

CURRENT AND FUTURE CLIMATE MODELS FOR TEN REMAINING SPECIES OF
ACHATINELLA TO INFORM POTENTIAL LOCATIONS OF *EX SITU* PREDATOR-FREE
EXCLOSURES

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF
HAWAI'I AT MĀNOA IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE

DEGREE OF
MASTER OF SCIENCE

IN

NATURAL RESOURCES AND ENVIRONMENTAL MANAGEMENT

AUGUST 2023

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Keywords: climate change, extinction, assisted colonization, conservation introductions,
ectotherms, species distribution modeling, conservation planning

ACKNOWLEDGEMENTS

I thank the following organizations for their funding and/or collaboration that made this research possible, including: the US Fish and Wildlife Service; the Hawai'i Department of Land and Natural Resources, Division of Forestry and Wildlife, and the Snail Extinction Prevention Program. This project would not have been possible without the help and guidance of my advisor, Dr. Melissa Price. Thank you for your patience and support throughout the whole process and pushing me to experience and learn as much as I can.

I thank my other committee members, Dr. Adam Vorsino and Dr. Kirsten Oleson. Adam for the countless hours of teaching me about the intricacies of modeling and providing the base code to develop into my own. And Kirsten, for giving me your time and mental capacity.

I also thank the following individuals for their collaboration, suggestions, and support: Derek Risch, Dr. Lucas Fortini, Dr. David Sischo. I thank everyone in the Hawai'i Wildlife Ecology lab for your friendship and endless support. From editing drafts, to R code, to bounce ideas off of, and to spending time with each other. It's been wonderful to work with all of you and share the last five years together. I thank my wife Alexis, my parents, friends, family and mentors for always supporting me in whatever endeavor I choose. And finally, I dedicate this to my little brother Ethan, whose love and support I cannot put into words, but who has fostered in me every possibility that has unfolded so far.

Abstract

Ectotherms are particularly sensitive to drought and extreme temperatures and may act as bellwethers of climate change, but declines are often attributed to other threats. As a result, the threat of climate change may be under-estimated. The decline of Hawaiian tree snails in the genus *Achatinella* has largely been attributed to over-collection, habitat loss, and introduced predators. Currently, most species remain only in captive rearing facilities or predator-free exclosures, following recent sharp declines and population “blink-outs”. In this study, I developed species distribution models for the ten remaining species in the genus *Achatinella* under present and future climate scenarios, within the historical range on O‘ahu, as well as areas outside the historical range across the Hawaiian Islands. I found that ~98% of suitable area across the Hawaiian Islands is outside of the historical range. Additionally, most of the climate-suitable habitat under future conditions on O‘ahu do not overlap with areas where populations are currently persisting, suggesting that without translocation, these species may become extinct sometime before the end of the century. Our results raise alarms regarding the likely impacts of climate change on wildlife long before the end of the century and highlight the importance of translocations outside the historical range for the persistence of climate-sensitive species.

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Introduction

Over the next century, many species around the world will become extinct or will only persist outside of historical ranges due to climate change, invasive species, disease, and habitat loss (Holland and Cowie 2009, Harley 2011, Vorsino et al. 2014, Hylander et al. 2015, Fortini et al. 2016, Manes et al. 2021, Sharma et al. 2021). These threats may reduce or eliminate suitable habitat within the historical range, so that if populations do not shift with the climate, they may decline to extinction (Hoegh-Guldberg et al. 2008, Scriber 2014, Gallagher et al. 2015). With climate warming likely to increase 1.5° C by 2040, actions to prevent further biodiversity loss must be implemented in a timely manner (Masson-Delmotte et al. 2021).

Ectotherms are particularly vulnerable to a changing climate, as they are adapted to daily fluctuations of temperature within their geographic range (Paaijmans et al. 2013), but may have limited capacity to acclimate outside the range of temperatures to which they have been exposed (Colwell et al. 2008, Bonebrake and Deutsch 2012). Further, phenological plasticity may be unlikely to offset the decreased fitness caused by climate change (Deutsch et al. 2008), resulting in an increased risk of extinction (Davis and Shaw 2001, Alan Pounds et al. 2006) if they are unable to shift geographic ranges under a rapidly changing climate (Bradshaw and Holzapfel 2001, Balanyá et al. 2006, Calosi et al. 2008). Thus, ectotherms may be excellent candidates for consideration of conservation introductions outside of the historical range to ensure species persistence.

To assist with achieving the geographic shifts in species range that are necessary to adapt to a changing global climate, conservation translocations are an increasingly important tool (Novak et al. 2021). Translocations may be useful for multiple purposes, including the reintroduction of a species within the historical range, augmentation of an existing population, genetic reinforcement, biocontrol introductions, or conservation introductions, which are translocations to a site outside of the historical range (Gallagher et al. 2015, Lawler et al. 2015, Bricchieri-Colombi and Moehrenschrager 2016, Zimmer et al. 2019, Berger-Tal et al. 2020). At least 30% of species recovered from the endangered species list experienced at least one of these types of translocations (Novak et al. 2021). Further, many species that are threatened or endangered include translocations as a recommendation in their recovery plan (Novak et al. 2021). Translocations within the historical range are useful provided that the range and habitat are still suitable for the species (Hylander et al. 2015). Given rapidly changing climates, translocations outside of the historical range may be increasingly necessary if we wish for endangered and threatened species to persist into the future (Gallagher et al. 2015, Lawler et al. 2015, Novak et al. 2021, Rivera et al. 2021).

Assisted gene flow and genetic rescue may occur by translocating donors from adjacent populations into isolated populations or into captive populations, following guidelines such as those developed by IUCN (IUCN 2012). In the face of a rapidly changing climate, management of adaptive potential and genomic diversity are critical to maintain the ability for species to adapt to changing conditions (Price et al. 2021) and may independently provide motivation for translocations. Population fragmentation contributes to inbreeding depression and low levels of genetic variation, potentially reducing the ability to adapt to changing climatic conditions (Price and Hadfield 2014, Sischo et al. 2016, Chan et al. 2019, Quilodrán et al. 2020). Thus,

translocations can play a vital role in amending the loss of genetic diversity resulting from habitat fragmentation increasing genetic diversity and the ability to adapt to changing climates (Hoffmann et al. 2015, Bohling 2016, Hamilton and Miller 2016, Harrisson et al. 2016).

Reintroductions within the historical range are already playing a critical role in the Hawaiian Islands for seabirds and plants (Reynolds et al. 2008, 2013, Baker et al. 2011, Farmer et al. 2011, Schultz et al. 2011, Freifeld et al. 2016). However, there is an increasing need to consider translocations outside of the historical range, as climate change is impacting species with limited capacity for dispersal and migration (Hall et al. 2010, Urban et al. 2012, Buckley et al. 2013). Many high-elevation species are predicted to lack climate-suitable habitat by end of century, as climates warm (Kidane et al. 2019, Tito et al. 2020, Barras et al. 2021, Manes et al. 2021, Sharma et al. 2021), but there may be climate-suitable habitat nearby on higher-elevation mountain ranges and islands (Vorsino et al. 2014, Fortini et al. 2015, 2016). Further, many of these potential sites for receiving translocated individuals have lost similar species to predation and climate change, minimizing potential for hybridization and competition (Fortini et al. 2017). Thus, a critical next step is the modeling of climate-suitable habitat under current and future conditions, both within the historical range and on nearby islands, to inform conservation planning efforts.

Despite growing certainty over the last 50 years that conservation introductions are likely necessary for a large number of species due to a rapidly changing climate, a relatively small number of species have been moved to habitats that will remain suitable under changing climates (Hoegh-Guldberg et al. 2008). Concerns regarding costs, impacts on the receiving habitat such as potential hybridization with closely related species and interspecific competition, as well as impacts to the donating population from removing individuals, and the high rate of mortality in translocated individuals, have often resulted in decisions to maintain species within their historical ranges despite ongoing declines (Rivera et al. 2021). Despite the legitimacy of these concerns given the well-documented impacts of invasive species (Novak et al. 2021), there is only a single documented incident of a conservation introduction of an endangered species that resulted in a negative impact to the receiving ecosystem (George et al. 2009), perhaps due to the life history characteristics that are typically associated with endangered species, such as low fecundity. Further, a number of protocols and guidelines have been developed to minimize potentially negative and unintended effects on the receiving system (Lawler et al. 2015).

The genus *Achatinella* is endemic to the island of O‘ahu in the Hawaiian Islands and is the only taxonomic group federally listed as endangered at the genus level (USFWS 1993). Historical declines and extinctions starting in the 1800s have been attributed to over-harvesting by shell collectors, inbreeding, predation by invasive rats, chameleons, and carnivorous snails (Hadfield et al. 1993, Hadfield and Saufler 2009, Holland et al. 2010, Gerlach et al. 2021). Today, species in the subfamily Achatinellinae are conservation reliant species, largely remaining in *ex situ* captive rearing facilities and inside predator-exclusion fences within the historic range (Yeung and Hayes 2018, Hadfield 2021). There are currently five exclosures that have been constructed on O‘ahu, and nine proposed exclosures across the Hawaiian Islands (D. Sisco, 2021, personal communication). Reintroductions to supplement populations in predator-

free exclosures within the historical ranges of species have been ongoing since 1998 on the island of O‘ahu, but there are few places where exclosures can be built due to both the limited historical ranges of these species, and the steep terrain. Further, as periods of drought and temperatures increase due to climate change, reproduction and survival are likely to decline within the historical range (Hadfield et al. 1993). Thus, Hawaiian tree snails are an optimal study system in which to evaluate the potential for conservation introductions outside of the historical range to alleviate extinction risk due to climate change. In this study we aimed to identify: (1) climate-suitable habitat for the remaining species of *Achatinella* within the historical range on O‘ahu and across the Hawaiian Islands; (2) climate-suitable habitat under climate change scenarios; and (3) suitable locations for predator-free exclosures under current and future scenarios.

Methods

Observation Data. Presence-observation data were compiled for all ten remaining species on O‘ahu in the genus *Achatinella*, based on surveys conducted by state and federal organizations from 1920 to 2012. The coordinates and year of survey were associated with presence points used in the model. Many of the presence points were from the last 50 years, and thus do not represent the current distribution due to population and species extirpation in a number of places (Figure 1). As some species had very few detections, resulting in limited representation of potentially suitable climatic ecotypes across the landscape, we generated a set of pseudo-absences that were randomly distributed after buffering the target-species presences by a 1 km radius (Pilsbry and Cooke Jr 1912, Cowie et al. 1995, Elith et al. 2011). We generated pseudo-absences at an average density of 1 per 500m². A smaller density resulted in less stable models and results. Duplicate records that occurred within 250 m² were removed to minimize spatial bias. These pseudo-absences provide more detail to the models resulting in a more definitive projection of potentially climate-suitable habitat on O‘ahu and reducing the error of projection into non-analog climate space.

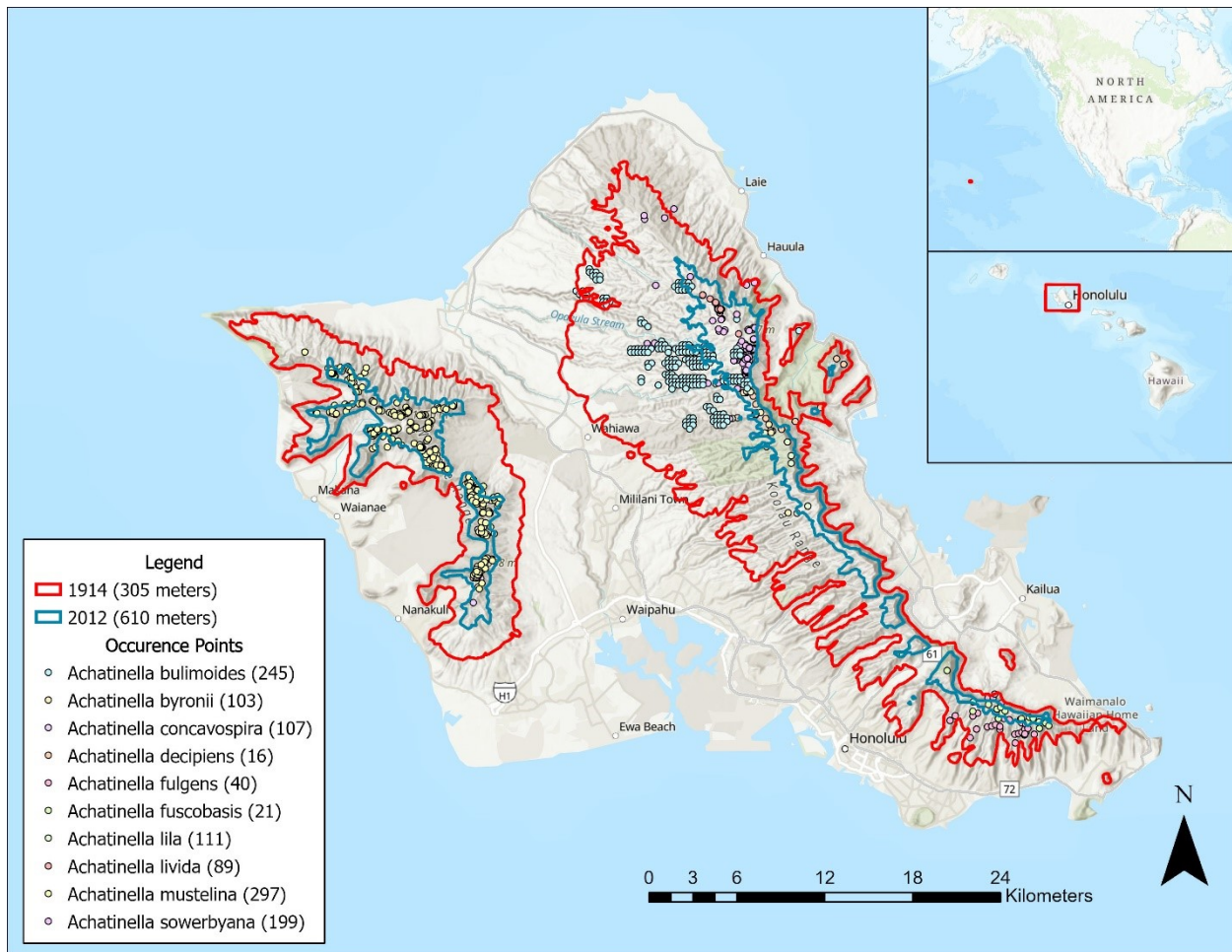


Fig. 1 Shifts in species ranges in the genus *Achatinella* from 1914 to 2012 (Rohrer et al. 2016). Red line indicates lowest elevation where species could be found in 1914, and blue line indicates lowest elevation where species could be found in 2012. Points indicate species detections from 1920 to 2013.

Bioclimatic Variable Development, Date Equivalence, and Selection. Bioclimatic variables are commonly used to define and project distributions of species in relation to potentially biologically relevant variables that may directly, or indirectly, influence an organism's climatic niche (Hijmans et al. 2005). These variables describe both the mean and variance in temperature and precipitation throughout the year. Although there are a large group of variables available, 19 are commonly used to assess and project biologically relevant distributions (Hijmans et al. 2005). Of these 19 commonly used variables, in this study annual temperature and annual precipitation were used (Price et al. 2007). These variables describe temperature and/or precipitation over a period of time, and as such require similar time points and resolutions to define an accurate projection of the bioclimatic variables. The presence data used in the analysis were collected over many decades and in many different seasons, and thus, it would be inappropriate to compile and use bioclimatic variables developed primarily from current

projections of precipitation. To address this issue, hindcasted bioclimatic variables were obtained for each year of the historic precipitation projections from 1920-2012 (Giambelluca et al. 2017). As only the current monthly mean annual temperature projections were available for immediate use, they were used to infer the temperature variance of the hind projections. This allowed a slightly more accurate representation of the species' climatic niche by matching its temporally defined precipitation with each point's collection year. Collection points without an associated year were discarded.

Historic and current 250 m² resolution monthly precipitation rasters were downloaded from the Online Rainfall Atlas of Hawai'i (Giambelluca et al. 2013). These precipitation projections were defined per month from 1920 to 2016 (Frazier and Giambelluca 2017). Mean monthly temperature rasters were downloaded from the Climate of Hawai'i website as maintained by the University of Hawai'i (Giambelluca et al. 2014). Although there is currently a hind projection for temperature predictions, it does not cover the same time period and processing the data for use was beyond the scope of this study.

Future Climate Models. For this assessment, the future predictors for 2080-2100 were derived from the Hawaiian Regional Climate Model projections (Zhang, Wang, Lauer, & Hamilton, 2012), using the Special Report on Emission Scenario (SRES) A1B. The dynamically downscaled SRES A1B scenario projects warmer and wetter future climatic conditions for Hawai'i (Fortini et al., 2017) and was used for this modeling effort because it is a standalone scenario and time period projection. SRES A1B can be easily compared to other Hawai'i climate models that have multiple scenarios with similar time periods (Rovzar et al. 2013, Vorsino et al. 2014, Fortini et al. 2015, 2016, 2017, Kim et al. 2019).

