few occurrence records. Models were trained using data from five chronologically cumulative sampling periods, which

ii

simulate stages of invasion. The effects of spatial extent and spatial filtering were also examined. All models achieved high AUC (area under the receiver operating curve) values > 0.93 and correctly classified  $87.7 \pm 18.8\%$  of independent test records, indicating high model performance regardless of the degree of temporal bias. The leading contributing variables were minimum temperature of the coldest month (for sixteen models) or percent impervious surface (for four models). Sensitivity was consistently higher for models that used the larger spatial extent, which suggests that for an emerging species, larger backgrounds may be less restrictive on model outcomes. Spatial filtering produced more discriminating results without compromising model sensitivity. The study finds that invasive SDMs can be useful in identifying areas vulnerable to invasion, particularly if they are integrated into adaptive management strategies. The thesis of Monica Dimson is approved.

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### TABLE OF CONTENTS

- 1. Introduction
- 2. Background
  - 2.1. Species Impact
  - 2.2. Study Area
  - 2.3. Modeling Method
- 3. Methods
  - 3.1. Species Data
  - 3.2. Environmental Variables
  - 3.3. Model Parameters
  - 3.4. Model Evaluation
- 4. Results
  - 4.1. Suitable Area
  - 4.2. Model Sensitivity
  - 4.3. Area Under the Receiver Operating Curve
  - 4.4. Variable Contribution
- 5. Discussion
  - 5.1. Utility of Temporally-Biased Models
  - 5.2. Effects of Spatial Filtering and Spatial Extent
  - 5.3. Limitations of the AUC
  - 5.4. Important Predictors of ISHB
- 6. Conclusion
- 7. Tables and Figures
- 8. Appendix
- 9. References

## TABLES AND FIGURES

| Table 1       | Environmental variables   |
|---------------|---|
| Table 2       | Description of model series   |
| Table 3       | Minimum training presence thresholds                                |
| Table 4       | Area predicted suitable   |
| Table 5       | Model sensitivity results   |
| Table 6       | Area under the receiver operating curve results                     |
| Table 7       | Mean variable contribution  |
| Table 8       | Mean, minimum, and maximum values of leading contributing variables |
| Figure 1      | Spatial extents   |
| Figures 2a-2e | California unfiltered model outputs                                 |
| Figures 3a-3e | California filtered model outputs                                   |
| Figures 4a-4e | Ecoregion unfiltered model outputs                                  |
| Figures 5a-5e | Ecoregion filtered model outputs                                    |
| Figure 6      | One-way ANOVA results   |
| Figure 7      | Two-way ANOVA results   |

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#### 1. INTRODUCTION

Species distribution models (SDMs) describe the relationship between species occurrence and environmental conditions at a given location. SDMs have a wide variety of applications, including risk assessment for biological invasion (Peterson 2003; Elith et al. 2010; Jiménez-Valverde et al. 2011). Invasive species can have a significant economic and ecological impact outside of their native range. In the United States, the annual cost of invasive species management is estimated at 219 billion USD (Pimentel 2011). Invasive species also threaten native biodiversity through interspecific interactions (e.g. competition, predation, parasitism) and habitat modification (Pimentel et al. 2005). Modeling the distribution of invasive species can help to identify areas that are most vulnerable to invasion, particularly when resources for full systematic surveys are limited.

Invasive species are typically in disequilibrium with a novel environment, which presents a challenge for correlative models like Maxent (Elith et al. 2010; Uden et al. 2015). A modeling study of incipient *Phytophthora ramorum* found that invasive SDMs are less accurate in the early stages of invasion and more likely to under-predict ranges (Vaclavik and Meentemeyer 2012). It takes time for a species to establish and realize its full potential range, and models trained on records from the onset of invasion will likely be affected by spatial (e.g. from uneven survey effort) and temporal (e.g. surveying during ongoing species expansion or contraction) sampling bias (Bean et al. 2012).

Several alternative approaches have been proposed to address the issue of disequilibrium. These include correlative models that project predictions from the native range onto introduced sites, mechanistic models based on species physiology, hybrid models that select environmental predictors according to species physiology, or collection of input data via planned, transect

sampling (Peterson 2003; Elith et al. 2011; Jiménez-Valverde et al. 2011; Vaclavik and Meentemeyer 2012; Brummer et al. 2013). Unfortunately, these data and methods are rarely readily available, and are often costly and time-consuming to acquire or implement.

There is a need to further examine the utility of correlative SDMs in the early stages of biological invasion, despite the implicit temporal bias. Many invasive SDM studies have focused on species that are well-established at the time of study (Welk et al. 2004; Lippitt et al. 2008; Elith et al. 2010; West et al. 2016). Though predictive ability has been found to increase as species near establishment, these studies do not address early detection, prevention, and containment objectives critical to successful invasive species management (Epanchin-Niell and Liebhold 2015). It is impractical to wait until a destructive species has spread and established before attempting to predict its potential extent. As newly introduced species approach equilibrium in the invaded range—itself a difficult threshold to identify—efficient control and total eradication become near impossible to achieve (Venette et al. 2010; Uden et al. 2015).

In this research, I modeled the distribution of the invasive shot hole borer (Coleoptera: Curculionidae: Scolytinae: *Euwallacea* sp. nr. *fornicatus*) (ISHB), an emerging invasive species in California that threatens commercial avocado industries, native forests, and urban landscapes (O'Donnell et al. 2016). A series of SDMs were produced using Maxent, a common correlative distribution model that consistently ranks among the most reliable species distribution modeling methods (Elith et al. 2006; Phillips et al. 2006; Wisz et al. 2008). Using ISHB survey data collected from 2012 to 2016, five chronologically cumulative sampling periods were created to simulate stages of invasion. Each sampling period was modeled 1) with and without spatial filtering and 2) using two different spatial extents. These additional parameters were examined

because the Maxent model is especially sensitive to sampling bias and can be greatly impacted by the size of the background area (VanDerWal et al. 2009; Elith et al. 2011).

The objectives of this study were to 1) determine the relative predictive ability of models trained on temporally-biased ISHB data, 2) examine the effects of spatial extent and spatial filtering on invasive SDM outcomes, and 3) determine how SDMs for emerging invasive species can serve early detection and prevention management objectives.

#### 2. BACKGROUND

#### 2.1. Species Impact

The common name invasive shot hole borer (ISHB) refers to two closely related ambrosia beetles that belong to genetically distinct clades of the *Euwallacea fornicatus* species complex (Stouthamer et al. 2017). The beetles are native to separate but overlapping regions of Asia. Each vectors a fungal symbiont (*Fusarium* spp.) that infects the xylem of the host plant and also serves as the insect's food source (Eskalen et al. 2013). The mutualistic beetle/disease complex causes limb failure, branch dieback, and in severe cases, tree mortality.

ISHB was first detected in 2003 in Los Angeles County, but its potential impact was not recognized until 2012 (Lynch et al. 2016). By 2013, ISHB/*Fusarium* had been observed on 112 tree species (Eskalen et al. 2013). Over fifty host species support both fungal growth and beetle reproduction. These reproductive hosts include nineteen California native species, six invasive plants, and many trees common in the urban forest. ISHB is also a pest of avocado (*Persea americana*) (Stouthamer et al. 2017), a major agricultural crop in California valued at 274 million USD (California Department of Food and Agriculture 2016). Avocado groves have been affected in Israel as well, where ISHB was first recorded in 2005 (Mendel et al. 2012).

