Mapping the Diversification of Hawaiian Swordtail Crickets using Ecological Niche Modeling

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ABSTRACT

The Hawaiian Islands offer a unique opportunity to study the diversification of species, particularly with the endemic Hawaiian swordtail crickets in the genera *Laupala* and *Prolaupala* (Orthoptera: Gryllidae), a radiation of species whose divergence in song promoted rapid diversification through sexual selection. This group's abiotic niches have never been formally studied, so the contribution of niche shifts to their evolution is not well understood. In this study, I generated species distribution models for all 37 species of *Laupala* and 3 species of *Prolaupala* in Maxent. I created predicted niche occupancy models to quantify niche overlap between species and analyzed niche divergence for a phylogenetic signal. Results showed that soil type was the most important environmental factor and maximum precipitation of the driest month was the most important climate variable constraining cricket distributions. Niche overlap showed *Laupala* contains both allopatric and sympatric species. However, there was no phylogenetic signal to niche divergence, indicating that niches have not been evolutionarily conserved. This analysis adds a layer to the substantial information already known about the processes important to generating and maintaining Hawaiian biodiversity.

KEYWORDS

Laupala, Hawaii, Maxent, niche overlap, phylogenetic signal

INTRODUCTION

Phylogeography, the study of phylogenetic relationships in the context of geographic information, provides a spatially explicit mechanism for examining evolutionary processes (Hickerson et al. 2010). As a result of their relatively small sizes and isolation oceanic islands serve as microcosms, providing optimal conditions for phylogeographic research. Particularly in the Hawaiian Islands, the geological chronosequence creates a natural laboratory for ecology and evolutionary biology (Simon 1987). The Hawaiian Archipelago is a chain of volcanic islands produced by a mantle plume in the middle of the Pacific plate, isolated by over 1000km from the nearest land mass, making it both ecologically and geologically one of a kind. Over 5 million years the tectonic movements of this plate created islands from the hot spot in a unique linear order, sequentially from oldest, Kauai, to youngest, Hawaii (Price and Clague 2002). After colonization of the older islands, organisms dispersed to newer islands before radiating into diverse species assemblages (Gruner 2007). Processes of speciation can thus be examined island to island as they progress.

Due to the influences of this unique geography on evolution, Hawaii also has both high levels of endemism and many taxonomic groups that radiated into species-rich lineages. Unlike many islands where colonization drives diversity, Hawaiian diversity has resulted from *in situ* speciation from only a few parental lineages (Simon 1987). This phenomenon occurred strikingly within the terrestrial arthropod fauna which constitute more than 75% of the endemic biota (Eldredge and Miller 1997). Interestingly, initial evidence suggests that groups that expanded within the Hawaiian Islands also tend to have diversified ecological tolerances, indicating that environmental factors have played an important role in the proliferation of the terrestrial arthropods (Roderick and Gillespie 1998). In particular, the endemic Hawaiian swordtail crickets in the genera *Laupala* and *Prolaupala* are a well documented species radiation within the islands (Shaw 1996a). Their divergence in sexual signals promoted their rapid diversification (Mendelson and Shaw 2005). However, their abiotic niches have never been formally examined, making it difficult to determine the relative importance of habitat, and specifically, niche differentiation to the diversification of this group.

Ecological Niche Modeling, a phylogeographic tool, predicts species distributions based on documented occurrences, allowing for the inclusion of abiotic characteristics in explaining the role of the environment in evolution (Chan et al. 2011). Models extrapolate habitat suitability based on each species ecological associations, using climatic and geographic variables like precipitation and temperature (Philips et al. 2006). This data can then create niche models which can be analyzed in the context of the phylogeny or evolutionary history for each group (Chan et al. 2011). Ultimately such techniques provide information on the species' fundamental niche, all tolerable habitat conditions, and corresponding patterns of diversification (Wies and Graham 2005). Distribution models have many applications; they facilitate more accurate predictions of the effects of biological invasions, climate change, and anthropogenic disturbances, all especially important in the fragile island ecosystems (Phillips et al. 2006). Ecological Niche Modeling has not previously been conducted with any Hawaiian arthropod, thus generating distribution models will provide critical information on the endemic organisms that live within this distinct Hawaiian environment.

In this study, I used cricket occurrence records and environmental layers to produce models for each species using the program Maxent (Phillips et al. 2006). This method provides information on the ranges of each cricket species and what environmental factors constrain their distributions. I then created predicted niche occupancy models (PNOs) and quantified niche overlap between species based on the published phylogeny to determine to what extent niches diverge (Evans et al. 2009). Each model was used to identify which clades have similar and evolutionarily conserved niches instead of novel shifted niches (Fitzpatrick and Turelli 2006). This project contributes a level of understanding to the information known about the processes important to generating and maintaining biodiversity in the fascinating Hawaiian biota.

METHODS

Focal taxa

I modeled the distributions of Hawaiian swordtail crickets in the endemic genera *Laupala* and *Prolaupala*. I modeled all 37 described species of *Laupala* contained in the Cerasina, Kauai, and Pacifica groups and the 3 species of *Prolaupala*. These genera are flightless detritivore crickets generally found in higher elevation forests in the leaf litter or on low vegetation (Figure 1; Otte 1994). They reproduce by transferring spermatophores through copulation and then depositing eggs with an ovipositor (de Carvalho and Shaw 2009). These crickets exhibit a huge range in male song type along with high selectivity in mate choice by female crickets and are cryptic, often only identifiable by the differences in song pulse rate (Mendelson and Shaw 2002, Mendelson and Shaw 2005, Otte 1994). This has led to extreme sexual selection based on small changes in acoustics and the highest documented rate of speciation of any arthropod in the world (Mendelson and Shaw 2005). Based on initial taxonomic descriptions ecological attributes do not distinguish species and many species are sympatric, thus it is thought that speciation is unlikely to be explained by shifts in niche (Shaw 2000, Otte 1994). However, abiotic ranges have never been systematically documented in *Laupala* or *Prolaupala*. More information is needed to understand the potential contribution of adaptive niche shifts in addition to sexual selection on swordtail cricket evolution.

Figure 1. *Laupala* crickets showing cryptic morphology. Photos courtesy of Kerry L. Shaw.

Data sources

This study focused on the largest Hawaiian Islands; Kauai, Oahu, Molokai, Lanai, Maui, and Hawaii. Datasets originated from published specimen localities assembled during previous collecting. I digitized the majority of localities from records in the book *The Crickets of Hawaii* and additional localities in papers by Kerry L. Shaw by geo-referencing (Otte 1994, Shaw 2000, de Carvalho and Shaw 2009, Fergus and Shaw 2011, LaPolla et al. 2000, Mendelson and Shaw

2002, Mendelson et al. 2004, Parsons and Shaw 2001, Shaw 1996a, Shaw 1996b). Geo-referencing entails manually looking up verbatim place names on a topographic map and recording the latitude and longitude digitally. I recorded presence data for the focal taxa in the form of latitude and longitude coordinates geo-referenced using the WGS-84 datum. I then mapped all points in ArcGIS 10.2 and transformed the data the datum (NAD83; ESRI 2011).

Maxent modeling

Through the species distribution modeling (SDM) program Maxent, which models distributions using presence only data, I correlated species occurrences with environmental data to determine each species abiotic niche (Philips et al. 2006). Maxent utilizes a statistical approach called maximum entropy to make predictions based on incomplete information, estimating the most uniform distribution across the designated area (Philips et al. 2006). It then uses a technique called 'relaxation' to combat over-fitting (Hernandez et al. 2006). Maxent is appropriate for this study because it does not require reliable absence data for the species, which is difficult to obtain from historic records that span multiple collecting expeditions. Maxent is also the most capable SDM modeling program for small sample sizes, producing meaningful models with as few as 5 occurrences (Hernandez et al. 2006). It is thus able to compensate for the small incomplete datasets available for *Laupala* and *Prolaupala*. In general Maxent has improved accuracy for species with restricted ranges and limited ecological tolerances as opposed to wide-ranging species, characteristics of *Laupala* (Hernandez et al. 2006). In rare range limited species like the swordtail crickets Maxent can successfully estimate species ranges and habitat (Philips et al. 2006). Maxent is also relatively insensitive to the spatial errors associated with location data, especially in historic data sets such as the data for this study (Baldwin 2009).

I assembled the geo-referenced presence coordinates and environmental raster layers, a continuous grid of data cells, clipped to the extent of the Hawaiian Islands in ArcGIS 10.2 (ESRI 2011). I obtained environmental datasets from online open access resources; BioClim for temperature and precipitation data (Hijmans et al. 2005), US Department of Agriculture (USDA) for soil data (APPENDIX A; Hawaii Soil Survey 2000) and the State of Hawaii's open access GIS maps for Digital Elevation Models (DEM 2007) and data on land use (APPENDIX A;

Hawaii GIS 2003). I transformed all layers from shape files to rasters and re-sampled from the original 1km² (BioClim) or 10m² (soil type, land cover, elevation) resolution to 30m² resolution to increase the detail of the output ranges given that Hawaii has such a small area (ESRI 2011). I based model resolution and the addition of soil type, land cover, and DEM layers on work conducted by the Hawai'i Cooperative Studies Unit (Price et al. 2008). While the scaled up resolution and mix of continuous (BioClim, DEM) and categorical (soil type, land cover) variables adds the potential for bias there is no alternative when dealing with multiple layers and such range restricted species.

I ran Maxent under the auto features setting with jackknifing, resulting in individual variable response curves and pictures of predictions (Phillips et al. 2006). I first ran a correlation analysis of the raster layers and selected variables by eliminating combined and correlated variables in ArcGIS (ESRI 2011). I then chose ecological characteristics likely to restrain range in the Hawaiian environment (Table 1). The final model included soil type, land cover, DEM, Bio2 (mean diurnal temperature range), Bio4 (temperature seasonality measured by the coefficient of variation), Bio5 (maximum temperature of the warmest month), Bio14 (precipitation of the driest month), and Bio15 (precipitation seasonality measured by the coefficient of variation). The jack-knife process provides information on how important each variable is individually at explaining the species distribution. Response curves illustrate the specific effects of each variable and percent contributions denote each variable's relative contribution to the generated distribution model. I ran the final model once with all points and a second time using 50% of the data to train and then validate the models.

Table 1. Methods of variable selection. Temperature is measured in (°C*10) and precipitation is measured by (mm). CORR= correlated, COMB= combined multiple variables (precipitation and temperature, or multiple temperature variables), CLIM= based on warm, wet, moderate Hawaiian climate, RANGE= likely to limit ranges.

Category	Name	Variable	Reason for Discarding or Selection	Correlations (> +/-0.7) Present in Final Model
Topographic	Soil Type (USDA Categories)	**SOIL**	RANGE	None
	Land Cover	**LAND**	RANGE	None
	Digital Elevation Model	**DEM**	RANGE	BIO2 (0.828), Bio5 (-1.056)
Temperature	Annual mean temperature	BIO1	CORR (BIO5)	---
	Mean diurnal temperature range (mean (period max-min))	**BIO2**	CLIM	DEM (0.828)
	Isothermality (Bio02 ÷ Bio07)	BIO3	COMB	---
	Temperature seasonality (Coefficient of Variation)	**BIO4**	CLIM	None
	Max temperature of warmest month	**BIO5**	RANGE	DEM (-1.056)
	Min temperature of coldest month	BIO6	CORR (BIO5)	---
	Temperature annual range (Bio05-Bio06)	BIO7	COMB	---
	Mean temperature of wettest quarter	BIO8	COMB	---
	Mean temperature of driest quarter	BIO9	COMB	---
	Mean temperature of warmest quarter	BIO10	CORR (BIO5)	---
	Mean temperature of coldest quarter	BIO11	CORR (BIO5)	---
Precipitation	Annual precipitation	BIO12	CORR (BIO14)	---
	Precipitation of wettest month	BIO13	CORR (BIO14)	---
	Precipitation of driest month	**BIO14**	CLIM	None
	Precipitation seasonality (Coefficient of Variation)	**BIO15**	CLIM	None
	Precipitation of wettest quarter	BIO16	CORR (BIO14)	---
	Precipitation of driest quarter	BIO17	CORR (BIO14)	---
	Precipitation of warmest quarter	BIO18	COMB	---
	Precipitation of coldest quarter	BIO19	COMB	---

Phylogenetic processing

To determine correlations between niche divergence and speciation I examined predicted ranges in the context of the most recent phylogeny (Figure 2). I first created Predicted Niche Occupancy Models (PNOs) for the top two most important continuous variables using the phyloclim package developed for R and then analyzed them for pair wise percent overlap (R

Core Team 2013). PNOs profile the response of each species to each individual climate variable by plotting variable range against the probability distributions generated in Maxent (Evans et al. 2009). This method allows determination of when and where niches are conserved and in the same place versus shifted and novel based on quantified overlap (Wies and Graham 2005, Evans et al. 2009). Finally I analyzed the trends in overlap for a phylogenetic signal using age-range correlation and MonteCarlo replicates test for significance (Fitzpatrick and Turelli 2006). This function compared amount of divergence genetically based on number of nodes separating species to amount of divergence in niche based on overlap using a linear regression (R Core Team 2013).

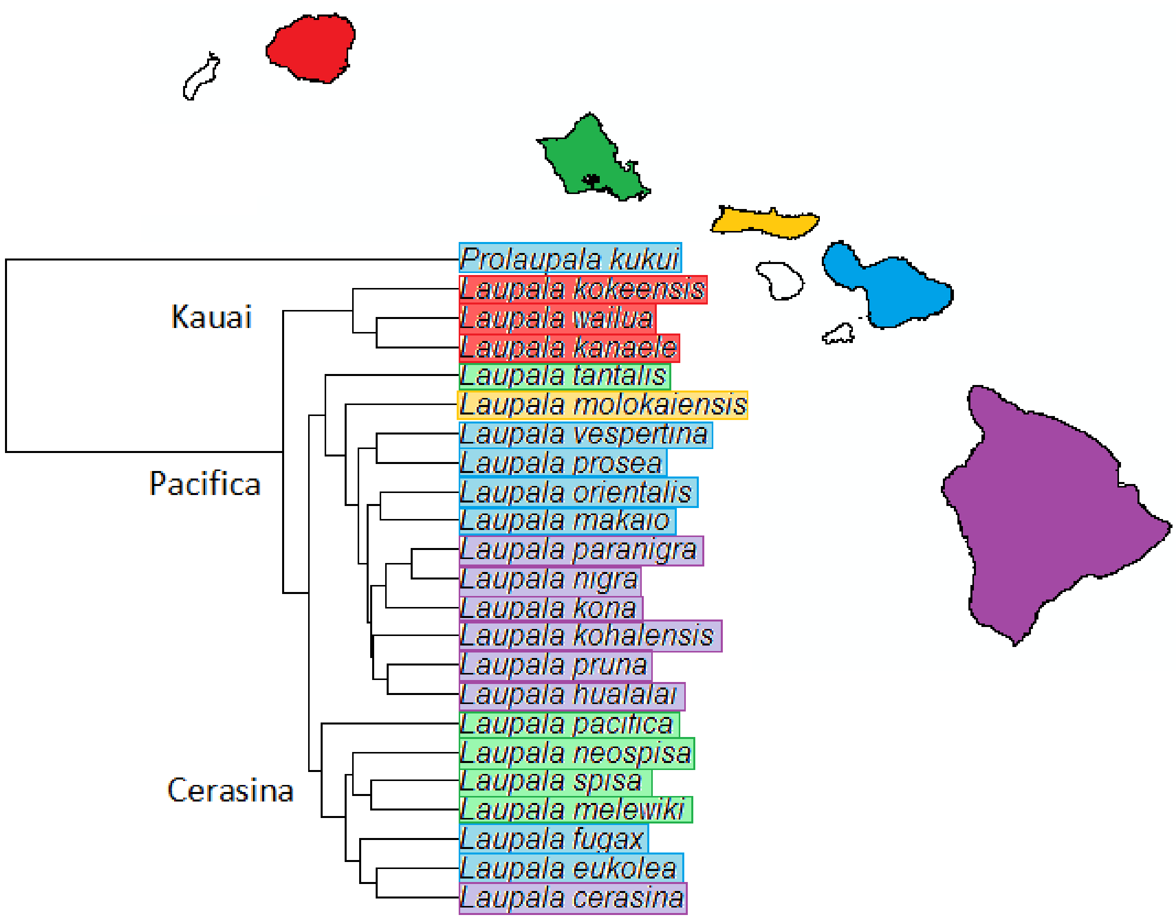

Figure 2. Cricket Phylogeny. *Prolaupala kukui* was used as the out-group, adapted from published phylogeny (Mendelson and Shaw 2005).

RESULTS

Maxent distribution models

The Maxent analysis yielded distributions for all species modeled (APPENDIX B). The 'area under the curve' (AUC) values, which measure model predictive ability, were all statistically significant when compared to the random prediction AUC value of 0.5. These results verify that the model can effectively predict the distribution of *Laupala* given enough presence values. Using the threshold of 5 minimum records for a meaningful model and p-values <.05 obtained from model validation not all niche models were significant. Seventeen of the total forty-nine documented *Laupala* species and all three documented *Prolaupala* species had insufficient presence records for niche examination (Table 2). Thus while all of the maps indicate ranges, only the 20 significant models were useful for examining environmental factors.

Geographically no species range covered an entire island and most were restricted to less than half of the island area. The 40 species modeled had narrow distributions with none present on multiple islands (Figure 3). In *Laupala* the Pacifica group had the largest range, followed by the Cerasina group, with the Kauai group having the smallest range. Total range size varied from ~40km² with *Laupala lanaiensis* to ~2500 km² with *Laupala hualalai* and 330km² with *Prolaupala perkinsi* to ~1600km² with *Prolaupala kaalensis*.

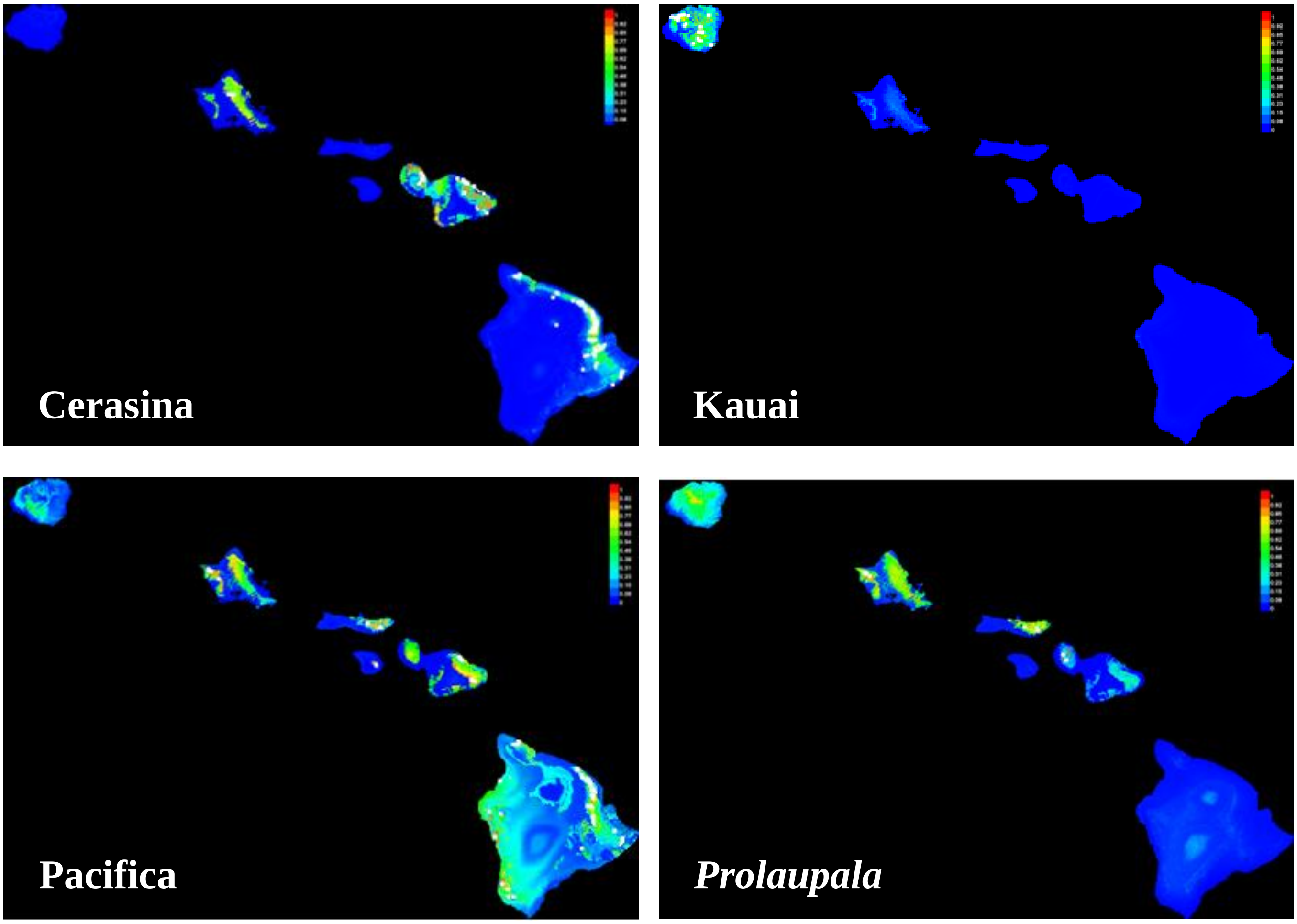

Figure 3. Map of cricket species distributions by phylogenetic group. Areas with warmer colors indicate higher habitat suitability (red= 100%) while areas with cooler colors indicate lower habitat suitability (dark blue= 0%).

