Assessing the Risks Posed by Goldspotted Oak Borer to California and Beyond[1]

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Abstract

Goldspotted oak borer, *Agrilus auroguttatus*, has killed approximately 27,000 mature oaks in southern California. Consequently, the future spread of this insect is a significant concern to many oak woodland managers in California and across the United States. "Risk" reflects the likelihood that *A. auroguttatus* will continue to spread in North America and the magnitude of ecological, economic, or social impacts that this insect may cause.

This research project measured several critical biological parameters to refine spatial risk assessments for this insect. Cold tolerance testing of prepupae, the primary overwintering stage, indicates that this insect should be unable to survive in U.S. Department of Agriculture (USDA) Plant Hardiness Zones 2b – 5b. Some survivorship might occur in Zone 6a, but this outcome depends on the degree of cold acclimation that larvae may achieve. Host range testing with cut logs confirmed expectations that California black oak, *Quercus kelloggii*, and coast live oak, *Q. agrifolia*, are hosts and that Engelmann oak, *Q. engelmannii*, is not a host for *A. auroguttatus*. Our assays suggest that interior live oak, *Q. wislizeni*, and valley oak, *Q. lobata*, could be hosts, whereas Oregon white oak, *Q. garryana*, is unlikely to be a host. More study is needed to determine conclusively the host status of blue oak, *Q. douglasii*, canyon live oak, *Q. chrysolepis*, and cork oak, *Q. suber*, though field observations suggest canyon live oak can be colonized and killed by this insect. Flight mill studies indicate that adult females might fly up to 4 to 5 km/day and 9.3 km in their lifetime.

Collectively, these results suggest that *A. auroguttatus* poses the greatest risk nationally to California and southern Oregon. If dispersal only occurs through flight, the effects from this insect will likely remain concentrated in southern California for the next 5 to 10 years. Potential movement of *A. auroguttatus via* infested firewood or other human-mediated pathways and the unknown host status of oak species from eastern North America introduce considerable uncertainty into these models. This refined risk assessment supports the value of efforts to slow the spread of *A. auroguttatus*.

Key words: cold hardiness, exotic invasive species, goldspotted oak borer, mortality agent, MaxEnt, spread

Introduction

Pest risk analysts face the daunting challenge of forecasting the potential spread and impact of non-native species, frequently in areas that have no historical association with that species (Venette 2015). "Risk," in this context, refers to (i) the probability that a non-native species will arrive, establish, and spread within an area of concern and (ii) the magnitude of economic, ecological, or social harm caused by the species. Pest risk maps are needed to support strategic and tactical risk management decisions, such as whether

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regulatory actions should be taken to restrict human-mediated spread of the species or where monitoring traps should be placed to detect the species.

Extensive oak mortality in southern California in the early 2000s, at the time known colloquially as “oak croak,” was later attributed to the effects of the goldspotted oak borer, *Agrilus auroguttatus* (Coleoptera: Buprestidae) (Coleman and Seybold 2008). This insect species is native to southeastern Arizona and likely present in southwestern New Mexico, Texas, and northern Mexico; the population in California likely originated from the Dragoon Mountains in Arizona (Lopez and others 2014). As such, *A. auroguttatus* may be considered a domestic invasive species because, although this insect is native to the United States, it is not native to the Californian ecosystems where it now occurs and is causing harm.

Initial field observations suggested that coast live oak, *Quercus agrifolia*, California black oak, *Q. kelloggii*, and canyon live oak, *Q. chrysolepis* were particularly sensitive to feeding damage from *A. auroguttatus* (Coleman and Seybold 2008). Another oak species, Engelmann oak, *Quercus engelmannii*, was also infested, but was not apparently killed by *A. auroguttatus*. Larvae feed beneath the bark in the phloem, cambium, and outer xylem. This feeding disrupts the vasculature of the trees and leads to large areas of necrotic tissue; collectively this damage can ultimately cause crown thinning and tree death. More than 27,000 trees have been killed in an area centered near Julian, California (Coleman and others 2012, Haavik and others 2014a, USDA 2014). The area in southern California with oak mortality attributed to *A. auroguttatus* continues to expand (Coleman and others 2012, 2015).