Control tactics for ambrosia beetles are limited. ISHB feeds and mates within the tree galleries and does not appear to use an aggregation pheromone (Umeda et al. 2016). Infection by *Fusarium* inhibits the host plant's ability to respond to chemical treatments (Eatough Jones et al. 2017). Early detection and containment are therefore critical management strategies for ISHB.

#### 2.2. Study Area

The current range of ISHB in California now includes Los Angeles, Orange, and San Diego Counties, as well as limited regions of Riverside, San Bernardino, Ventura, Santa Barbara, and San Luis Obispo Counties. ISHB models were created at two spatial extents: 1) the state of California and 2) an ecological sub-set defined by Level III Ecoregions (Fig. 1). Ecoregions describe areas of similar ecosystem type, resource quality and availability, and probable response to disturbance (Griffith et al. 2016). The Ecoregion hierarchy classifies ecosystems at different spatial scales, providing an adaptable framework for ecosystem research and management.

The geographical and biological diversity of California divides the state into 13 Level III ecoregions. In Southern California, the Mediterranean climate produces cool, wet winters and warm, dry summers (Franklin 1998). This climate regime supports some of the highest levels of regional biodiversity in the world; Mediterranean California is home to 4,300 native plant species, 35% of which are endemic to the region (Cowling et al. 1996). Urbanization and agriculture are the main threats to regional diversity.

The urban forest of Los Angeles is also extremely diverse and supports a higher number of tree species (both native and exotic) than some native forests in the U.S. (Gillespie et al. 2016). Many of these species are susceptible to ISHB/*Fusarium*.

The modeled subset includes Ecoregions 8 and 85. Ecoregion 85, the Southern

Californian/Northern Baja Coast, is an area characterized by coastal sage scrub and chaparral, as well as major urban areas and some agricultural land (Griffith et al. 2016). Ecoregion 8 describes the Southern California Mountains, an area of higher elevations, cooler summers, and higher precipitation than Ecoregion 85. It is also less developed, as much of the area is National Forest public land, and dominated by chaparral, oak woodlands, and coniferous woodlands.

#### 2.3. Modeling Method

Maxent is a machine-learning program that predicts species geographic distributions using species point data and environmental variables (Phillips et al. 2006). It performs well with limited occurrence records and produces robust results with small sample sizes, compared to other correlative SDM methods (Hernandez et al. 2006; Anderson and Gonzalez 2011). Maxent is a presence-only model and does not require field records of species absence. Instead, pseudoabsences are drawn from the background data (Phillips and Dudík 2008). This makes Maxent a valuable tool for modeling incipient species like ISHB, for which absence data in the novel range is often unavailable or unreliable (Phillips et al. 2006; Jiménez-Valverde et al. 2008).

Presence-only models have a few disadvantages. True-absences can be valuable in providing a more complete picture of sampling bias, and may also help to produce more robust predictions if they are truly representative of unsuitable habitat (Elith and Leathwick 2009). Inclusion of true-absences, together with dispersal constraints, has been shown to improve invasive SDM performance (Vaclavik and Meentemeyer 2009). However, absence from a given area is difficult to verify for mobile species (Jiménez-Valverde et al. 2008). Observed absences could equally signify that habitat is unsuitable, or that it is suitable but currently unoccupied

(Elith and Leathwick 2009; Jiménez-Valverde et al. 2011). For an emerging species like ISHB, it is difficult to confirm the exact significance of observed absence.

#### 3. METHODS

#### **3.1. Species Data**

Presence-only occurrence data for ISHB were obtained from University of California (UC) Riverside; UC Cooperative Extension, Orange County; and USDA Forest Service, Forest Health Protection. The dataset was compiled from reports and informal surveys that recorded ISHB observations in Southern California from 2012 to 2016. Point locations were collected using hand-held GPS devices and represent individual ISHB-infested trees. Infestation was confirmed by trained experts using direct beetle observations, beetle signs and/or symptoms of attack, and/or *Fusarium* infection.

The original dataset is the most spatially and temporally comprehensive dataset currently available and includes 9,530 ISHB presence records. By default, Maxent removes duplicate points that occur within a single grid cell, the size of which is determined by the spatial resolution of the environmental layers, in this case 100-meters (Fourcade et al. 2014). This reduced the dataset to 1,052 unique records. Though the ISHB point data are highly accurate and precise, they are affected by an unquantified degree of spatial sampling bias, which is primarily the result of uneven sampling effort. Much of the data was collected not during transect surveys, but during visual tree assessments within artificial boundaries where researchers have had permission to survey (e.g. county parks, riparian corridors, university campuses) (Umeda et al. 2016). This resulted in clusters of dozens of points within a single 100-meter grid cell. Spatial sampling bias is a common obstacle in species distribution modeling, and the utility of data

despite these limitations is a point of investigation in this study (Rushton et al. 2004; Newbold 2010).

#### **3.2. Environmental Variables**

Bioclimatic variables were downloaded from WorldClim 1.4, a popular dataset in species distribution modeling because it provides publicly available, global coverage at a relatively fine spatial resolution of 1-kilometer (Hijmans et al. 2005). Rasters were resampled to 100-meters using bilinear interpolation, which has been used, with robust results, to resample 250-meter climate data to as fine a scale as 10-meters (Rovzar et al. 2016). Resampling from this relatively coarser resolution may obscure microclimates in areas of high topographic relief, however, the topographic data have a finer resolution and may help to preserve this variability.

Topographic, impervious surface, tree canopy cover, and NDVI (normalized difference vegetation index) data were acquired at a 30-meter resolution. These layers were aggregated by mean and resampled to 100-meter resolution using bilinear interpolation. Elevation, percent impervious surface, and percent tree canopy cover rasters were downloaded from the U.S. Geological Survey National Elevation Dataset and National Land Cover Database, respectively (Xian et al. 2011; Homer et al. 2015; USGS 2016). Aspect and slope were calculated from a mosaic of elevation rasters. Dry-season NDVI was calculated from August through September 2016 Landsat 8 scenes (data obtained from the U.S. Geological Survey's Earth Resources Observation and Science Center). NDVI is a remotely-sensed measure of greenness often used to quantify vegetation distribution and density.

Lastly, a categorical shapefile for geologic substrate was acquired from the U.S. Geological Survey (Ludington et al. 2005). Vector to raster conversion was performed in

ArcMap 10.4.1 using a 100-meter cell size and the Maximum Area setting, which assigns values based on the majority area of the destination cell. This technique has been shown to be more accurate that alternative methods (Congalton 1997).

ArcMap 10.4.1 was used to process all environmental layers to identical spatial resolution and extent, as required by Maxent. Rasters were projected to an equal area coordinate system (NAD 1983 California Teale Albers) before resampling. Outputs were then re-projected to WGS 1984 and extracted by the two spatial extents used in the study (Fig. 1). A resolution of 100 meters was selected so that results would be more applicable to management and conservation decision-making (Brummer et al. 2013).