In the species modeled soil had the highest percent contribution and permutation importance to the Maxent models (APPENDIX B). Based on the jackknife of variable results established soil type was the best predictor of suitable areas when determining a species' distribution (Figure 4). Based on the response curves *Laupala* were found most often in well drained loamy soils (Table 2). Kaalualu (moderately deep, excessively drained soils formed in volcanic ash over \`a\`a lava, temperature 74°F) and Mokuleia (well drained soils formed in alluvium deposited over coral sand, temperature 74°F) were the most common soil types occupied (Table 2; APPENDIX A; Hawaii Soil Survey 2000). *Laupala* were most often found in forest type habitats. Open habitats like shrub land and developed areas had fewer predicted *Laupala*. Alien Forest and Closed Koa-Ohia Forest were the most commonly predicted land covers (Table 2). Elevation, obtained from the response curves to DEM, showed *Laupala kokeensis* occurred at the highest elevation 1150m and *Laupala vespertina* (and others; Table 2) occurred at the lowest 0m. *Laupala* as a group had a mean elevation of 230m above sea level.

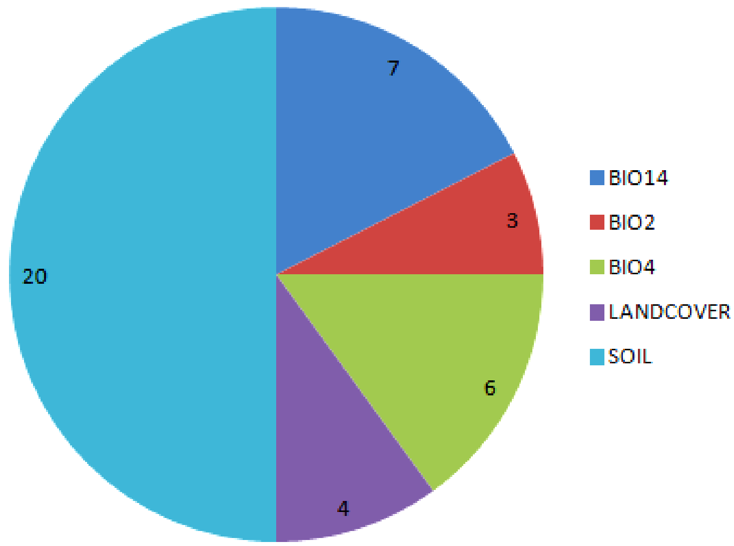

Figure 4. Chart of top two predictors of range based on jackknife results. Soil was the best predictor, followed by precipitation in the driest month (Bio14), then temperature seasonality (Bio4), land cover, and mean diurnal range (Bio2) (Table 2).

In general *Laupala* were constrained to wetter areas with less fluctuation in temperature. Based on the response curves produced by the predicted distributions, diurnal temperature fluctuations ranged from 7.5°C with *Laupala kolea* (and others; Table 2) to 9.6°C with *Laupala kauaiensis* and *Laupala makaweli* with a median of 8.0°C. Temperature seasonality varied from 94.5°C with *Laupala kohalensis* to 176.0°C with *Laupala kolea* and others with a median of 151.0°C. Maximum temperature of the warmest month varied from 23.8°C with *Laupala kokeensis* to 30.5°C with *Laupala kohalensis* with a median of 28.0°C. Precipitation seasonality ranged from 10 mm with *Laupala tantalis* and others to 100 mm with *Laupala makaweli* with a median of 20mm. Precipitation of the driest month ranged from 65mm with *Laupala kokeensis* to 400mm with *Laupala pruna* and others with a median of 350mm. See APPENDIX B for distribution maps and environmental characteristics by species.

Table 2. Summary of Maxent results for 20 significant models. This table is based on response curves and jackknife of variable importance results in APPENDIX B. Models were considered significant with a p-value less than 0.05. See APPENDIX A for explanation of soil type by name. BIO 14 and Bio15 are precipitation measured in mm. BIO 2, BIO4, and BIO5 are temperature variables measured in °C x 10. DEM is measured in m above sea level.

Phylo Group	Species	# Pts.	Island	Top Layers >0.5 gain	p-value (5)	BIO 14	BIO 15	BIO 2	BIO 4	BIO 5	DEM	LANDCOVER	SOIL
Cerasina	***L. cerasina***	82	Hawaii	1- bio14, 2- soil, 3- bio5, 4- bio4, 4-dem, 6- bio2, 7- bio15	1.11E-19	255	26	83.5	1085	270	275	Uluhe Shrubland, Closed Koa-Ohia Forest, Closed &Open Ohia Forest, Cultivated Cropland, Alien Forest, Uncharacterized Forest	Puu Pa, Olaa-Hydrudands-Hilo, Waimea-Kikoni, Waikaloa-Waiaha-Pakini-Kaalualu
	L. eukolea	18	Maui	1- soil, 2- bio2, 3- landcover, 4- bio4, 5- bio14	0.001185	200	24	77.5	1250	280	200	Alien Forest, Uncharacterized Shrubland	Tantalus-Makiki-Koko-Cinder land, Pulehu-Mala-Kealia-Ewa
	L. kolea	7	Maui	1- soil, 2- bio2	0.007194	400	10	75	1760	305	0	Closed Ohia Forest, Alien Forest, Uncharacterized Open-Sparse Vegetation	Tantalus-Makiki-Koko-Cinder land, Pulehu-Mala-Kealia-Ewa
	L. spisa	6	Oahu	1- soil, 2- bio14, 3- bio15	0.007592	400	10	75	1760	305	0	Ohia Forest, Alien Forest	Waikane-Lolekaa-Kemoo-Alaeloa, Kekake-Keei-Kahaluu
Kauai	***L. kauaiensis***	12	Kauai	1- soil, 2- bio4, 3- landcover	6.3E-05	400	10	96	1760	305	260	Native Wet Forest&Shrubland, Developed, High Intensity, Alien Shrubland	Mokuleia-Jaucas, Pakala -Kolokolo-Hanalei, Waikomo
	L. kokeensis	15	Kauai	1- bio4, 2- soil, 3- landcover, 3- dem, 5- bio5, 6- bio15	1.18E-07	65	54	87.5	1760	238	1150	Closed Koa-Ohia Forest, Closed&Open Ohia Forest, Native Mesic to Dry Forest&Shrubland, Native Wet Forest&Shrubland, Open Koa-Ohia Forest, Developed, Low Intensity, Alien Forest	Pakala-Mokuleia variant-Kolokolo-Hanalei, Mokuleia-Jaucas Puhi-Makaweli-Lihue-Hanamaulu
	L. koloa	12	Kauai	1- soil, 2- landcover, 3- bio4, 4- bio14, 5- bio15, 6-dem	8.67E-10	400	10	75	1760	NA	0	Alien Forest	Waikomo
	L. makaweli	9	Kauai	1- bio4, 2- soil, 3- landcover	0.000238	NA	100	96	1760	NA	NA	Closed & Open Koa-Ohia Forest, Native Wet Forest&Shrubland, Alien Forest	Waikomo, Mokuleia-Jaucas Puhi-Makaweli-Lihue-Hanamaulu
	L. olohena	24	Kauai	1- soil, 2- bio4, 3- landcover, 4- bio14, 5- bio5, 6- dem, 7- bio15	1.83E-14	195	22	86.5	1510	280	295	Native Wet Forest&Shrubland, Alien Forest	Pakala-Mokuleia variant-Kolokolo-Hanalei, Waikomo, Mokuleia-Jaucas

	L. wailua	22	Kauai	1- soil, 2- bio4, 3- landcover, 4- bio14, 5- bio5, 6- dem, 7- bio15	5.87E-15	200	23	86.5	1510	280	300	Native Wet Forest&Shrubland, Alien Forest	Pakala-Mokuleia variant-Kolokolo-Hanalei, Waikomo, Mokuleia-Jaucas
Pacifica	***L. kohalensis***	5	Hawaii	1- soil, 2- landcover, 3- bio2	0.03227	NA	10	75	945	305	0	Closed Ohia Forest, Alien Shrubland	Waimea-Kikoni
	L. nigra	34	Hawaii	1- soil, 2- bio14, 3- bio5, 4- bio2, 5- dem, 6- bio4, 7- bio15, 8- landcover	3.56E-22	245	26	83.5	1090	270	340	Uluhe Shrubland, Closed&Open Koa-Ohia Forest, Cultivated Cropland, Alien Forest	Puu Pa, Olaa-Hydrudands-Hilo
	L. paranigra	20	Hawaii	1- bio14, 2- soil, 3- bio15, 4- bio4, 5- bio5, 6- dem	4.83E-06	300	24	84.5	1085	270	400	Closed Koa-Ohia Forest, Closed&Open Ohia Forest, Cultivated Cropland, Alien Forest, Uncharacterized Forest, Uncharacterized Open-Sparse Vegetation	Pakala-Mokuleia variant-Kolokolo-Hanalei Waialeale-Hulua-Alakai, Puu Pa, Olaa-Hydrudands-Hilo
	L. pruna	25	Hawaii	1- bio14, 2- soil, 3- bio4, 4- bio15, 5- bio5, 6- dem	4.15E-10	400	26	83.5	1095	270	320	Closed&Open Koa-Ohia Forest, Closed&Open Ohia Forest, Cultivated Cropland, Alien Forest, Uncharacterized Forest	Pakala-Mokuleia variant-Kolokolo-Hanalei Waialeale-Hulua-Alakai, Puu Pa, Olaa-Hydrudands-Hilo, Waikaloa-Waiaha-Pakini-Kaalualu
	L. prosea	10	Maui	1- bio2, 2- soil, 3- landcover, 4- dem, 5- bio14	9.91E-08	400	17	75	1470	305	150	Developed, Low Intensity, Alien Forest, Uncharacterized Shrubland	Tantalus-Makiki-Koko-Cinder land, Pulehu-Mala-Kealia-Ewa
	L. vespertina	9	Maui	1- soil, 2- landcover	0.01276	0	98	75	1760	305	0	Uluhe Shrubland, Ohia Forest, Alien Forest	Tantalus-Makiki-Koko-Cinder land
	L. kai	7	Oahu	1- soil, 2- landcover, 3- bio4	0.000133	400	10	75	1760	305	0	Mixed Native-Alien Forest, Ohia Forest, Alien Forest	Waikane-Lolekaa-Kemoo-Alaeloa
	L. nui	5	Oahu	1- soil, 2- bio14, 3- bio 15, 4- landcover	0.01394	400	10	75	1760	305	0	Alien Forest	Waikane-Lolekaa-Kemoo-Alaeloa, Kekake-Keei-Kahaluu
	L. pacifica	26	Oahu	1- soil, 2- bio4, 3- landcover, 4- bio 14, 5- bio15, 6- bio2	8.06E-15	400	17	82.5	1380	275	300	Native Wet Cliff Vegetation, Ohia Forest, Open Koa-Ohia Forest, Alien Forest	Waikane-Lolekaa-Kemoo-Alaeloa, Kekake-Keei-Kahaluu
	L. tantalis	12	Oahu	1- soil, 2- bio14, 3- landcover, 4- bio15	0.000787	400	10	75	1505	305	650	Native Wet Cliff Vegetation, Ohia Forest, Developed, Low Intensity, Alien Forest	Waikane-Lolekaa-Kemoo-Alaeloa, Kekake-Keei-Kahaluu

Phylogenetic niche analysis

The generated PNOs quantified cumulative likelihood of presence for the 20 modeled species by clade based on BIO14 and BIO4. In general *Laupala* showed a greater responses to temperature than precipitation. The Kauai group had high occupancy at large temperature variations while the Cerasina and Pacifica groups had higher occupancies at low variation. All groups required moderate to high amounts of precipitation for occupancy with the exception of *L. makaweli*, *L. kohalensis*, *L. tantalis*, and *L. eukolea*. No species had high occupancy with zero precipitation. The pair wise overlap analysis showed *Laupala* has a wide range in amount of niche overlap (Figure 5). Overlap of Bio4 varied from 1.8% between *L. pruna* and *L. makaweli* to 95.8% between *L. pacifica* and *L. tantalis*. Overlap of Bio14 varied from 15.9% between *L. pruna* and *L. kohalensis* to 99.6% between *L. olohena* and *L. wailua*. Of well studied species boundaries *L. paranigra* and *L. kohalensis* overlapped 31.7% in Bio4 and 21.5% in Bio14, *L. cerasina* and *L. kohalensis* overlapped 83.4% in Bio4 and 73.1% in Bio14. Age range correlation yielded no correlation between amount of genetic divergence and niche divergence.

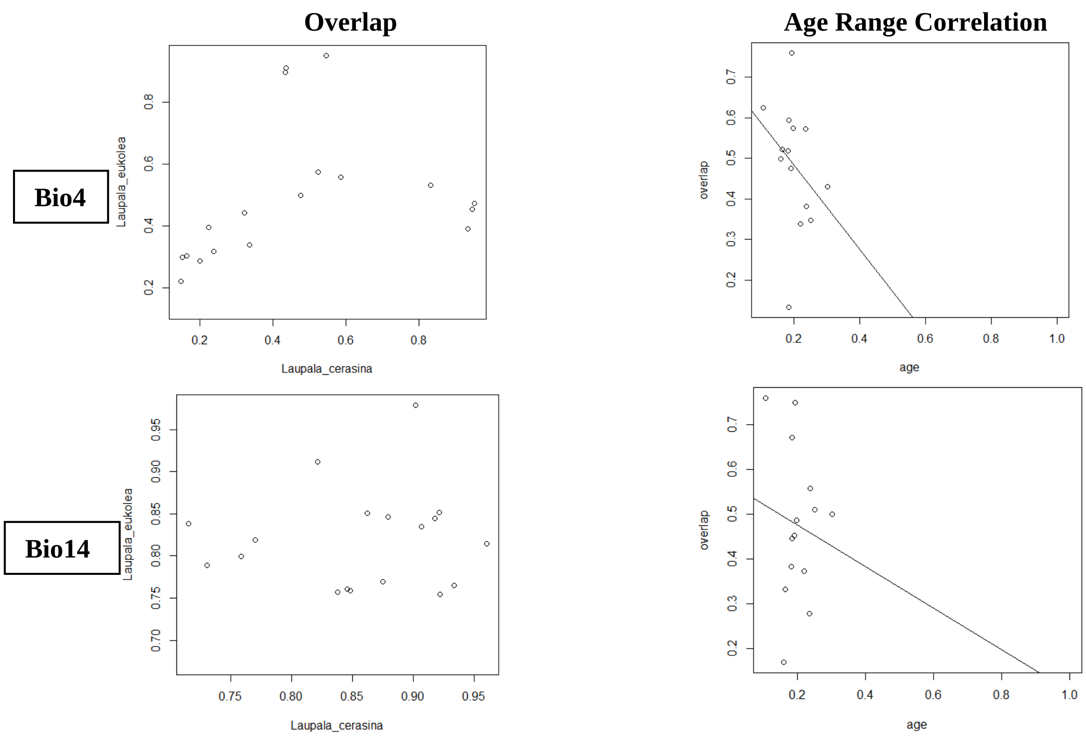

Figure 5. Plot of pair-wise overlap and age range correlation with a linear regression line. Overlap is a paired plot showing overlap between two representative species. Points closer together have more sililar niches. The age range correlation shows overlap plotted against phylogenetic age. Trend lines show no phylogenetic signal.

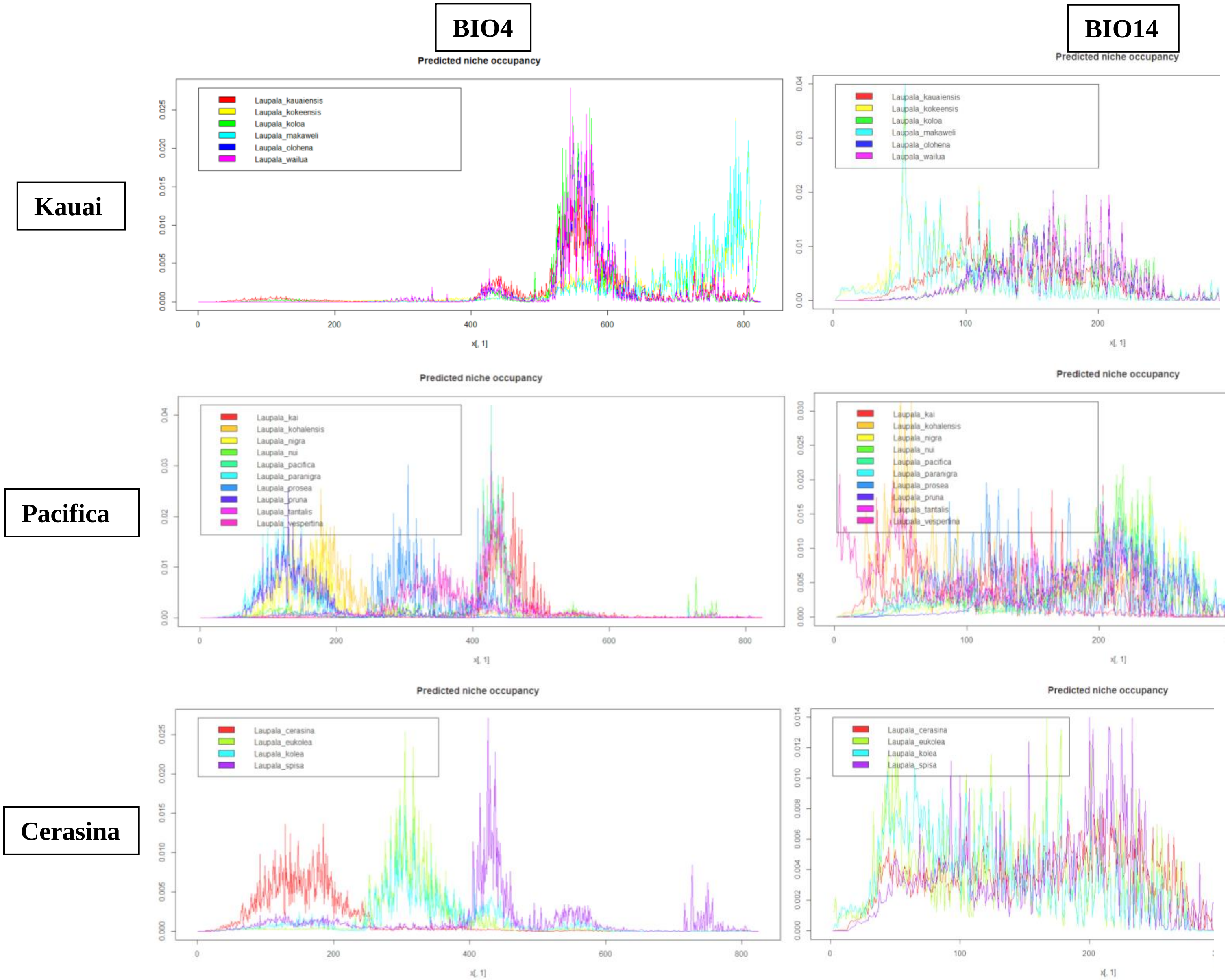

Figure 6. PNOs for *Lapaua* by group. Show probability of occupancy at each value of the environmental variable based on the Maxent output suitability map and original environmental layer.

DISCUSSION

In this project I quantified the ecological niches of Hawaiian Swordtail crickets in the endemic genera *Laupala* and *Prolaupala*. Soil was the best predictor of cricket range which reflects the underlying biology of these detritivores. Maximum precipitation of the driest month was the most important climate variable, which likely stems from the cricket's preferred habitats of moist forest environments. Based on pair wise percent overlap I found that *Laupala* contains both allopatric and sympatric species. The age range correlation showed no relationship between genetic divergence and niche divergence, indicating species closely related genetically did not necessarily have similar niches. This study provided further insight into the processes important to maintaining diversity and the future conservation of the Hawaiian Islands.

Range characteristics

Isolation of islands results in the diversification of organisms into novel habitats. Each cricket species was endemic to a single island which is characteristic of Hawaiian arthropods (Price and Clague 2002, Roderick and Gillespie 1998). This general trend of small range sizes and extreme endemism also likely stems from constraints in dispersal because crickets in *Laupala* and *Prolaupala* had an evolutionary loss of flight (Otte 1994, Mendelson and Shaw 2005). There are biotic implications of small ranges including higher degrees of endemism and potentially increased vulnerability to invasive species (Krushelnycky and Gillespie 2010). As species diverge into narrower ranges and smaller populations they become more susceptible to stochastic events (Gruner 2007). Research has shown that range restricted are at a higher risk of extinction (Knapp 2011). The cricket species *Laupala lanaiensis* with the smallest predicted range size for example has not been found since the 1970s (Otte 1994).

Influence of habitat on distributions

The jackknife results and high contribution of soil type to the model predictions supports that soil is an important characteristic of cricket niches. This relationship reflects the reliance of crickets on substrates for important life history events and suggests that soil may be more important to ranges than previously thought (Mendelson et al. 2004, Otte 1994). Hawaii has eight of the 10 world soil orders despite its small total area (Hawaii Soil Survey 2000). This may have contributed to associations between endemic organisms and soil type. Correlations of cricket distributions with soils likely stem from their feeding as detritivores by foraging in the leaf litter and soil matter (Otte 1994). This has potential consequences due to anthropogenic impacts such as changing land use, particularly for urban development and farming or ranching which can degrade soils.

Land use correlations indicated a strong preference for forests by *Laupala* and few species predicted in developed areas. In an area limited location like the Hawaiian Islands this has conservation implications because development for expanding human populations often comes at the cost of habitat destruction. While the large association with alien vegetation and forests indicates that crickets may not be extremely sensitive to vegetation type it also has potential consequences. For example, crickets in the Kauai group showed associations with almost exclusively degraded ecosystems; *L. wailua* and *L. olohena* occurred in native wet forest and shrub land and alien forest, *L. koloa* occurred in only alien forest. Research has shown that areas of non-native vegetation have experienced an increase in invasive ants and recent local extirpations of *L. wailua*, *L. koloa*, and *L. olohena* from collecting localities used in this study (LaPolla et al. 2000). Crickets were generally found at mid-elevations. However, DEM was not an important variable to cricket ranges, which likely results from correlations with climate variables.