Ecological niche models and Model Parameter Tuning. All analyses were conducted in the R statistical environment (Team, 2019). A total of four ecological niche model algorithms were selected for the analysis based on their predictive accuracy, including Maxent, Maxnet, Boosted Regression Trees, and Random Forest (Dicko et al. 2014, Vorsino et al. 2014). These ecological niche modeling approaches were implemented within the SDMtune package (Vignali et al., 2020). All four models were combined to create a model ensemble.

All model parameters were optimized with the algorithm in the SDMtune package using the default parameters for each model (Vignali et al. 2020). The SDMtune algorithm utilizes the average and standard deviation of the Area Under the Curve (AUC) metric to estimate the degree of fit and select optimal model parameters. The average AUC value was used to estimate degree of fit based on the training dataset, whereas the Δ AUC was employed as a means of estimating overfitting with the testing dataset (Muscarella et al. 2014). For reproducibility, all seeds were set to 96,782.

Default model settings were used for each individual model at first. These settings were then tuned and optimized through SDMtune algorithm setting for maximum transferability and low sample sizes. The resulting baseline O'ahu and Hawaiian Islands projections were then checked and verified by expert knowledge of species distributions. These settings were then reinserted and run into the SDMtune algorithm until there was no improvement in model performance that could be verified by expert knowledge. If a model could not provide an adequate baseline performance, it was discarded before the ensemble step.

The R package ENMEVAL split the data for cross-fold validation to assess the accuracy of the trained model predictions through comparison to testing datasets. Data split for cross-fold validation occurred as follows: for species with over 50 records, the function “checkerboardpattern2” partitioned presence and absences by four groups, by two neighboring cells, to correct spatial autocorrelation and improve transferability. For species with over 30 records, function “checkerboardpattern1” was used to partition the data into 2 groups, by two neighboring cells, to correct for autocorrelation and improve transferability (Kass et al. 2021). For species with less than 30 records, the function “k-fold” ($k = n - 1$) partitioning was used where the data was jackknifed for k-combinations to train and evaluate a model for each combination, then averaged (Muscarella et al. 2014).

All models were evaluated and verified using expert knowledge before combining the four models into an ensemble. Tuned models were inspected for an AUC greater than 0.5 which signals model prediction accuracy was better than random; models with less than an AUC of 0.5 were dropped. The models were then ensembled through a combined weighted mean of the AUC and the Maximum Testing Specificity and Sensitivity (TSS) of the four models to dictate species presence/absence. TSS is a statistic that quantifies a model’s performance on false positives such as a modeled absence where data show a presence, or a modeled presence where data would suggest otherwise (Allouche et al. 2006). Each ensemble model was evaluated with expert knowledge to set presence-suitability thresholds for each species ensemble model using baseline projections. A presence-suitability threshold sensitivity analysis was also conducted for each species at each baseline projection by increasing the presence-suitability threshold cutoff by 0.1.

Presence-Suitability Threshold Sensitivity Analysis. The presence-suitability threshold cutoff selected for all models and all species was 0.5. These threshold values were handpicked based on field observations, laboratory rearing observations, and expert derived species ranges. Although the literature recommends choosing thresholds based on the model statistics such as AUC, TSS, and kappa, preliminary analysis often found that the presence-suitability threshold selected from AUC and TSS was often unstable between model runs causing the baseline climate suitability maps to vary wildly, either over or under predicting habitat suitability and mismatching those from expert derived species ranges. Therefore, we chose 0.5 as the threshold to allow the baseline models to match with expert derived species ranges. There were minimal consequences of changing the threshold values for most of the modeled species of *Achatinella* using the baseline climate and O’ahu projection, excluding *A. fulgens* and *A. fuscobasis* who had the strongest relationship between climate-suitable area and the threshold cutoff (Fig.2). However, the relationships of the threshold cutoff and climate-suitable area were more pronounced when examining the baseline projection of the main Hawaiian Islands. *Achatinella fulgens*, *A. fuscobasis*, *A. bulimoides*, *A. byronii*, *A. concavospira*, *A. lila*, *A. livida*, and *A. sowerbyana* have strong relationships with the threshold cutoff with greater suitable area to lose as the threshold cutoff increased (Fig. 3).

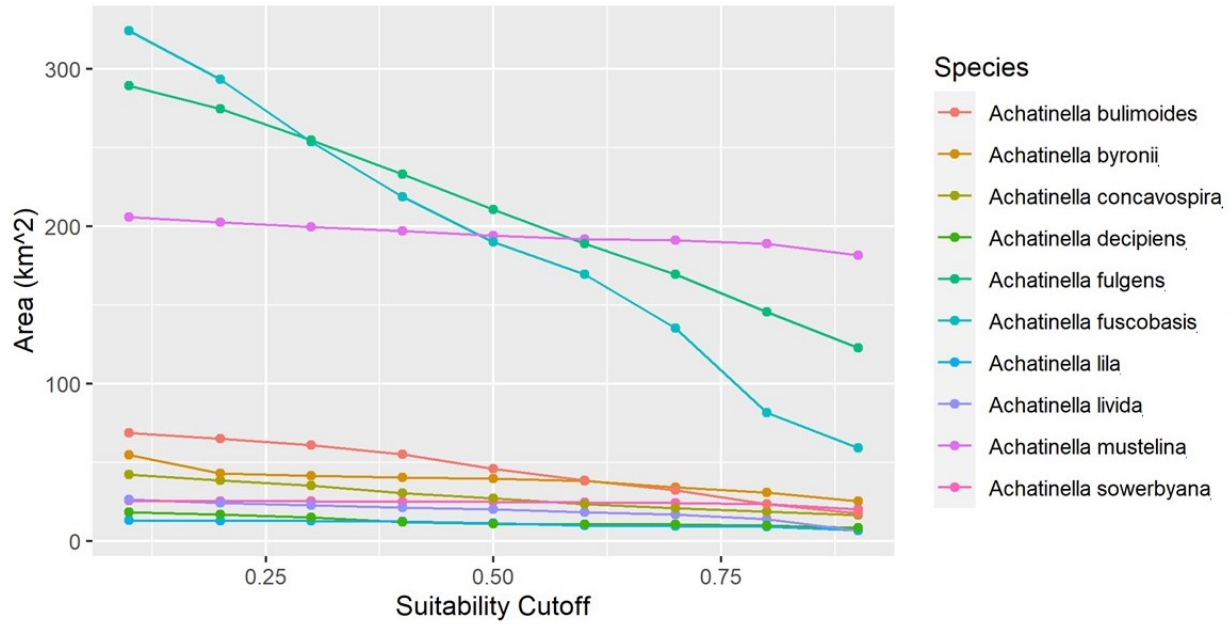


Fig. 2 Baseline suitable area of O'ahu along an increasing presence-suitability threshold. The total suitable area by species under the baseline climate model.

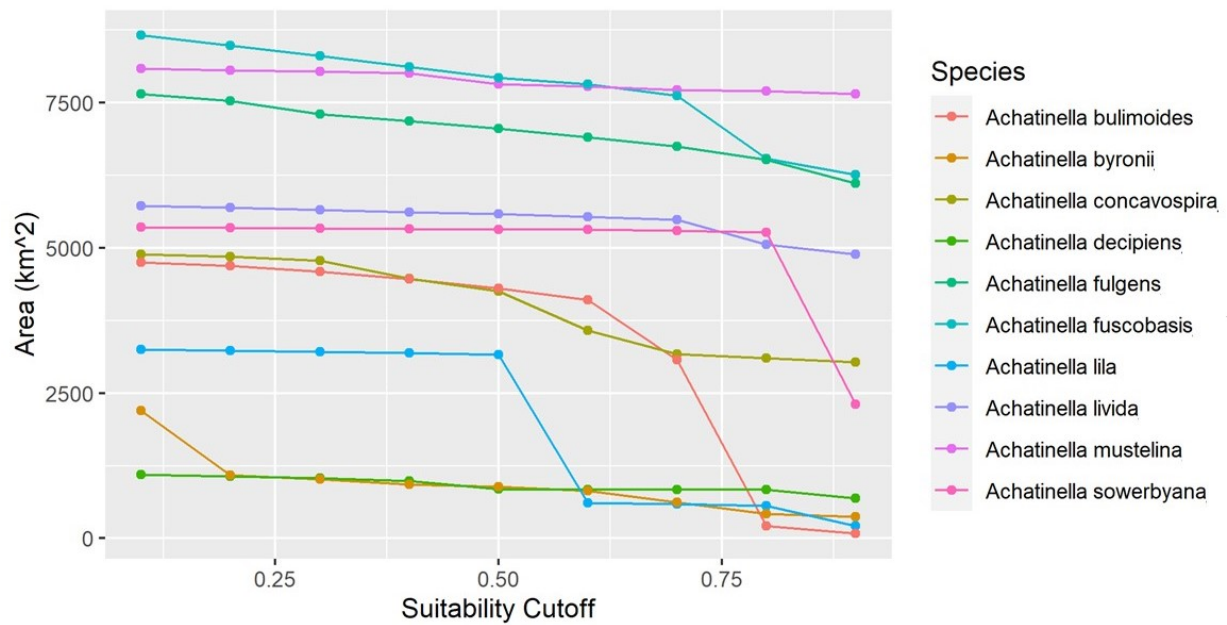


Fig. 3 Baseline suitable area of the main Hawaiian Islands along an increasing presence-suitability threshold. The total suitable area by species under the baseline climate model.

Spatial Planning and Prioritization. Using the packages “prioritizr” and “gurobi” (Gurobi Optimization, LLC 2021, Hanson et al. 2021), three scenarios were developed to identify the minimum number of exclosures that would protect three populations of each species in: (1) current climate-suitable habitat; (2) end-of-century climate-suitable habitat; (3) overlapping

current and future climate-suitable habitat. Prioritizr is a systematic conservation prioritization interface within R that uses integer linear programming techniques to build and solve conservation planning problems. This package was chosen for its integer linear programming that yields more effective and faster solutions than Marxan (Beyer et al. 2016). Gurobi is a commercial mathematical optimization solver; Gurobi is the best supported solver to use with Prioritizr for maximum performance (Schuster et al. 2020, Gurobi Optimization, LLC 2021). Climate-suitable habitat was determined by species suitability thresholds from the previous models and constrained with enclosure requirements, such as a maximum slope of 30 degrees (D. Sicho, 2018, personal communication). The resolution of the output was 5655.83 m² for each pixel, and a constraint of two neighboring suitable pixels was specified to ensure suitable area for enclosure construction. Areas with low vegetation and urban development were excluded from consideration (Jacobi et al. 2017). Lastly, solutions were prioritized that maximized the distance between enclosures to minimize the chances that a single stochastic event, such as a hurricane, would impact multiple enclosures. To reduce computation time, each problem was solved with multi-threading and run to find a solution in the 90th percentile (gap = 0.1).

Spatial prioritization produced solutions when the neighboring cell requirements were $n = 2$. Solutions were produced with species that were projected to persist based on the climate scenario and the island(s); species that were projected to lack climate-suitable habitat on O‘ahu under future conditions (*Achatinella bulimoides*, *A. concavospira*, *A. lila*, *A. sowerbyana*) were dropped from subsequent enclosure site analyses (Table 1).

Results

Most species in the genus *Achatinella* will have less than 6 km² of climate-suitable area remaining on O‘ahu under end of the century climate models; *Achatinella bulimoides*, *A. concavospira*, *A. lila*, and *A. sowerbyana* are likely to lose all climate-suitable habitat on O‘ahu by the end of the century (Table 2). All species are predicted to lose at least 86% of climate-suitable habitat by the end of century. *Achatinella mustelina* is predicted to have the most climate-suitable area on O‘ahu at 25 km²; in contrast, *A. bulimoides*, *A. concavospira*, *A. lila*, *A. livida* and *A. sowerbyana* are predicted to have 1 km² or less of climate-suitable habitat on O‘ahu at the end of the century. Total climate-suitable habitat on O‘ahu for species in the genus *Achatinella* is expected to decrease from 755 km² to 61 km², an overall decrease of 88%, largely driven by *A. fulgens*, *A. fuscobasis*, and *A. mustelina*, the three species that have the most suitable habitat to lose (Table 1, Fig. 4).

When considering potentially suitable areas outside of the historical range under current conditions, nearly 100-fold more area is available than within the historical range (47,086 km²; Fig. 5, Table 2). Less than 4% of potential climate-suitable habitat under current conditions is within the historical range on O‘ahu for the ten remaining species in the genus *Achatinella*. The results from the baseline model projection to the Hawaiian Islands show that three species, *Achatinella fulgens*, *A. fuscobasis*, and *A. mustelina*, have the largest potential climate-suitable habitat across the Hawaiian Islands (Table 1). *Achatinella decipiens* has the least amount of total potential climate-suitable habitat across the Hawaiian Islands at 652 km².

By the end of the century, potential climate-suitable habitat across the Hawaiian Islands will decrease by about 32% for species in the genus *Achatinella* (from 47,086 to 30,926 km²) (Table 1; Fig. 5). Climate-suitable habitat will decrease for all ten species by an average of 34%,

with *A. byronii* losing the least amount of range at 24%, and *A. concavospira* experiencing a 58% range loss across the archipelago. Maps of each projection are included in Appendix 1-36.

Table 1. Climate-suitable habitat that meets exclusion requirements within the historical island of O‘ahu and the potential range across the Hawaiian Islands under current and future projections.

Species	Current O‘ahu km ²	Future O‘ahu km ²	Percent Change	Current Statewide km ²	Future Statewide km ²	Percent Change
<i>A. bulimoides</i>	44	<1	-100%	4297	2742	-36%
<i>A. byronii</i>	37	4	-90%	862	652	-24%
<i>A. concavospira</i>	26	<1	-100%	4254	1774	-58%
<i>A. decipiens</i>	11	1	-86%	854	581	-32%
<i>A. fulgens</i>	203	14	-93%	7036	5063	-28%
<i>A. fuscobasis</i>	192	17	-91%	7943	5241	-34%
<i>A. lila</i>	11	<1	-100%	3148	2093	-33%
<i>A. livida</i>	19	<1	-99%	5575	3883	-30%
<i>A. mustelina</i>	189	25	-87%	7810	5436	-30%
<i>A. sowerbyana</i>	23	<1	-100%	5308	3461	-35%
Total Climate-suitable habitat (km ²)	755	61	-88%	47086	30926	-32%
Average Climate-suitable habitat (km ²)	75	6.1	-95%	4707	3093	-34%

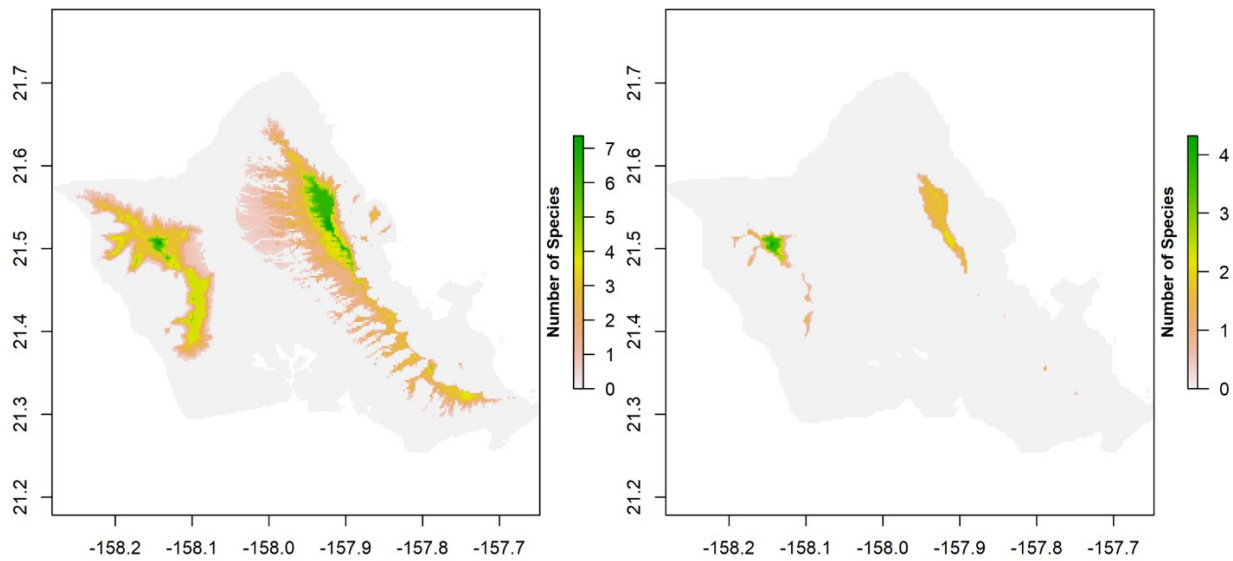


Fig. 4 Current (left) and future (right) tree snail number of species based on modeled range of all modeled species. All 10 extant species of *Achatinella* modeled on the island of O‘ahu at the present and future time periods.