Correlation analysis was performed for all continuous variables using the principal component analysis tool in ArcMap 10.4.1. Highly correlated variables ( $\geq$ |0.75|) in the correlation matrix were removed so that only one of the variables remained. In selecting and refining the predictors, I prioritized variables of ecological relevance to insect development, host availability and conditions, and disturbance (Elith et al. 2011). Twelve variables were used as predictors for all ISHB models (Table 1).

The predictor set is limited in that it does not include biotic interactions that may influence beetle distribution. This is a common restriction on correlative SDMs, particularly for an invasive species that is relatively new to science. Little is known about ISHB's life history in terms of interspecific competition or predation, especially in California (Umeda et al. 2016), or about specific host characteristics that influence vulnerability.

Dry-season NDVI and land cover variables were intended to serve as proxies for host plant material, but host availability does not guarantee susceptibility. Likelihood of infestation is also influenced by host vigor and stand conditions (Paine et al. 1997), which can vary from year to year. Because the bioclimatic variables are averaged over a thirty-year period, conditions that induce drought or moisture stress are not represented by these predictors.

#### **3.3. Model Parameters**

Maxent version 3.3.3 k was used to create twenty ISHB models at a 100-meter spatial resolution (Phillips et al. 2004). I tested models using three parameters: length of sampling period, spatial extent, and spatial filtering (Table 2). Default settings and 10,000 background points were used for all models. Each model used in the analyses was the average of ten cross-validation replicates. This form of replication randomly splits the records into equal-size "folds," each of which was used for model evaluation in one of the replicates. In this case, each run used nine of the folds for model training and the remaining fold—approximately 11% of the total sample size—for model testing.

#### **3.3.1.** Length of Sampling Period

In this research, temporal sampling bias was represented by the length of the sampling period from which ISHB records were taken. Five chronologically cumulative datasets, referred hereto after as sampling periods, were derived from the occurrence records. I refer to the models by the last year of data in the sampling period (e.g. models based on 2012-2015 records are called "2015 models"). There were four iterations of each sampling period, using different combinations of spatial extent and spatial filtering (described below).

Models with a longer sampling period had a larger training dataset (Table 2) that was potentially more environmentally representative of the ISHB niche. This research did not control for differences in sample size, the effects of which may be less important than those of sampling

bias (Bean et al. 2012; Boria et al. 2014). Improvements in model performance are more often due to spatial bias treatment, rather than larger sample size alone. Bean et al. (2012) observed that "well-sampled data with few records are better than biased data of any sample size" (p. 255). Sample size also has an inconsistent relationship with area under the receiver operating curve (AUC), a common SDM performance metric. AUC has been found to both increase with (Hernandez et al. 2006) and be relatively unaffected by changes in sample size (Wisz et al. 2008; Anderson and Gonzalez 2011).

#### **3.3.2.** Spatial Extent

Ideally, areas that have not been surveyed should be excluded from the background area in Maxent (Elith et al. 2011). In a presence-only model, selecting too large a background may produce misleading model results, including inflated performance statistics (VanDerWal et al. 2009). ISHB models were thus created using two spatial extents: 1) the state of California and 2) the external boundary of Ecoregions 8 and 85 (Environmental Protection Agency, Level III) (Fig. 1). The outputs are referred to as California and Ecoregion models, respectively. Ecoregions 8 and 85 were merged in ArcMap 10.4.1 to obtain a single outer boundary for the area. The small portion of Ecoregion 85 that extends into Mexico was clipped from the extent. The vast majority of ISHB records have been collected, coincidentally, from Ecoregion 85. Few areas outside of this extent have been surveyed, and this may have inflated some performance metrics for the California models. However, the political boundary of California was tested because it reflects the likely jurisdiction of policymakers. The future distribution of ISHB may concern resource managers at the state level, particularly if preventative strategies outside of Southern California are to be implemented.

#### **3.3.3.** Spatial Filtering

A study by Yackulic et al. (2013) found that 87% of Maxent modeling studies are affected by spatial sampling bias. A spatially biased model is often fitted more closely to survey effort, rather than the actual distribution of a species (Phillips et al. 2009). Spatial filtering can help mitigate this bias by reducing clusters of geographic records. It has been shown to improve model predictive accuracy and improve representation of non- or less-surveyed areas in the modeled extent (Kramer-Schadt et al. 2013).

In order to examine the impact of spatial sampling bias on emerging, invasive SDMs, ISHB models were created both with and without spatial filtering. I used a method similar to the rarefied unfiltered treatment in Boria et al. (2014) and the systematic sampling treatment in Fourcade et al. (2014), in which records are subsampled at a coarser resolution than that of the model. To create the spatially filtered dataset, NOAA Biogeography Branch's Sampling Design Tool was used to randomly sample records from a 500-meter fishnet generated in ArcMap 10.4.1. This further reduced the number of ISHB observations to 372. Models that have been treated with this method are hereafter referred to as "filtered," versus "unfiltered."

#### **3.4. Model Evaluation**

The primary metric of model performance in this study was sensitivity, or the proportion of true-presences correctly classified by each model. Sensitivity was calculated using 150 ISHB records that were excluded from model training (Appendix A). Thirty records were randomly selected from each survey year using NOAA Biogeography Branch's Sampling Design Tool.

The predicted values at each of the model-independent test points were extracted from the Maxent outputs using ArcMap 10.4.1. Correctly classified records were those points with

values greater than or equal to the minimum training presence (MTP) threshold of each respective model (Table 3).

Thresholds are often used to create binary maps of habitat suitability, and should be selected based on study objectives and restrictions (Hernandez et al. 2006; Holcombe et al. 2010). Fixed thresholds (e.g. threshold=0.5, 10 percentile training presence) omit a defined percentage of training records, which can help to account for varying quality of input data (Ward and Morgan 2014). The MTP, which sets the threshold to the lowest probability predicted for any of the true positives that trained the model, was selected because confidence in the precision and accuracy of the ISHB records is high.

In addition to sensitivity, MTP was used to calculate suitable area. The range of suitable values, based on MTP, were also calculated for the leading contributing variables.

Metrics based on specificity, the proportion of correctly classified true-absences, should be avoided for presence-only models (Hernandez et al. 2006; Merow et al. 2013). Errors of commission (true-absences classified as presences) are difficult to interpret, not only because true-absences are lacking, but because they could indicate sites where the species could exist and does not yet. For such species (e.g. rare, endangered, or invasive), which are known to presently occupy a limited part of their potential range, omission (true-presences classified as absences) is of greater concern than commission (Uden et al. 2015; Rovzar et al. 2016). Commission errors could also be caused by factors not included in the model, e.g. dispersal limitations and biotic interactions (Jiménez-Valverde et al. 2011).

One of the most common threshold-independent metrics used in model assessment is the area under the receiver operating curve (AUC), which relies on measures of both sensitivity and specificity (Elith and Leathwick 2009; Merow et al. 2013). AUC describes the probability that

the model can randomly predict a higher probability for a presence cell versus an absence (or pseudo-absence) cell (Phillips and Dudík 2008). Values range from 0 to 1.0, where AUC = 0.5 indicates model predictive ability equal to that of random prediction. Models with AUC  $\geq$  0.75 are generally considered suitable for use in conservation planning (Elith et al. 2006).