Influence of climate on distributions

Based on variable importance the distribution models suggest that in a low-seasonality tropical system like Hawaii the most physiologically taxing and thus range-limiting aspect of climate is precipitation of the driest month rather than maximum temperature of the warmest month. This suggests that *Laupala* may be more sensitive to a lack of precipitation rather than temperature extremes. At higher elevations with *L. kokeensis*, temperature seasonality had the largest contribution to predicting ranges. Given that maximum temperature of the warmest month was not an important climate variable for any cricket species, crickets are more likely to be sensitive to variability in temperature due to seasonality or diurnal fluctuations. As global climate change accelerates the Hawaiian crickets will become more vulnerable to extinction due to decreases in precipitation and fluctuating temperatures, particularly at high elevations.

Phylogeography of niches

Based on niche overlap, *Laupala* showed both allopatric distributions with low overlap (eg. *L. pruna* and *L. makaweli*) and sympatric distributions with high overlap (eg. *L. pacifica* and *L. tantalis*). Moving to another island caused allopatric speciation (divergence due to moving geographically to different habitats) and diversification in the Pacifica and Cerasina clades, congruent with genetic analyses (Shaw 1996a). Sympatric speciation (divergence due to biotic interactions in the same habitat) likely occurred via sexual selection in *Laupala* based on divergence in song (deCarvalho and Shaw 2010).

Niche overlap results were congruent with previous research done on species boundaries. *L. paranigra* and *L. kohalensis* are allopatric based on minimal overlap in both responses to precipitation and temperature, but both found on Hawaii so they do not exhibit zero overlap and can in fact hybridize (Shaw 1996b). It would be interesting to see what kind of climate tolerances hybrids possess. *L. cerasina* and *L. kohalensis*, a cryptic species boundary, are sympatric and overlap higher in responses to temperature (Mendelson and Shaw 2002). Given that their divergence due to male song differentiation has been well documented, perhaps the high niche overlap in temperature is due to a higher tendency to sing at certain temperatures. Although results show that clades did differ in occupancy by environmental variables, the lack of a phylogenetic signal means that more closely related species were not more likely to have more similar niches. Niches were not conserved evolutionarily, thus natural selection from environmental tolerances probably did not play a large role in cricket diversification. This is congruent with the well documented radiation of *Laupala* crickets due to sexual selection (Mendelson and Shaw 2005).

Limitations and future directions

This study was successful in characterizing the ranges of crickets especially given the limited records for some species. The biggest restriction to this study was the lack of digitized data and collecting localities on the majority of the *Lauapala* and all of the *Prolaupala* species. Most observations were obtained from the duplicate collection localities which hinders a broad picture of ranges if areas are not sampled. Collections were also often without GPS coordinates for individual specimens and some records had confusing or vague localities that were difficult to georeference. There was also a lack of fine scale climate data as Bioclim only has data to a 30 arc minute or ~1km² resolution (Hijmans et al. 2005). I had to clip to fine scale, which can bias results but is necessary for Hawaii (Price et al. 2008). However, given the low mobility of the crickets given the loss of flight and oceanic barriers to dispersal, the models are reasonably accurate despite these limitations.

The next step to species distribution modeling in Hawaii is to model all arthropod groups and conduct more multi-island collections of all arthropods to advance the currently limited data sets. The only distribution modeling previously conducted in Hawaii has been range mapping done with plants (Rovzar et al. 2013, Price et al. 2012) and expanding this research to invertebrates will contribute an additional layer of knowledge to the current understanding of the niches of Hawaiian biota. Additionally collecting expeditions are needed before species distributions or biological processes are altered by humans. Many historical collections were limited to easily accessible areas (such as where *L. cerasina* is found, hence 82 records but only 2 for *Laupala molokaiensis*) so future trips should investigate new areas of cricket habitat as predicted by the Maxent models generated in this study. In general it is essential to digitize historic museum collections and field notes to facilitate distribution studies. Most importantly, to advance an understanding of Hawaiian swordtail crickets, future studies should collect more examples of organisms with limited documentation and record fine scale climate data.

Broader implications

Unique processes generate and maintain Hawaiian biodiversity and range maps provide invaluable data sets for future studies on Hawaiian Swordtail Crickets. For the first time with the

Laupala and *Prolaupala* genera, which have been highly studied for biotic interactions, we have a systematic documentation of the abiotic components of niches and associated speciation implications. This study showed that *Laupala* species do in fact differ in ecological niches, which has not previously been demonstrated. SDMs also have many applications in addition to evolutionary studies including conservation planning, invasive species mapping, and modeling the effects of climate change (Rovzar et al. 2013, Brummer et al. 2013, Rinnhofer et al. 2012). Such usage is particularly important for Hawaiian arthropods like *Laupala* due to their loss of competitive advantage from evolutionary isolation and narrow ranges, which makes them more susceptible to stochastic events. Arthropods represent the majority of invasive species introduced to Hawaii, which makes the native arthropods especially vulnerable to associated adverse effects and understanding their ranges the first step in their protection. The models produced can also be used as a template for expanding ecological niche modeling to additional Hawaiian taxa. This project was successful in expanding knowledge of the endemic Hawaiian swordtail crickets, an amazing component of the world's biodiversity.

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APPENDIX A. Categorical Variables

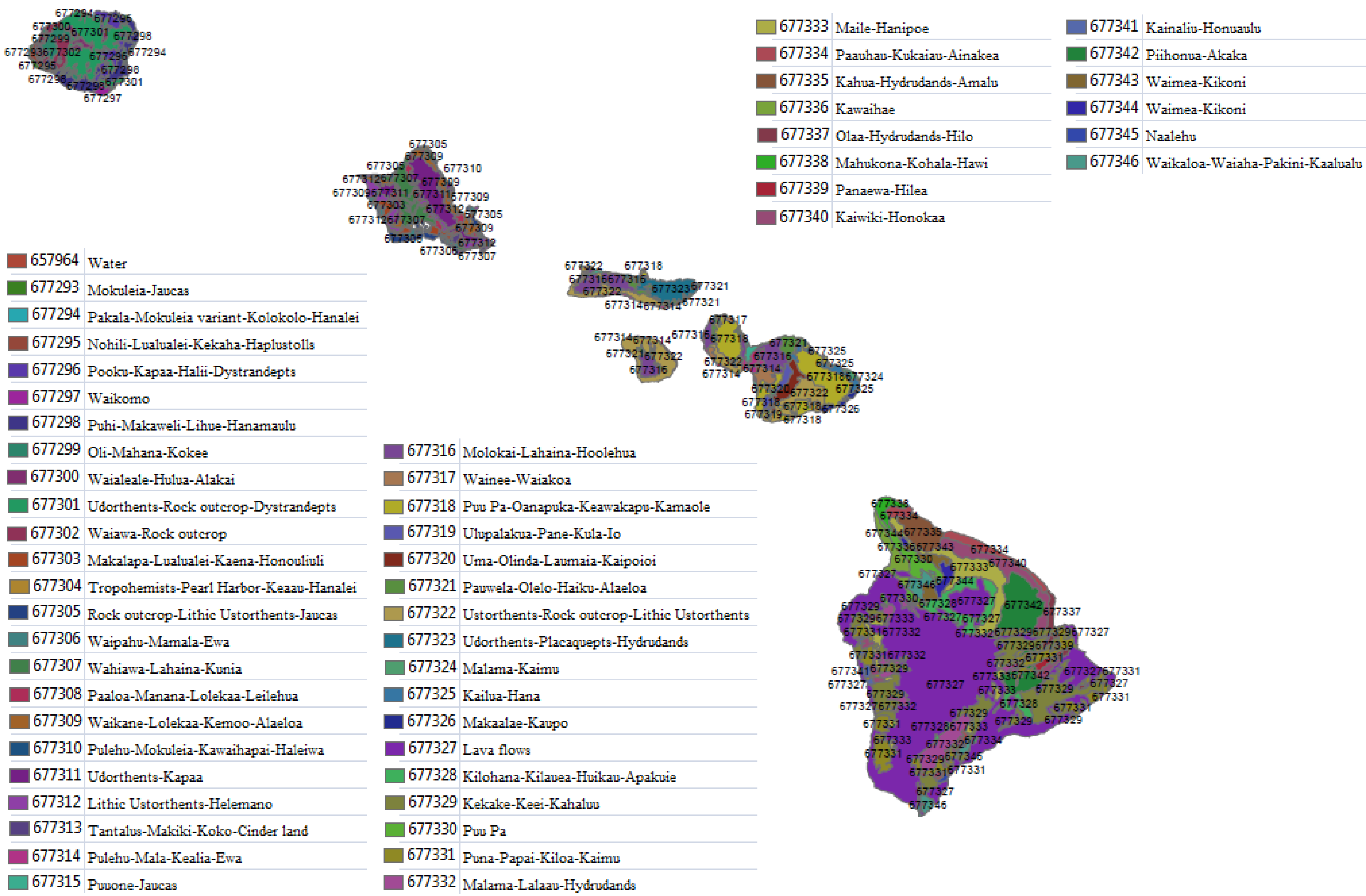


Figure 7. Map of Soil Type (Hawaii Soil Survey 2000).

Table 3. Soil Type Descriptions. Adapted from Official Soil Series Descriptions (https://soilseries.sc.egov.usda.gov/OSD_Docs/A/ALAELOA.html, by name; Hawaii Soil Survey 2000)

Name	Description	Rainfall	Soil Temp.	Slope	Taxonomic Class	Type
Alaeloa	Deep, well drained soils that formed in material weathered from basic igneous rock.	48 in	72 F	Uplands: 3-70%	Fine, parasesquic, isohyperthermic Ustic Palehumults	Alaeloa silty clay--pasture
Alakai	Deep, poorly drained soils, formed in organic material overlaying clay weathered from basalt.	280 in	56 F	Ridges: 0-30%	Clayey, ferrihumic, dysic, isomesic Terric Haplosaprists	Alakai mucky peat--rain forest
Cinder-land	Cinder fields	NA	NA	NA	NA	NA
Ewa	Deep, well drained soils that formed in alluvium weathered from basaltic rock.	24 in	73 F	Alluvial Fans and Terraces: 0-12%	Fine, kaolinitic, isohyperthermic Aridic Haplustolls	Ewa silty clay loam--irrigated sugarcane
Hanalei	Poorly drained soils that formed in alluvium derived from basic igneous rock.	80 in	72 F	Bottom Lands: 0-6%	Very-fine, mixed, semiactive, nonacid, isohyperthermic Typic Endoaquepts	Hanalei silty clay - pasture
Hanamaulu	Very deep, well drained soils that formed in alluvium from basic igneous rocks.	80 in	73 F	Terraces: 3-40%	Very-fine, ferruginous, isohyperthermic Humic Kandiudox	Hanamaulu silty clay - sugarcane
Hilo	Deep, well drained soils that formed in material weathered from volcanic ash.	145 in	72 F	Ashfields: 0-35%	Medial over hydrous, ferrihydritic, isohyperthermic Acrudoxic Hydrudands	Hilo medial silty clay loam
Hulua	Poorly drained soils, formed in material weathered from basic igneous rock.	150 in	66 F	Uplands: 3-70%	Hydrous, amorphic, isothermic Placic Petraquepts	Hulua gravelly silty clay - brush and scrubby ohia
Hydru-lands	Waterlogged land	NA	NA	NA	NA	NA
Jaucas	Very deep, excessively drained, very rapidly permeable soils on vegetated beach areas along the sea coast. They formed in calcareous sand deposits.	40 in	80 F	Coast: 0-15%	Carbonatic, isohyperthermic Typic Ustipsamments	Jaucas sand
Kaalualu	Moderately deep, excessively drained soils formed in basic volcanic ash over \`a\`a lava.	25 in	74 F	Ashfields: 2-70%	Medial-skeletal over fragmental or cindery, amorphic over mixed, isohyperthermic Typic Haplotorrands	Kaalualu cobbly loamy sand, under pasture, at an elevation of 140 m
Kealia	Deep, poorly drained soils that formed in alluvium. Found on level coastal flats.	20 in	75 F	Coast: 0%	Fine-loamy, mixed, subactive, isohyperthermic Typic Aquisalids	Kealia silt loam - pasture

Keei	Very shallow to shallow, well drained soils that formed in a thin mantle of organic material and small amounts of volcanic ash overlying pahoehoe lava.	120 in	63 F	Volcanos: 2-10%	Euic, isothermic, micro Lithic Udifolists	Keei highly decomposed plant material under ohia lehua and guava forest
Kekake	Very shallow, moderately well drained organic soils. These soils formed in organic material mixed with minor amounts of basic volcanic ash over pahoehoe lava.	35 in	55 F	Ashfields: 2-20%	Euic, isomesic, micro Lithic Ustifolists	Kekake gravelly highly decomposed plant material, under pasture at an elevation of 1417 m
Kemoo	Deep, well drained soils that have formed in material weathered from basalt.	47 in	72 F	Uplands: 2-70%	Fine, parasesquic, isohyperthermic Vertic Paleustolls	Kemoo silty clay - pasture
Kikoni	Deep, well drained soils that formed in basic volcanic ash overlying \`a\`a lava.	40 in	65 F	Ashfields: 0-12%	Medial, amorphic, isothermic Humic Haplustands	Kikoni medial very fine sandy loam - pasture
Koko	Deep, well drained soils that formed in material weathered from cinders and tuff.	20 in	74 F	Uplands: 2-25%	Medial, amorphic, isohyperthermic Typic Haplotorrands	Koko silt loam - cultivated
Kolokolo	Detailed description not in database	NA	NA	NA	Fine, mixed, isohyperthermic Cumulic Hapludolls	NA
Lihue	Deep, well drained soils that formed in material weathered from basic igneous rock and influenced by tropospheric dust.	50 in	73 F	Uplands: 0-40%	Very-fine, ferruginous, isohyperthermic Rhodic Eutrustox	Lihue silty clay - sugarcane
Lolekaa	Very deep, well drained soils that formed in alluvium and colluvium.	80 in	72 F	Alluvial Fans and Terraces: 3-70%	Very-fine, parasesquic, isohyperthermic Typic Palehumults	Lolekaa silty clay - pasture
Makaweli	Very deep well drained soils that formed in material weathered from basic igneous rock and volcanic ash.	28 in	74 F	Uplands: 0-35%	Fine, parasesquic, isohyperthermic Torroxic Haplustolls	Makaweli silty clay loam - sugarcane
Makiki	Deep, well drained soils that formed in material weathered from alluvium mixed with ash and cinders.	45 in	73 F	Alluvial Fans and Terraces: 0-3%	Fine, mixed, active, isohyperthermic Typic Haplustepts	Makiki clay loam - irrigated sugarcane
Mala	Well drained soils that formed in recent alluvium. Mala soils are on bottoms of drainageways and on alluvial fans on coastal plains.	15 in	75 F	Coast and Alluvial Fans: 0-7%	Fine, kaolinitic, nonacid, isohyperthermic Typic Torrifluvents	Mala silty clay - pasture
Mokuleia	Well drained soils that formed in recent alluvium deposited over coral sand.	40 in	74 F	Coastal Plains: 0-2%	Clayey over sandy or sandy-skeletal, mixed, active, isohyperthermic Entic Haplustolls	Mokuleia clay loam - pasture
Olaa	Moderately deep, well drained soils formed in basic volcanic ash overlying \`a\`a lava.	154 in	73 F	Lava: 2-10%	Hydrous-skeletal, ferrihydritic, isohyperthermic Typic Hydrudands	Olaa cobbly hydrous loam in lowland forest, elevation 322 m

Pakala	Deep, well drained soils formed in alluvium weathered from basic igneous rock.	30 in	74 F	Valleys, Alluvial Fans: 0-12%	Fine-loamy, parasesquic, isohyperthermic Oxic Haplustepts	Pakala clay loam - sugarcane
Pakini	Deep and very deep, well drained soils formed in basic volcanic ash.	25 in	74 F	Ash Fields: 2-10%	Medial, amorphic, isohyperthermic Typic Haplotorrands	Pakini medial fine sandy loam, under pasture elevation 122 m
Puhi	Deep, well drained soils that formed in material weathered from basic igneous rock.	70 in	73 F	Uplands: 3-40%	Very-fine, ferruginous, isohyperthermic Humic Kandiustox	Puhi silty clay loam - sugarcane
Pulehu	Well drained soils that formed from alluvium washed from basic igneous rock.	25 in	74 F	Stream Terraces, Alluvial Fans: 0-12%	Fine-loamy, mixed, semiactive, isohyperthermic Cumulic Haplustolls	Pulehu clay loam - irrigated sugarcane
Puu Pa	Deep, well drained soils that formed in basic volcanic ash in \`a\`a lava.	20 in	64 F	Ash Fields: 6-20%	Medial-skeletal, amorphic, isothermic Humic Haplustands	Puu Pa very cobbly medial very fine sandy loam, under grasses, at an elevation of 495 m
Tantalus	Moderately deep, well drained soils that formed in material weathered from volcanic ash and cinders.	100 in	70 F	Uplands: 8-70%	Medial over pumiceous or cindery, ferrihydritic, isothermic Typic Hapludands	Tantalus silt loam - woodland
Waiaha	Shallow, well drained soils that formed in basic volcanic ash over \`a\`a or pahoehoe lava.	40 in	74 F	Ash Fields: 2-50%	Medial-skeletal, amorphic, isohyperthermic Lithic Haplustands	Waiaha cobbly medial silt loam, in pasture at an elevation 165 m
Waialeale	The Waialeale series consists of moderately deep, somewhat poorly drained soils that formed in material weathered from basic igneous rock.	175 in	56 F	Uplands: 30-70%	Very-fine, isotic, isothermic Typic Epiaquods	Waialeale peaty silty clay loam - rain forest
Waikaloa	The Waikaloa series consists of deep and very deep, well drained soils that formed in basic volcanic ash.	15 in	64 F	Ash Fields: 2-20%	Medial, amorphic, isothermic Typic Haplotorrands	Waikaloa medial fine sandy loam, under pasture, elevation 792 m
Waikane	The Waikane series consists of deep, well drained soils that formed in material weathered in alluvium and colluvium from basic igneous rock.	60 in	72 F	Alluvial Fans and Terraces: 3-70%	Very-fine, isotic, isohyperthermic Typic Haplohumults	Waikane silty clay - pasture
Waikomo	The Waikomo series consists of shallow, well drained stony soils, formed in material weathered from basic igneous rock.	45 in	74 F	Uplands: 2-6%	Clayey, mixed, active, isohyperthermic Lithic Haplustolls	Waikomo stony silty clay - sugarcane
Waimea	The Waimea series consists of deep, well drained soils that formed in material weathered from volcanic ash underlain by andesite and basalt.	30 in	60 F	Ash Fields: 6-20%	Medial, amorphic, isothermic Humic Haplustands	Waimea medial silt loam, under grasses, at elevation 991 m

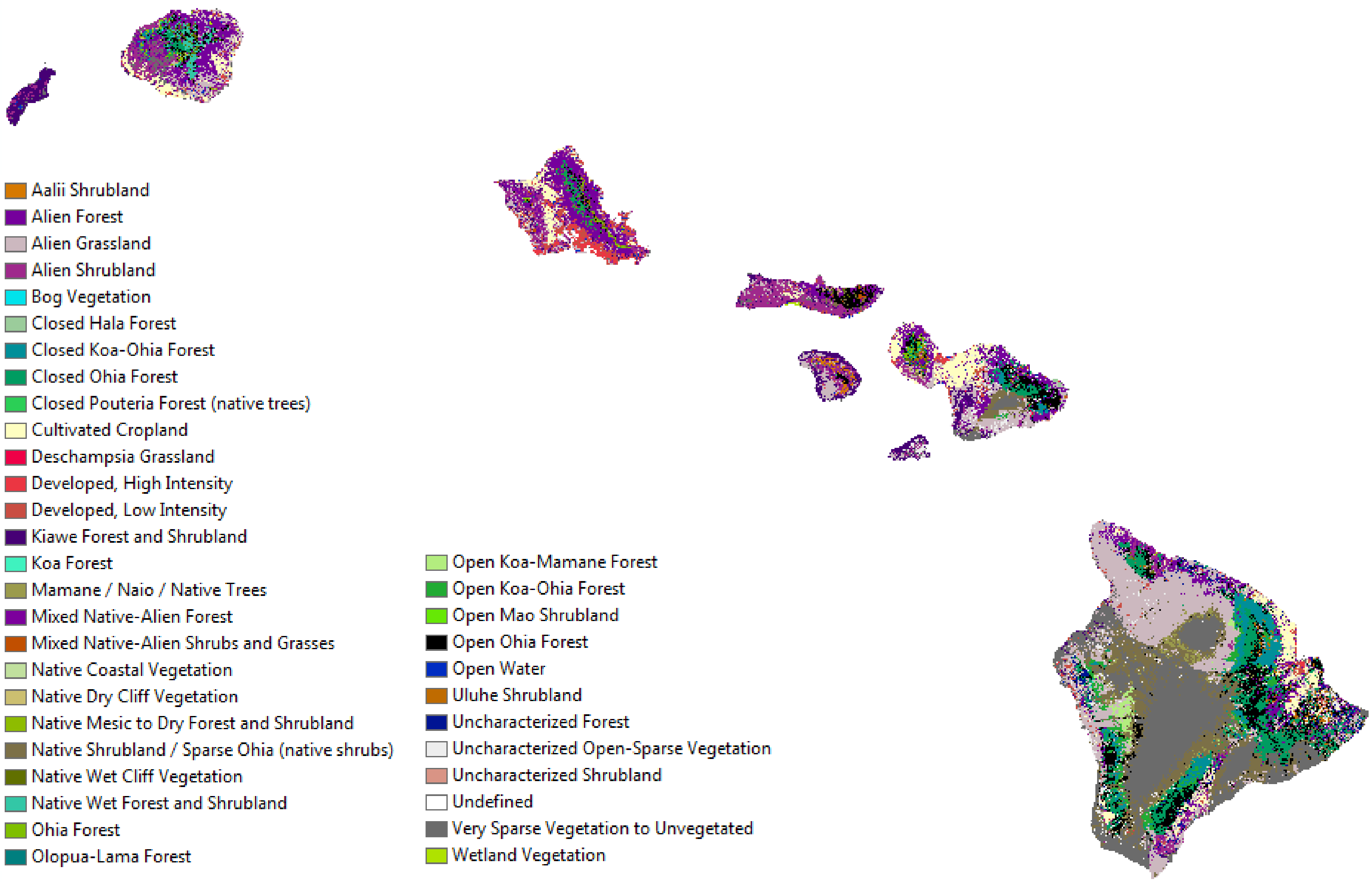


Figure 8. Map of Land Cover (Hawaii GIS 2003).