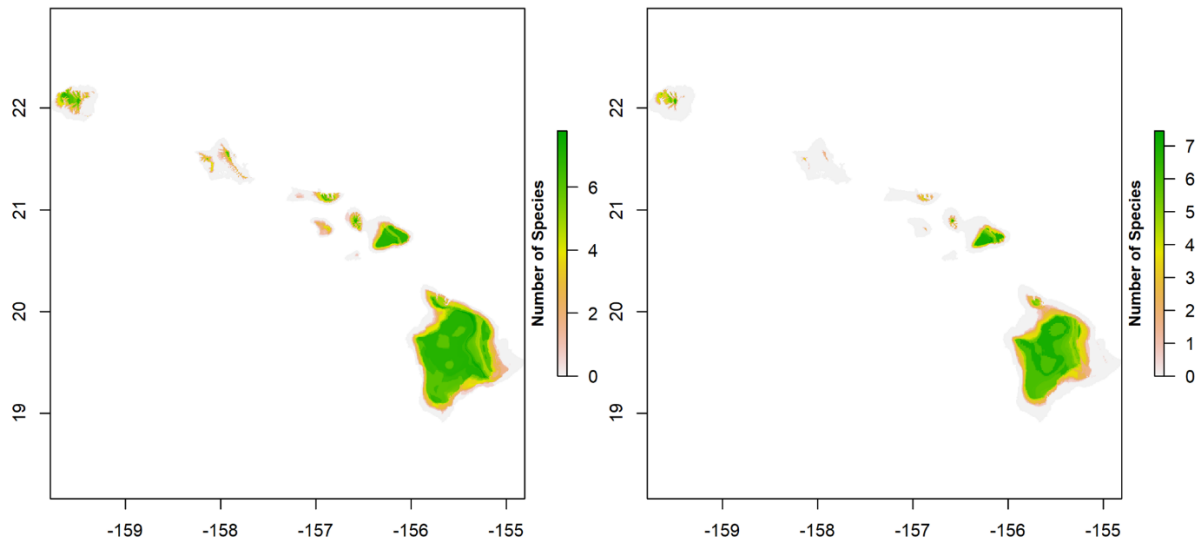


Fig. 5 Current (left) and future (right) tree snail number of species per area based on modeled range of all remaining species in the genus *Achatinella*.

Table 2. Composition of O‘ahu climate-suitable habitat when compared to the total potential climate-suitable habitat across all Hawaiian Islands in baseline and end of century climates (this study) and current species persistence in the wild (D. Sischo, 2023, personal communication).

Species	Current O‘ahu Climate Compared to Total Potential Climate	Future O‘ahu Climate Compared to Total Potential Climate	Extant in the Wild in 2023?
<i>A. bulimoides</i>	1%	<1%	no
<i>A. byronii</i>	4%	<1%	no
<i>A. concavospira</i>	<1%	<1%	no
<i>A. decipiens</i>	1%	<1%	no
<i>A. fulgens</i>	3%	<1%	no
<i>A. fuscobasis</i>	2%	<1%	no
<i>A. lila</i>	<1%	<1%	no
<i>A. livida</i>	<1%	<1%	no
<i>A. mustelina</i>	2%	<1%	yes
<i>A. sowerbyana</i>	<1%	<1%	no
Total Climate-suitable habitat	2%	<1%	

Spatial Planning Results. In the baseline scenario, solutions for O‘ahu needed the same number of exclosures required for areas outside the historical range across the archipelago (Table 3). To protect three populations from each of the ten remaining species in the genus *Achatinella*, a minimum of 14 exclosure sites are needed on O‘ahu under current climate conditions. By the end of century, despite the inclusion of only six of the ten species due to a lack of suitable habitat for the remaining four species, 18 exclosures are necessary to protect three populations of each of the remaining species. A “hedge-your-bets” strategy in which exclosures are developed in overlapping current and future suitable areas would require 18 exclosures on O‘ahu. In contrast, if climate-suitable habitat outside the historical range but within the Hawaiian Islands is included, 14 exclosures would be needed to protect three populations of all species under both current and overlapping models, and by the end of the century a minimum of 16 exclosures protects three populations of all ten species of *Achatinella*.

Table 3. The number of exclosures needed on each island to protect three populations of each species of *Achatinella*. Due to the lack of suitable habitat, the asterisk indicates that only six species of *Achatinella* are protected.

O‘ahu Exclosures	Hawai‘i Exclosures	Time Period
14	14	Baseline
18*	16	End of Century
18*	14	Overlap

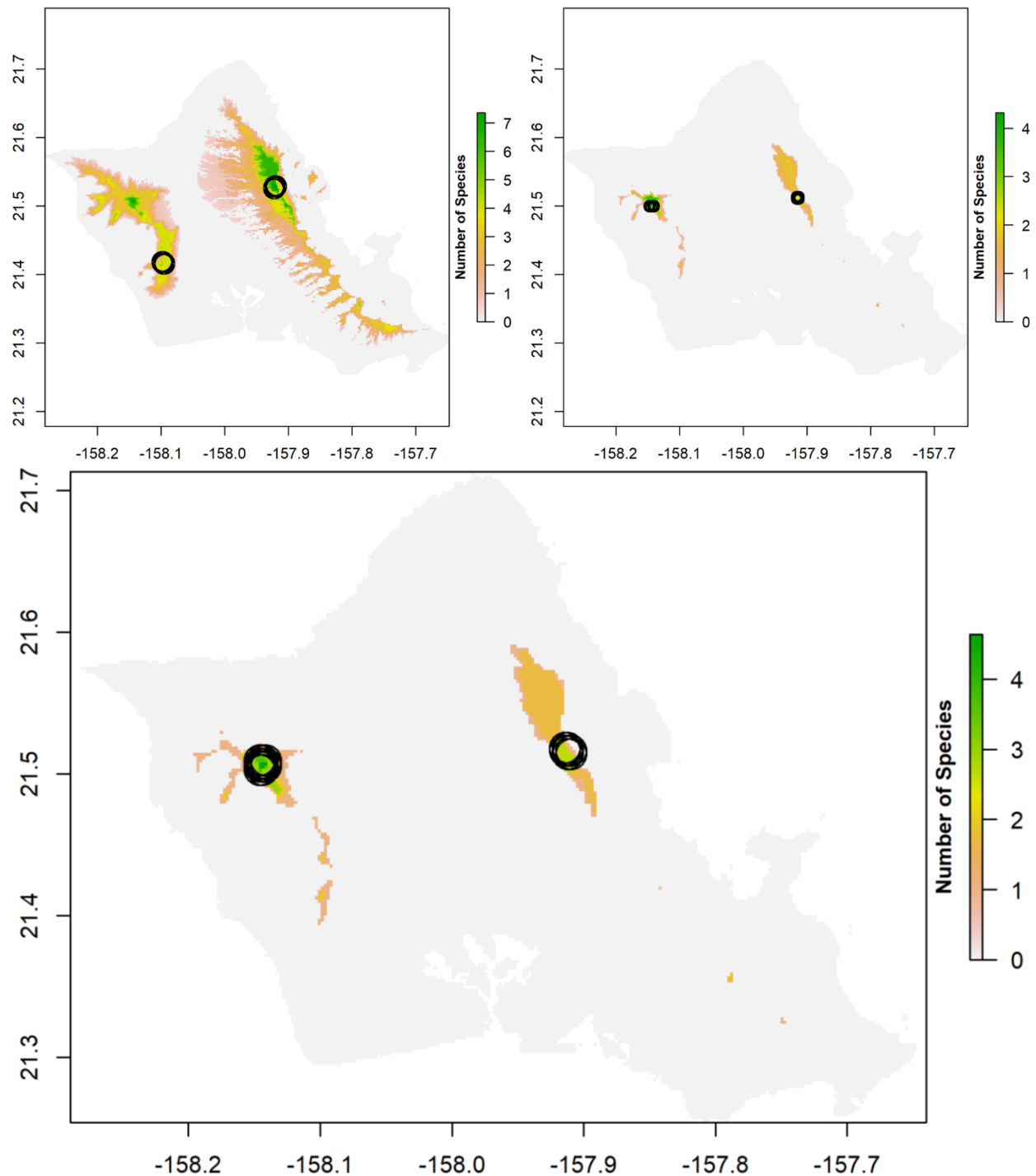


Fig. 6 Current (top left), future (top right), and overlapping (bottom) tree snail number of species based on modeled range of all modeled species. Optimal locations for all species of *Achatinella* to persist in the minimum number of exclosures for three populations across O'ahu in climate-suitable habitat that exist under current, future, and overlapping climate scenarios.

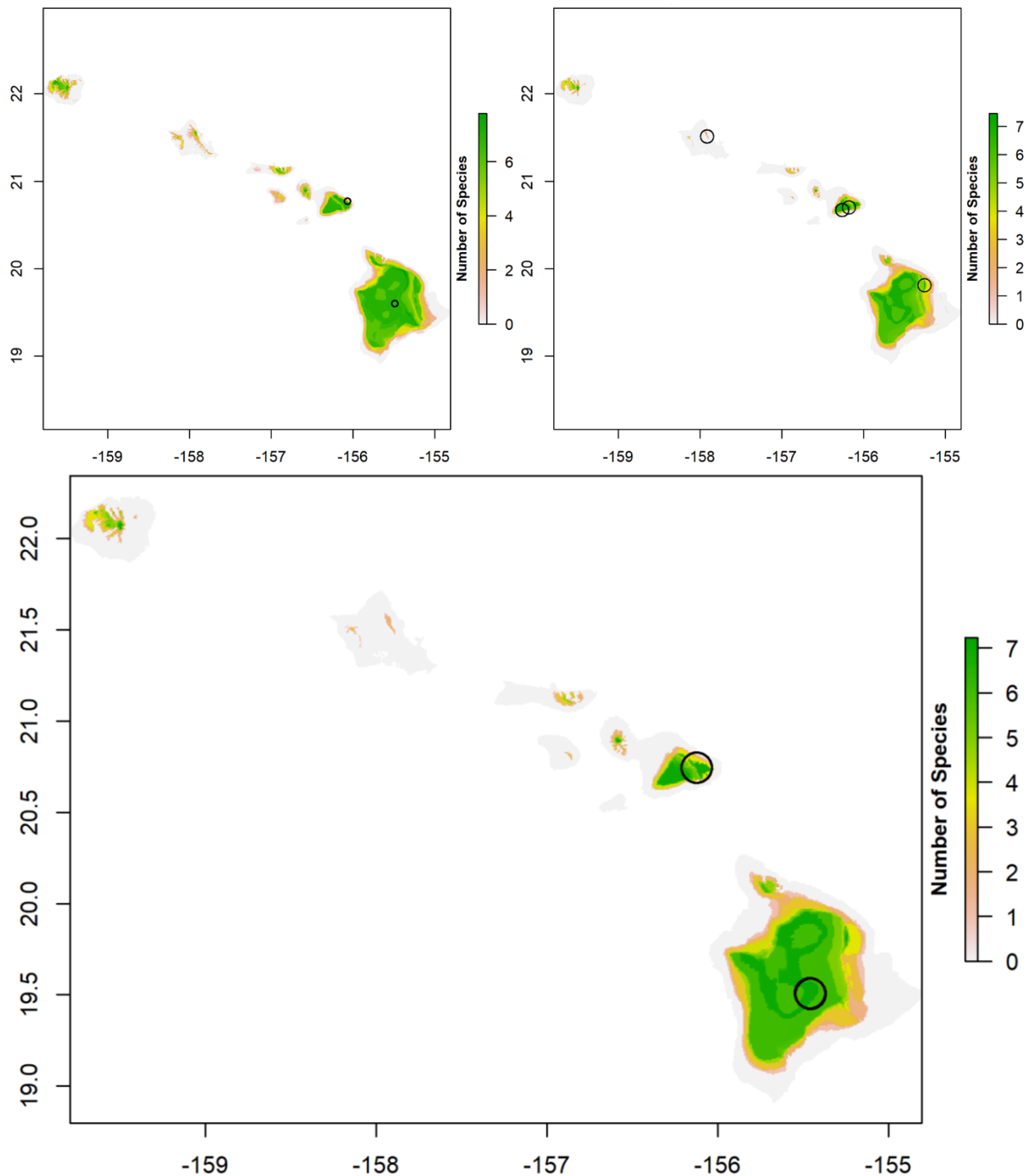


Fig. 7 Current (top left), future (top right), and overlapping (bottom) tree snail number of species based on modeled range of all modeled species. Optimal locations for three populations of each species in the genus *Achatinella* to persist in the minimum number of exclosures across the Hawaiian Islands in climate-suitable habitat that exist under current, future, and overlapping climate scenarios.

Exclosure Elevation Changes. Few exclosures will be suitable under both current and future climate scenarios (Fig 10). Species of *Achatinella* are projected to have the most climate-suitable area for exclosures around 400-600 meters in elevation under baseline climate scenarios on O‘ahu (Fig 8). The average elevation range for climate-suitable exclosures is predicted to increase for O‘ahu by the end of century to 600-800 meters (Fig 9). All species in the genus *Achatinella* are predicted to need habitat at higher elevations than the maximum elevation on O‘ahu (1200 m; Fig. 11, Fig. 12, Fig. 13). The average exclosure elevation range for the Hawaiian archipelago under current conditions is estimated to be approximately 600-1500 meters, with an elevation maximum of 2200 meters (Fig. 11). The end of century model for the Hawaiian archipelago projects a higher elevation range for exclosures of 1200-2000 meters. *Achatinella concavospira*, *A. fulgens*, *A. fuscobasis*, and *A. mustelina* are predicted to utilize elevations higher than the 1600 meters in locations where the rest of the species are unlikely to persist (Fig. 12).

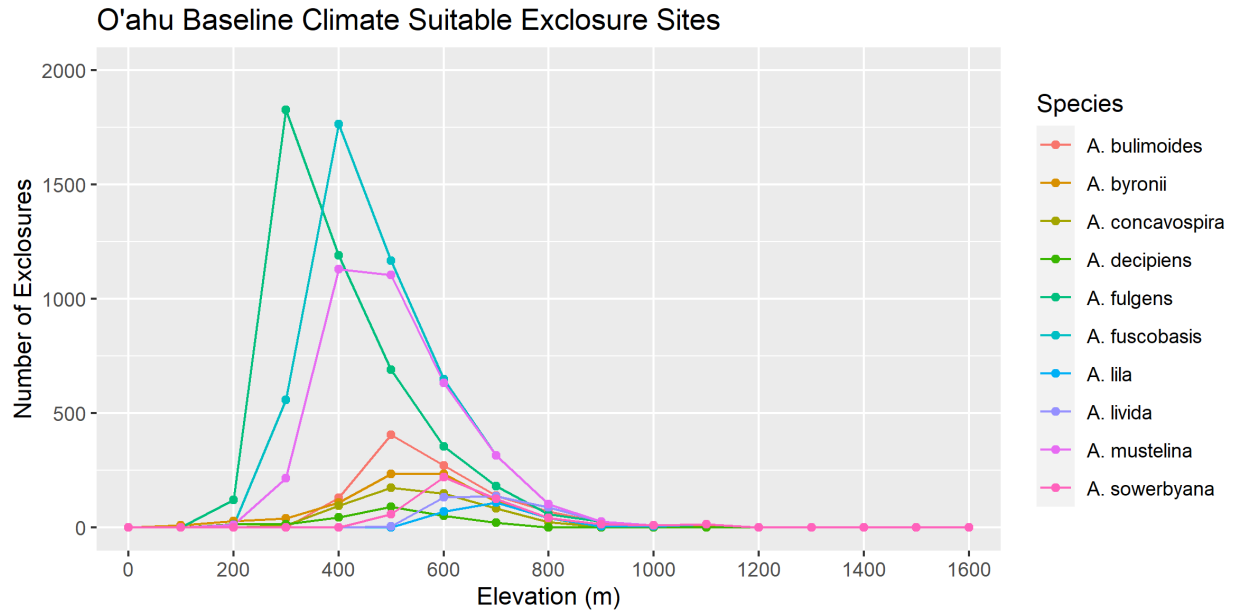


Fig. 8 Current number of exclosures along elevation for O‘ahu. Climate-suitable exclosure sites on O‘ahu by species under baseline climate.