Though AUC is the only measure of predictive accuracy in some SDM studies (Broennimann et al. 2007; Wisz et al. 2008; Brummer et al. 2013), it is not an ideal performance metric of presence-only models due to the lack of true-absence data (Lobo et al. 2008; Pearson 2010). In Maxent, AUC has been found to increase when using too large a background area (VanDerWal et al. 2009; Merow et al. 2013). AUC values remain high even when spatial sampling bias is deliberately added to a model, but also decrease when that same bias is corrected through spatial filtering (Kramer-Schadt et al. 2013; Syfert et al. 2013; Fourcade et al. 2014). Because alternative metrics for presence-only models are few, AUC continues to be used in model evaluation. However, it is recommended that a secondary metric be used to corroborate high values and justify confidence in the model (Warren and Seifert 2011; Merow et al. 2013).

This study used mean AUC as a comparative metric between models, rather than as an absolute measure of model performance. Four one-way analysis of variance (ANOVA) tests were used to compare the effect of different sampling periods on AUC within each model series. I refer to the model series by spatial extent and spatial filtering, where +F indicates filtered models (i.e. California, California+F, Ecoregion, Ecoregion+F). Two-way ANOVA was also used to compare models within the same sampling period (i.e. all 2012 models, all 2013 models, etc.). All ANOVA and post hoc Tukey tests were conducted in RStudio (RStudio Team 2016).

#### 4. **RESULTS**

#### 4.1. Suitable Area

Area predicted suitable increased with length of sampling period, all other parameters being equal (Table 4). Filtered models were generally more conservative than their unfiltered counterparts (Fig. 2a-2e, 3a-3e, 4a-4e, 5a-5e). Spatial filtering decreased area predicted suitable by  $35.2 \pm 10.3\%$  in the California extent and  $22.7 \pm 10.8\%$  in the Ecoregion extent (excluding 2012 Ecoregion models). Area predicted suitable was 5.8% greater for the filtered versus unfiltered 2012 Ecoregion model. Due to the areal difference of the spatial extents, the suitable area of the California models cannot be directly compared to that of the Ecoregion models.

#### 4.2. Model Sensitivity

Mean sensitivity increased with length of sampling period, all other parameters being equal (Table 5). The largest increase in sensitivity occurred between the 2012 and 2013 models. On average, sensitivity of each 2013 model was  $42.9 \pm 6.9$  percentage points higher than that of its 2012 counterpart. Average sensitivity of the 2014, 2015, and 2016 models was consistently high at 99.3  $\pm 0.6\%$ .

Sensitivity was higher to test records from the modeled sampling period (e.g. 2013 models were more sensitive to 2012-2013 records than records after 2013). All models correctly predicted 97.9  $\pm$ 1.6% of the 2012 test records. However, average sensitivity to the 2015 test records (77.5  $\pm$ 29.8%) was lower than that of the 2016 test records (82.0  $\pm$ 28.5%).

Spatial filtering did not have a consistent effect on sensitivity. The largest increase in sensitivity due to spatial filtering occurred among the 2012 models. Sensitivity of the 2012 California and 2012 Ecoregion models both increased by eight percentage points when training

records were filtered. The largest decrease occurred in the sensitivity of the 2013 Ecoregion models, which decreased by ten percentage points when records were filtered.

The effect of spatial extent on sensitivity depended on sampling period. Average sensitivity of the 2012, 2013, and 2014 Ecoregion models was  $5.7 \pm 4.3$  percentage points lower than that of their California counterparts. Among 2015 and 2016 models, however, the difference in sensitivity between California and Ecoregion models was less than one percentage point.

#### **4.3.** Area Under the Receiver Operating Curve

All twenty ISHB models performed better than random prediction and obtained AUC greater than 0.93 (Table 6). Within each model series, AUC decreased with length of sampling period, which had a statistically significant effect on AUC at the p < 0.001 level as determined by one-way ANOVA. Post hoc Tukey tests showed multiple pairwise differences among the AUC values of each model series (Fig. 6). The AUC of each 2012 model was statistically significantly higher than that of its 2016 counterpart (p < 0.001).

In each sampling period, spatial extent had a statistically significant effect on AUC as determined by two-way ANOVA. The AUC of each California model was statistically significantly higher than that of its Ecoregion counterpart (e.g. 2015 California+F > 2015 Ecoregion+F) (p < 0.001; p < 0.01 for 2012 CA/Ecoregion pair) (Fig. 7).

All else being equal, there was no statistically significant effect of spatial filtering alone on AUC, as determined by two-way ANOVA, except in the 2016 model group. Post hoc Tukey tests showed no statistically significant difference between the AUC of an Ecoregion model and its filtered Ecoregion counterpart (Fig. 7). Among California models, spatial filtering increased AUC for the 2014 (p < 0.01), 2015 (p < 0.01), and 2016 (p < 0.001) models only.

#### 4.4. Variable Contribution

The leading contributing variables were minimum temperature of the coldest month (for sixteen models) or percent impervious surface (for four models) (Table 7). Both were among the top three contributing variables for nineteen out of twenty models. Also among the top three contributing variables were isothermality (more important in California models) and dry-season NDVI (more important in Ecoregion models). Slope and aspect contributed least to the models. Precipitation metrics, percent tree canopy cover, and geologic substrate contributed less than 4% to the models. Variable contribution differed somewhat between the two spatial extents.

Within the suitable area determined by MTP, mean minimum temperature of the coldest month was  $3.97 \pm 1.13$ °C (Table 8). Mean suitable surface imperviousness was  $14.0 \pm 10.1\%$ , mean isothermality was  $52.9 \pm 2.5\%$ , and mean dry-season NDVI was  $0.19 \pm 0.04$ .

#### 5. **DISCUSSION**

The results of this study show that temporally-biased sampling data can be used to train high-performing SDMs for an incipient invasive species like ISHB, albeit with a limited shelflife. All models achieved AUC > 0.93 and correctly classified 98.8  $\pm$ 1.1% of the independent test records from their sampling period. In discussing model predictive ability, I focus primarily on sensitivity and use AUC only as a relative measure of performance. Limitations of AUC are discussed below.

#### **5.1. Utility of Temporally-Biased Models**

Unsurprisingly, predictive ability was more robust for the time period on which the model was trained, then deteriorated with time after sampling period. This suggests that invasive

SDMs will more effectively meet detection and prevention aims if incorporated into an adaptive ecological management system, in which the results of management actions continuously inform subsequent decisions and strategies (Uden et al. 2015). There is no "best" or "final" model for an emerging invasive species. Model-informed surveys will yield additional species records, which should be added to training datasets as they become available. It is important to acknowledge that models have a temporal limit, but these actions may prolong the utility of the model.

Despite these limits, the ISHB models were also able to predict records from the year subsequent to the training sampling period, i.e. the 2012 models predicted  $60.0 \pm 14.7\%$  of the 2013 records; the 2013 models predicted  $94.6 \pm 7.9\%$  of the 2014 records; the 2014 models predicted  $87.5 \pm 7.4\%$  of the 2015 records; and the 2015 models predicted  $97.5 \pm 1.7\%$  of the 2016 records (Table 5). This sensitivity suggests that Maxent models for emerging invasive species are able to anticipate new occurrences up to a certain threshold. That threshold is likely species-dependent and requires further investigation.

