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Africanized honeybee habitat suitability: a comparison between models for southern Utah and southern California

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ABSTRACT

The Africanized honeybee (AHB; *Apis mellifera scutellata*) is an invasive species which poses a threat to the United States' agricultural industry because of potential decline in pollination services. Previous research has confirmed that the AHB may still expand its range farther north and that limiting environmental factors for AHB distribution vary across the country. This study examines similarities and differences in AHB distribution and the relative importance of environmental factors between two regions of the southwestern United States: southern Utah and southern California. The Maximum Entropy (MaxEnt) modeling approach was used to create two species distribution models of the AHB. First a model was created based on AHB presence data in Utah. This model was used to estimate the Utah distribution and also to project the California distribution based on Utah environmental preferences. The second model was created to predict distribution in California and to project distribution in Utah based on AHB environmental preferences in California. The level of influence of each variable was measured through percent contribution and permutation importance. Model performance was assessed through the area under the receiver operating characteristic curve (AUC). Models estimated AHB presence with high accuracy (AUC > 0.95) in original environments, but were less accurate (AUC < 0.8) in novel environments. Minimum temperature was the primary controlling factor of AHB distribution in each model, and other variables followed similar ranking of importance between the two models. Species response curves varied substantially between the two models. Models did not transfer well from one region to the other because of local differences in response curves and the relative importance of environmental variables, suggesting that AHB in these regions may not have realized their potential geographic range.

1. Introduction

Species Distribution Modeling (SDM) is a useful and widely-implemented approach to examine the relationships between plants or animals and their physical environment (Elith and Leathwick, 2009; Miller, 2010). SDM has been of particular importance to the study of invasive species (Peterson, 2003; Shatz et al., 2013). When a species establishes itself in a novel environment outside its historic range, it can greatly affect the processes and organisms of that ecosystem (Badano & Marquet, 2008; Pejchar & Mooney, 2009). Often these invasive species are considered pests because they possess undesirable characteristics such as competition with native species that can affect ecosystem services (Funk et al., 2014). Moreover, populations of these invasive species may not be controlled by local fauna, resulting in population increases as they thrive in new geographic regions without natural predators. The Africanized honeybee (AHB; *Apis mellifera scutellata*) is an invasive insect that reached the United States in the 1990s, posing a threat to the U.S. agricultural industry, and, to a lesser degree, the health and safety of American citizens. Since 1990, the AHB has expanded its range throughout the southern U.S. with established populations spanning across the southern U.S. border and reaching as far north as southern Utah by 2008 (ARS, 2011). Since that time, the rate of expansion has slowed considerably. As the AHB approaches the realization of its potential niche, the questions of how far it may spread and what environmental factors may influence its

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distribution remain largely unanswered. Our understanding of AHB current and future distribution is critical for the agricultural industry and the comfort and safety of U.S. residents. Recent research has demonstrated that the AHB poses an economic threat to U.S. agriculture (National Research Council, 2007). European honeybees (EHB; *Apis mellifera* spp.) are kept in apiaries across the nation for agriculture pollination and honey production, but more of these bees are becoming Africanized every year (ARS 2011) through hybridization. The AHB produces less honey and pollinates less than the EHB (Macias-Macias et al., 2009), affecting agriculture production. The AHB inherits this tendency to yield smaller quantities of honey from its African honeybee predecessor, perhaps due to its evolution in tropical climates where it is unnecessary to store large honey reserves for winter (Schneider, 1997). While the AHB (also known as the "killer bee") is indeed a more aggressive subspecies of honeybee compared to the commonly domesticated European honeybee (EHB), chances of human fatality are actually quite low. Studies in South America showed that direct effects of AHB on humans are not as severe as experts initially thought prior to invasion (Kent, 1989). An Africanized colony is thought to be more difficult and expensive to manage because of its aggressive behavior and tendency to swarm to new locations frequently (Winston, 1992). Because of decreased honey yields, lower pollination rates, and added expenses of colony management, hybridization of EHB and AHB has important economic consequences. The U.S. Department of Agriculture has estimated that European swarms provide $20 billion in pollination services that are jeopardized by the AHB (McDowell, 1984), and more recent estimates from the National Research Council put this number at $57 billion (National Research Council, 2007). However, research has shown that up to 2010, economic damage resulting from AHB invasion may have been less severe than first anticipated (Livanis & Moss, 2010). Debate around the level of impact the AHB will have on the U.S. agricultural industry has remained unresolved, especially in light of Colony Collapse Disorder (CCD),[1] which has become of highest priority in the discussion and funding of honeybee research in the U.S. (CCD Steering Committee 2010).