Field observations and collection records provide strong evidence that Emory oak, *Quercus emoryi*, and silverleaf oak, *Q. hypoleucoides*, are hosts for *A. auroguttatus* in Arizona (Coleman and Seybold 2008, 2011; Haavik and others 2014a) and *Q. kelloggii* and *Q. agrifolia* are hosts in California (Coleman and Seybold 2008, 2011; Coleman and others 2011; Haavik and others 2014a). In both states, the density of emergence holes created by adults, the numbers of adult *A. auroguttatus* that emerged from bark samples, or the proportion of affected trees suggested that these oak species supported positive rates of population growth, the ultimate test of host status. In contrast, *Q. engelmannii* was initially presumed to be a host based on widespread mortality of this species in areas known to be infested with *A. auroguttatus* (Coleman and Seybold 2008); however, subsequent, detailed field observations confirmed that although some *A. auroguttatus* can complete development on this species, it is not preferred and unlikely to support positive population growth (Coleman and others 2012). Similarly, extensive mortality of *Q. chrysolepis* has been observed in areas with *A. auroguttatus*. Coleman and others (2012) reported that although the proportion of living and dead *Q. chrysolepis* with injury from *A. auroguttatus* was 48 percent and 60 percent, neither estimate was different from injury levels on comparable *Q. engelmannii*. This lack of a statistical difference may be due to a small sample size. Field surveys in Arizona failed to detect any evidence of feeding or development on Arizona white oak, *Q. arizonica*, or gray oak, *Q. grisea*, in areas where *A. auroguttatus* occurs (Coleman and Seybold 2011). The pattern of host utilization suggested a rule of thumb that red oaks (Section *Lobatae*) are more likely to be hosts whereas white oaks (Section *Quercus*) are unlikely to be hosts. This generalization led us inadvertently to characterize interior live oak, *Q. wislizeni*, as a known host (Downing and others 2009) when no direct evidence supported that conclusion.

The objective of this study was to gather additional biological information to better estimate where *A. auroguttatus* might locate suitable climate and hosts and when it might spread into these suitable areas. A previous assessment described the distribution and density of oak species that were thought to be hosts (Downing and others 2009). The current assessment builds from this foundation by using climate suitability models and empirical measures of cold tolerance to determine where temperature and moisture might be appropriate for *A. auroguttatus*. We incorporate new information about the potential host status of several *Quercus* spp. that occur at low densities or do not currently co-occur with *A. auroguttatus*. Lastly, we estimate rates of geographic range expansion (spread rates) by measuring flight distance on flight mills as a function of adult age.

Materials and methods

Climate suitability

Temperature and moisture frequently dictate the limits to the geographic distribution of invasive alien species. Several models, variously called species distribution models, ecological niche models, or environmental suitability models, are available to characterize the impact of abiotic factors such as climate on species distributions. Deductive models depend on a deep understanding of the impact of temperature or moisture on population growth rates; this understanding comes from appropriately designed experiments. In contrast, inductive models statistically relate species occurrence records to environmental covariates and forecast species occurrence based on those statistical relationships. For *A. auroguttatus*, we relied on a hybrid approach to characterize the suitability of the climate in North America. We measured the cold tolerance of this insect and relied on an inductive model, MaxEnt (Phillips and others 2006), to characterize climate suitability in areas where winter temperatures will not preclude establishment of this insect.

Empirical measurements of cold tolerance

For many temperate insects cold temperatures are likely to dictate the northern limits to the distribution of a species. Consequently, we assessed the cold tolerance of *A. auroguttatus* by measuring supercooling points of immature individuals, especially fourth (prepupae, “j-stage”) instars. *Agrilus auroguttatus* and other buprestids typically pass the winter in the j-stage, though the insect may pass the winter in earlier instars (Coleman and Seybold 2008). The supercooling point is the temperature at which insect body fluids spontaneously begin to freeze. Many temperate and subtropical insects are chill tolerant/freeze intolerant (in other words, individuals can survive exposure to temperatures below 0 °C, but die when fluids begin to freeze), so, the supercooling point represents the lowest temperature at which freeze intolerant insects might survive. Little is known about the cold tolerance of buprestids in general, but *Agrilus planipennis*, emerald ash borer, was found to be predominantly chill tolerant/freeze intolerant (Christianson 2014, Crosthwaite and others 2011). We suspect that this cold tolerance strategy is also true for *A. auroguttatus*.