The 2016 models performed best in terms of sensitivity. These models were trained on a larger and presumably more diverse dataset that covered a broader geographic extent. However, the 2015 test records were the most difficult to classify among all models, and yielded higher omission rates than the 2016 test records (Table 5). This suggests that fewer novel environments were sampled in 2016 than in 2015, despite the discovery of ISHB in new counties. SDMs are often fitted to environmental rather than geographic space (Phillips et al. 2009), which is why the 2012 and 2013 (Fig. 2a-b, 3a-b, 4a-b, 5a-b) models could identify suitable habitat in San Diego County before ISHB was observed there in 2014 (Fig. 2c, 3c, 4c, 5c). Sampling across geographic space is thus less important than sampling across environmental space (Vaughan and Ormerod 2003).

It can be difficult to anticipate monitoring needs for a new invasive species before its full, potential threat has been recognized. But the sensitivity results in this study indicate that biases in species occurrence data can be minimized by balancing survey efforts across environmental space as well as geographic space. If this results in inconsistent geographic coverage across the landscape, correlative distribution models may help to fill in the gaps.

ISHB continues to spread, but it is already well-established in many regions of Southern California. Detection and monitoring efforts are still limited to visual surveys and, more recently, trapping using the lure quercivorol, which is attractive to several other species of ambrosia beetle (Carrillo et al. 2015; Umeda et al. 2016). SDMs can contribute to management efforts for ISHB and other incipient invasive species in a cost-effective, adaptive way. The results of this study show that these models were able to reliably detect new occurrences, and that this ability would be complemented by concurrent field surveys in novel environmental conditions. The average 2012 model was trained on the most biased data, but predicted over half of the 2013 test records (Table 5). Such predictions may have aided early containment of ISHB and identified vulnerable areas in and immediately surrounding Los Angeles.

#### 5.2. Effects of Spatial Filtering and Spatial Extent

Spatial filtering is recommended if geographic clustering attributable to sampling bias occurs in the species presence data. Filtered models were generally more discriminating in terms of suitable area (Table 4), but did not inhibit sensitivity. Sensitivity of the 2014, 2015, and 2016 models was high ( $\geq$  94%) for both the filtered and unfiltered series (Table 5). Spatial filtering also increased sensitivity of the 2012 models, for which sampling bias was highest, by 15.6%

(California extents) and 17.9% (Ecoregion extents). This suggests that filtered models can guide the identification of priority conservation areas without compromising model sensitivity.

It is generally recommended that presence-only SDMs utilize a more conservative spatial extent, so that pseudo-absences drawn from the background area do not inflate performance metrics (Lobo et al. 2008). In this study, however, each California model achieved higher sensitivity and AUC than that of its Ecoregion counterpart. The surveyed Ecoregions may have been too narrow an extent (VanDerWal et al. 2009) that fitted the model too closely to the training data. On the other hand, California may be an unnecessarily broad extent for a species like ISHB. There is likely an intermediate extent that would better serve ISHB detection. Including a buffer around the surveyed area may help to produce less restrictive predictions for invasive species that have yet to establish.

While it is clear that the 2016 models were the most successful (within each series), it is more difficult to identify the spatial extent and spatial filtering settings that optimize model performance. Among the series in this study, the filtered 2016 California model provided the most accurate predictions of ISHB presence. But the "best" model in any comparative assessment will be constrained to the parameters of the study. In other words, there may be an inbetween spatial extent that better serves ISHB prediction. Selection of spatial extent, and the level of filtering, should be species- and data-oriented.

#### **5.3. Limitations of the AUC**

Though I discuss AUC as a comparative metric within and among model series, I attribute no ecological significance to the absolute AUC values, especially as a standalone performance metric.

AUC should not be used to compare invasive SDMs affected by varying degrees of bias. In the ISHB models, sensitivity increased as length of sampling period expanded, but AUC values decreased (Table 6). The 2012 models had the highest AUC values, but the lowest sensitivity to all records after 2012. The 2016 Ecoregion and 2016 Ecoregion+F models, despite achieving 100% sensitivity to the independent test records, achieved the lowest AUC values.

Spatial filtering is known to reduce geographic bias in model results (Kramer-Schadt et al. 2013; Syfert et al. 2013), but the effect of spatial filtering on AUC was inconsistent (Fig. 7). AUC also failed to reflect the improved sensitivity of the 2012 filtered models. Selection of spatial extent should not be based on AUC alone, as large background areas often inflate AUC values (Lobo et al. 2008; Wisz et al. 2008; VanDerWal et al. 2009).

#### **5.4. Important Predictors of ISHB**

The two most important predictors of ISHB were minimum temperature of the coldest month and percent impervious surface. Relative variable contribution differed by spatial extent, so that the third leading contributor was isothermality for the California models and dry-season NDVI for the Ecoregion models. The climate variables are likely linked to beetle physiology, while the land cover variables help to describe host availability.

The importance of the minimum temperature of the coldest month variable suggests that ISHB, like many species in the subfamily Scolytinae, is freeze-susceptible (Lombardero et al. 2000). Temperature minimums are often an important determinant of insect distributions (Ungerer et al. 1999). Cold temperatures may induce mortality and constrain reproduction, development, flight, and overwintering survival (Lombardero et al. 2000; Sidder et al. 2016). For ISHB, the lower limit of suitable minimum temperature was  $0.36 \pm 2.56^{\circ}$ C (Table 8), but care

should be taken in projecting this lower limit to other regions, as cold tolerance of other Scolytinae has been shown to vary geographically (e.g. due to microclimates) (Régnière and Bentz 2007; Sidder et al. 2016).

Isothermality, a measure of diurnal temperature oscillations relative to the annual temperature range, was also an important climatic predictor. Suitable isothermality ranged from  $43.8 \pm 3.3$  to  $62.3 \pm 4.0\%$  (Table 8), suggesting a preference for milder climates with less short-term variation in temperature. This may help to explain the predicted distribution of ISHB along the coast of California (Fig. 2a-2e, 3a-3e, 4a-4e, 5a-5e).

Apart from percent impervious surface, the California models are dominated by climate variable contributions (Table 7). Isothermality (and to some extent, minimum temperature) may have been more prominent for the California extent because Ecoregions are, by definition, areas of similar climate. A more limited spatial extent may allow models to be more discriminating in terms of non-climatic variables, such as dry-season NDVI, which contributed significantly more to the Ecoregion models.

Dry-season NDVI and percent impervious surface were intended to describe host availability. Average suitable surface imperviousness  $(14.0 \pm 10.1\%)$  is skewed towards the lower end of the range, where a higher density of host material could be expected (Table 8). The range maximum ( $85.0\pm22.3\%$ ) supports field observations that ISHB will readily infest hosts in the urban forest as well as natural areas. The high contribution of surface imperviousness also suggests that indicators of anthropogenic activity (disturbance/development) are highly relevant to invasive species SDMs, as they indicate the probability of introduction (Lippitt et al. 2008).