In order to evaluate potential areas at risk of AHB infestation, this project aims to identify the environmental factors driving the distribution of the AHB in the southwestern United States using the presence-only Maximum Entropy method (MaxEnt; Phillips et al., 2004) at the forefront of the bee's current range. This study also aims to evaluate the transferability of the models in evaluating potential new infestation areas and evaluate similarities and differences in patterns of AHB distribution across two regions of the southwestern United States.

2. Study areas

Models were created from data representing two regions of the southwestern United States: southern Utah and southern California. We define southern Utah as the entire portion of the state south of 40° N, beyond which no AHB have been reported in any state. This portion of Utah receives extremely varied levels of precipitation, with annual averages exceeding 100 cm in the higher elevations, while the lower-lying areas across much of the southern portion of the region receive less than 25 cm per year. The Wasatch Mountains and other mountain ranges run north and south through the center of the region, exceeding 3000 m in elevation, and the lowest region of the state lies in the southwest corner at about 900 m. Temperatures throughout Southern Utah occasionally reach below −18 °C, and can exceed 38 °C.

Southern California (south of 36.5° N) has a broad diversity of physical environments, from the Mediterranean climate along the coast, to the low-lying Death Valley at 84 m below sea level, to the southern portion of the Sierra Nevada mountain range and the Tehachapi Mountains, which close off the southern end of the Central Valley as they reach the coast. The leeward side of these mountain ranges can receive under 38 cm of precipitation per year, while the western slopes receive more than 127 cm of rainfall per year. Mild coastal areas see maximum summer temperatures of about 24 °C while hot, dry regions raise the state average maximum temperature to 35 °C (Western Regional Climate Center 2015). The two study areas were selected due to data availability and the opportunity to compare two areas within the broader region of the southwestern United States.

3. Methods

SDM requires the parameterization of environmental limits of a species' suitable range. This parameterization is frequently performed through the use of locations where the species is known to be present. Through the MaxEnt algorithm version 3.3.3k (Phillips et al. 2004), we implemented this presence data approach to predict habitat suitability for the AHB in southern California and southern Utah.

A total of 88 AHB presence locations was collected in southern Utah between 2007 and 2011 by the Utah Department of Agriculture and Food. Presence data were collected from randomly-located traps across ten counties in southern Utah, supplemented by other observations when the presence of AHB was confirmed following reports of AHB from apiaries and citizens. In order to model AHB distribution in California we used presence locations ($n = 142$) recorded by the state government of California between 1990 and 2005 (USGS, 2005). For both California and Utah, all presence data are confirmed AHB observations (through DNA testing).

Bioclimatic variables were derived from Oregon State's PRISM Climate Group climatic datasets (Oregon State University, 2014), as it is considered more accurate than other datasets for mountainous and coastal regions (Daly et al. 2008). Six MODIS-derived Enhanced Vegetation Index (EVI) datasets representing spatial and temporal variations in vegetation density were also considered (see Supplemental Information), as well as data representing vegetation and land cover, vegetation diversity, and topographic aspect. Vegetation cover and diversity influence AHB foraging, while topographic aspect was also considered as it influences the length of daylight for foraging activity, especially in complex terrain like that found in southern Utah and California. Data for all biophysical parameters were collected for the same region across which AHB were sampled.

In order to identify the variables to use in the model, Pearson's r correlation coefficient was calculated for each variable pair (Williams et al., 2012). Groups of variables that correlated strongly with each other ($r > 0.7$) were reduced to a single factor, selected according to current scientific understanding of biological limitations of *A. mellifera*. A preliminary MaxEnt model was run with the selected variables that helped refine the set of variables further (Phillips et al. 2004). Variable importance was measured through percent contribution and permutation importance. The percent contribution method assesses the increase in gains with each step of the MaxEnt algorithm, and those variables which lead to the highest increases in gains are considered to be most important. This approach is useful but dependent on the particular iteration of the MaxEnt algorithm, and is especially sensitive if any variables correlate with each other (Phillips, Anderson, & Schapire, 2006).

[1] Colony Collapse Disorder is the name given to the recent decline of honeybees throughout North America and elsewhere, the causes of which are currently under debate. For more see Stankus, 2014.