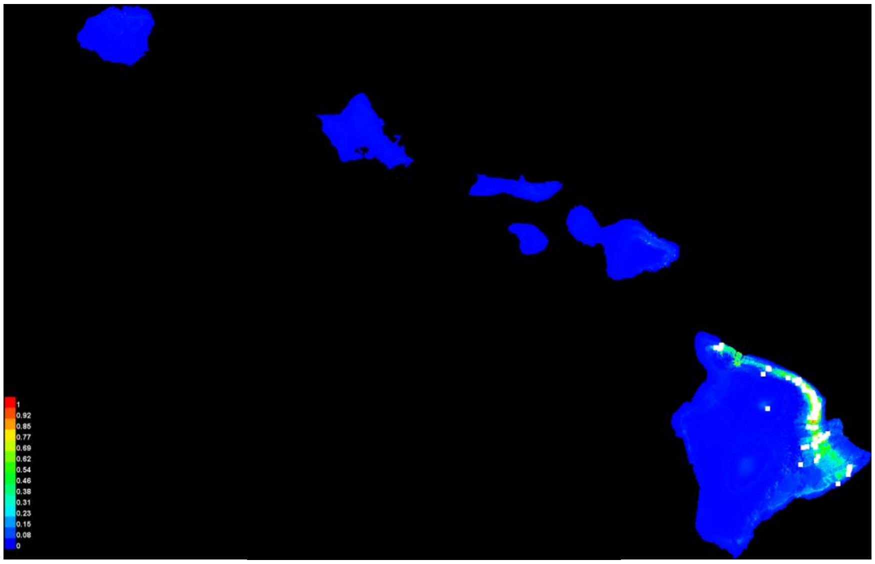
APPENDIX B. Maxent Results

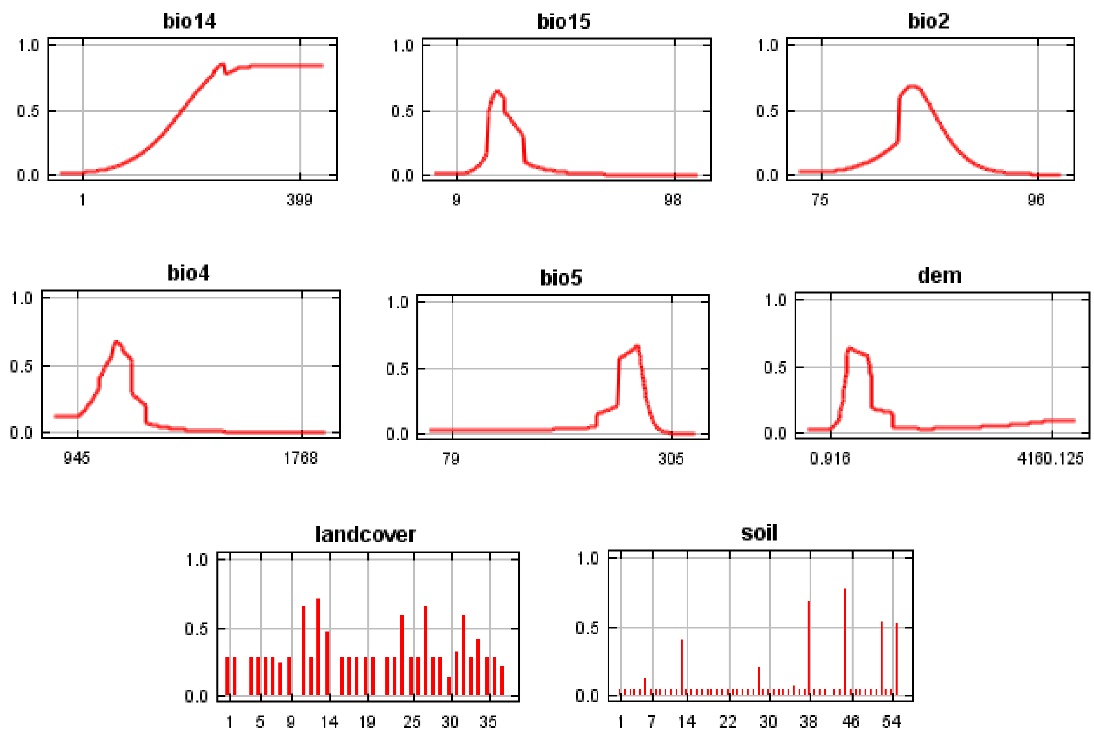
Table 4. Maxent Model Construction.

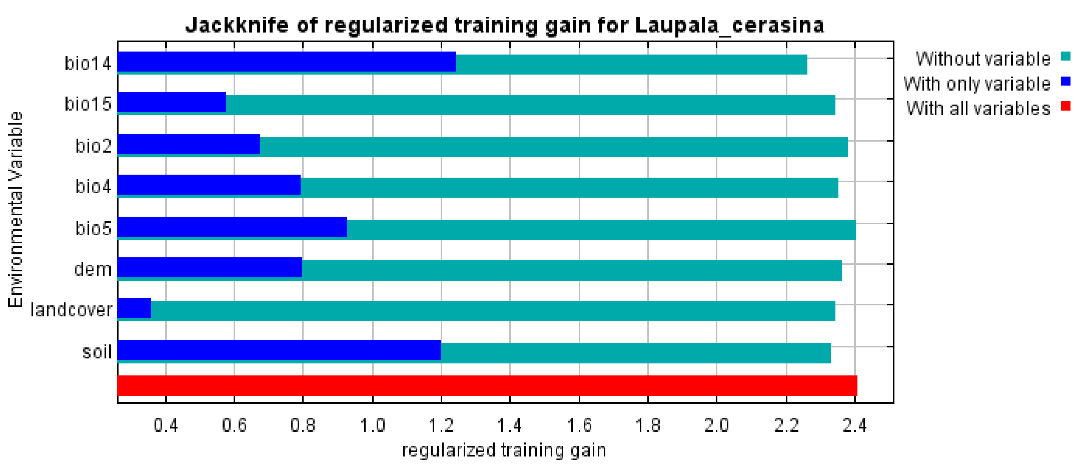
Species	#	AUC	BIO14 contribution	BIO15 cont.	BIO2 cont.	BIO4 cont.	BIO5 cont.	DEM cont.	Land Cover cont.	Soil cont.	BIO 14 permutation importance	BIO15 p.i.	BIO2 p.i.	BIO4 p.i.	BIO5 p.i.	DEM p.i.	Land Cover p.i.	Soil p.i.
L. cerasina	82	0.971	36.085	3.926	8.787	19.758	1.773	10.019	3.728	15.924	37.628	19.310	8.288	18.035	1.433	7.251	3.099	4.957
L. eukolea	18	0.996	0.994	0.038	15.162	0.000	0.007	1.367	13.942	68.491	0.468	0.000	2.135	0.000	0.083	1.697	3.853	91.764
L. eupacifica	6	0.992	0.000	0.000	0.000	0.000	0.000	0.000	0.188	99.812	0.000	0.000	0.000	0.000	0.927	0.000	1.426	97.648
L. fugax	6	0.992	14.137	0.000	0.000	0.165	0.000	8.320	14.543	62.835	2.047	0.000	0.000	0.000	0.000	4.455	12.856	80.642
L. hapapa	4	0.997	2.722	4.065	4.555	9.030	2.007	0.148	2.392	75.080	5.221	2.617	2.459	16.603	22.935	6.464	0.727	42.974
L. hualalai	4	0.987	2.696	20.852	0.000	7.030	0.000	0.000	43.314	26.108	12.841	50.255	0.000	11.296	0.000	0.000	16.067	9.541
L. kai	7	0.998	0.000	0.011	9.364	3.691	0.000	0.000	3.068	83.867	0.000	0.004	1.548	1.624	0.000	0.000	0.048	96.777
L. kanaele	4	0.999	0.129	6.651	9.090	14.430	5.845	0.000	23.566	40.289	0.253	4.563	3.014	74.440	0.000	0.000	17.259	0.472
L. kauaiensis	12	0.994	0.000	14.142	0.202	12.264	0.000	4.866	25.630	42.897	0.000	17.999	1.955	33.472	0.000	43.013	3.242	0.319
L. kohalensis	5	0.998	0.000	0.851	4.493	0.000	0.000	0.000	14.702	79.953	0.000	0.000	7.438	0.000	0.000	0.000	0.930	91.632
L. kokeensis	15	0.995	0.336	0.000	0.836	87.464	0.000	0.000	2.163	9.202	0.192	0.000	0.388	98.875	0.000	0.005	0.226	0.314
L. kolea	7	0.997	0.000	2.456	30.150	0.087	0.000	1.259	6.200	59.847	0.000	4.741	75.574	0.040	0.000	5.837	1.537	12.273
L. koloa	12	0.997	11.945	0.052	0.039	0.144	0.263	1.231	21.842	64.485	2.615	0.000	0.039	0.797	0.000	90.129	1.696	4.724
L. kona	8	0.990	0.002	0.073	5.026	0.052	0.000	0.136	39.163	55.549	0.000	0.000	20.102	10.537	0.000	2.643	49.599	17.119
L. lanaiensis	3	0.999	0.477	2.256	0.290	0.000	0.496	0.000	43.519	52.962	0.000	0.434	0.000	0.000	0.000	0.000	13.703	85.863
L. makaio	3	0.997	0.000	0.000	0.000	0.000	0.000	4.950	3.761	91.289	0.000	0.000	0.000	0.000	0.000	7.780	1.288	90.933
L. makaweli	9	0.997	0.000	0.000	0.000	54.841	0.000	0.000	5.140	40.019	0.000	0.000	0.000	99.396	0.000	0.000	0.452	0.152
L. media	4	0.999	0.000	4.470	40.046	0.000	0.000	13.386	8.370	33.728	0.000	0.586	38.391	0.000	0.000	56.739	0.252	4.033
L. mediaspisa	4	0.993	0.000	0.767	0.017	0.161	0.005	0.000	5.725	93.325	0.000	0.000	0.000	2.160	0.000	0.000	5.280	92.560

L. melewiki	4	0.999	9.611	0.529	0.000	0.298	0.000	1.135	20.771	67.656	7.458	4.407	0.000	8.814	0.000	4.068	40.000	35.254
L. molokaiensis	2	0.999	0.000	4.024	0.000	0.000	0.000	0.000	26.549	69.427	0.000	2.436	0.000	0.000	0.000	0.000	39.513	58.051
L. neospisa	2	0.999	7.588	12.251	0.000	0.669	0.349	0.012	18.723	60.409	25.187	0.000	0.000	0.373	0.000	0.933	1.866	71.642
L. nigra	34	0.994	39.614	1.375	2.757	0.245	0.154	2.961	4.701	48.193	57.620	3.294	7.361	2.564	0.000	7.122	3.212	18.826
L. nui	5	0.998	30.205	5.587	1.077	0.096	0.000	1.120	13.807	48.108	3.985	59.562	24.785	0.196	0.000	9.525	1.615	0.332
L. oahuensis	4	0.994	0.000	2.205	1.592	9.362	0.000	0.000	5.053	81.789	0.000	0.000	0.964	17.532	0.000	0.000	3.685	77.819
L. olohena	24	0.996	18.146	2.828	0.779	10.566	0.000	3.190	22.400	42.090	1.091	1.502	0.720	23.918	0.000	71.807	0.939	0.024
L. pacifica	26	0.994	8.197	0.000	0.530	0.908	0.000	0.605	7.778	81.983	0.082	0.000	2.896	0.197	0.000	3.579	4.500	88.748
L. paranigra	20	0.979	73.606	0.000	0.000	7.524	0.000	1.138	1.359	16.373	72.004	0.000	0.000	5.933	0.000	0.000	4.517	17.546
L. parapacifica	4	0.997	25.300	8.319	4.621	2.347	0.000	0.000	2.987	56.425	0.197	52.606	32.506	10.411	0.000	0.000	2.888	1.392
L. paraprosea	4	0.998	12.192	0.378	7.741	0.404	0.412	0.000	13.253	65.621	5.260	0.000	60.334	1.243	3.367	0.000	0.064	29.732
L. prosea	10	0.998	0.000	8.421	34.614	0.000	0.277	2.796	13.313	40.579	0.000	22.414	57.121	0.000	1.153	18.526	0.143	0.643
L. pruna	25	0.982	69.821	2.930	0.000	8.697	0.000	0.921	3.709	13.922	80.167	3.123	0.000	6.343	0.000	5.661	2.568	2.139
L. spisa	6	0.999	19.793	4.688	0.167	2.009	0.000	0.170	1.459	71.714	0.000	75.240	0.418	3.664	0.000	2.041	2.188	16.450
L. tantalis	12	0.996	5.352	3.995	0.098	0.594	0.000	0.511	11.308	78.143	0.000	46.057	1.636	3.708	0.000	1.410	4.282	42.907
L. vespertina	9	0.992	5.548	0.000	0.000	0.427	2.290	0.000	13.030	78.705	3.778	0.000	0.000	1.710	2.368	0.000	7.485	84.659
L. waikemoi	1	0.996	0.000	0.000	0.000	0.000	0.000	0.000	38.415	61.585	0.000	0.000	0.000	0.000	0.000	0.000	18.729	81.271
L. wailua	22	0.996	17.502	1.020	0.821	3.256	0.000	2.132	25.892	49.377	6.906	2.041	1.484	44.413	0.000	43.192	1.792	0.173
P. kaalensis	4	0.996	0.000	6.385	1.425	28.151	0.000	0.000	12.763	51.276	0.000	0.000	0.358	51.205	0.000	0.000	2.966	45.471
P. kukui	3	0.999	0.000	0.000	0.000	0.000	0.000	0.821	42.385	56.794	0.000	0.000	0.000	0.000	0.000	8.538	25.109	66.353
P. perkinsi	3	0.998	0.000	1.307	0.265	0.000	0.000	0.000	6.123	92.305	0.000	5.812	4.756	0.000	0.000	0.000	16.777	72.655

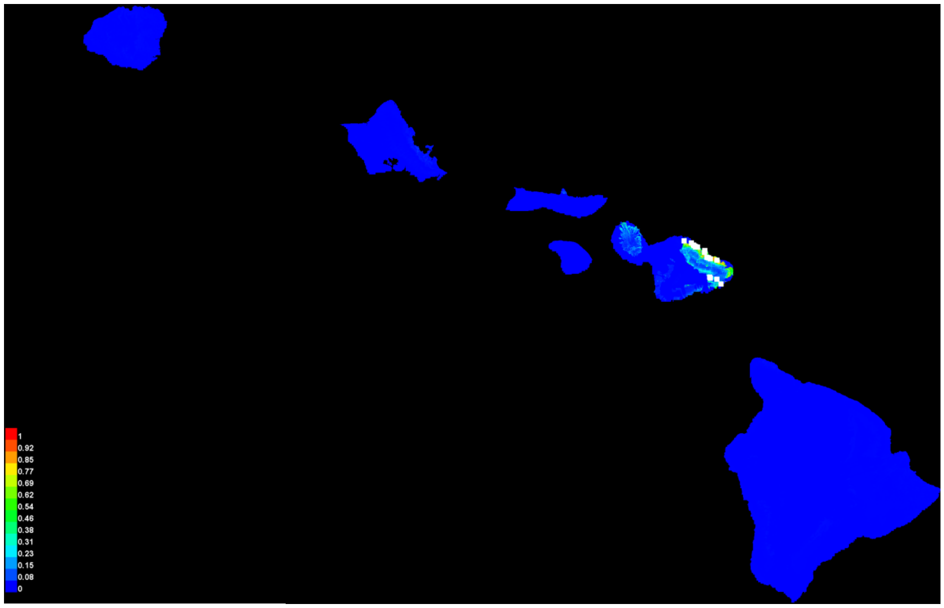
L. cerasina

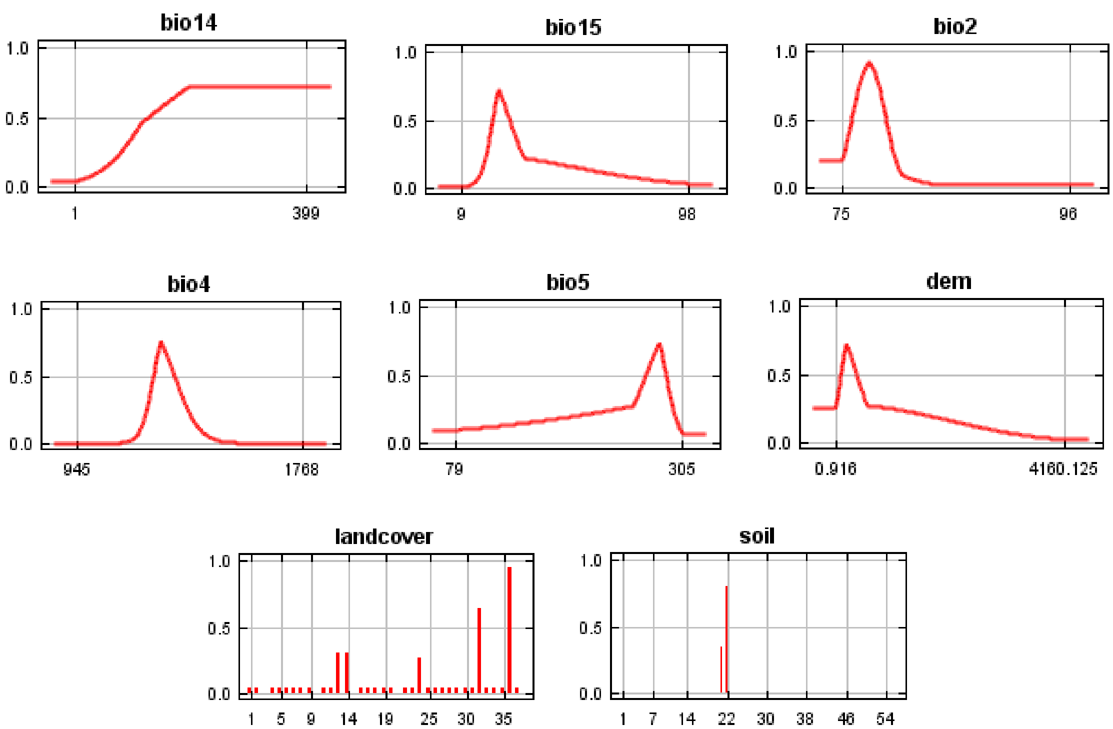


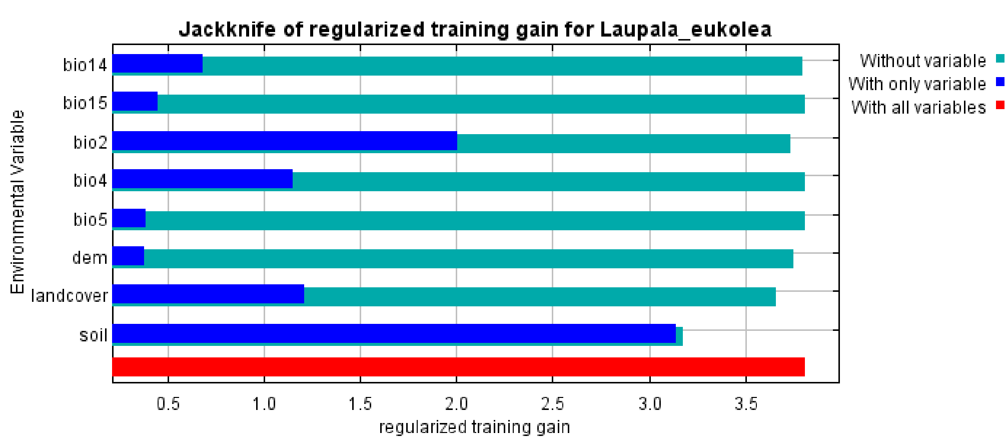

bio14
1.0
0.5
0.0
1
399
bio15
9
98
bio2
75
96
bio4
945
1768
bio5
79
305
dem
0.916
4160.125
landcover
1
5
9
14
19
25
30
35
soil
1
7
14
22
30
38
46
54


Jackknife of regularized training gain for Laupala_cerasina
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
Without variable
With only variable
With all variables
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
2.4
regularized training gain