Prepupae of *A. auroguttatus* were collected monthly in the fall and winter from the Cleveland National Forest in San Diego County, California by removing bark from naturally infested oaks. Extracted prepupae were placed in 24-well plastic plates and covered with cotton plugs. Plates were sealed (triple contained) inside insulated coolers and shipped *via* overnight courier to St. Paul, Minnesota. In a biosecurity level-2 quarantine laboratory, larval supercooling points were measured within 72 hours of receipt by following protocols from Carrillo and others (2004) with coiled copper-constantan thermocouples (Hanson and Venette 2013). Prepupae were held on the thermocouple with high vacuum grease. Thermocouples inside plastic syringes were placed near the center of 20 x 20 x 20 cm polystyrene cubes. When these cubes were placed in a -80 °C freezer, the insect cooled at a rate of approximately 1 °C/minute. Temperatures were recorded once per second. The supercooling point was the lowest temperature recorded before detection of an exotherm (a sudden increase in temperature as the heat of crystallization was released).

For purposes of the risk assessment, we presumed that larvae would achieve the lowest mean supercooling point recorded (in other words, would always achieve the maximum degree of cold tolerance). We then projected the extent of mortality by comparing the distribution of supercooling points with historical records of low temperatures as summarized in USDA Plant Hardiness Zones. This analysis was used to identify Plant Hardiness Zones where *A. auroguttatus* would be unlikely to establish because temperatures are likely to be too cold. In ArcMap, polygons that represented the unsuitable Plant Hardiness Zones were used to mask portions of the conterminous United States.

MaxEnt models of climate suitability

We followed procedures for the development of a MaxEnt model as described by Phillips and others (2006) with modifications proposed by Jarnevich and Young (2015). We began by assembling published distribution records for *A. auroguttatus* (Coleman and Seybold 2008, 2011; Coleman and others 2012; Haavik and others 2014a, 2015). We verified that location records were accurate and corrected latitude or longitude when necessary (for example, when coordinates placed a location in Mexico or the Pacific Ocean but the written description was for southern California or Arizona). This exercise produced a list of 66 presence points for *A. auroguttatus*. We then downloaded the 19 bioclimatic variables from WorldClim.org at 30 arc-second resolution (Hijmans and others 2005). We limited the extent of the analysis to North America.

A significant concern with inductive distribution models is the potential for overfitting environmental covariates (in other words, suggesting a more restricted distribution for a species than can be supported statistically or biologically). We limited the potential for overfitting by taking four precautionary steps (Jarnevich and Young 2015). First, we limited the geographic area from which background samples could be drawn by creating a minimum convex polygon around all presence points in California and Arizona with an additional 2.5 arc-minute buffer. Second, we restricted the analysis to bioclimatic variables that were not correlated (correlation coefficient, $|r| < 0.7$). Cross correlation analysis (Proc CORR in SAS 9.13) was performed with climatic records extracted from the area within the minimum convex polygon. Third, we excluded variables that gave a discontinuous (jagged) response. Lastly, we compared the area under the receiver operating characteristic curve (AUC) from a model training set of presence points to the AUC from a model testing set of presence points. Because the AUC is scaled from 0 – 1, a difference greater than 0.1 in AUC provided evidence of overfitting (Jarnevich and Young 2015).

The MaxEnt model was initially run with presence points from California and Arizona, background data points drawn from the buffered minimum convex polygon, and all 19 bioclimatic variables. This run was used to identify the variables with the greatest percentage contribution to the overall model. Of the variables that contributed at least 2 percent to the overall model, variables with discontinuous response functions were removed from further consideration. We identified bio10 (in other words, mean temperature of the warmest quarter) as the variable that contributed the most to the model. We then found bio14 (precipitation of the driest month) to be the only other climatic variable that (i) was not correlated with bio10, (ii) gave a continuous response function, and (iii) contributed more than 2 percent to the overall model. We re-ran the MaxEnt model with this restricted set of bioclimatic variables to generate 25 replicate models. For each model, MaxEnt randomly selected 20 percent of the 66 presence points to train the model, the remaining presence points were used for model testing. Model performance was evaluated by the AUC and a comparison with aerial sketchmaps of oak mortality caused by *A. auroguttatus*.