ISHB distribution cannot be explained solely by climate, especially if more discriminating predictions are required. Variables that describe host conditions are just as

influential, and potentially more so (DeRose et al. 2013), because ISHB occurrence is necessarily linked to host presence. Predictions of ISHB habitat suitability are effectively predictions of host availability, if not actual susceptibility (based on host vigor). It is therefore important to account for finer-scale temporal variations in local climate conditions that affect host vigor. This cannot be provided by the thirty-year averages of the WorldClim variables, but change in NDVI, rather than dry-season NDVI alone, may be serve as a useful predictor for future models.

#### 6. CONCLUSION

The results of this research indicate that SDMs can be used to predict new occurrences of an emerging invasive species, in spite of temporal sampling bias. Model performance can be improved, and temporal sampling bias mitigated, by approaching the modeling process through an adaptive management strategy that continuously incorporates new field data into updated models. Management objectives should be considered in the implementation of spatial filtering and selection of spatial extent, which can produce more or less discriminating predictions as well as influence relative contributions of environmental predictors.

It is recommended that AUC be used cautiously in the interpretation of presence-only SDMs. A sensitivity metric should be used to corroborate and provide context for AUC values. One limitation of the sensitivity results in this study is that the test records, while independent from model training, were randomly subsampled from the original ISHB dataset and thus potentially affected by the same biases as the training data (Boria et al. 2014). Field validation would provide completely independent test records, as well as temporally novel 2017 records with which to test the 2016 models. Ground-truthing would also yield both sensitivity and

specificity results. Collection of true-absence data is needed to determine whether models are over-predicting ISHB occurrence.

Whether the modeled species is emerging or established, invasive or native, SDMs are subject to bias in occurrence records. In a presence-only correlative model like Maxent, invasive SDMs will only be sensitive to environments represented by or similar to the training data. This may be inadequate if the goal is to describe the species' full, potential range or niche. If, however, the objective is to detect and protect environments with conditions similar to those that have already proven suitable, then the methods in this paper provide a framework for creating reliable invasive SDMs.

# **TABLES AND FIGURES**

### Table 1

Descriptions of variables and rationale for inclusion in models.

| Variable                      | Rationale  | Source                          |
|-------------------------------|--|---------------------------------|
| Isothermality                 | Insect development                                   | WorldClim 1.4                   |
| Max Temp. of Warmest Month    | Insect development                                   | WorldClim 1.4                   |
| Min Temp. of Coldest Month    | Insect development                                   | WorldClim 1.4                   |
| Temperature Annual Range      | Insect development/<br>Host environmental conditions | WorldClim 1.4                   |
| Precipitation of Wettest Qtr. | Host environmental conditions                        | WorldClim 1.4                   |
| Precipitation of Driest Qtr.  | Host environmental conditions                        | WorldClim 1.4                   |
| Slope                         | Host environmental conditions                        | USGS 3D Elevation Program       |
| Aspect                        | Host environmental conditions                        | USGS 3D Elevation Program       |
| Geologic substrate            | Host environmental conditions                        | USGS Open-File Report 2005-1305 |
| Percent Impervious Surface    | Disturbance/Host availability                        | National Land Cover Database    |
| Percent Tree Canopy Cover     | Host availability                                    | National Land Cover Database    |
| Dry-season NDVI               | Host availability                                    | USGS EROS Center                |

Descriptions of model outputs created in the study. Sampling period refers to the temporal range of occurrence records used in model training and testing. Ecoregion Spatial Extent refers to ecoregions 8 and 85 (EPA Level III).

| Model Series  | Sampling<br>Period | Spatial Extent | Spatial<br>Filtering | Sample Size<br>(Training<br>records) |
|---------------|--------------------|----------------|----------------------|--------------------------------------|
|               | 2012               | California     | No                   | 120                                  |
| O allifa main | 2012-2013          | California     | No                   | 239                                  |
| unfiltered    | 2012-2014          | California     | No                   | 530                                  |
| unnitered     | 2012-2015          | California     | No                   | 637                                  |
|               | 2012-2016          | California     | No                   | 1052                                 |
|               | 2012               | California     | Yes                  | 64                                   |
|               | 2012-2013          | California     | Yes                  | 116                                  |
| filtered      | 2012-2014          | California     | Yes                  | 215                                  |
| intered       | 2012-2015          | California     | Yes                  | 267                                  |
|               | 2012-2016          | California     | Yes                  | 372                                  |
|               | 2012               | Ecoregion      | No                   | 120                                  |
|               | 2012-2013          | Ecoregion      | No                   | 239                                  |
| Ecoregion     | 2012-2014          | Ecoregion      | No                   | 530                                  |
| unntereu      | 2012-2015          | Ecoregion      | No                   | 637                                  |
|               | 2012-2016          | Ecoregion      | No                   | 1052                                 |
|               | 2012               | Ecoregion      | Yes                  | 64                                   |
|               | 2012-2013          | Ecoregion      | Yes                  | 116                                  |
| Ecoregion     | 2012-2014          | Ecoregion      | Yes                  | 215                                  |
| intered       | 2012-2015          | Ecoregion      | Yes                  | 267                                  |
|               | 2012-2016          | Ecoregion      | Yes                  | 372                                  |

Minimum training presence (MTP) threshold of each model output.

| Model Series | Sampling<br>Period | МТР    |
|--------------|--------------------|--------|
|              | 2012               | 0.1036 |
|              | 2012-2013          | 0.048  |
| California   | 2012-2014          | 0.0209 |
|              | 2012-2015          | 0.0287 |
|              | 2012-2016          | 0.017  |
|              | 2012               | 0.2534 |
|              | 2012-2013          | 0.0571 |
| filtered     | 2012-2014          | 0.0501 |
|              | 2012-2015          | 0.0686 |
|              | 2012-2016          | 0.0296 |
|              | 2012               | 0.0532 |
| Feenenien    | 2012-2013          | 0.0293 |
| unfiltered   | 2012-2014          | 0.0159 |
|              | 2012-2015          | 0.0158 |
|              | 2012-2016          | 0.0073 |
|              | 2012               | 0.1386 |
| Farmation    | 2012-2013          | 0.1181 |
| filtered     | 2012-2014          | 0.065  |
|              | 2012-2015          | 0.0351 |
|              | 2012-2016          | 0.0221 |

Area predicted suitable by the minimum training presence threshold, expressed as a percentage of the total spatial extent. California models cannot be compared to Ecoregion models.

| (                  | California Models |           |                    | Ecoregion Models | S          |
|--------------------|-------------------|-----------|--------------------|------------------|------------|
| Sampling<br>Period | Unfiltered        | Filtered  | Sampling<br>Period | Unfiltered       | Filtered   |
| 2012               | 2.1%              | 1.6%      | 2012               | 12.0%            | 12.8%      |
| 2013               | 4.7%              | 3.5%      | 2013               | 21.9%            | 13.3%      |
| 2014               | 8.1%              | 4.4%      | 2014               | 28.4%            | 21.1%      |
| 2015               | 9.1%              | 5.3%      | 2015               | 33.5%            | 29.7%      |
| 2016               | 12.9%             | 7.5%      | 2016               | 44.5%            | 37.9%      |
| Average            | 7.4 ±3.7%         | 4.4 ±1.9% | Average            | 28.1 ±10.9%      | 23.0 ±9.7% |