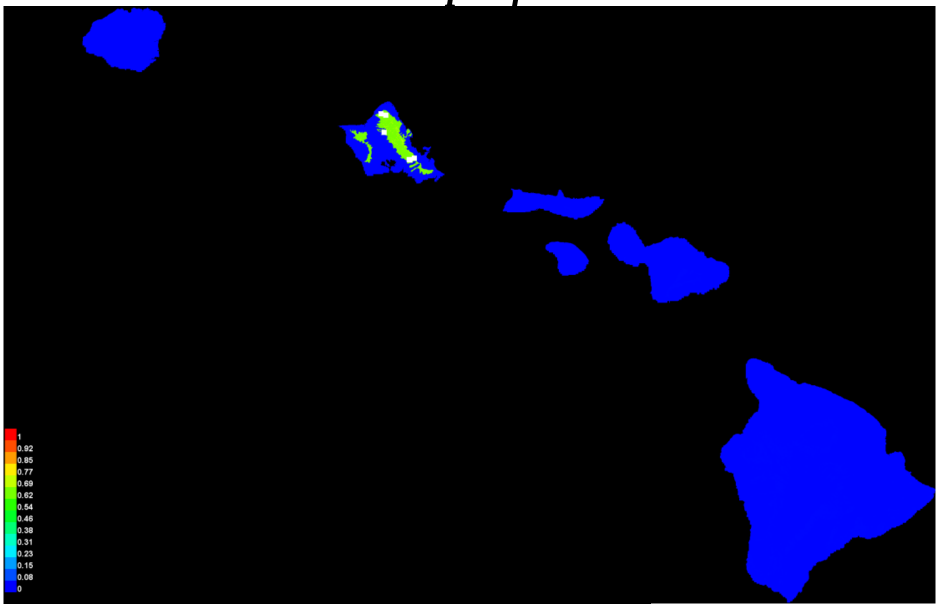
L. eukolea

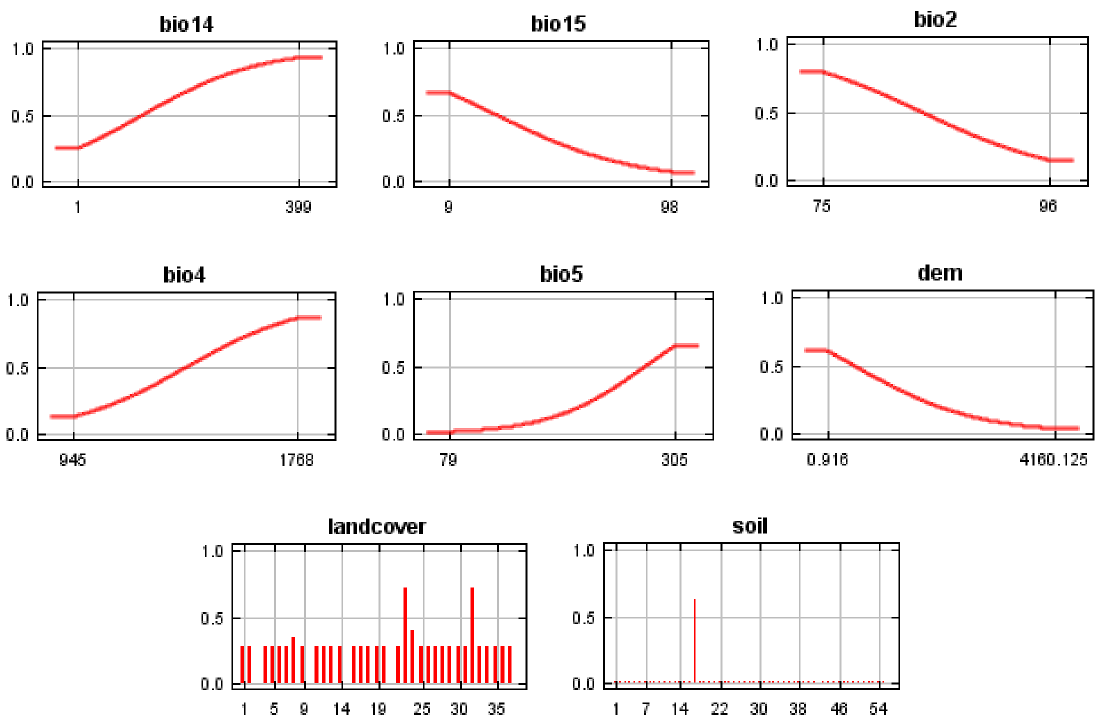


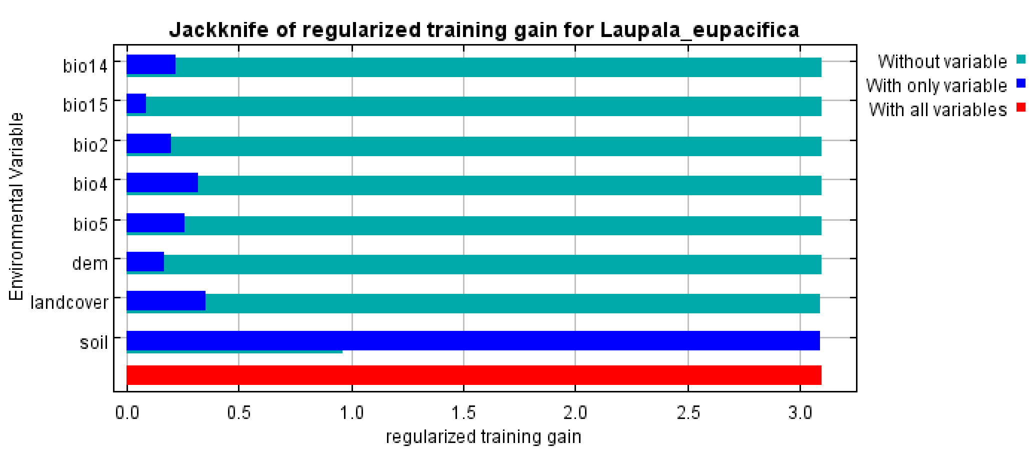

bio14
1
399
bio15
9
98
bio2
75
96
bio4
945
1768
bio5
79
305
dem
0.916
4160.125
landcover
1 5 9 14 19 25 30 35
soil
1 7 14 22 30 38 46 54
1.0
0.5
0.0


Jackknife of regularized training gain for Laupala_eukolea
Without variable
With only variable
With all variables
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
0.5 1.0 1.5 2.0 2.5 3.0 3.5
regularized training gain

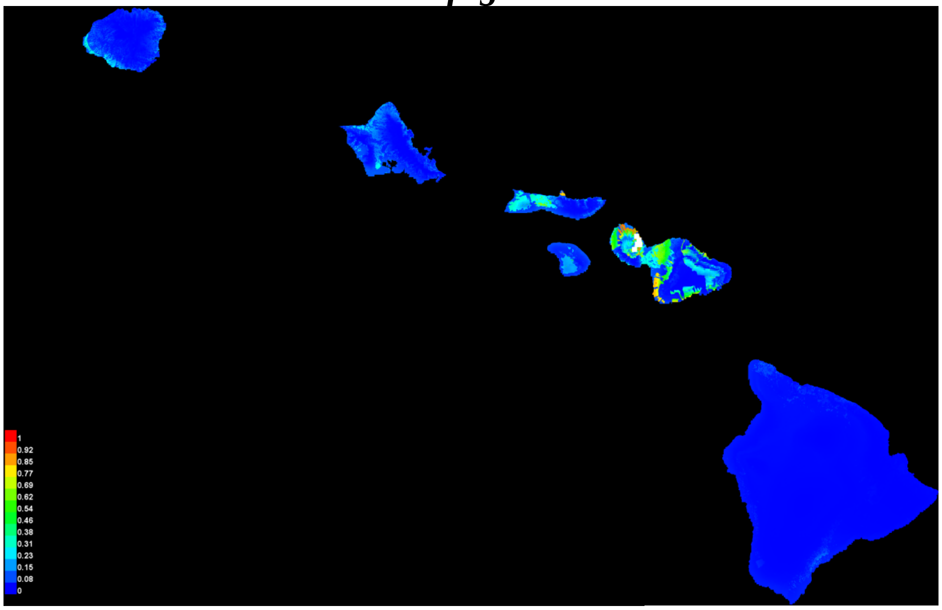
L. eupacifica

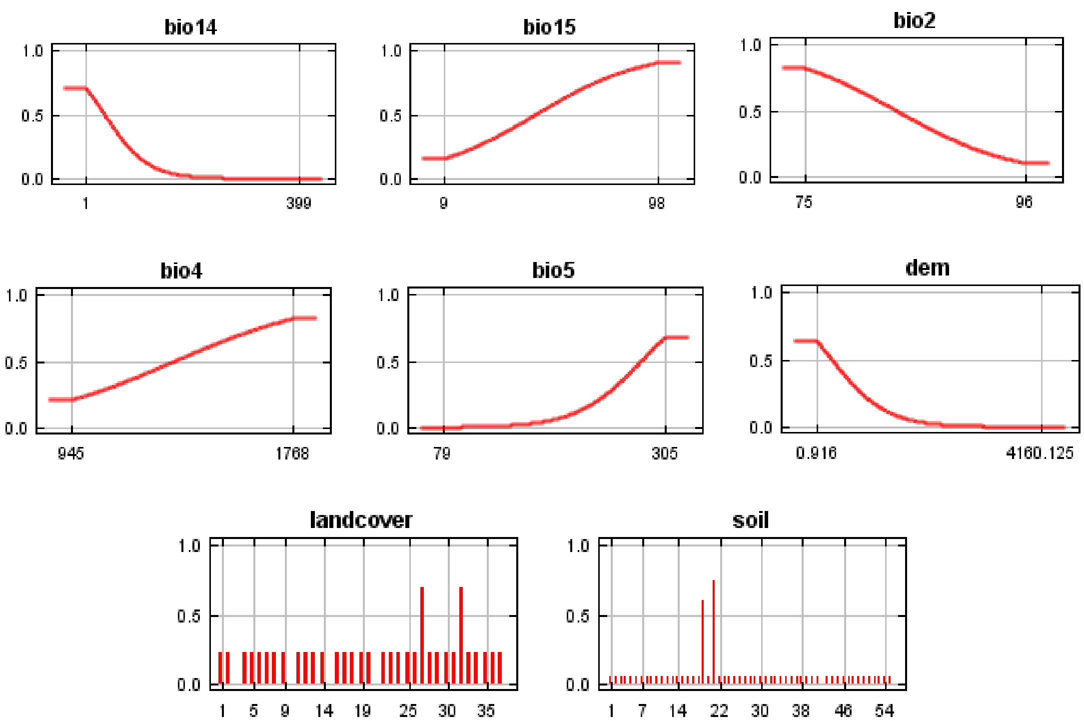






L. fugax




bio14
1.0
0.5
0.0
1
399
bio15
9
98
bio2
75
96
bio4
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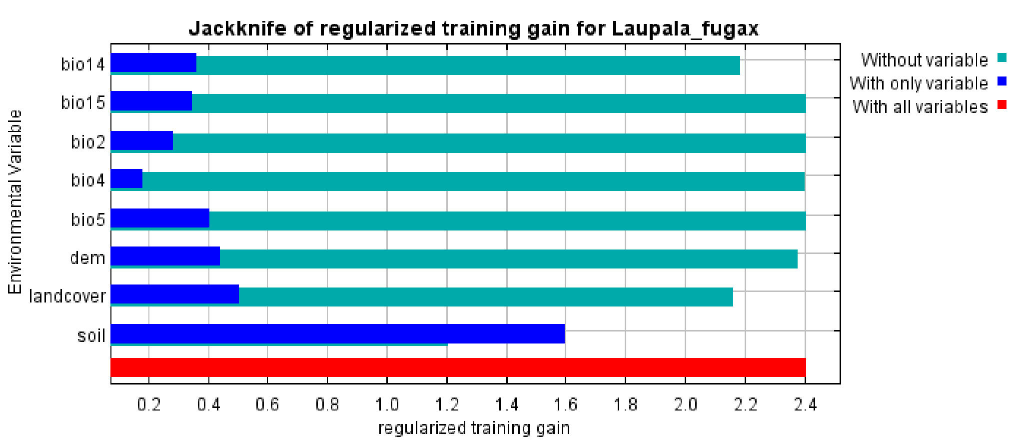
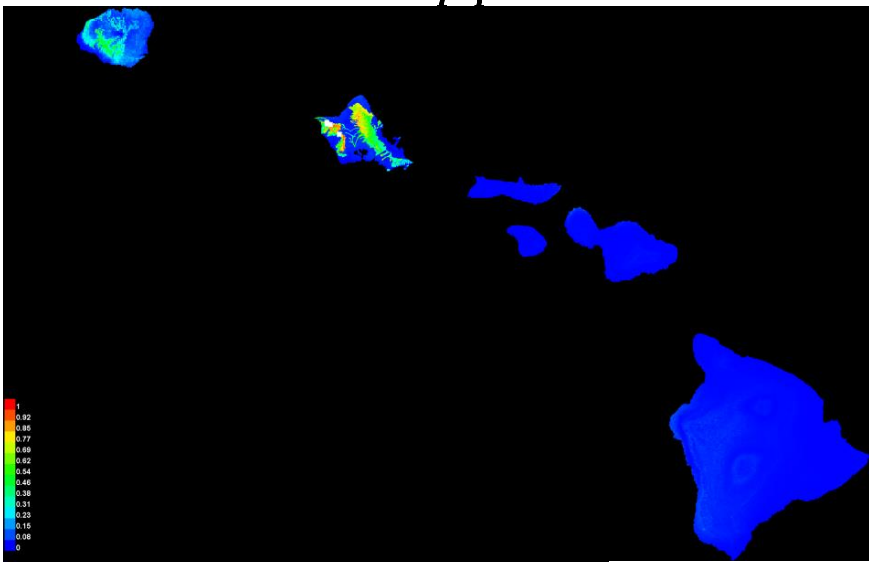
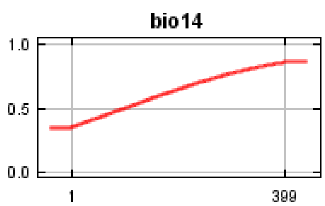
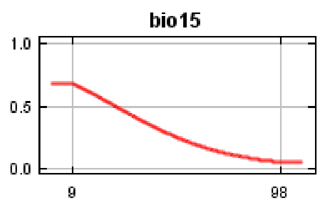
1768
bio5
79
305
dem
0.916
4160.125
landcover
1 5 9 14 19 25 30 35
soil
1 7 14 22 30 38 46 54

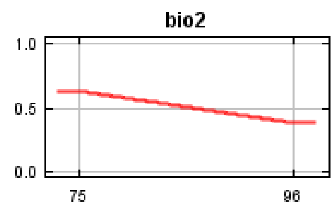

Jackknife of regularized training gain for Laupala_fugax
Without variable
With only variable
With all variables
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
0.2 0.4 0.6 0.8 1.0 1.2 1.4 1.6 1.8 2.0 2.2 2.4
regularized training gain

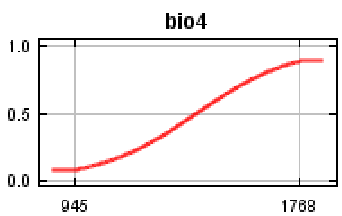
L. hapapa

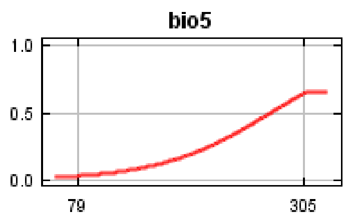


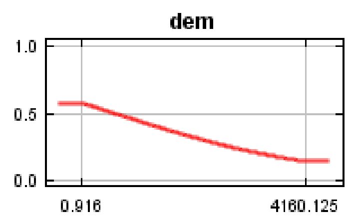

bio14
1.0
0.5
0.0
1
399

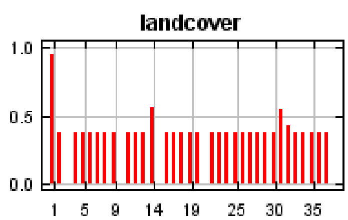

bio15
1.0
0.5
0.0
9
98

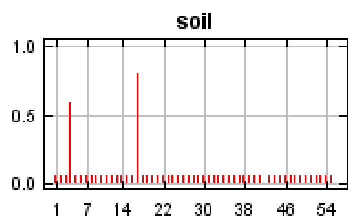

bio2
1.0
0.5
0.0
75
96

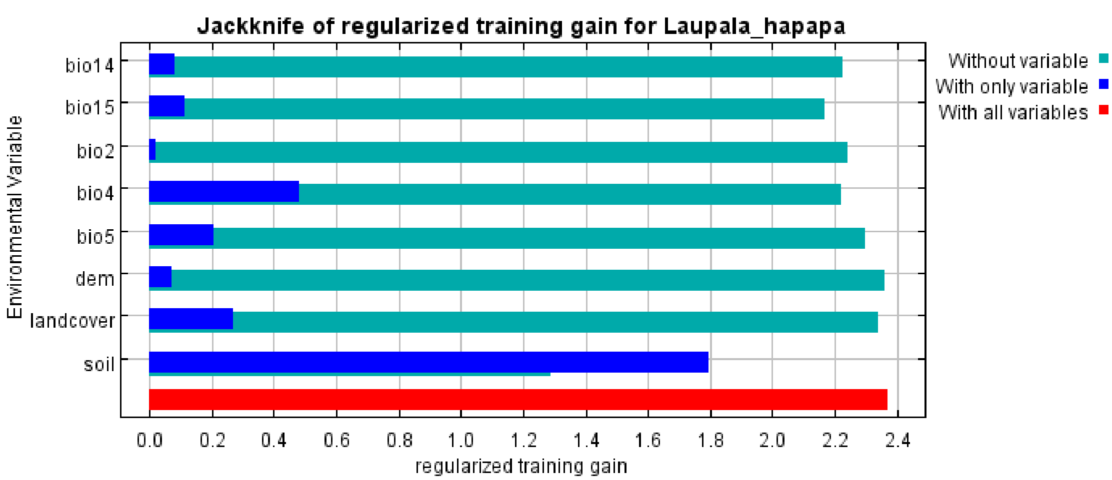

bio4
1.0
0.5
0.0
945
1768


bio5
1.0
0.5
0.0
79
305

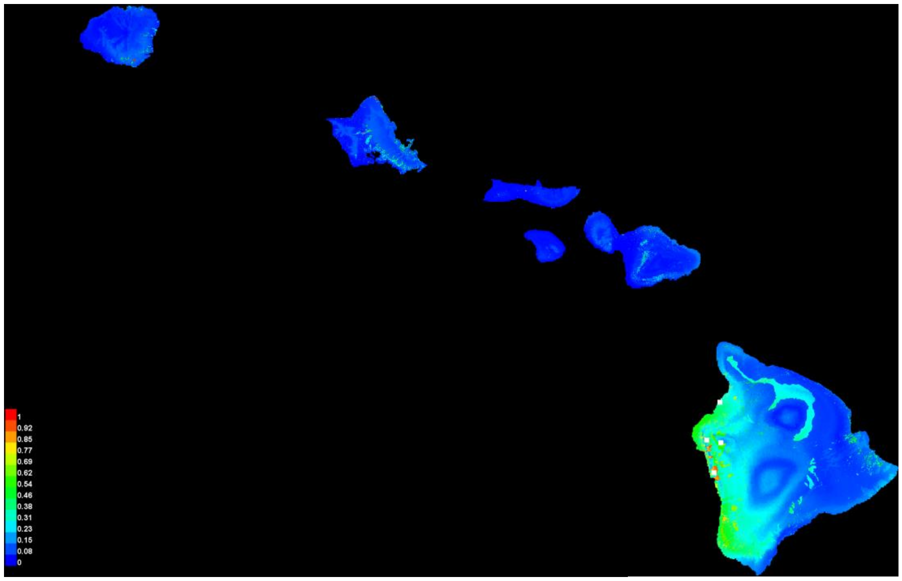

dem
1.0
0.5
0.0
0.916
4160.125

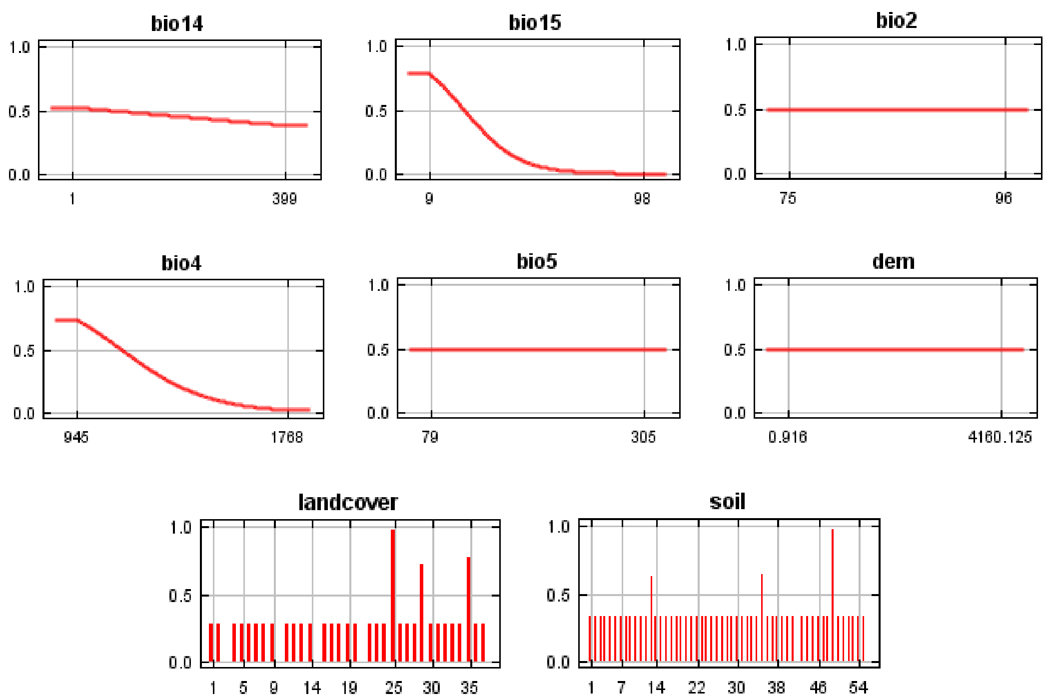

landcover
1.0
0.5
0.0
1 5 9 14 19 25 30 35

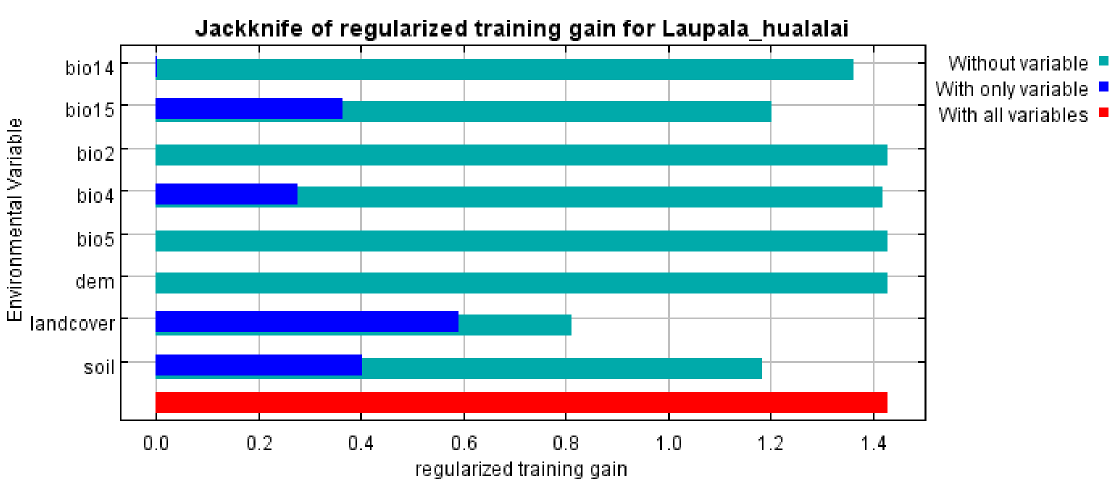

soil
1.0
0.5
0.0
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Laupala_hapapa
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
0.0 0.2 0.4 0.6 0.8 1.0 1.2 1.4 1.6 1.8 2.0 2.2 2.4
regularized training gain
Without variable
With only variable
With all variables