MaxEnt generated a surface for North America that described the suitability of the climate in each 30-arc-second grid cell as the mean of the 25 replicate models. Values near 1.0 were considered highly suitable, whereas values near 0 were completely unsuitable.

Host status of oaks

The potential suitability of oak species that have not yet been colonized extensively by *A. auroguttatus* was determined through a combination of no-choice host range experiments and Monte Carlo simulation. Haavik and others

(2014b) artificially infested cut logs of known hosts (*Q. agrifolia* and *Q. kelloggii*), non-hosts (*Q. engelmannii*) and several species of unknown host status (Q. *chrysolepis*, *Q. wislizeni*, blue oak, *Q. douglasii*, Oregon white oak, *Q. garryana*, valley oak, *Q. lobata*, and cork oak, *Q. suber*) with neonates of *A. auroguttatus* and recorded the proportions of larvae that entered the host, established a gallery, and developed to fourth instar. In addition, fecundity was measured for females that were fed foliage from these species. These data were used in Monte Carlo simulations (@Risk 4.5, Palisade Software, Ithaca, NY) to generate a probability density function of the number of adult female daughters produced per mother under the assumption that mothers could only feed on one species. Haavik and others (2014b) reported results for two rounds of host testing. We adopted a risk-averse approach and relied on those results that were most favorable for *A. auroguttatus* in either year to characterize the host suitability of the species. Fecundity was described by a normal distribution, limited to values ≥ 0, and proportions were described by beta distributions. The simulation was run 10,000 times. The resulting probability density function allowed us to estimate the probability that *A. auroguttatus* would produce more than one daughter per mother if the mother only was allowed to feed upon one host species. Geographic distributions of oak species determined to be hosts were obtained from USGS (2013). Geographic areas without suitable hosts were clipped from the MaxEnt map in ArcMap 10.1.

Spread potential for A. auroguttatus

An initial attempt was made in 2011 to conduct an in-field mark-release-recapture experiment to determine how far adult *A. auroguttatus* might fly. Over 300 beetles were marked with fluorescent dust and released in the center of a trapping array, but none was recaptured on a purple prism trap. Because large numbers of adult beetles were difficult to collect and the traps were inefficient at attracting adult *A. auroguttatus*, we elected not to repeat this study.

We used flight mills to estimate the dispersal potential of *A. auroguttatus* adults. Adults and pupae were collected from the field, triple contained, and shipped via overnight courier to the biosecurity level-2 laboratory in St. Paul, Minnesota. Adults and pupae were held in individual rearing cups, and adults were provided with freshly cut foliage from *Q. lobata* for at least 2 days.

The general design and operation of the mill are described in Fahrner and others (2014). The arm of the flight mill was affixed to the pronotum of adults with superglue. Adults were placed on the flight mill for 24 hours and allowed to fly with a photoperiod of 24:0 (L:D) hours or 8:16 hours. The flight period always began in light. Under both conditions, adults flew more than 80 percent of the total flight distance within the first 6 hours of being placed on the mill, so we restricted the analysis to this period, which allowed us to combine data from both photoperiod treatments. Flight distance was measured as a function of age, sex, and mating status. A total of 223 beetles were attached to the mill, of which 179 engaged in flight. Beetles were removed from the mill and observed daily until death. Age-at-death data were used to construct a life table with age measured in days from adult eclosion.

To estimate flight potential, we focused on results for females. Female dispersal is likely to dictate the unaided rate of range expansion of *A. auroguttatus*. As before, we adopt a risk-averse approach. So, for each age (x), the mating status (virgin or mated) that led to the greater mean flight distance was used as the measure of flight distance for that age (f_x). Maximum net lifetime flight distance (d) was calculated as the sum of the product of $L_x f_x$, where L_x is the number of days an average individual lives from age x to $x+1$ (Carey 1993). To calculate the population spread rate, we followed procedures modified from Shigesada and Kawasaki (1997). The diffusion coefficient (D) was calculated as $D = (d^2)/\pi$. The population spread rate is $2\sqrt{\varepsilon D}$, where ε is the intrinsic population growth rate, which was estimated to be 0.634 from annual changes in densities of *A. auroguttatus* at three sites reported in Haavik and others (2015).