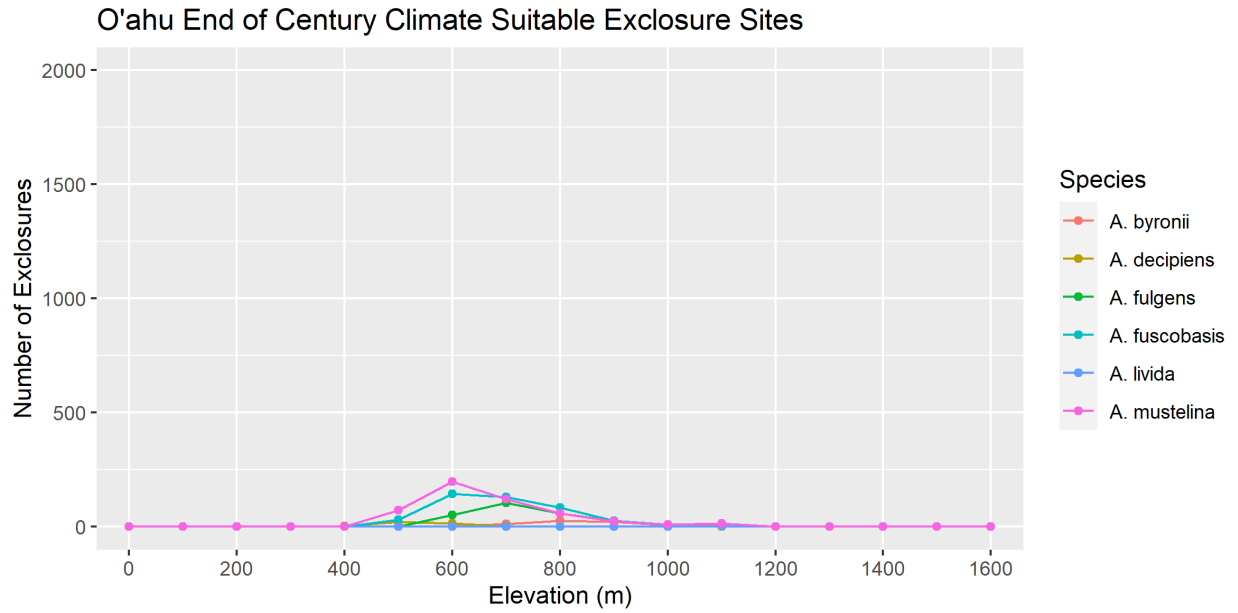


Fig. 9 Future number of potential exclosures by elevation for O'ahu. Suitable exclosure sites by species on O'ahu under end of century climate.

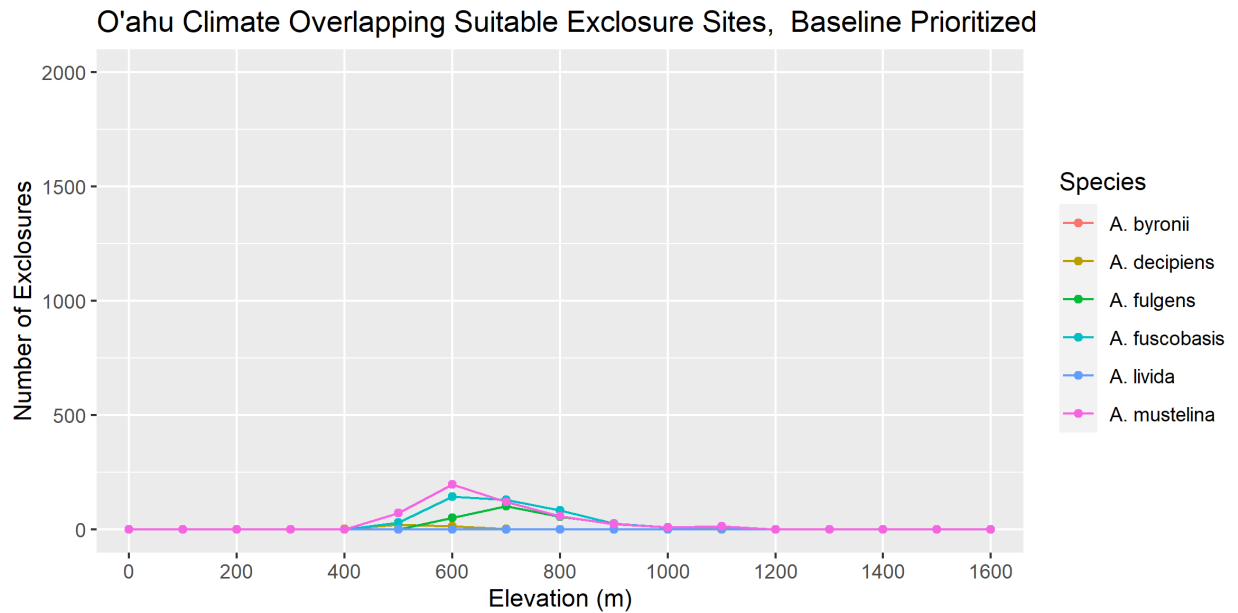


Fig. 10 Overlapping number of exclosures along elevation for O'ahu. Sustained suitable exclosure sites by species on O'ahu under both baseline and end of century climates.

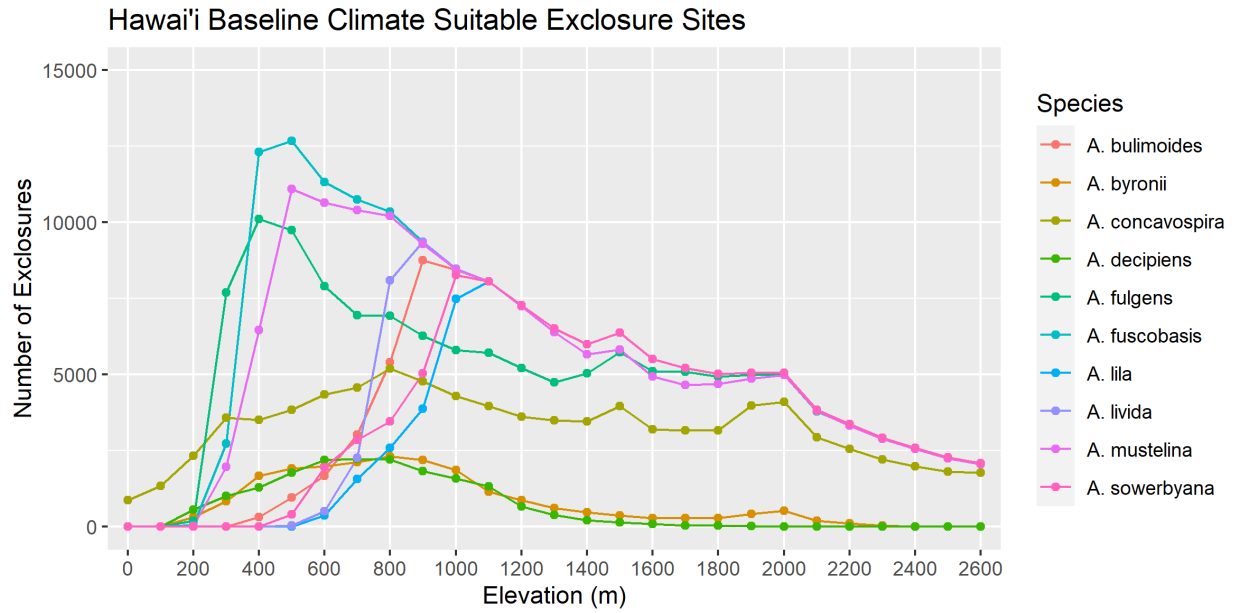


Fig. 11 Current number of exclosures along elevation for the Hawaiian Islands. Suitable exclosure sites by species in Hawai'i under baseline climate.

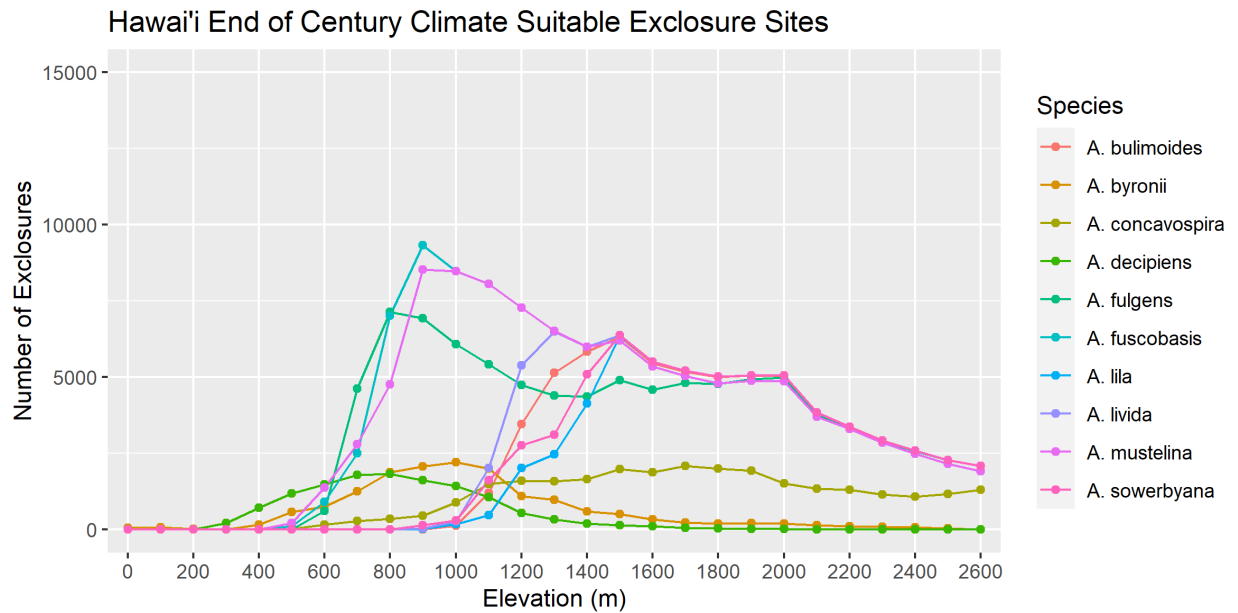


Fig. 12 Future number of exclosures along elevation for the Hawaiian Islands. Suitable exclosure sites by species in Hawai'i under end of century climate.

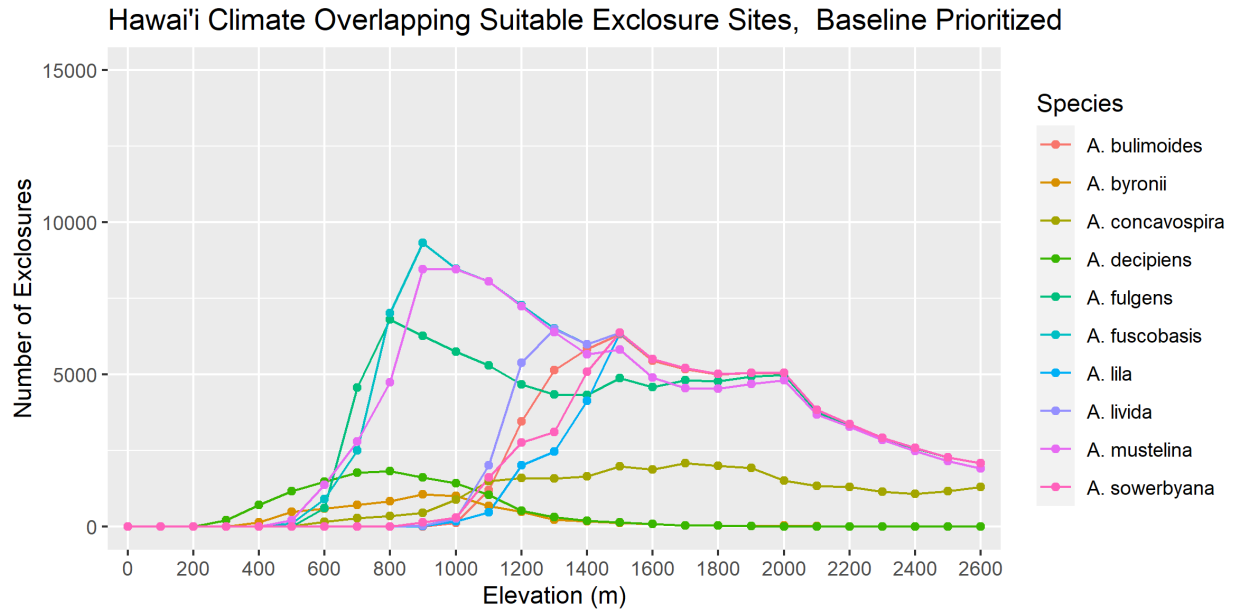


Fig. 13 Overlapping number of exclosures along elevation for the Hawaiian Islands. Sustained suitable exclosure sites by species on Hawai‘i under both baseline and end of century climates.

Discussion

Given their sensitivity to extreme climate events, ectotherms are particularly likely to be impacted by climate change. In this study, we found that climate-suitable habitat projections for species in the genus *Achatinella* that incorporated end-of-century climate projections generally matched the species extant today, potentially suggesting that climate change impacts have contributed to declines in the species over the last few decades. Generally, species that were predicted to have little to no climate-suitable habitat remaining at the end of century were, in fact, currently estimated to be extinct in the wild in the near future. As such, this study underscores the likely role of ongoing climate change in the declines of ectotherms over the last few decades, and the urgent need for consideration of translocation outside of the historic range if we wish for sensitive species to persist into the future.

Consistent with expectations for island endemic species (Gaston 2003), climate-suitable area within the historical range was found to be very small, with less than 75 km² of climate-suitable area for most species (Table 1). Given that most species are found at the highest elevations on the island of O‘ahu, it is not surprising that most of the suitable area under future conditions was found to be on higher-elevation islands outside the historical range on O‘ahu (Fig. 11, Fig 12). The subfamily Achatinellinae was considered to be a relatively young taxonomic group in its “first flower of evolution” according to early naturalists (Pilsbry and Cooke Jr 1912). Given the emergence of the islands in the archipelago over time, most species in this subfamily evolved on the older islands of O‘ahu and Maui Nui, with only a few species occurring on the newest island, Hawai‘i, with the largest area and the highest elevation. Thus, it is likely that models for species in the other genera in this subfamily, *Newcombia*, *Partulina*, *Perdicella*, will show similar patterns, with a large amount of climate-suitable habitat on other islands.

Our models showed that by considering islands outside the historical range, we can substantially reduce the number of predator-free exclosures needed to protect the remaining ten species, minimizing costs, and increasing the likelihood that recovery measures will be implemented in a timely manner. Each of the Hawaiian Islands host similar ecosystems, plant species and predator suites, minimizing concerns regarding impacts on translocation sites. Translocation to suitable areas is particularly important for species that do not appear to have suitable areas remaining today, based on observations of declines across the landscape that are consistent with end-of-century models (Fortini et al. 2017). In particular, investment in predator-free exclosures in areas predicted to be unsuitable today or in the near future could result in sunk costs that divert resources from locations where they could persist into the next century.

Predator-free exclosures on neighboring islands are also likely to benefit other land snails. While there are no members of the genus *Achatinella* present on the neighboring islands, members of the subfamily Achatinellinae in the genera *Newcombia*, *Partulina* and *Perdicella* are still extant and declining due to invasive predators on Hawai‘i island and Maui Nui (Moloka‘i, Lāna‘i, and Maui) (Holland and Cowie 2009). Extant populations are low enough in numbers that competition for food resources is unlikely to be a threat within exclosures. Hawaiian tree snails graze the microbial communities on the surfaces of leaves, and ingest a varied diet across their ranges (O’Rorke et al. 2015), suggesting there would be suitable food resources available as long as suitable plant host species were present (Sischo et al. 2016, Meyer et al. 2021). Thus, translocation to suitable locations on other islands, outside of the historical range of species in

the genus *Achatinella*, presents a timely solution to mitigating the loss of climate-suitable habitat within the historical range due to climate change.

This is not the first time that conservation introductions have been considered for species in the genus *Achatinella*. There have been multiple translocation attempts to the island of Kauaʻi (Christensen 1985). Some individuals of the species *A. bellula* were translocated to the island of Kauaʻi in 1892 and last seen as late as 1911. With more success, *A. vulpina* was translocated to the island of Kauaʻi from 1903–1907 and was last seen as late as 1973, indicating establishment success of the initial founding population (USFWS 1993). More recently, there has also been a conservation introduction completed by the state Department of Land and Natural Resources Snail Extinction Prevention Program in 2019 with *A. concavospira*, translocating them from the southern end of the Waiʻanae mountain range to the northern end of the Waiʻanae mountain range, well outside of their historical range (D. Sischo personal communication 2023). While the movement of species outside of their historic range should not be undertaken frivolously, given the history of invasive species impacts, many species across the Hawaiian Islands are likely to benefit from conservation introductions (Fortini et al. 2015).

We note there were multiple challenges in modeling current and future climate-suitable areas for these species. Many of the tree snails had less than 40 recorded occurrence points to inform the models. Many of these points were from prior to the last 50 years, and thus do not represent the current distribution. Pseudo-presence points could not be extracted from the historical species distribution maps used for the endangered species listing of *Achatinella* due to later taxonomic revisions (Cowie et al. 1995). Thus, there was potential for overfitting and high uncertainty within the models. We attempted to bound spatial-autocorrelation using k-fold validation and two group checkerboard cross-validation (Muscarella et al. 2014). While we used the extensive experience of experts regarding current and historical distributions, we matched our resulting baseline ecological niche models by changing the suitability cut off to 0.5.