Sensitivity of model outputs, calculated using the minimum training presence threshold. Thirty model-independent test records were randomly selected from each sampling year (columns indicate sensitivity to test records from that year only). Filtered models are indicated by +F.

|                    |                 |       | 9     | 6 Correctly | / Classifie | d Test Re | cords          |                       |
|--------------------|-----------------|-------|-------|-------------|-------------|-----------|----------------|-----------------------|
| Sampling<br>Period | Model<br>Series | 2012  | 2013  | 2014        | 2015        | 2016      | All<br>Records | In Sampling<br>Period |
| 2012               | CA              | 96.7  | 53.3  | 50.0        | 20.0        | 36.7      | 51.3           | 96.7                  |
|                    | CA +F           | 96.7  | 76.7  | 53.3        | 40.0        | 30.0      | 59.3           | 96.7                  |
|                    | Ecoregion       | 96.7  | 43.3  | 50.0        | 13.3        | 20.0      | 44.7           | 96.7                  |
|                    | Ecoregion +F    | 100.0 | 66.7  | 50.0        | 23.3        | 23.3      | 52.7           | 100                   |
|                    | CA              | 96.7  | 100.0 | 100.0       | 86.7        | 93.3      | 95.3           | 98.4                  |
| 2012               | CA +F           | 96.7  | 100.0 | 100.0       | 90.0        | 93.3      | 96.0           | 98.4                  |
| 2013               | Ecoregion       | 96.7  | 100.0 | 93.3        | 83.3        | 90.0      | 92.7           | 98.4                  |
|                    | Ecoregion +F    | 96.7  | 100.0 | 83.3        | 53.3        | 80.0      | 82.7           | 98.4                  |
|                    | CA              | 96.7  | 100.0 | 100.0       | 93.3        | 100.0     | 98.0           | 98.9                  |
| 2012               | CA +F           | 96.7  | 100.0 | 100.0       | 90.0        | 96.7      | 96.7           | 98.9                  |
| 2014               | Ecoregion       | 96.7  | 100.0 | 100.0       | 90.0        | 93.3      | 96.0           | 98.9                  |
|                    | Ecoregion +F    | 100.0 | 100.0 | 100.0       | 76.7        | 93.3      | 94.0           | 100                   |
|                    | CA              | 96.7  | 100.0 | 100.0       | 100.0       | 100.0     | 99.3           | 99.2                  |
| 2012               | CA +F           | 96.7  | 100.0 | 100.0       | 96.7        | 96.7      | 98.0           | 98.4                  |
| 2015               | Ecoregion       | 100.0 | 100.0 | 100.0       | 96.7        | 96.7      | 98.7           | 99.2                  |
|                    | Ecoregion +F    | 100.0 | 100.0 | 100.0       | 96.7        | 96.7      | 98.7           | 99.2                  |
|                    | CA              | 96.7  | 100.0 | 100.0       | 100.0       | 100.0     | 99.3           | 99.3                  |
| 2012               | CA +F           | 100.0 | 100.0 | 100.0       | 100.0       | 100.0     | 100.0          | 100                   |
| 2016               | Ecoregion       | 100.0 | 100.0 | 100.0       | 100.0       | 100.0     | 100.0          | 100                   |
|                    | Ecoregion +F    | 100.0 | 100.0 | 100.0       | 100.0       | 100.0     | 100.0          | 100                   |
| Average            | Sensitivity     | 97.9  | 92.0  | 89.0        | 77.5        | 82.0      | 87.7           | 98.8                  |
| Standar            | d Deviation     | 1.6   | 17.4  | 20.0        | 29.8        | 28.5      | 18.8           | 1.1                   |

Test area under the receiver operating curve (AUC) and standard deviation. Sampling periods are described by the last year of test data. Filtered models are indicated by +F.

|               | Sampling Period |               |               |               |               |  |  |  |
|---------------|-----------------|---------------|---------------|---------------|---------------|--|--|--|
| Model Series  | 2012            | 2013          | 2014          | 2015          | 2016          |  |  |  |
| California    | 0.993 ±0.0015   | 0.986 ±0.0023 | 0.974 ±0.0026 | 0.970 ±0.0028 | 0.954 ±0.0032 |  |  |  |
| California +F | 0.994 ±0.0016   | 0.991 ±0.0022 | 0.987±0.0023  | 0.983 ±0.0028 | 0.978 ±0.0027 |  |  |  |
| Ecoregions    | 0.977 ±0.0088   | 0.969 ±0.0084 | 0.958 ±0.0069 | 0.948 ±0.0078 | 0.933 ±0.0069 |  |  |  |
| Ecoregions +F | 0.966 ±0.0108   | 0.965 ±0.0111 | 0.954 ±0.0112 | 0.941 ±0.0135 | 0.935 ±0.0122 |  |  |  |

Mean variable contribution to all twenty ISHB models (second column) and to individual model series.

|                               | Mean Contribution |           |                |                     |                       |  |  |  |
|-------------------------------|-------------------|-----------|----------------|---------------------|-----------------------|--|--|--|
| Variable                      | All models        | CA series | CA+F<br>series | Ecoregion<br>series | Ecoregion+F<br>series |  |  |  |
| Min temp. coldest month       | 34.5 ±13.3        | 45.3 ±8.7 | 35.7 ±12       | 31.0 ±9.9           | 26.2 ±13.9            |  |  |  |
| Percent impervious surface    | 24.9 ±9.5         | 19.1 ±7.1 | 28.0 ±11.8     | 21.8 ±5.2           | 30.6 ±7.8             |  |  |  |
| Isothermality                 | 13.7 ±6.3         | 18.0 ±4.5 | 18.9 ±4.0      | 10.9 ±3.3           | 7.2 ±4.1              |  |  |  |
| Temperature annual range      | 5.9 ±3.3          | 8.4 ±3.3  | 6.8 ±3.2       | 3.2 ±1.3            | 5.4 ±2.7              |  |  |  |
| Dry-season NDVI               | 5.4 ±5.4          | 0.6 ±0.1  | 0.9 ±0.5       | 12.0 ±3.0           | 7.9 ±3.7              |  |  |  |
| Max temp. warmest month       | 4.9 ±2.6          | 5.2 ±2.4  | 5.1 ±0.6       | 5.6 ±4.0            | 3.6 ±1.6              |  |  |  |
| Percent tree canopy cover     | 3.3 ±2.3          | 1.2 ±0.5  | 2.4 ±1.4       | 3.3 ±1.3            | 6.2 ±1.8              |  |  |  |
| Geologic substrate            | 2.4 ±2.7          | 0.6 ±0.5  | 0.8 ±0.7       | 3.5 ±2.0            | 4.8 ±3.4              |  |  |  |
| Precipitation of driest qtr.  | 2.0 ±2.8          | 0.5 ±0.5  | 0.4 ±0.2       | 4.3 ±3.7            | 2.9 ±2.3              |  |  |  |
| Precipitation of wettest qtr. | 1.9 ±2.2          | 1.0 ±1.2  | 0.8 ±0.8       | 2.7 ±2.8            | 2.9 ±2.5              |  |  |  |
| Slope                         | 0.8 ±0.9          | 0.1 ±0.1  | 0.1 ±0.1       | 1.2 ±0.5            | 1.8 ±0.9              |  |  |  |
| Aspect                        | 0.3 ±0.4          | 0.1 ±0.1  | 0.2 ±0.2       | 0.6 ±0.5            | 0.5 ±0.4              |  |  |  |