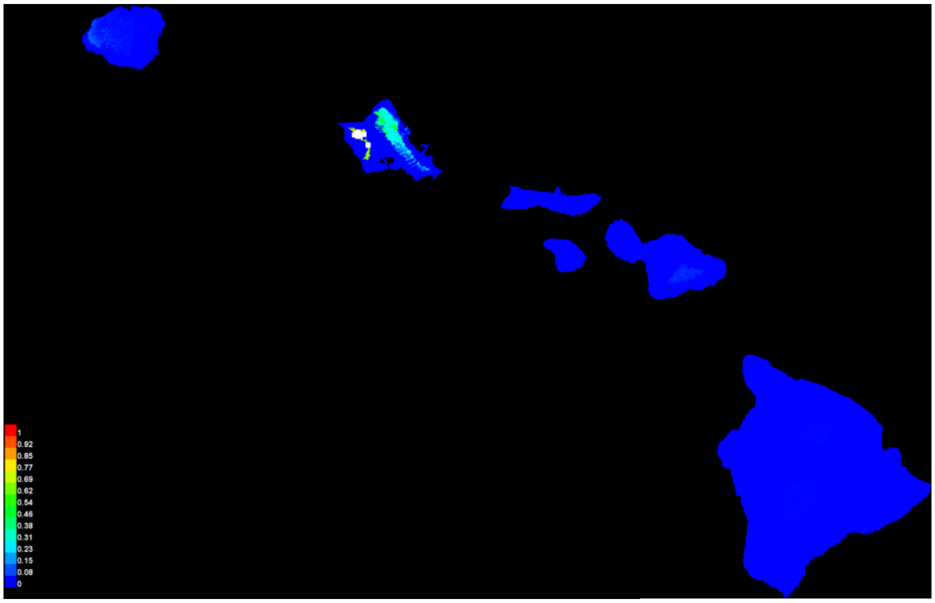
L. hualalai

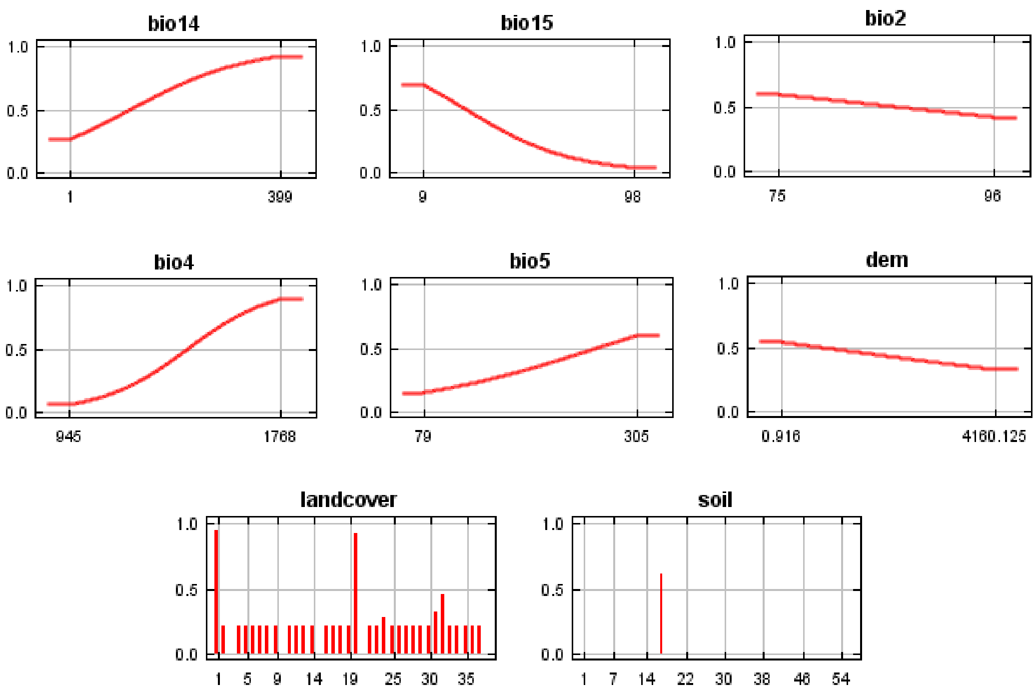



bio14
bio15
bio2
bio4
bio5
dem
landcover
soil


Jackknife of regularized training gain for Laupala_hualalai
Without variable
With only variable
With all variables
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
regularized training gain

L. kai

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bio2
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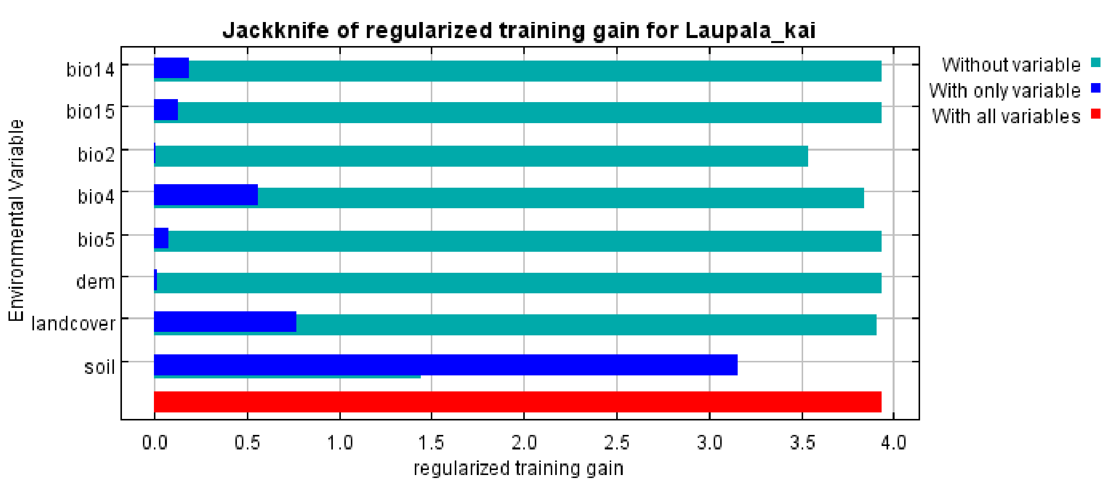
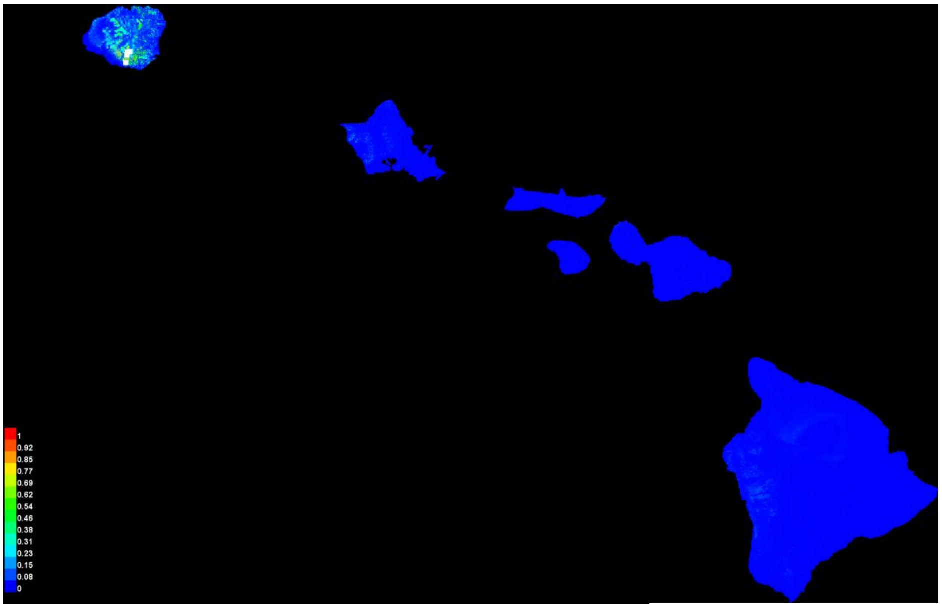
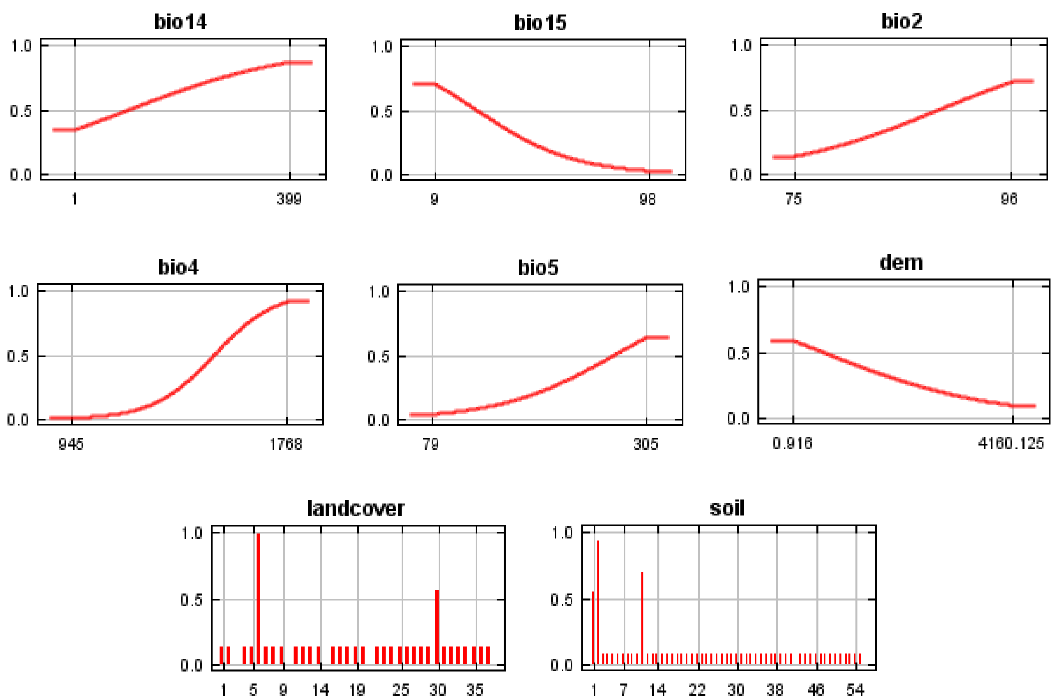
0.5
0.0
75
96
bio4
1.0
0.5
0.0
945
1768
bio5
1.0
0.5
0.0
79
305
dem
1.0
0.5
0.0
0.916
4160.125
landcover
1.0
0.5
0.0
1 5 9 14 19 25 30 35
soil
1.0
0.5
0.0
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Laupala_kai
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
Without variable
With only variable
With all variables
0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0
regularized training gain

L. kanaele




bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
1.0
0.5
0.0
1
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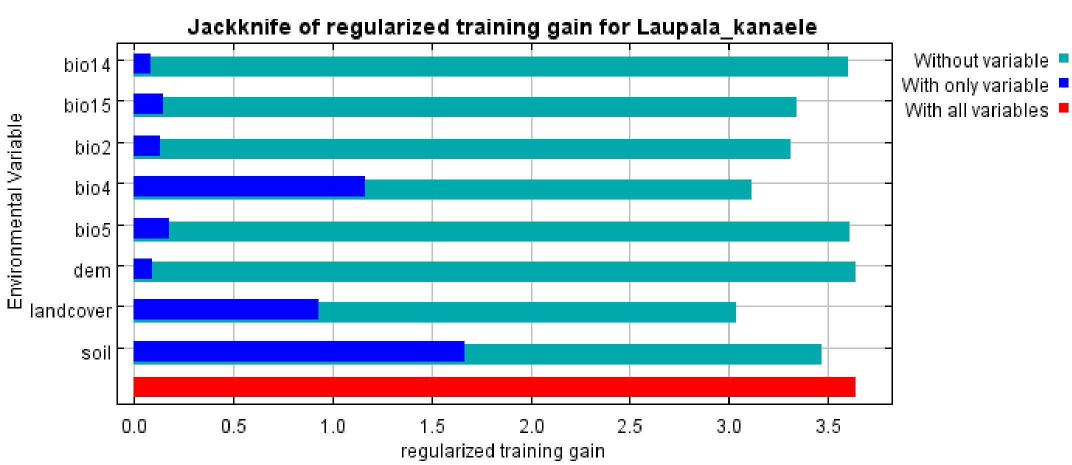
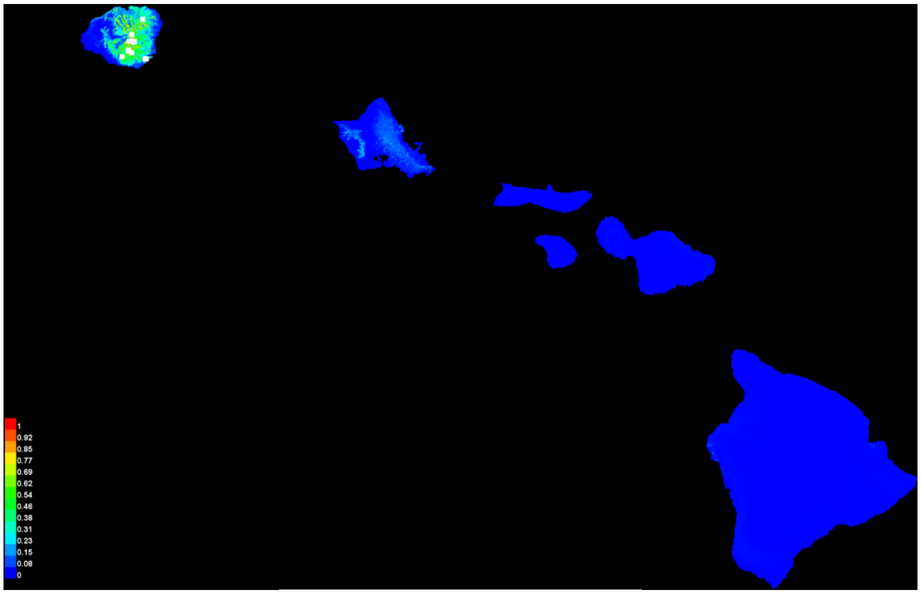
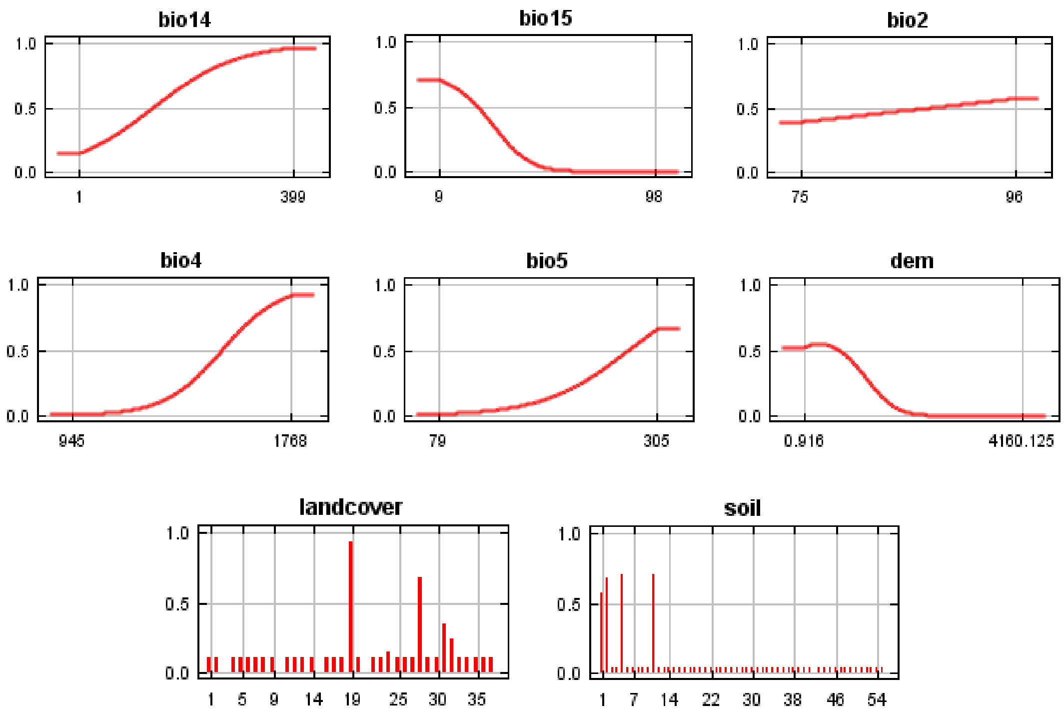
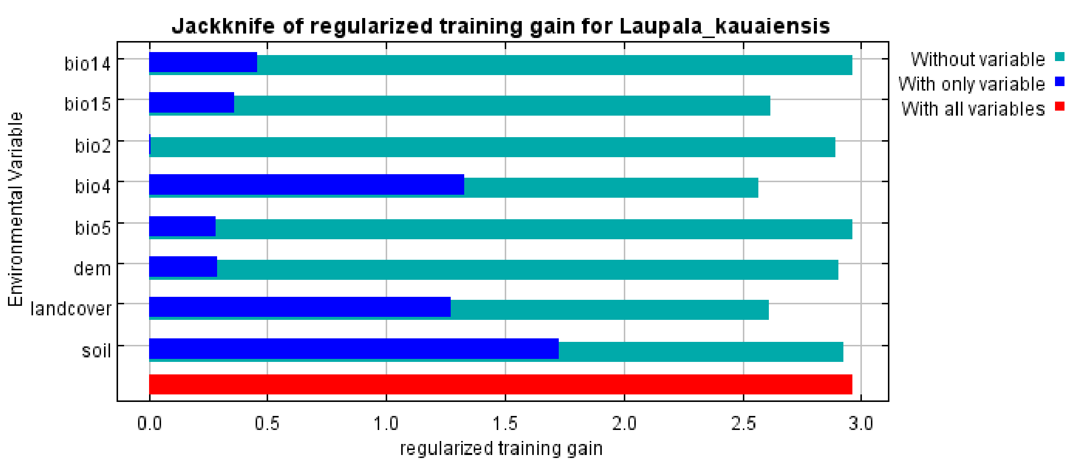
945
1768
79
305
0.916
4160.125
1 5 9 14 19 25 30 35
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Laupala_kanaele
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
Without variable
With only variable
With all variables
0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
regularized training gain