SDMtune lacks many important features of the package biomod2 including ensemble modeling by statistical evaluation, the utilization of several PA draws over model iterations, the subsequent several draws of model withholding over those model iterations, and then model averaging over the runs of model iterations. These features are key for getting statistically sound and stable species distribution models, especially with small sample sizes, such as *Achatinella decipiens* where $n = 16$, where withholding 20% of the data for model validation results in 12 presence points, with each point removed having a relatively large impact on the model. Any interpretation of the results and outputs must be taken with extreme caution. Each time the models are run, the results and their respective statistics vary somewhat unpredictably. Due to this inconsistency, it was difficult to derive and trust the habitat suitability thresholds from the model statistics because when doing so, the models would fail to accurately describe the historical range, either by overestimation or underestimation. Varying between runs while projecting outside of the historical suitable habitat, most suitable islands are consistent but the suitable area within the islands are inconsistent, flipping between the windward and leeward sides or summit compared to areas surrounding the summit. There are also some areas on Hawaiʻi island and Maui that consistently project suitable habitat, but their extent may vary. We are confident in the findings that there is more available suitable habitat outside of historical ranges and that each species will experience some kind of range reduction in the future. As a result of the discrepancies, this study should not be referenced for any future work outside of the

scope of discussions for the next modeling effort and exploring other islands for current suitable habitat by using environmental data loggers and ground-truthing.

Spatial prioritization analysis was optimized to minimize the number of exclosures, but did not consider cost, as exclosure cost is influenced by the ease of access, need for restoration actions, and other costs for preparation and maintenance. Our analyses suggest suitable vegetation may not occur in areas where climate is suitable, and larger areas are unlikely to be available for exclosures.

The end of century climate scenario used in this study is considered moderate, and it is predicting a warmer and wetter climate. It is highly likely that climate change is impacting species more rapidly than indicated by our models, as noted by the sharp declines in snail populations in the last few decades (D. Sischo personal communication 2021). The findings and species distribution maps generated from this study should be used as a guide to narrow down potential areas for predator proof exclosures. Further investigation in these areas will be necessary to confirm suitable environmental conditions, slope, and vegetation for predator proof exclosures. Future studies should use models consistent with current trends (Fortini et al. 2017). Using multiple climate scenarios will increase confidence in the predicted climate-suitable areas. Areas identified as suitable across climate scenarios, or perhaps by less conservative models that predict warming and drying sooner and to greater extremes, should be prioritized to account for uncertainty within climate projections and regarding species responses, future human actions and climate policy.

Future efforts to model snail distributions should utilize all RCP scenarios, including both statistically downscaled and dynamic downscaled projections due to differences in bioclimatic variable effects (Fortini et al. 2015). Running each scenario at each available time period will help further fine-tune exclosure placements and species responses. Additionally, a simple test of reversing the projections, to ensure that the base model is working, would show the opposite effect for species range, adding or subtracting climate-suitable habitat area. To reduce and account for uncertainty, multiple pseudo-absence draws should be made for each model to create an accurate average ensemble, identifying areas of agreement and even any areas of uncertainty to increase the precision for climate-suitable habitat in the future (Zurell et al. 2020). Furthermore, when removing duplicates, the collections with the earliest record date in the same location would be preferred over later dates because the environmental variables would be truer to the historical climate-suitable habitat models. Development of a more robust suitability cut off would also be ideal, so that the biological significance between projections is not altered.

Here I have presented evidence needed to support discussions around the topic of conservation introductions for species in the genus *Achatinella*. Long-term persistence of tree snails in the genus *Achatinella* will likely require conservation introductions outside of historical ranges across the Hawaiian archipelago. The results of this study are consistent with predictions that terrestrial gastropods are particularly susceptible to extreme weather events associated with climate change (Nicolai and Ansart 2017). Based on my study results, I suggest that climate change over the last century, combined with high temperature events and extreme droughts associated with climate change, are likely to impact terrestrial gastropods and other ectotherms much earlier than end-of-century models suggest.

Appendix

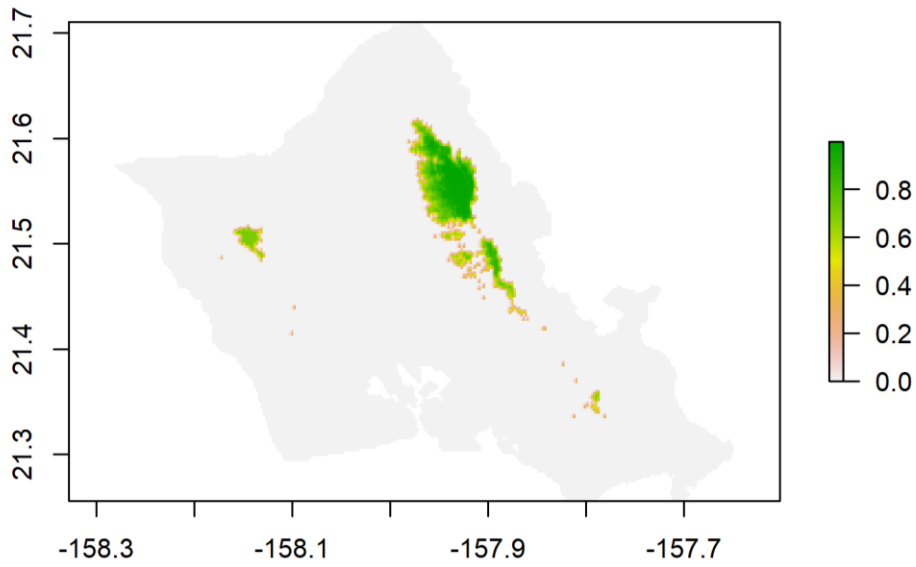


Figure A.1. Baseline species distribution of *Achatinella bulimoides* on O‘ahu with a threshold cutoff of 0.5.

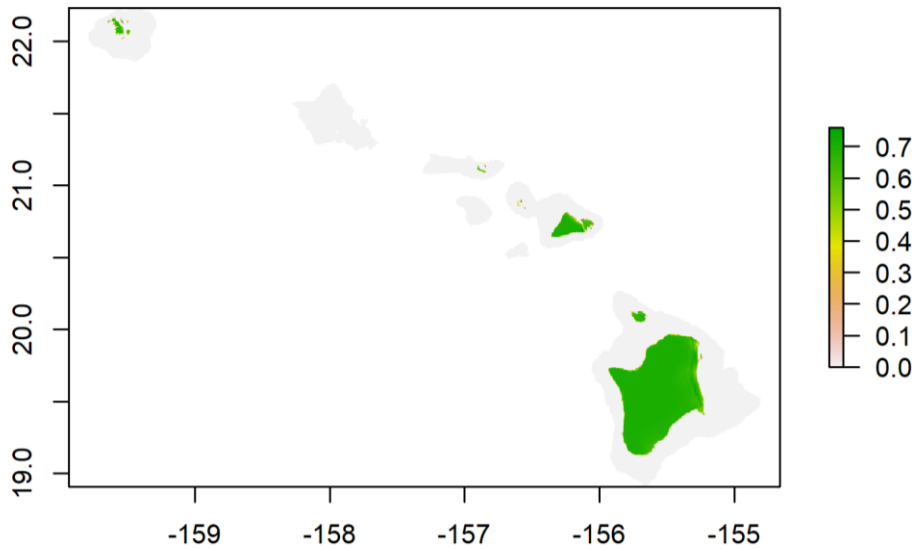


Figure A.2. Baseline species distribution of *Achatinella bulimoides* on the Hawaiian Islands with a threshold cutoff of 0.5.

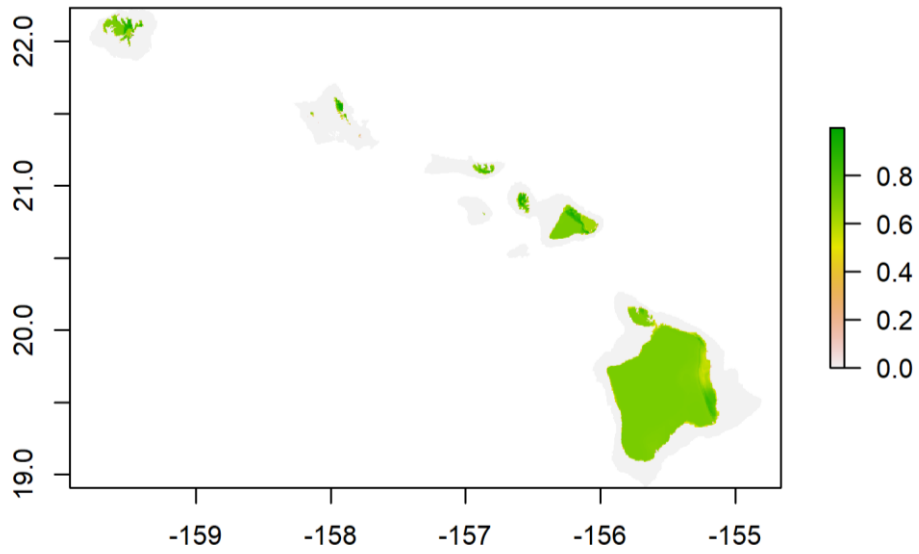


Figure A.3. End of century species distribution of *Achatinella bulimoides* on the Hawaiian Islands with a threshold cutoff of 0.5.

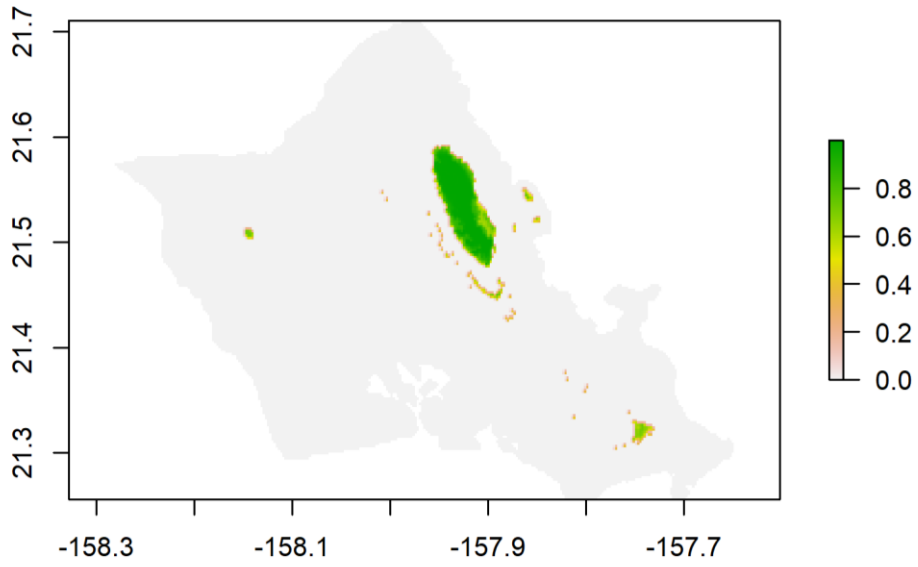


Figure A.4. Baseline species distribution of *Achatinella byronii* on O‘ahu with a threshold cutoff of 0.5.

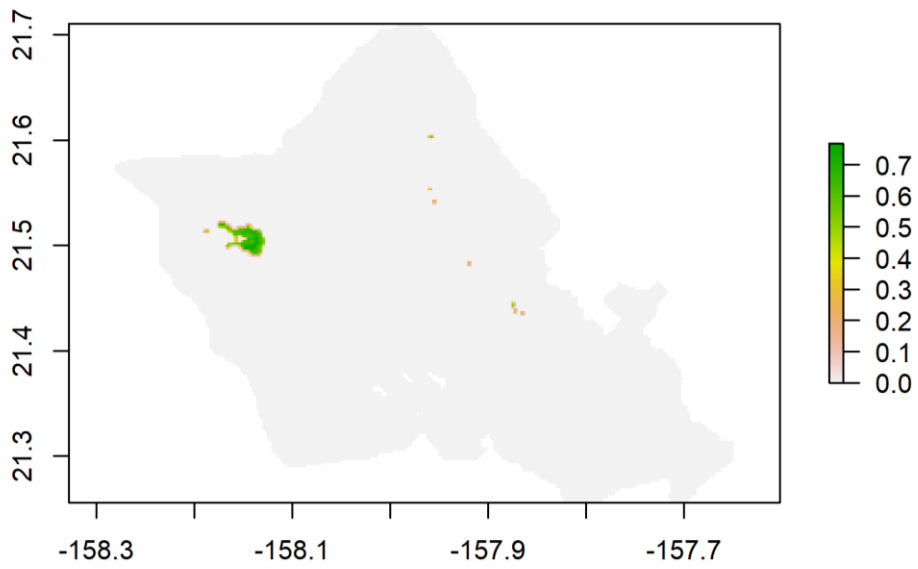


Figure A.5. End of century species distribution of *Achatinella byronii* on O‘ahu with a threshold cutoff of 0.5.

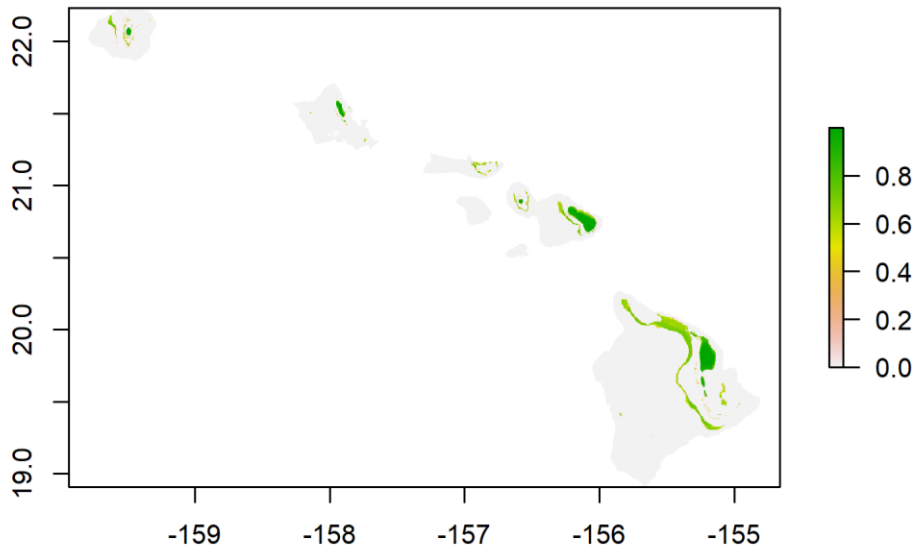


Figure A.6. Baseline species distribution of *Achatinella byronii* on the Hawaiian Islands with a threshold cutoff of 0.5.

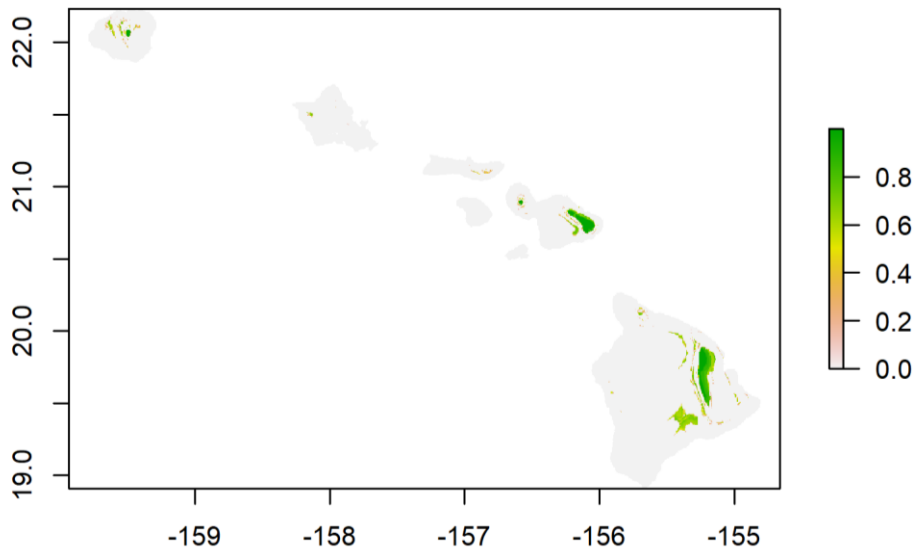


Figure A.7. End of century species distribution of *Achatinella byronii* on the Hawaiian Islands with a threshold cutoff of 0.5.