Shapefiles describing the distribution of oaks killed by *A. auroguttatus* in 2010 were obtained from the Insect and Disease Detection Survey Data Explorer (USDA 2015). These polygons were used as the starting locations. Buffers were created around these polygons to represent potential spread in 3-year increments through 2022 by assuming a constant annual rate of spread.

Results and discussion

The composite risk map

The updated national risk map for *A. auroguttatus* (fig. 1) illustrates the degree of climatic suitability for this insect within the geographic range of oak species that are known or potential hosts. The radiating rings indicate the maximum expected natural spread of *A. auroguttatus* every 3 years from 2010.

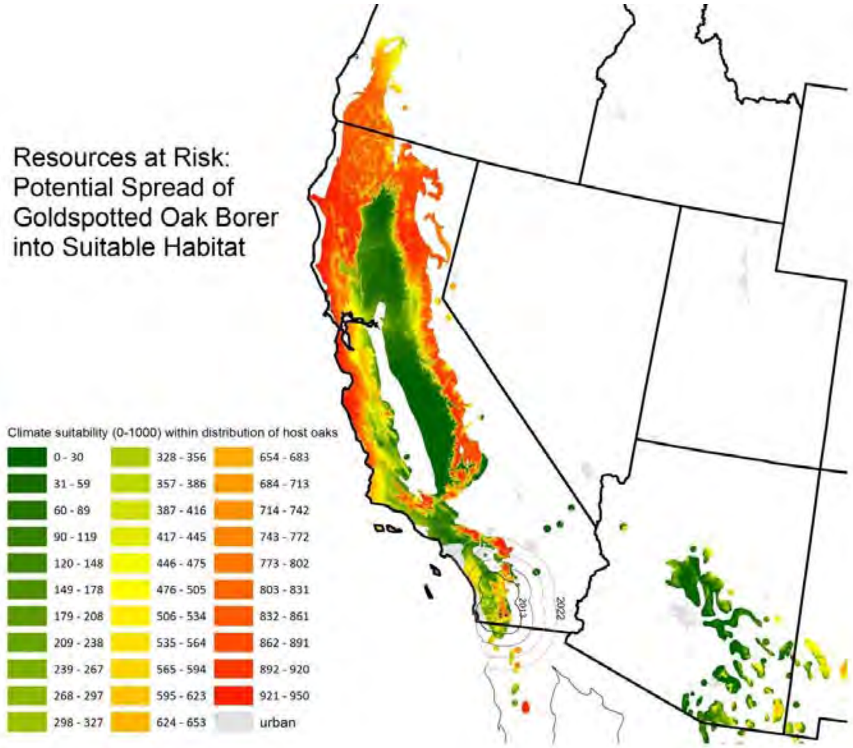

Figure 1—Composite risk map for *Agrilus auroguttatus* depicting the degree of climate suitability and potential extent of natural spread from 2013 – 2022 within the range of confirmed and suspected hosts. United States states outside New Mexico, Arizona, California, and Oregon are presumed to have little to no risk based the current understanding of host and climate requirements for this insect.

The map illustrates that *A. auroguttatus* has the potential to spread beyond Orange, San Diego, and Riverside Counties, the only three counties in California currently known to be infested (Coleman and others 2015). Each county has large areas with hosts, and these areas are projected to be very suitable climatically for this insect. Indeed, oaks killed by *A. auroguttatus* in San Diego County in 2010 occur in areas of the county that are characterized as among the most climatically suitable for the insect. These observed patches of oak mortality were not explicitly considered during the development of the climate suitability model, so the concurrence of oak morality in areas projected to be climatically suitable provides some degree of confidence in the underlying model.