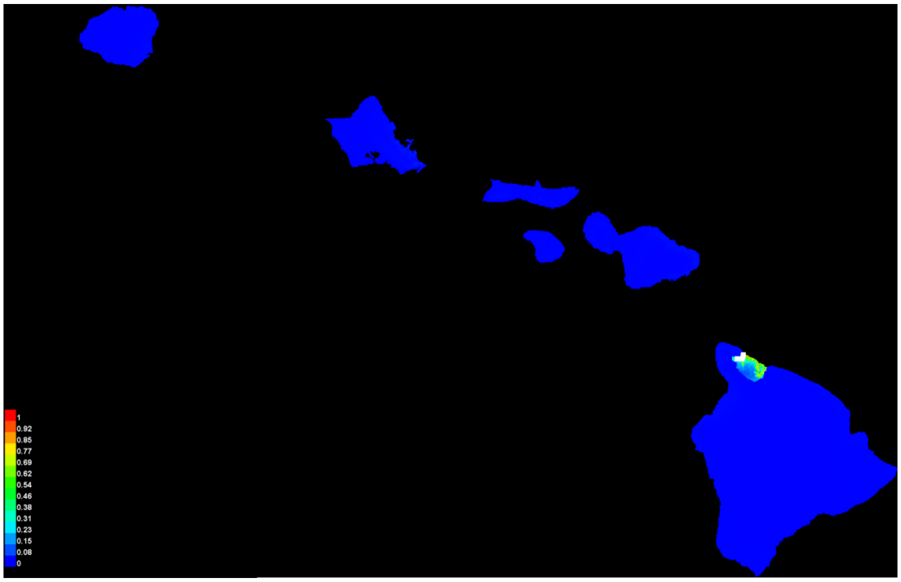
L. kauaiensis

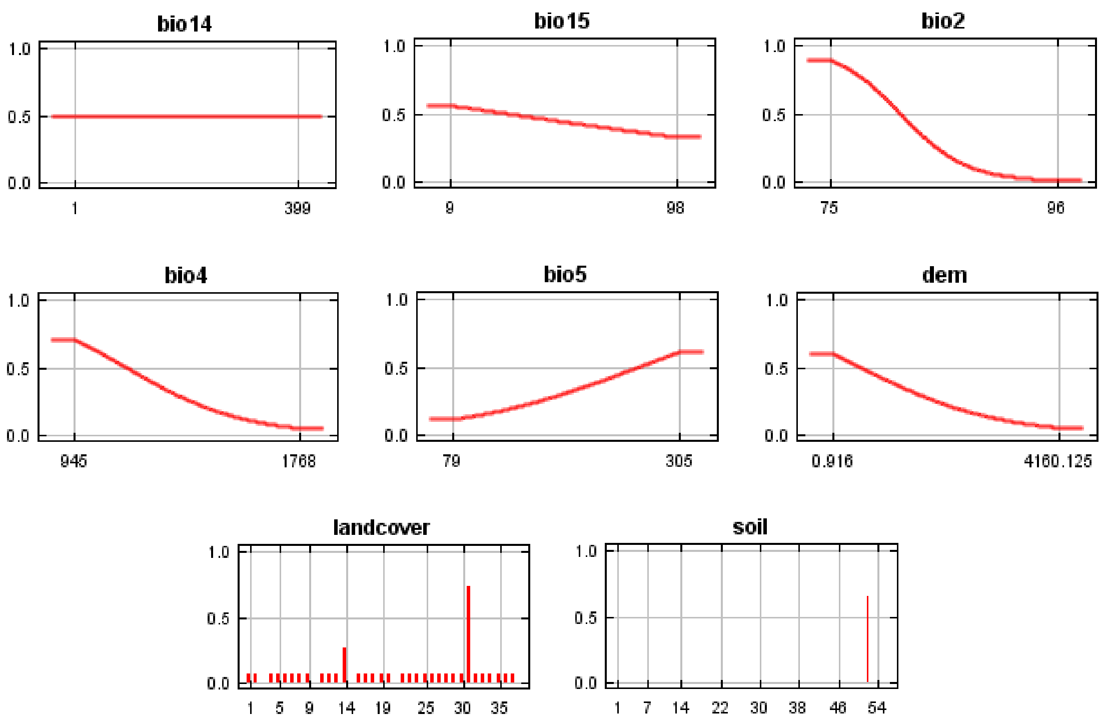


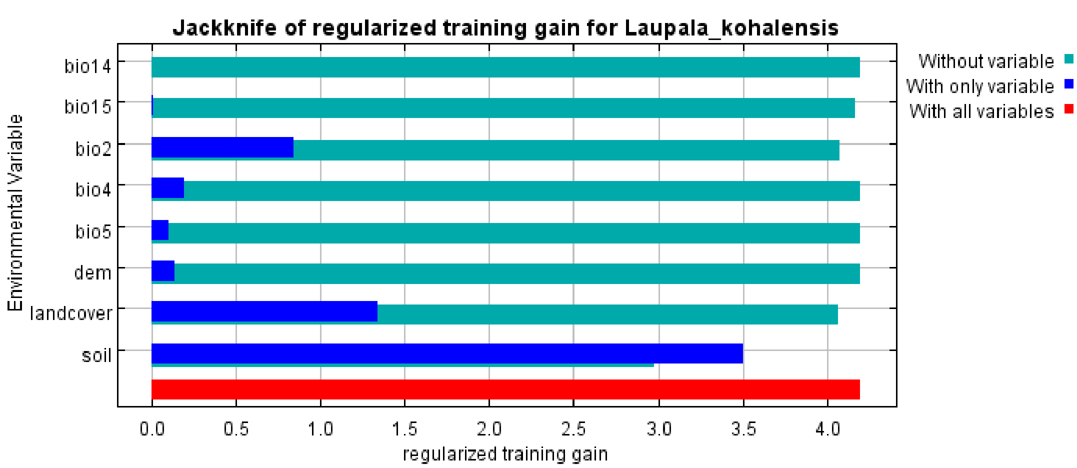




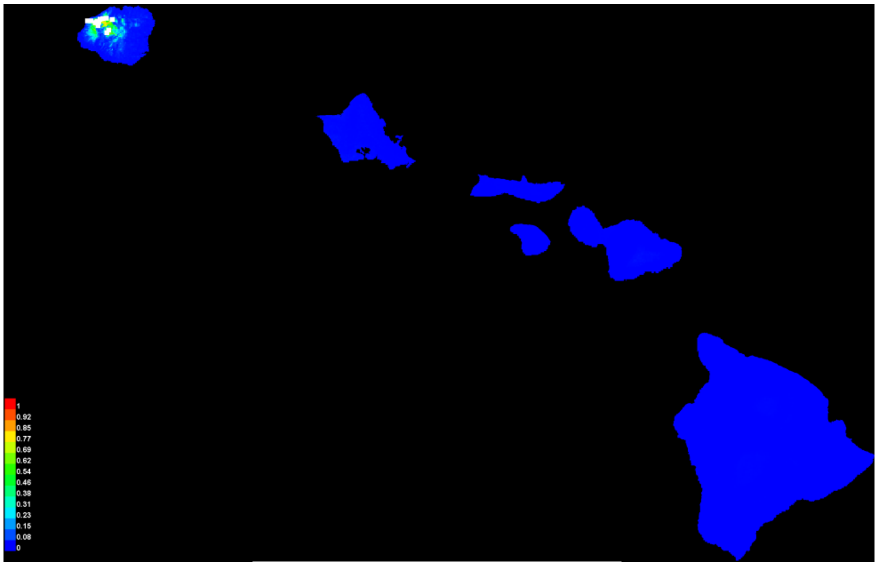
L. kohalensis

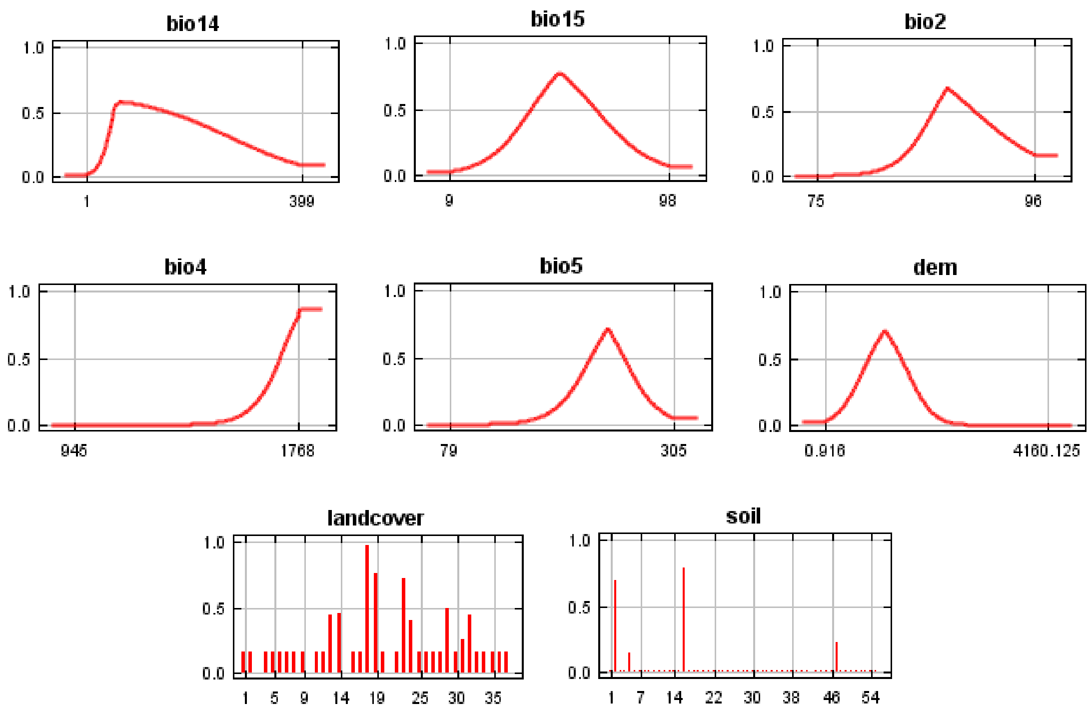






L. kokeensis




bio14
1.0
0.5
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bio2
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0.0
75
96
bio4
1.0
0.5
0.0
945
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bio5
1.0
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79
305
dem
1.0
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0.916
4160.125
landcover
1.0
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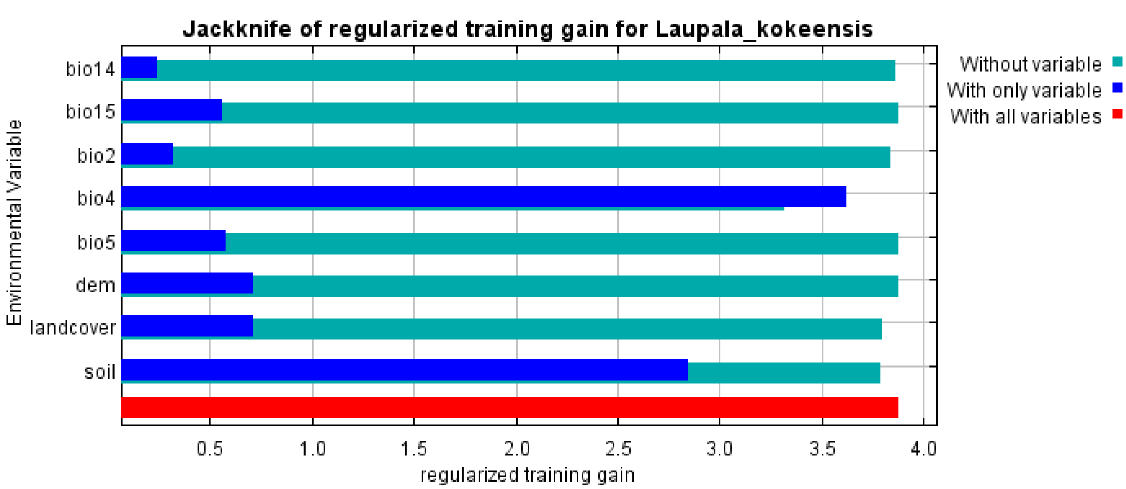
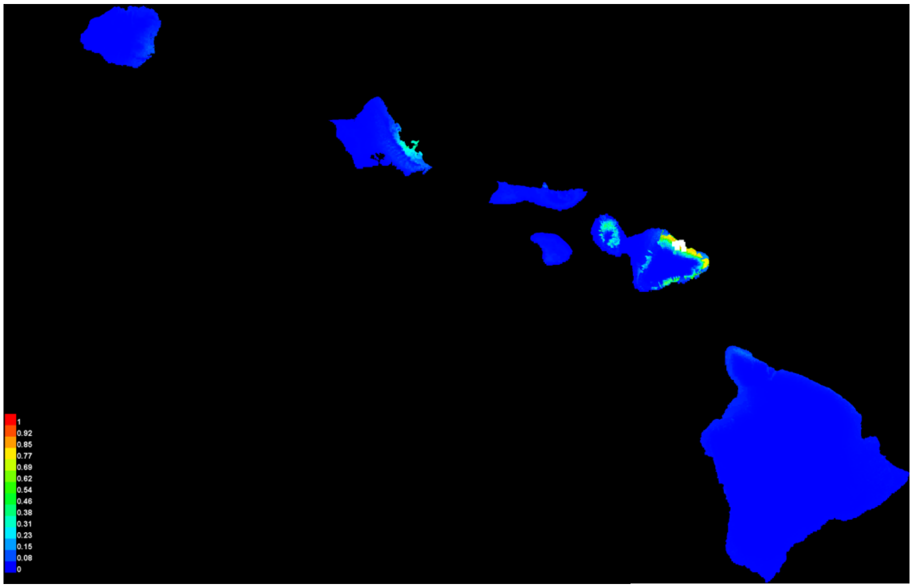
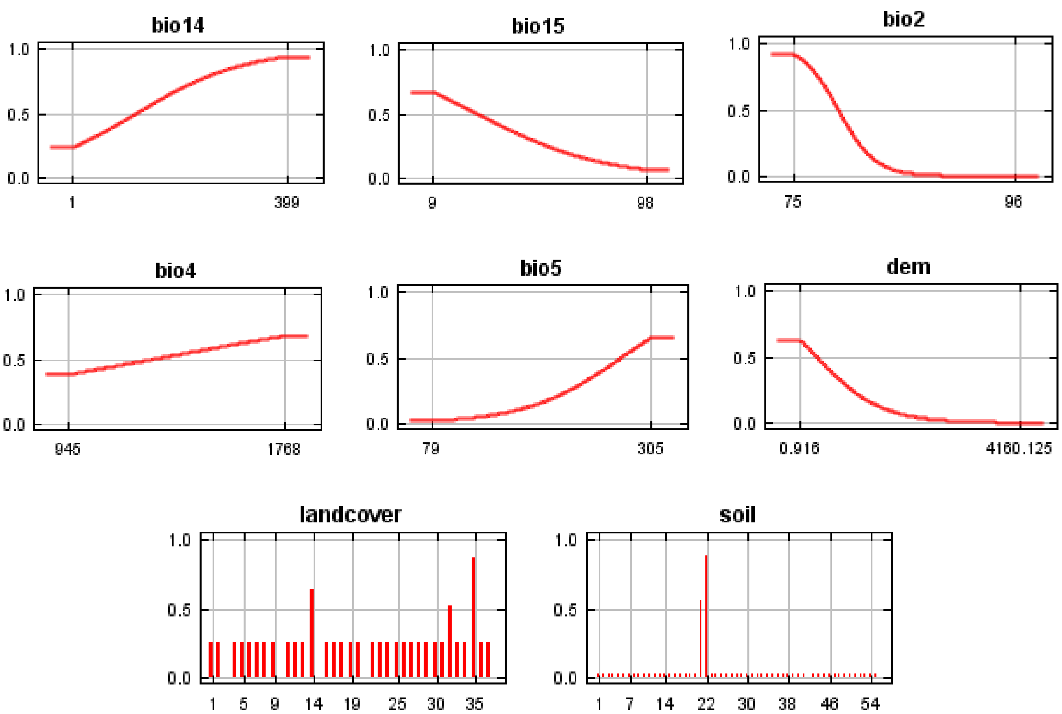
1 5 9 14 19 25 30 35
soil
1.0
0.5
0.0
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Laupala_kokeensis
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0
regularized training gain
Without variable
With only variable
With all variables

L. kolea

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1.0
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0.0
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0.0
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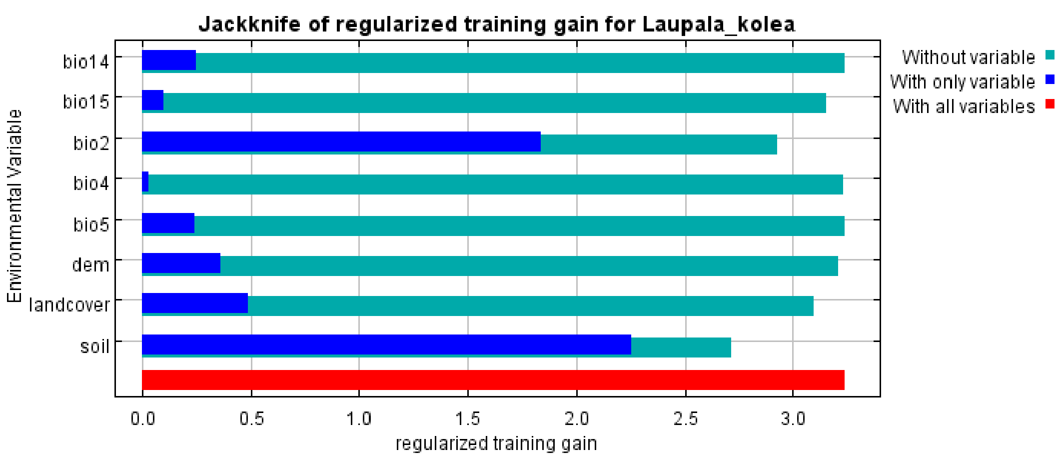
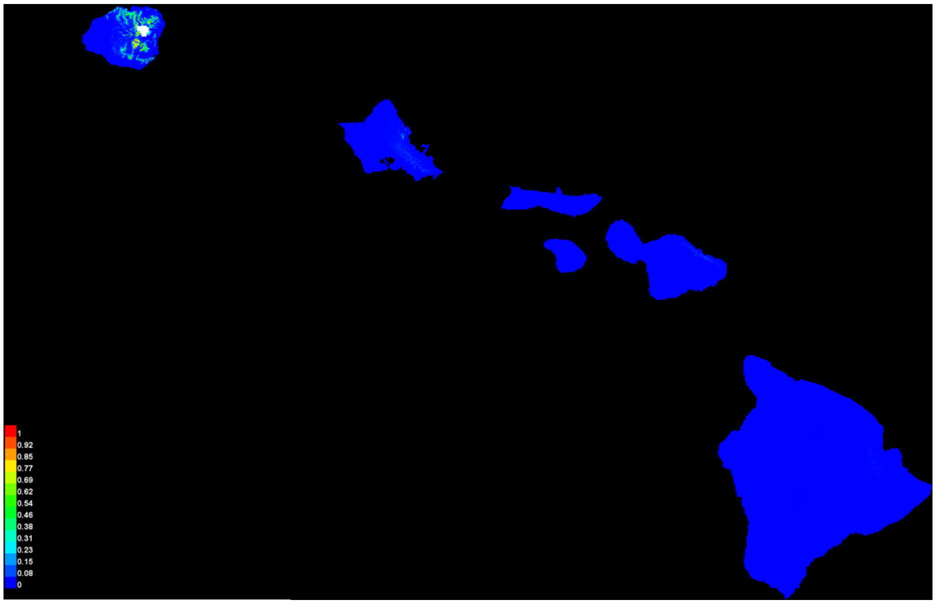
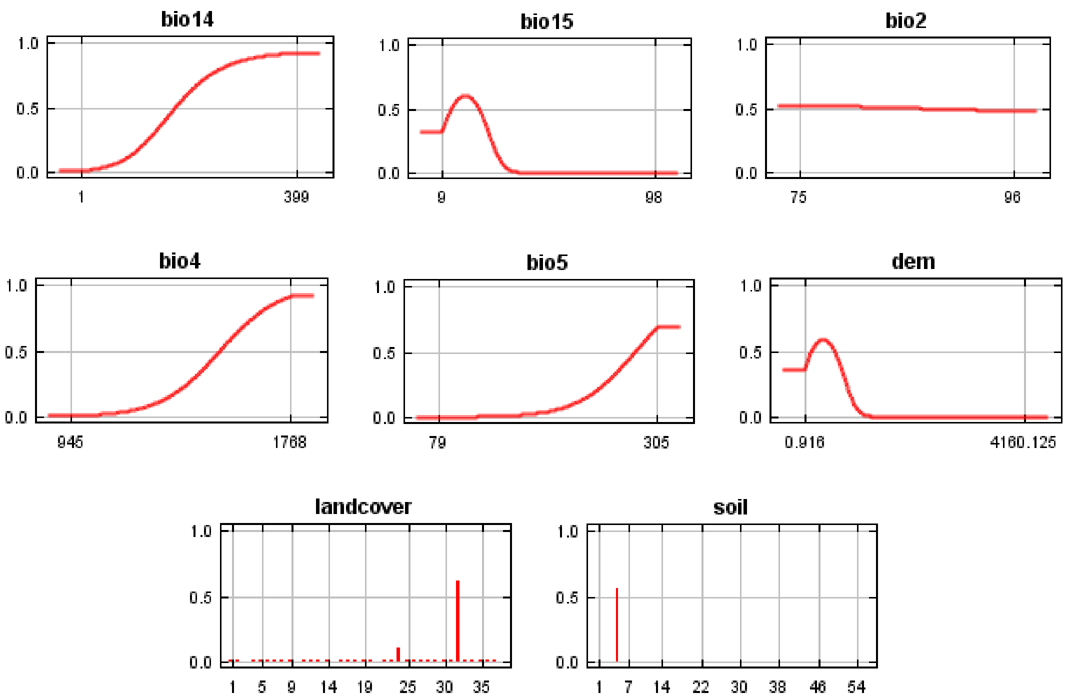
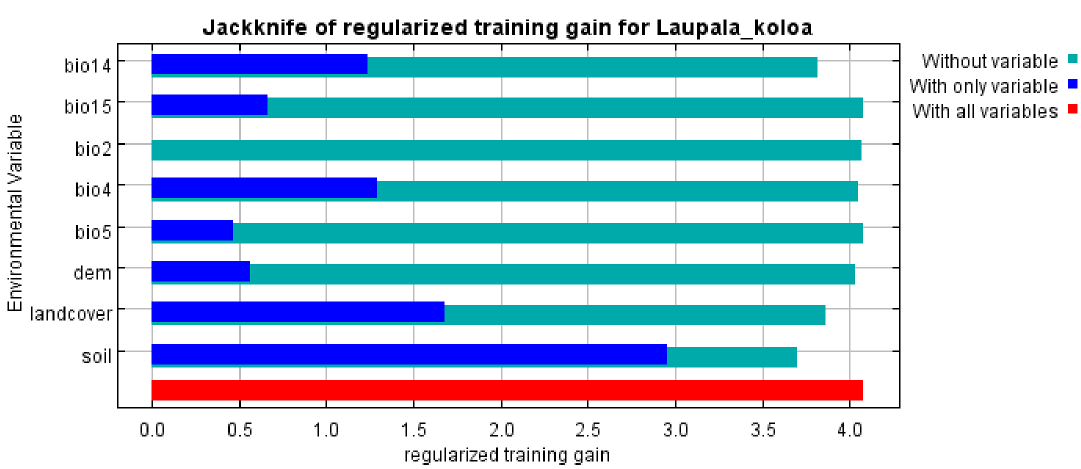
98
bio2
1.0
0.5
0.0
75
96
bio4
1.0
0.5
0.0
945
1768
bio5
1.0
0.5
0.0
79
305
dem
1.0
0.5
0.0
0.916
4160.125
landcover
1.0
0.5
0.0
1 5 9 14 19 25 30 35
soil
1.0
0.5
0.0
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Laupala_kolea
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
0.0 0.5 1.0 1.5 2.0 2.5 3.0
regularized training gain
Without variable
With only variable
With all variables

L. koloa




bio14
1 399
bio15
9 98
bio2
75 96
bio4
945 1768
bio5
79 305
dem
0.916 4160.125
landcover
1 5 9 14 19 25 30 35
soil
1 7 14 22 30 38 46 54
1.0
0.5
0.0