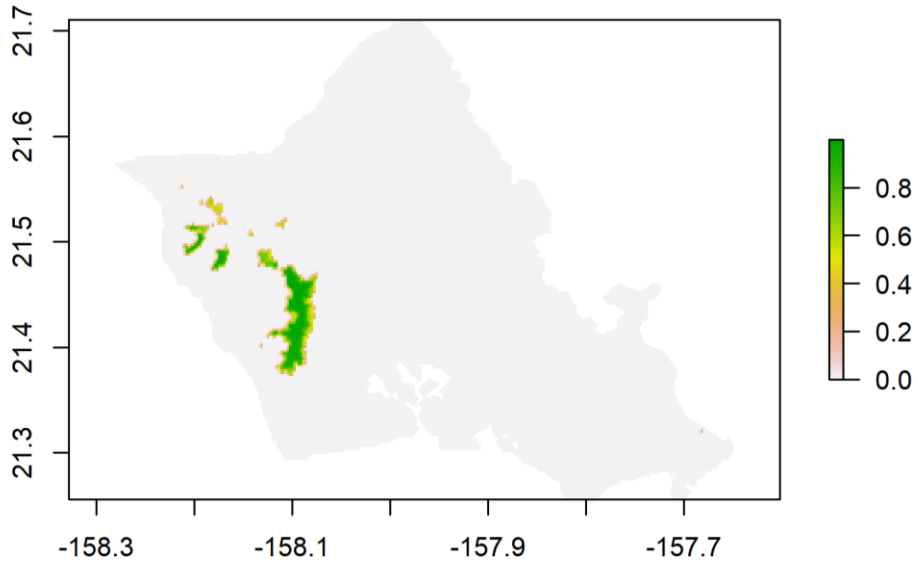


Figure A.8. Baseline species distribution of *Achatinella concavospira* on O‘ahu with a threshold cutoff of 0.5.

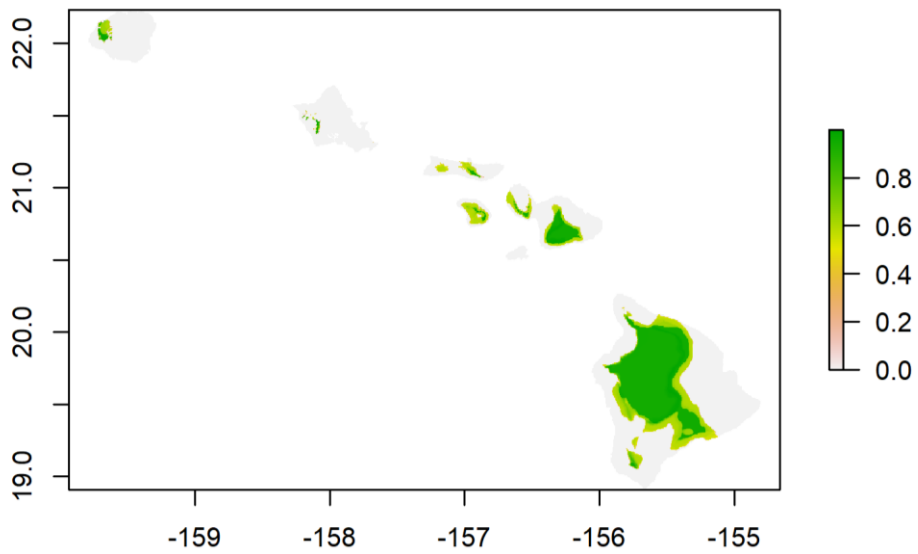


Figure A.9. Baseline species distribution of *Achatinella concavospira* on the Hawaiian Islands with a threshold cutoff of 0.5.

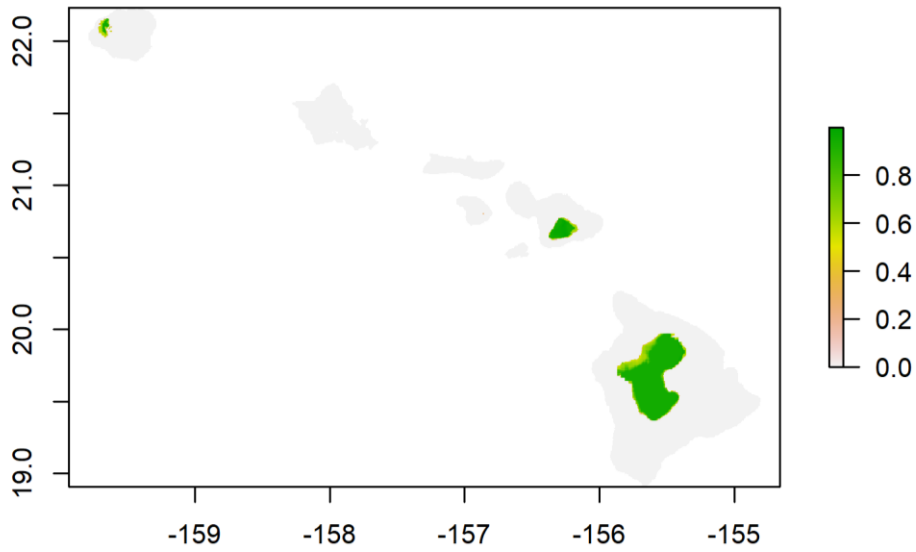


Figure A.10. End of century species distribution of *Achatinella concavospira* on the Hawaiian Islands with a threshold cutoff of 0.5.

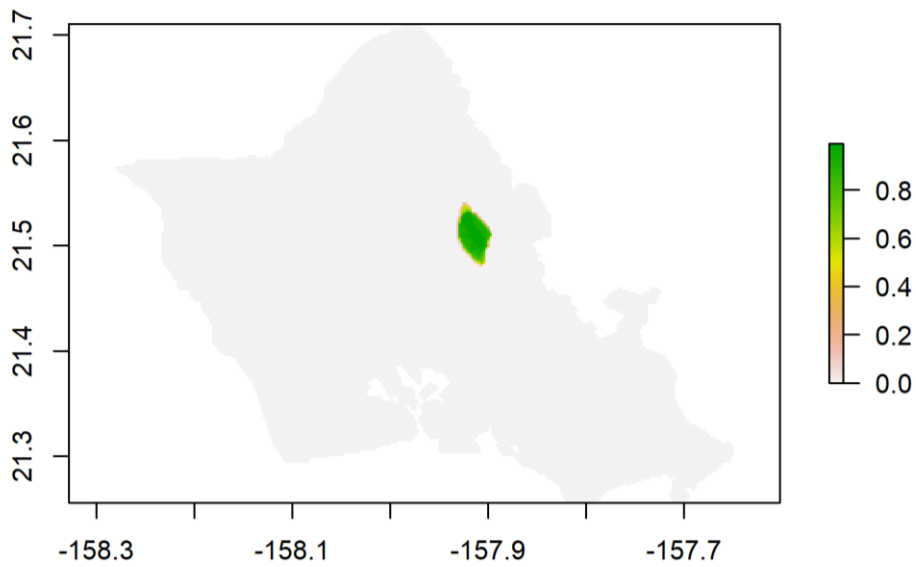


Figure A.11. Baseline species distribution of *Achatinella decipiens* on O‘ahu with a threshold cutoff of 0.5.

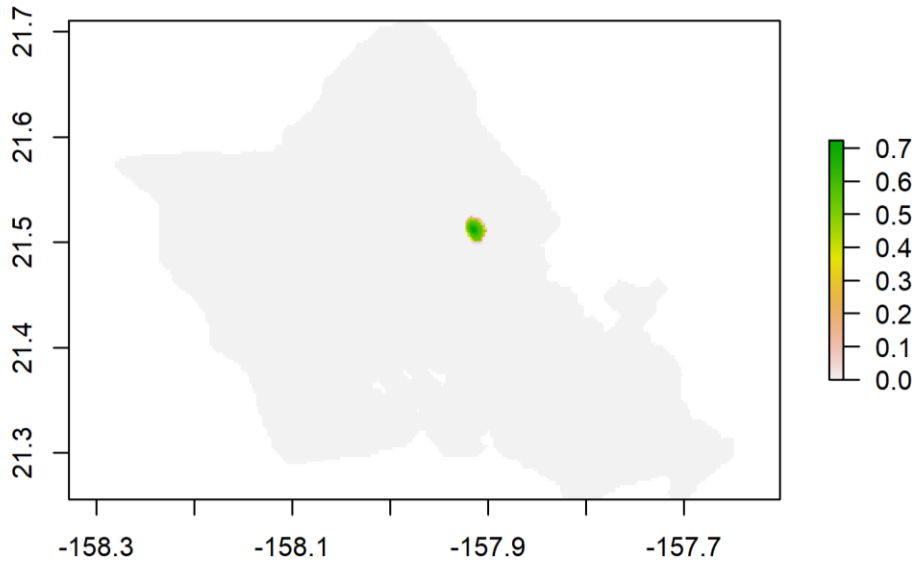


Figure A.12. End of century species distribution of *Achatinella decipiens* on O‘ahu with a threshold cutoff of 0.5.

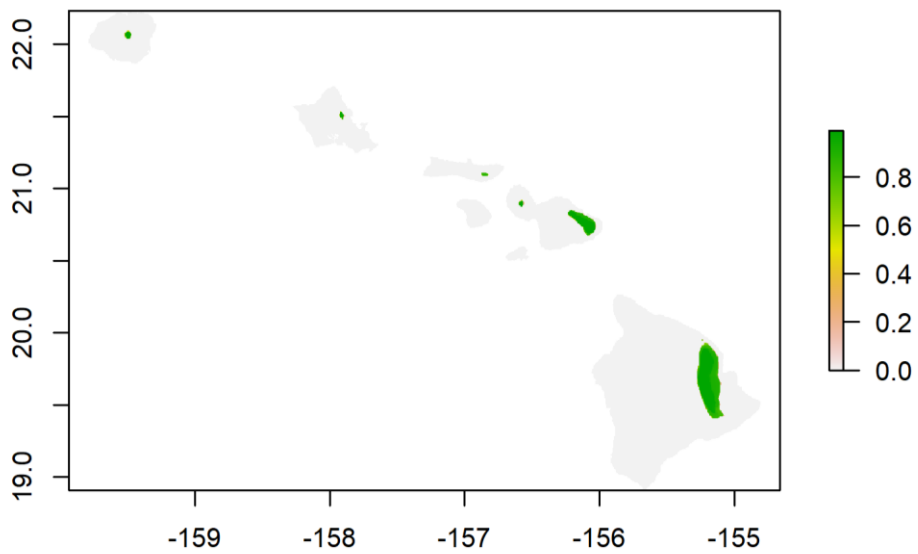


Figure A.13. Baseline species distribution of *Achatinella decipiens* on the Hawaiian Islands with a threshold cutoff of 0.5.

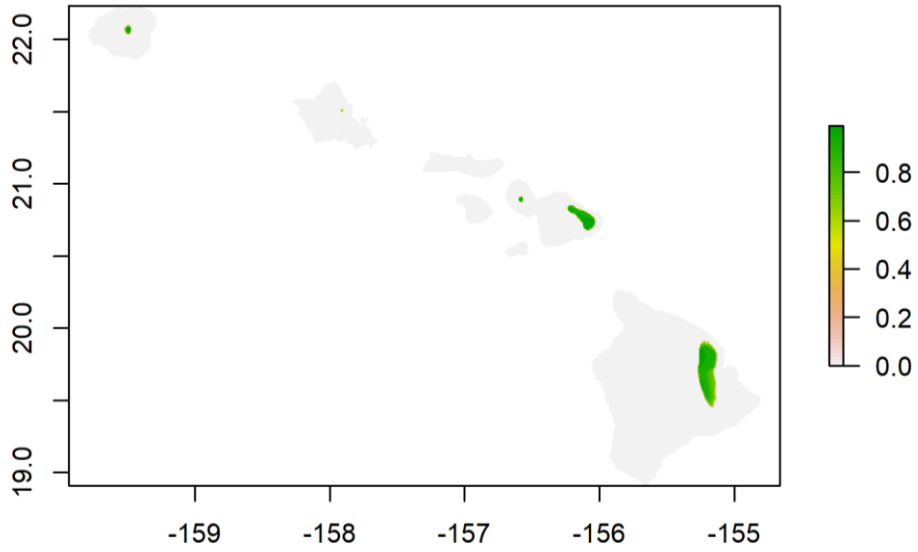


Figure A.14. End of century species distribution of *Achatinella decipiens* on the Hawaiian Islands with a threshold cutoff of 0.5.

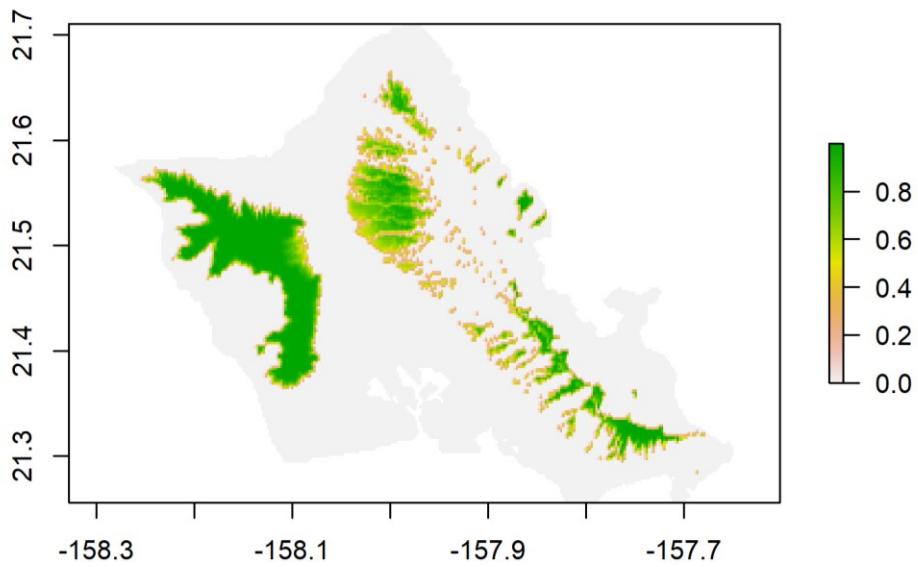


Figure A.15. Baseline species distribution of *Achatinella fulgens* on O'ahu with a threshold cutoff of 0.5.

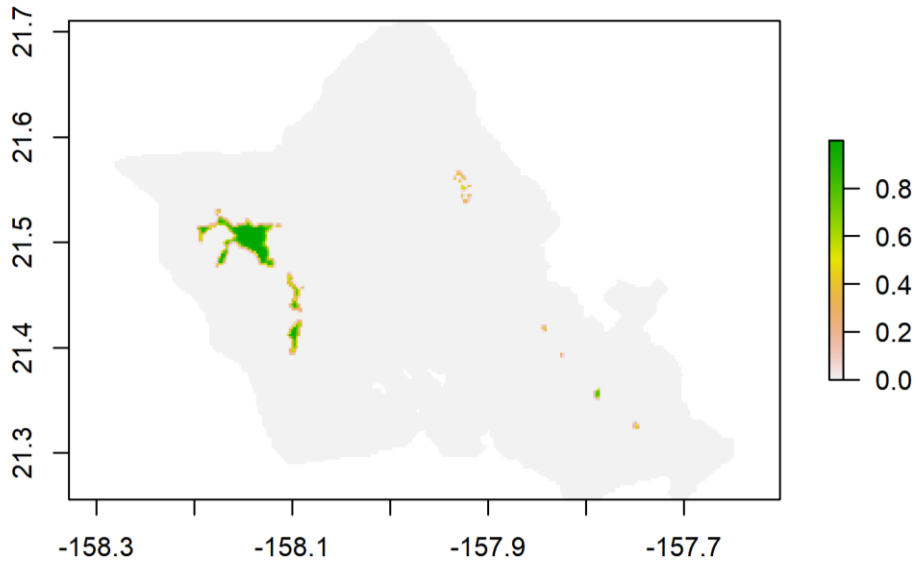


Figure A.16. End of century species distribution of *Achatinella fulgens* on O'ahu with a threshold cutoff of 0.5.

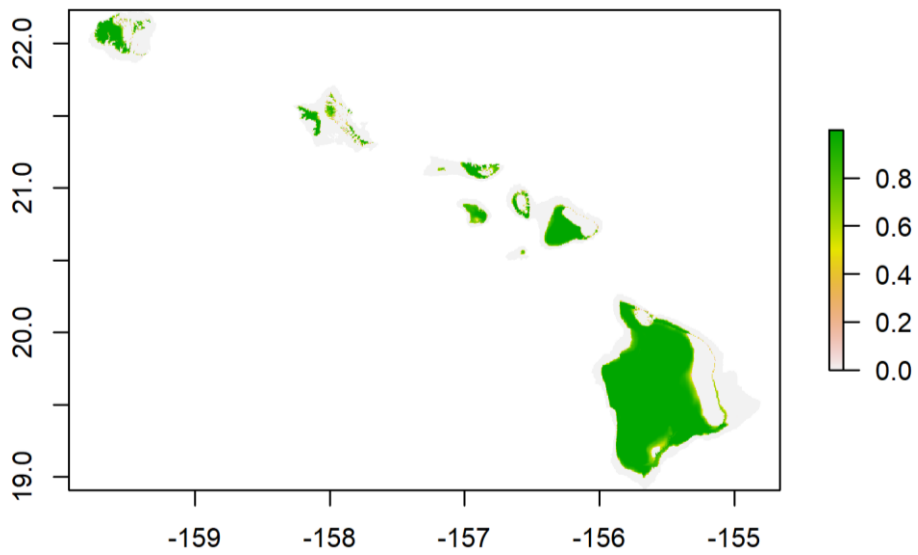


Figure A.17. Baseline species distribution of *Achatinella fulgens* on the Hawaiian Islands with a threshold cutoff of 0.5.