The risk map suggests some interesting possibilities about the previous and future course of the invasion by *A. auroguttatus*. In San Diego County, the landscape appears to be heterogeneous with respect to climatic suitability. This heterogeneity is created by the variations in temperature and moisture associated with topographic changes. In some cases, abiotic factors may change dramatically over relatively short distances, especially in canyons and ravines. As a result, areas in southern California that are climatically suitable tend to be somewhat fragmented. This fragmentation may have helped to slow the natural rate of spread of the insect as it has not yet fully occupied the areas considered to be suitable and within is natural dispersal capacity.

Our risk map suggests large areas with suitable climate and hosts occur near the Pacific coast, along the Sierra Nevada, and in northern California. *Quercus agrifolia* tends to be more widespread along the coast, whereas *Q. wislizeni* and *Q. kelloggii* tend to be more widespread in the lower elevations of the Sierra Nevada Range and in the north. In areas that are highly suitable for *A. auroguttatus*, we might expect more rapid population growth, faster local spread, and shorter intervals between the colonization and death of a tree. Thus, the spread of the insect into these areas is a significant concern.

However, our risk map also suggests that while *Q. douglasii* and *Q. lobata* might be hosts, they tend to grow in areas that are climatically less suitable for *A. auroguttatus*. The areas in and around the Central Valley where these oak species occur tend to be too hot and potentially too dry for *A. auroguttatus* to do well. Careful field monitoring is needed to confirm this projection.

Biology underlying the map

The coldest supercooling points for *A. auroguttatus* prepupae, mean of approximately -22 °C, were recorded in October 2010. This temperature typically occurs in USDA Plant Hardiness Zone 6a. In this zone, we would expect about 50 percent mortality of *A. auroguttatus* if it were present in a typical winter. In USDA Plant Hardiness Zones 2b-5b, the mean annual extreme low temperature is <-26.1 °C, so larval mortality would be expected to be much greater than 50 percent in most winters, often approaching 100 percent. Our laboratory measures of the cold tolerance of *A. auroguttatus* are consistent with the known, native distribution of the insect in southeastern Arizona. The annual extreme low temperature in the coldest locations within its native range is about -20.6 °C, and most *A. auroguttatus* larvae are sufficiently cold hardy to survive brief exposures to this temperature.

Two climatological factors contributed to the maximum entropy model for *A. auroguttatus*: the mean temperature during the warmest quarter of the year and precipitation during the driest quarter. The temperature component contributed 94.7 percent and the moisture component contributed 5.3 percent to the overall model. The analysis suggested that *A. auroguttatus* may have some sensitivity to heat, as the probability of it being present declined from 95 percent when the mean temperature during the warmest quarter was 16.0 °C to <10 percent when this temperature was 26.0 °C. The probability of *A. auroguttatus* being present with respect to precipitation in the driest month was more complex. This probability was greatest (65 percent) when precipitation in the driest month was approximately 2.3 mm. The probability of *A. auroguttatus* being present declined with either less or more precipitation.

The maximum entropy model revealed considerable variation in climatic suitability for *A. auroguttatus* across the conterminous United States. In general, the eastern half of the country was considerably less suitable than the western half. The model suggested that areas of moderately suitable habitat might occur in New England, the mid-Atlantic states, and in the Appalachian Highlands, but most areas would be climatically unsuitable. In contrast, relatively few areas in the western United States were classified as climatically unsuitable. Across the conterminous United States, many suitable sites became climatically unsuitable when the effects of cold were considered.

Simulation models of the number of adult daughters produced per female suggested interesting possibilities about the host range of *A. auroguttatus* (table 1). The simulation results were consistent with prior knowledge of the host status for three oak species. For the known hosts, *Q. kelloggii* and *Q. agrifolia*, the probability that a female would give rise to at least one adult daughter (in other words, the probability of replacement) was >90 percent. For the known non-host, *Q. engelmannii*, this probability was <10 percent. For oak species which *A. auroguttatus* has only rarely encountered or has yet to encounter, the probability of replacement on *Q. wislizeni* and *Q. lobata* was >90 percent, indicating that these species could be hosts. On *Q. suber*, *Q. douglasii*, and *Q. chrysolepis*, this probability was 0.58, 0.48, and 0.34, respectively. For the purposes of this analysis, we considered these probabilities sufficient to classify these three species as hosts, but recognize that additional field observations are needed to confirm these classifications. In contrast, the probability of replacement on *Q. garryana* was <10 percent, so we consider this species not to be a host. Although this analysis provides support for the general rule of thumb that red oaks tend to be hosts while white oaks tend not to be, the results also reveal that this pattern may not be absolute. In this case, the simulations suggested that three of the three red-oak species should be hosts, but so should two of the four white-oak species (table 1). In these instances, additional field observations will be necessary to confirm these classifications as well.