### Table 8

Mean, minimum, and maximum values of the leading contributing variables across all ISHB models, calculated within the suitable area defined by the minimum training presence threshold.

| Variable                     | Mean       | Minimum    | Maximum    |
|------------------------------|------------|------------|------------|
| Min temp. coldest month (°C) | 3.97 ±1.13 | 0.36 ±2.56 | 7.27 ±2.18 |
| Percent impervious surface   | 14.0 ±10.1 | 0 ±0       | 85.1 ±22.3 |
| Isothermality (%)            | 52.9 ±2.5  | 43.8 ±3.3  | 62.3 ±4.0  |
| Dry-season NDVI              | 0.19 ±0.04 | -0.1 ±0.15 | 0.57 ±0.06 |

# Figure 1

Model outputs were produced for two spatial extents: California and Ecoregions (8 and 85 combined).



# Figures 2a-2e

California unfiltered model outputs. Gray areas are unsuitable, based on the minimum training presence threshold.



# Figures 3a-3e

California filtered model outputs. Gray areas are unsuitable, based on the minimum training presence threshold.



### Figures 4a-4e

Ecoregion unfiltered model outputs. Gray areas are unsuitable, based on the minimum training presence threshold.



### Figures 5a-5e

Ecoregion filtered model outputs. Gray areas are unsuitable, based on the minimum training presence threshold.



### Figure 6

Mean area under the receiver operating curve (AUC). Models are grouped by series (spatial extent and spatial filtering). Shared letters indicate that there is no statistically significant difference between the sampling periods (within that model series only) as determined by one-way ANOVA and post hoc Tukey tests. Filtered models are indicated by +F.



Model Series Groups

### Figure 7

Mean area under the receiver operating curve (AUC). Models are grouped by length of sampling period. Shared letters indicate that there is no statistically significant difference between those model series (within that sampling period only) as determined by two-way ANOVA and post hoc Tukey tests. Filtered models are indicated by +F.



### APPENDIX

Longitude, latitude, and year observed for 150 model-independent ISHB test records. Thirty records were randomly selected from each year of sampling. Records are listed by original identification number (OID).

| OID | Longitude      | Latitude      | Year | OID | Longitude      | Latitude      | Year |
|-----|----------------|---------------|------|-----|----------------|---------------|------|
| 0   | -117.063398997 | 32.5506940184 | 2015 | 37  | -117.797007186 | 33.6505815464 | 2016 |
| 1   | -116.881833594 | 32.7742398614 | 2014 | 38  | -117.820096428 | 33.6526805684 | 2016 |
| 2   | -116.872387995 | 32.7784379054 | 2014 | 39  | -117.802254741 | 33.6526805684 | 2016 |
| 3   | -116.884982127 | 32.7794874164 | 2014 | 40  | -117.801205230 | 33.6526805684 | 2015 |
| 4   | -116.882883105 | 32.7794874164 | 2014 | 41  | -117.800155719 | 33.6526805684 | 2015 |
| 5   | -116.880784083 | 32.7794874164 | 2014 | 42  | -117.831641049 | 33.6537300794 | 2013 |
| 6   | -116.879734572 | 32.7826359494 | 2014 | 43  | -117.830591538 | 33.6537300794 | 2013 |
| 7   | -117.031913667 | 33.1216280024 | 2015 | 44  | -117.829542027 | 33.6537300794 | 2013 |
| 8   | -117.029814645 | 33.1226775134 | 2015 | 45  | -117.828492516 | 33.6547795904 | 2013 |
| 9   | -117.019319535 | 33.1405192004 | 2014 | 46  | -117.802254741 | 33.6547795904 | 2015 |
| 10  | -117.025616601 | 33.1436677334 | 2014 | 47  | -117.801205230 | 33.6547795904 | 2015 |
| 11  | -117.019319535 | 33.1436677334 | 2014 | 48  | -117.835839093 | 33.6558291014 | 2013 |
| 12  | -117.163102542 | 33.2591139434 | 2015 | 49  | -117.833740071 | 33.6558291014 | 2013 |
| 13  | -117.249162444 | 33.2633119874 | 2016 | 50  | -117.828492516 | 33.6558291014 | 2013 |
| 14  | -117.703600707 | 33.5435314244 | 2013 | 51  | -117.811700340 | 33.6558291014 | 2016 |
| 15  | -117.707798751 | 33.5498284904 | 2014 | 52  | -117.833740071 | 33.6568786124 | 2014 |
| 16  | -117.706749240 | 33.5508780014 | 2014 | 53  | -117.821145939 | 33.6568786124 | 2016 |
| 17  | -117.713046306 | 33.5519275124 | 2016 | 54  | -117.813799362 | 33.6568786124 | 2016 |
| 18  | -117.708848262 | 33.5519275124 | 2013 | 55  | -117.811700340 | 33.6568786124 | 2016 |
| 19  | -117.707798751 | 33.5519275124 | 2013 | 56  | -117.590253519 | 33.6579281234 | 2015 |
| 20  | -117.714095817 | 33.5529770234 | 2013 | 57  | -117.643778580 | 33.6621261674 | 2016 |
| 21  | -117.713046306 | 33.5529770234 | 2013 | 58  | -117.943938726 | 33.6631756784 | 2015 |
| 22  | -117.711996795 | 33.5529770234 | 2014 | 59  | -117.943938726 | 33.6652747004 | 2015 |
| 23  | -117.710947284 | 33.5529770234 | 2013 | 60  | -117.624887382 | 33.6715717664 | 2016 |
| 24  | -117.708848262 | 33.5529770234 | 2014 | 61  | -117.650075646 | 33.6726212774 | 2016 |
| 25  | -117.741383103 | 33.5571750674 | 2016 | 62  | -117.664768800 | 33.6810173654 | 2015 |
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| 29  | -117.868373934 | 33.6295913264 | 2014 | 66  | -117.943938726 | 33.7208987834 | 2016 |
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| OID | Longitude      | Latitude      | Year | OID | Longitude      | Latitude      | Year |
|-----|----------------|---------------|------|-----|----------------|---------------|------|
| 74  | -118.091919777 | 33.7765228664 | 2012 | 112 | -117.972275523 | 33.9633358244 | 2012 |
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| 77  | -118.102414887 | 33.8248003724 | 2012 | 115 | -117.979622100 | 33.9801280004 | 2012 |
| 78  | -118.103464398 | 33.8258498834 | 2012 | 116 | -117.408688116 | 33.9906231104 | 2016 |
| 79  | -118.102414887 | 33.8258498834 | 2012 | 117 | -118.050988848 | 34.0168608854 | 2012 |
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| 81  | -117.717244350 | 33.8667808124 | 2015 | 119 | -118.024751073 | 34.0724849684 | 2012 |
| 82  | -117.767620878 | 33.8678303234 | 2015 | 120 | -117.760274301 | 34.0745839904 | 2012 |
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