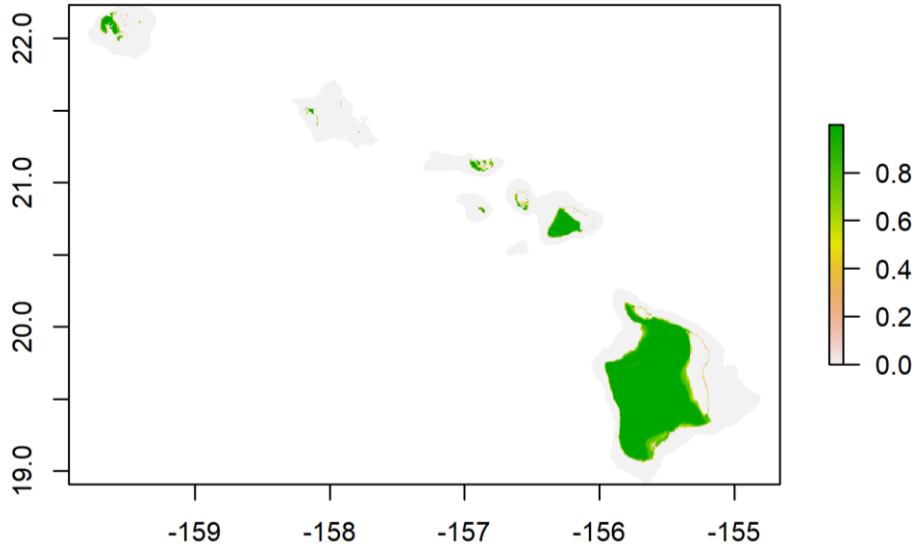


Figure A.18. End of century species distribution of *Achatinella fulgens* on the Hawaiian Islands with a threshold cutoff of 0.5.

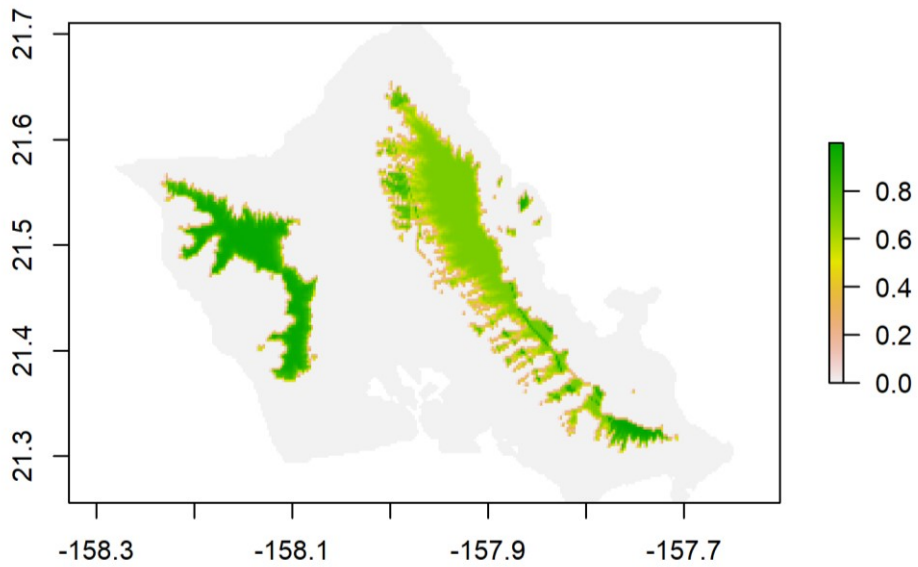


Figure A.19. Baseline species distribution of *Achatinella fuscobasis* on O‘ahu with a threshold cutoff of 0.5.

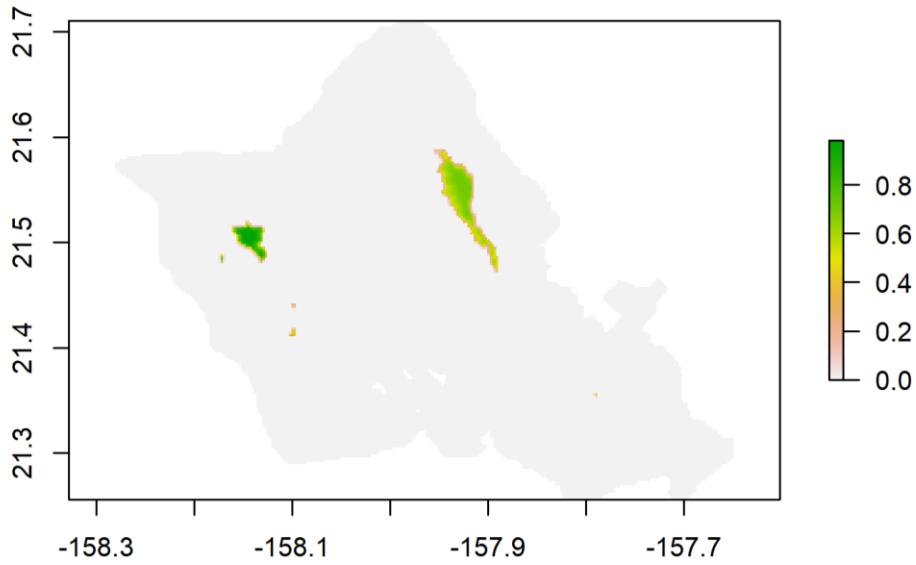


Figure A.20. End of century species distribution of *Achatinella fuscobasis* on O‘ahu with a threshold cutoff of 0.5.

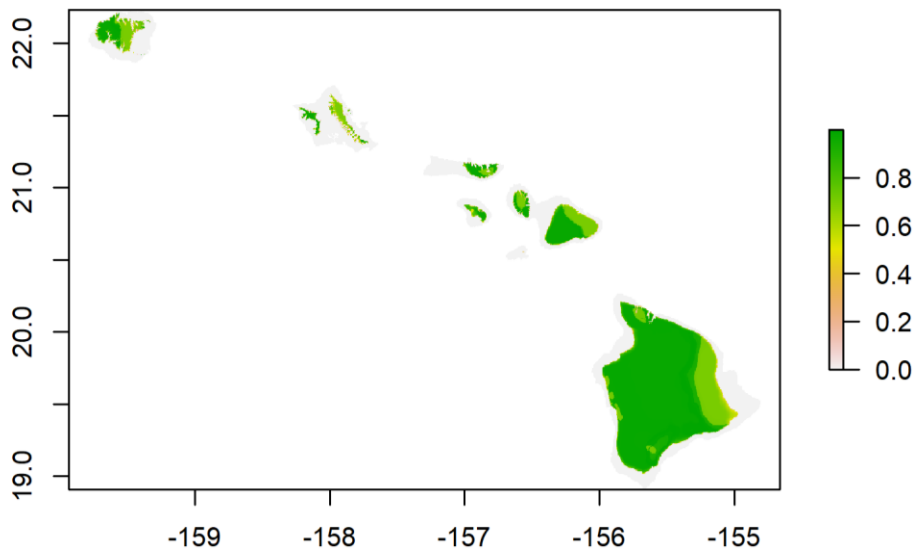


Figure A.21. Baseline species distribution of *Achatinella fuscobasis* on the Hawaiian Islands with a threshold cutoff of 0.5.

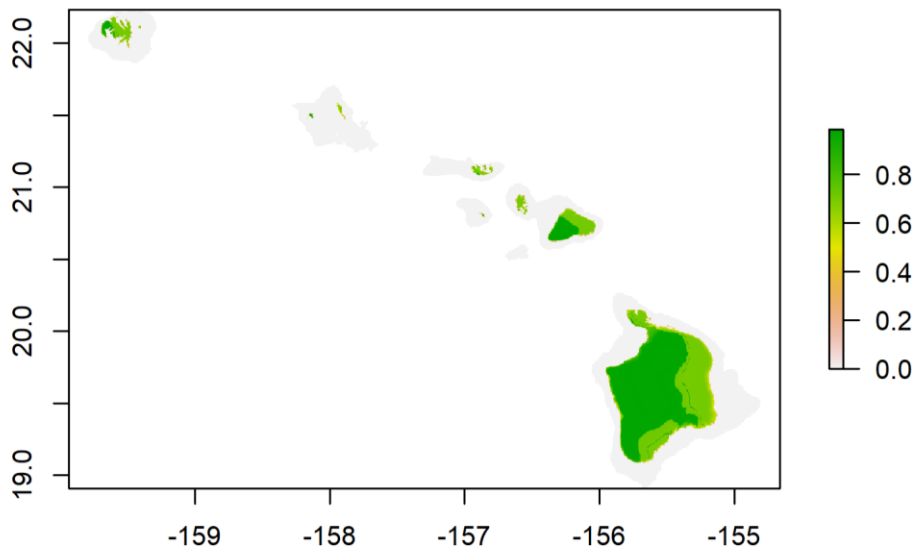


Figure A.22. End of century species distribution of *Achatinella fuscobasis* on the Hawaiian Islands with a threshold cutoff of 0.5.

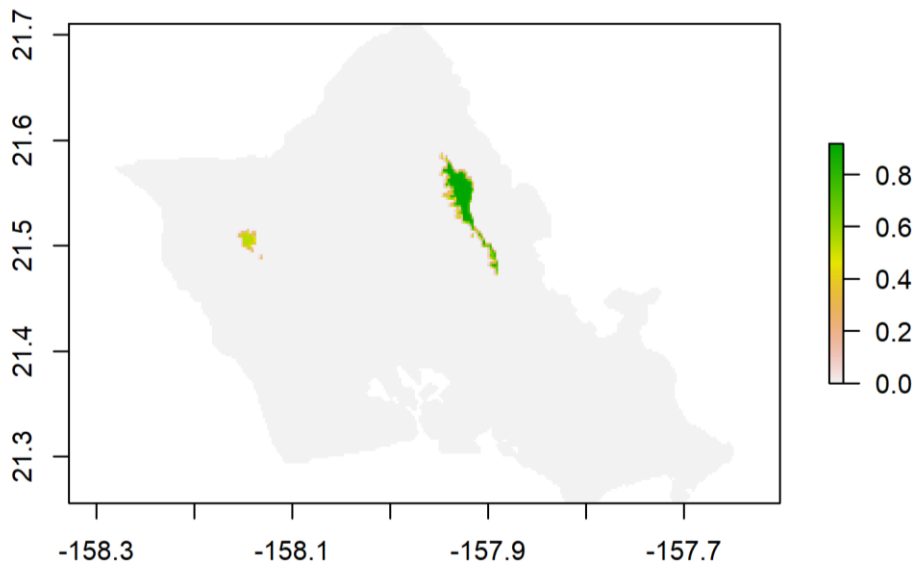


Figure A.23. Baseline species distribution of *Achatinella lila* on O‘ahu with a threshold cutoff of 0.5.

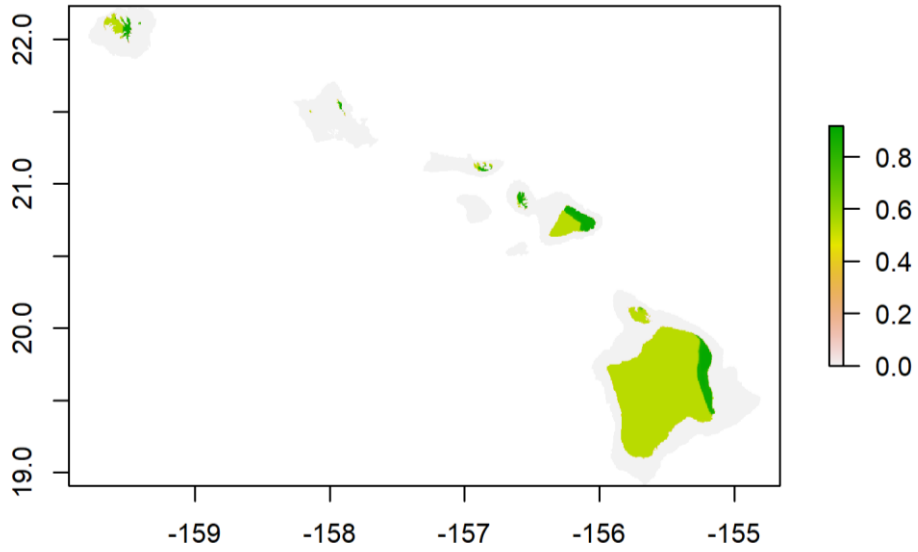


Figure A.24. Baseline species distribution of *Achatinella lila* on the Hawaiian Islands with a threshold cutoff of 0.5.

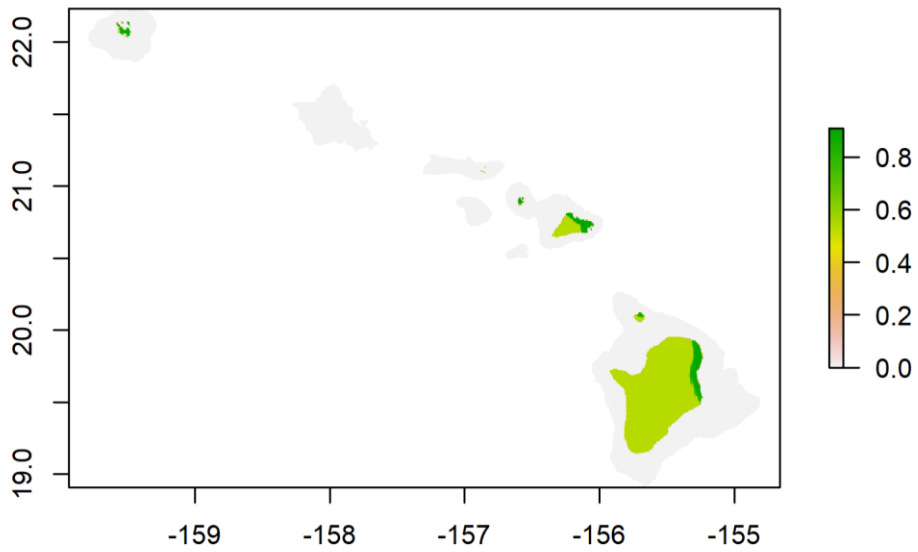


Figure A.25. End of century species distribution of *Achatinella lila* on the Hawaiian Islands with a threshold cutoff of 0.5.

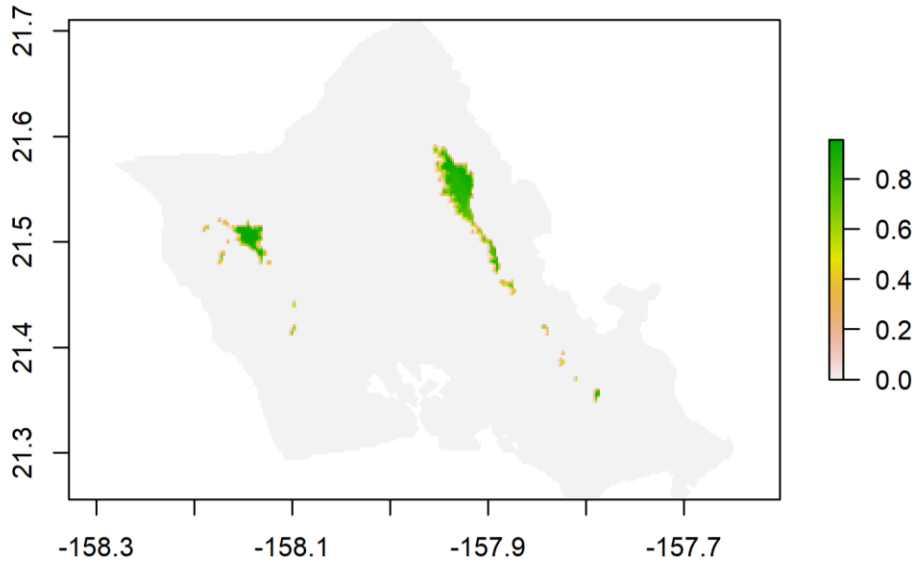


Figure A.26. Baseline species distribution of *Achatinella livida* on O'ahu with a threshold cutoff of 0.5.