Table 1—Potential host status of several oaks, *Quercus* spp., for *Agrilus auroguttatus* based on the probability that a female will give rise to an adult daughter (in other words, replace herself in the population)

Species	Expected (adult daughters/mother)	Prob. (replacement)[a]	Status
Section *Lobatae*			
Q. wislizeni, Interior live oak	6.5	0.996	Host
Q. kelloggii, California black oak	8.2	0.958	Host[b]
Q. agrifolia, Coast live oak	4.8	0.906	Host[b]
Section *Cerris*			
Q. suber, Cork oak	2.0	0.579	Host
Section *Protobalanus*			
Q. chrysolepis, Canyon live oak	1.2	0.342	Host
Section *Quercus*			
Q. lobata, Valley oak	5.6	0.947	Host
Q. douglasii, Blue oak	1.6	0.487	Host
Q. garryana, Oregon white oak	0.3	0.081	Non-host
Q. engelmannii, Engelmann oak	0.3	0.067	Non-host[b]

[a] Probability of replacement determined through 10,000 runs of a Monte Carlo simulation of *A. auroguttatus* development on artificially-infested, cut logs.

[b] Known before this study.

The distance a female can fly in general increases with age, from an average of approximately 0.15 km/day at 3 days after adult eclosion to 2.7 km/day at 26 days after eclosion. Daily survivorship of females remains high (≥90 percent) through 11 days after eclosion and declines steadily thereafter. In this study, the oldest adult female survived for 28 days. The maximum net lifetime displacement was estimated at 10.4 km/generation, which gave a diffusion coefficient of 34.1 km^2/generation. Because this species is univoltine, these rates equate to distances moved within a year. This calculation assumed that a female would fly for 6 hours along a linear path that radiated from the center of the population distribution and would feed and re-hydrate on oak foliage for 18 hours; if the female survived, flight would resume the next day with no carryover effects from the previous day's flight. Mortality is assumed to be independent of flight. Population range expansion is also a function of the intrinsic population growth rate. Thus, with diffusion and reproduction combined, we estimate an annual spread rate of 9.3 km/year. This projected spread rate is similar to the rate at which the area in southern California with oak mortality from *A. auroguttatus* increased from 2008-2010 (Coleman and others 2012).

Conclusions

Relative to other United States states, *A. auroguttatus* appears to pose the greatest threat to oaks in California and Oregon. Large areas within these states have suitable hosts and climate. In Arizona, a combination of natural enemies and host-plant resistance may keep this insect from building to damaging levels (Coleman and others 2015). Our forecasts of the potential geographic range for this insect are based upon the best available scientific information, yet we recognize that significant knowledge gaps remain. Extreme uncertainty in risk assessment as a consequence of poor biological understanding is a frequent circumstance among newly invading species. Empirical observations are essential to support or refute the forecasts made in this map and to provide a basis for its refinement.

More research is needed to evaluate the host status of oak species from eastern North America. If the rule of thumb about the suitability of red oaks continues to hold true for eastern oak species, considerable forested acreage would be at risk. Yet, most red and white oaks of California do not appear to have close relatives outside of the region (Nixon 2002).

We hope the updated risk map will help forest health specialists with their efforts to limit the potential damage from this insect. This map should be of immediate benefit in the design of early detection surveys and to help characterize the total area that might be affected if this insect is not effectively managed. We should emphasize that this map focuses on where *A. auroguttatus* might become established. Different factors may be needed to forecast the rate and extent of tree mortality within these areas. The magnitude of impact remains the most difficult component of any pest risk assessment to forecast (Venette and others 2010).

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