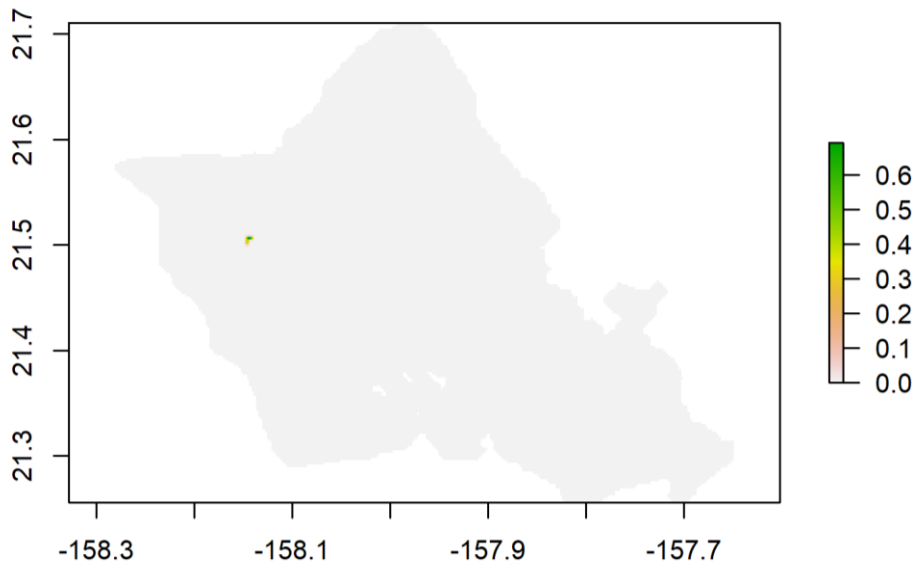


Figure A.27. End of century species distribution of *Achatinella livida* on O'ahu with a threshold cutoff of 0.5.

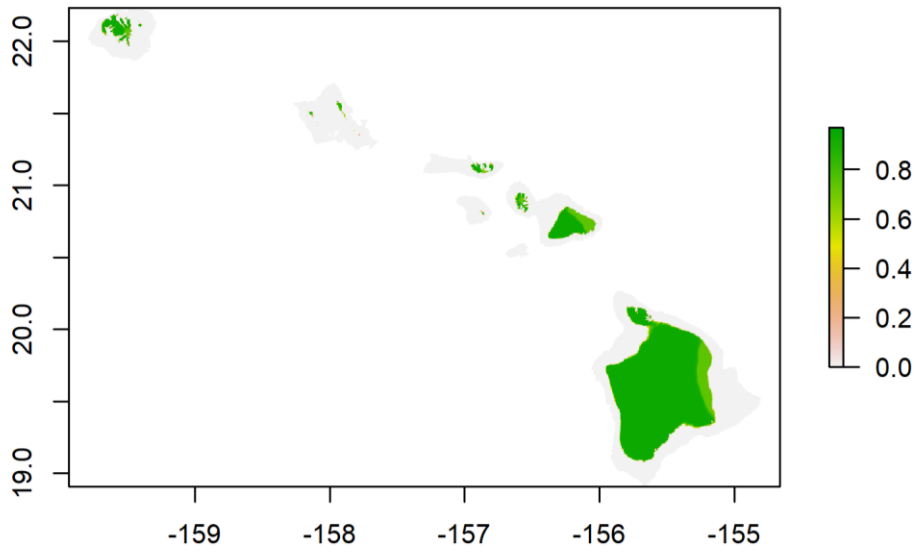


Figure A.28. Baseline species distribution of *Achatinella livida* on the Hawaiian Islands with a threshold cutoff of 0.5.

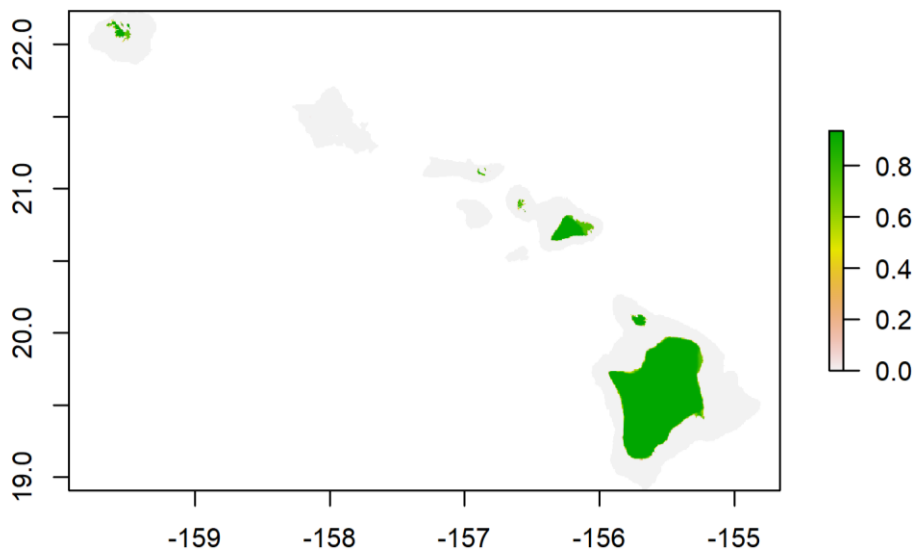


Figure A.29. End of century species distribution of *Achatinella livida* on the Hawaiian Islands with a threshold cutoff of 0.5.

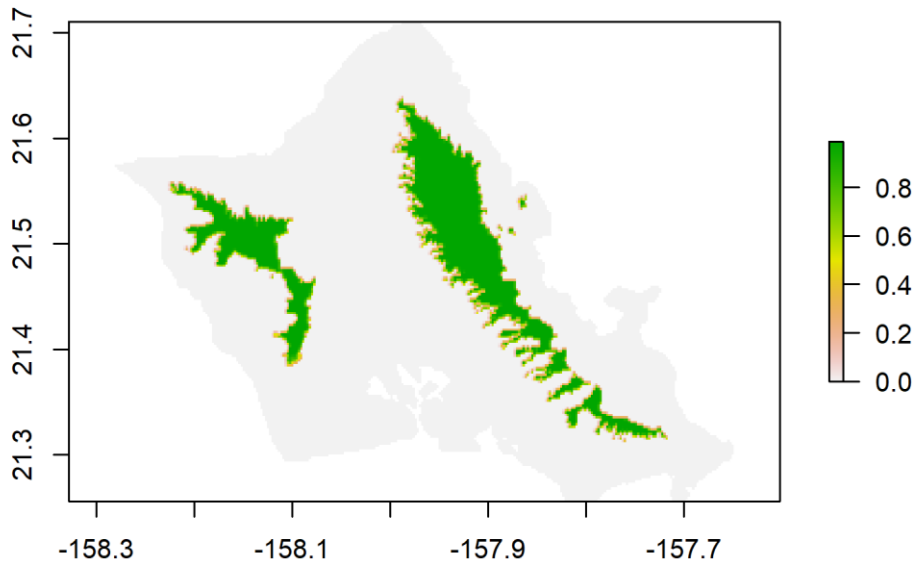


Figure A.30. Baseline species distribution of *Achatinella mustelina* on O'ahu with a threshold cutoff of 0.5.

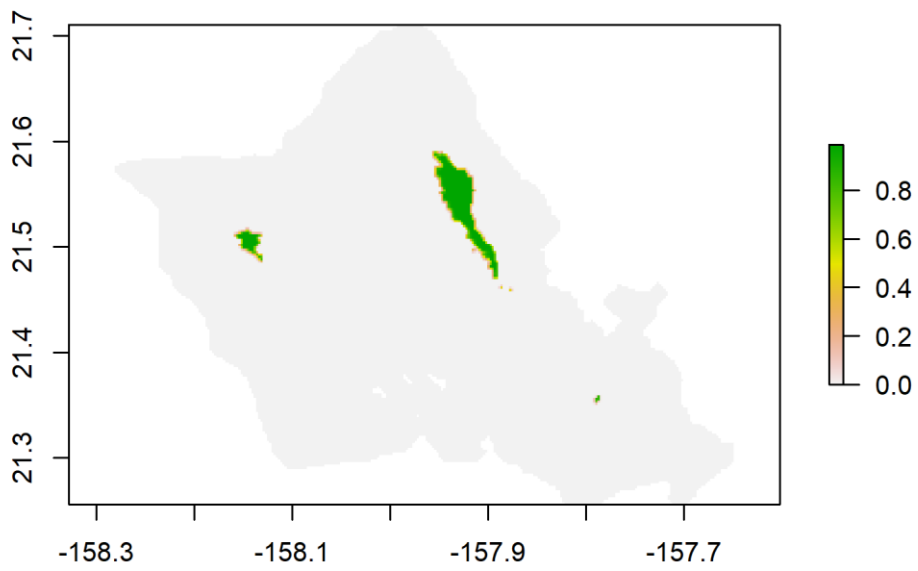


Figure A.31. End of century species distribution of *Achatinella mustelina* on O'ahu with a threshold cutoff of 0.5.

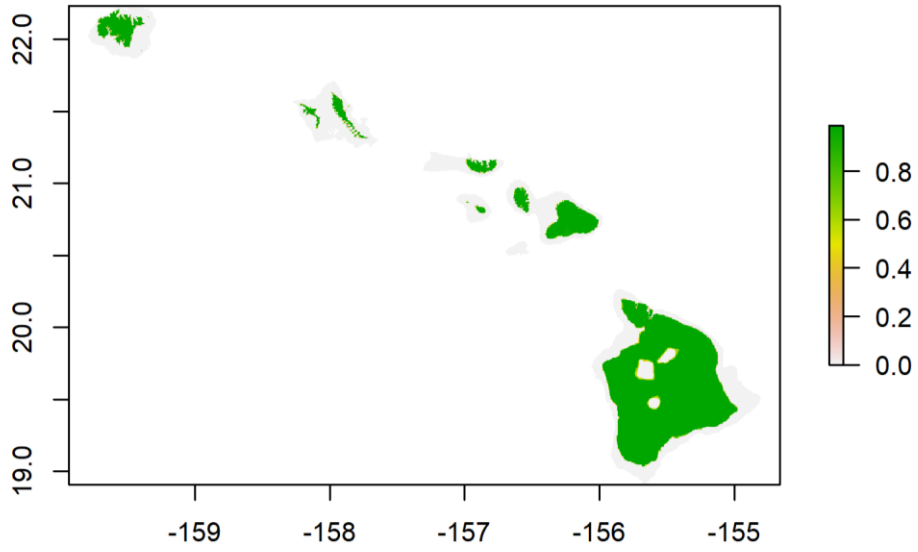


Figure A.32. Baseline species distribution of *Achatinella mustelina* on the Hawaiian Islands with a threshold cutoff of 0.5.

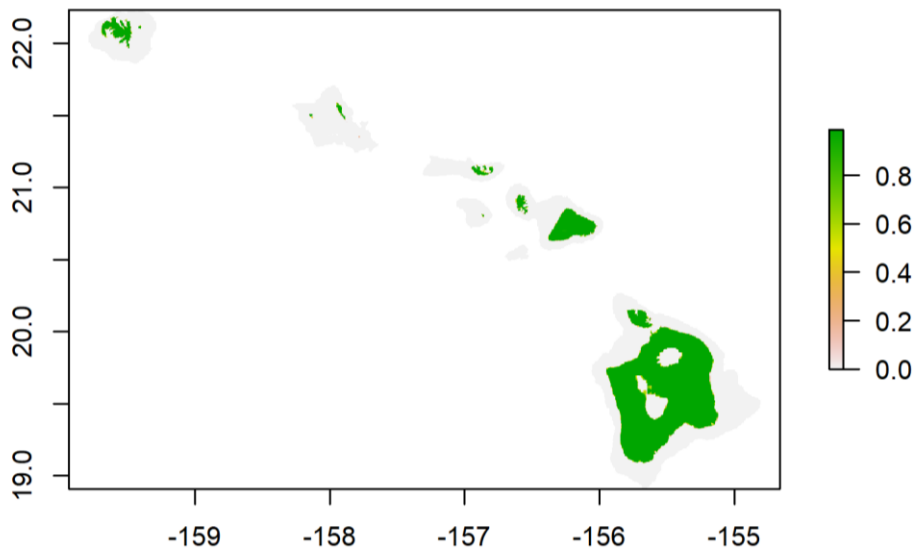


Figure A.33. End of century species distribution of *Achatinella mustelina* on the Hawaiian Islands with a threshold cutoff of 0.5.

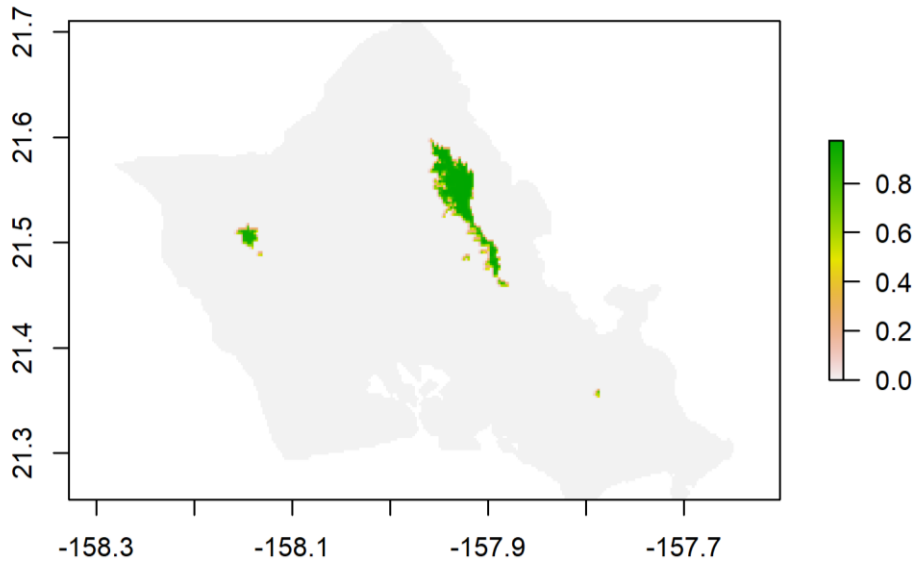


Figure A.34. Baseline species distribution of *Achatinella sowerbyana* on O‘ahu with a threshold cutoff of 0.5.

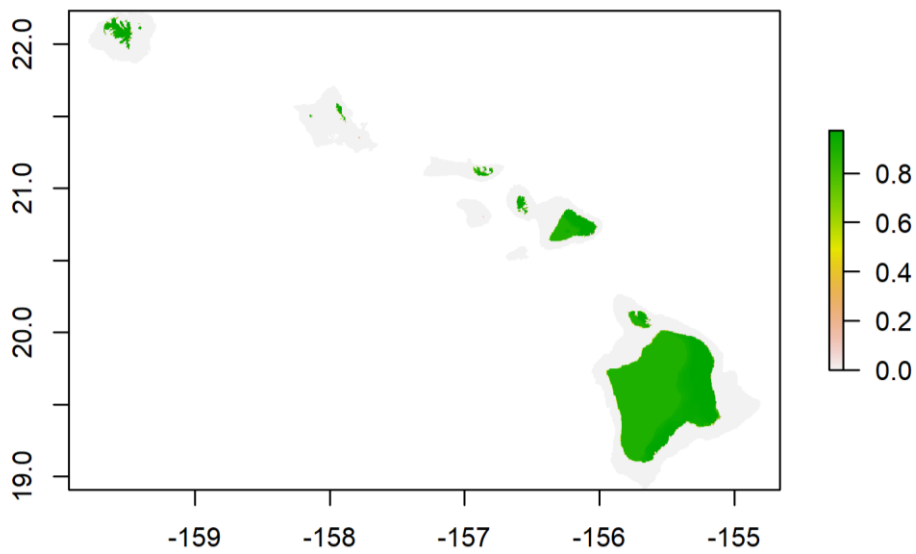


Figure A.35. Baseline species distribution of *Achatinella sowerbyana* on the Hawaiian Islands with a threshold cutoff of 0.5.

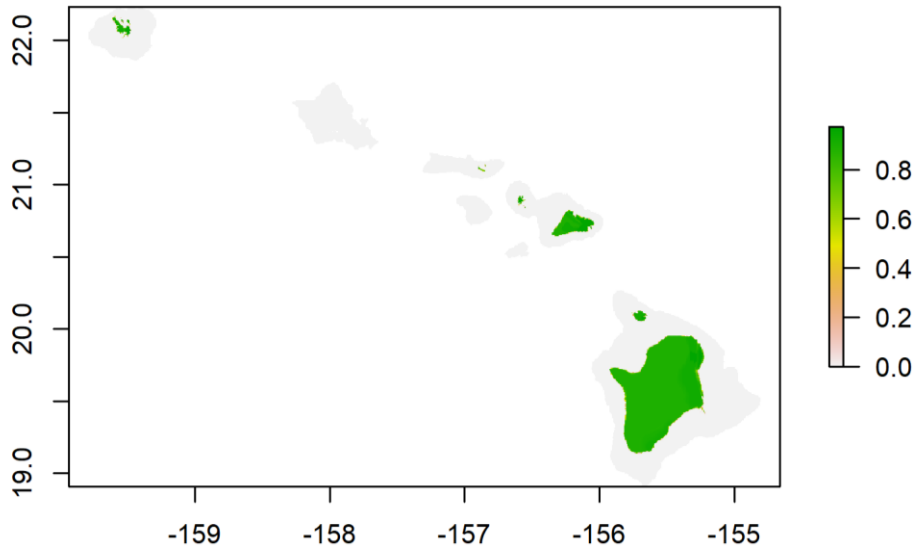


Figure A.36. End of century species distribution of *Achatinella sowerbyana* on the Hawaiian Islands with a threshold cutoff of 0.5.

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