Jackknife of regularized training gain for Laupala_koloa
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
Without variable
With only variable
With all variables
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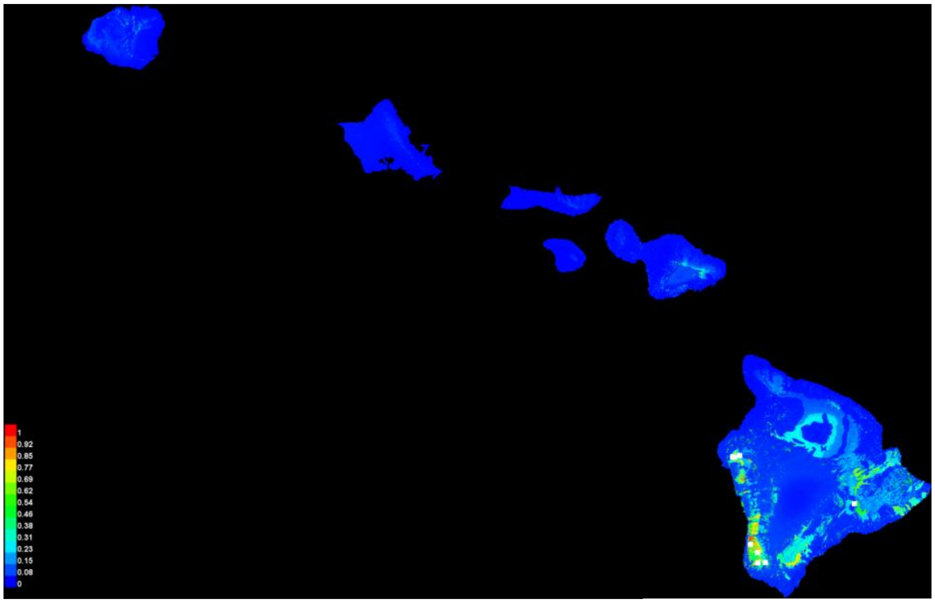
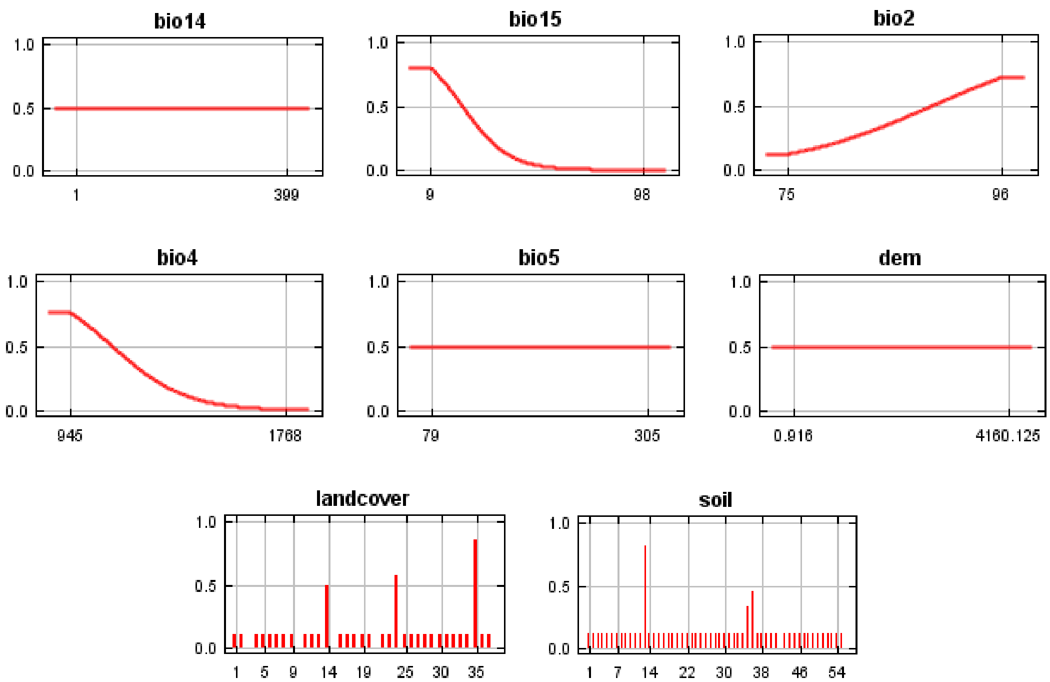
regularized training gain

L. kona

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landcover
soil
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1
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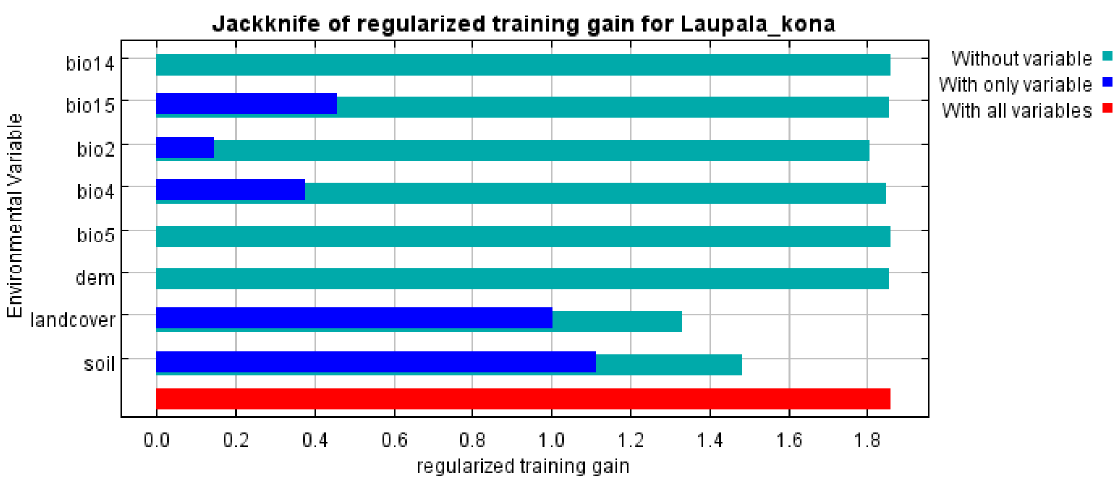
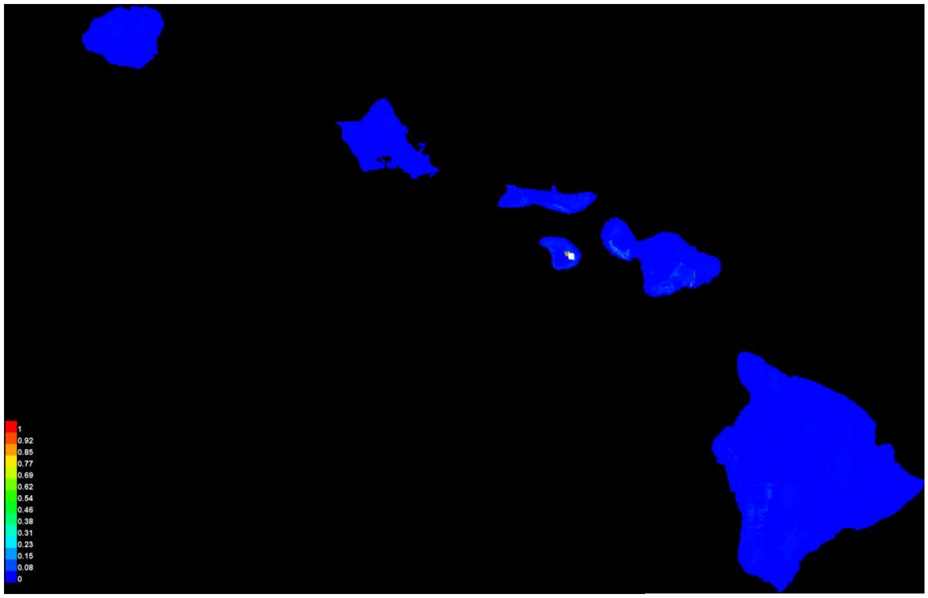
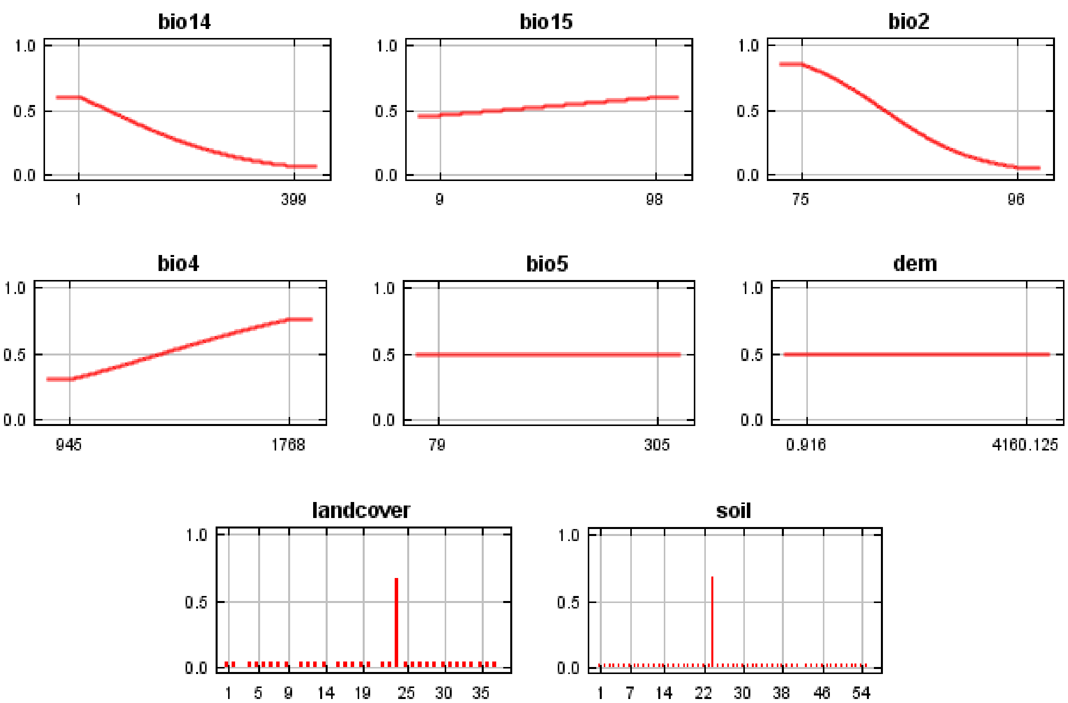
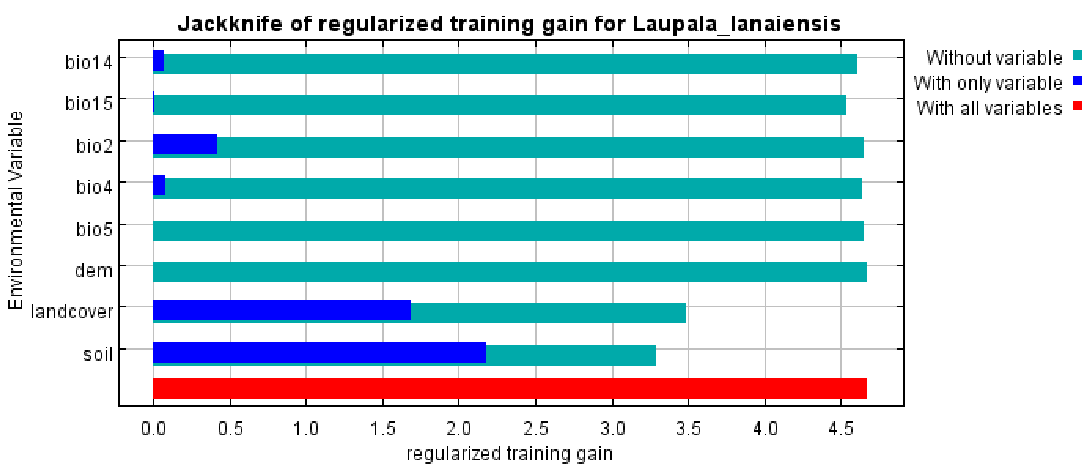
1768
79
305
0.916
4160.125
1 5 9 14 19 25 30 35
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Laupala_kona
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
Without variable
With only variable
With all variables
0.0 0.2 0.4 0.6 0.8 1.0 1.2 1.4 1.6 1.8
regularized training gain

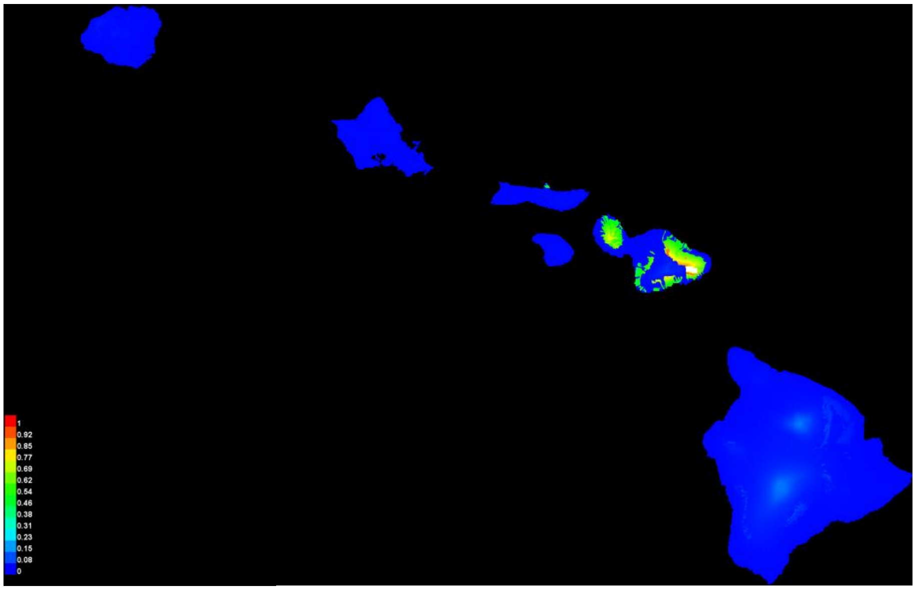
L. lanaiensis

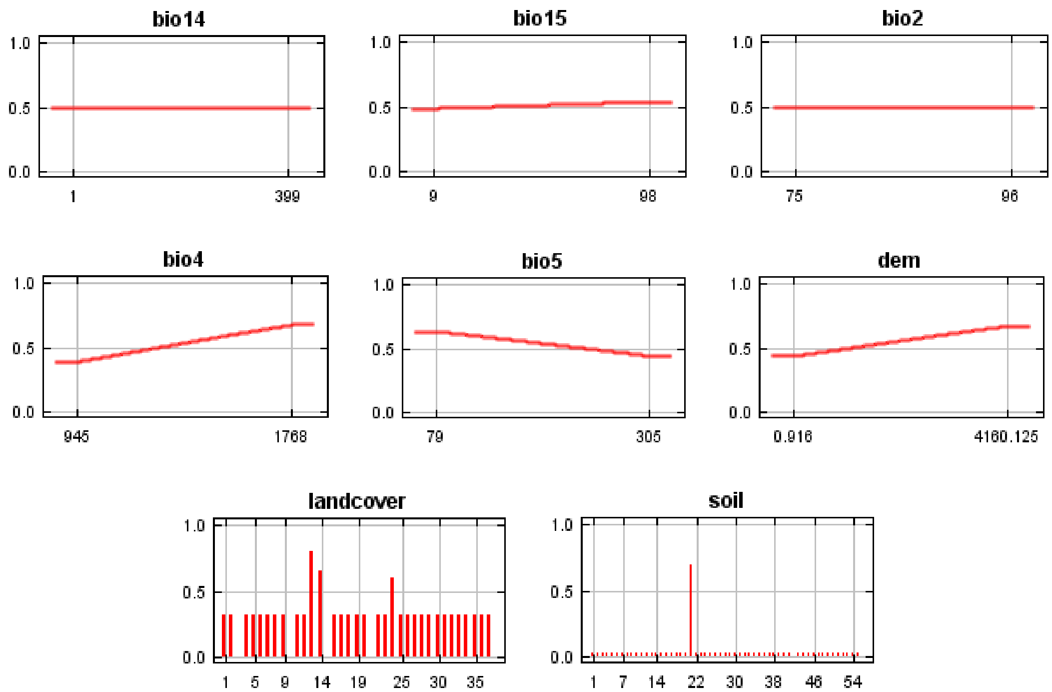






L. makaio

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bio15
9
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bio2
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96
bio4
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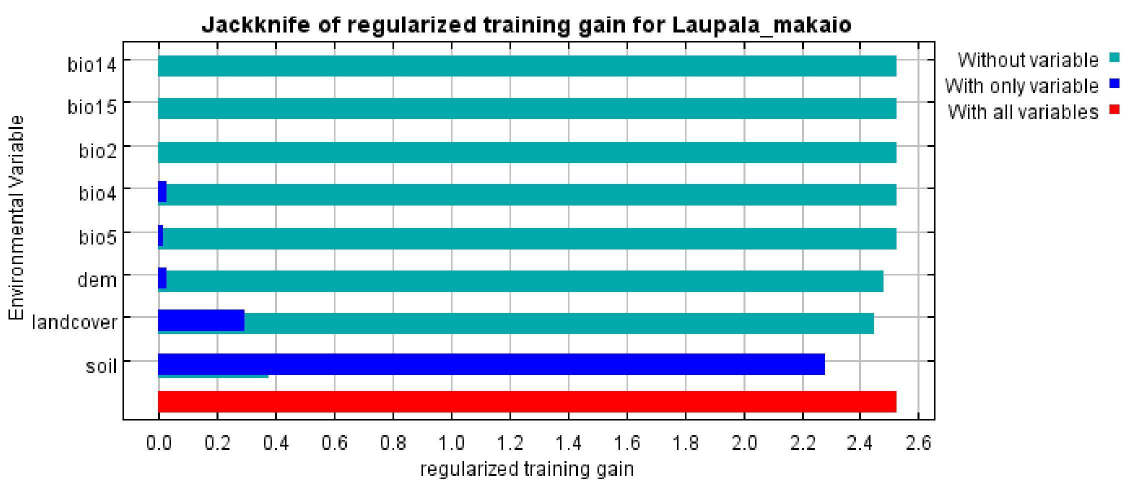
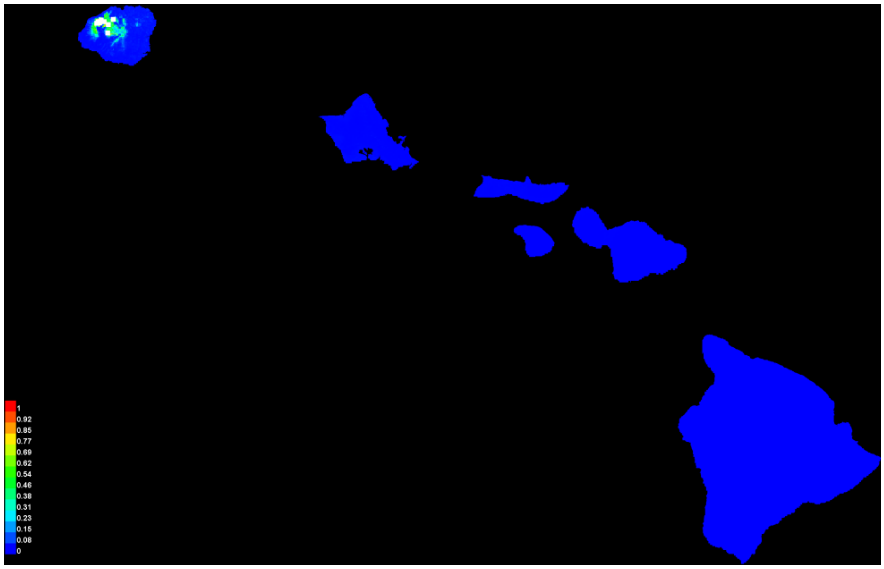
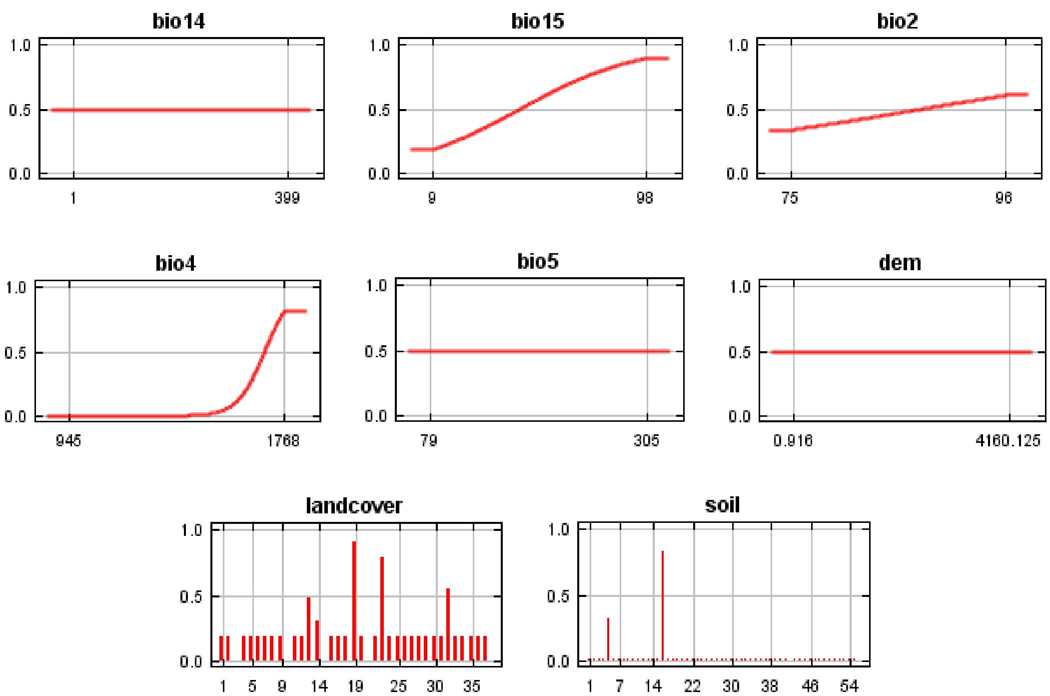
bio5
79
305
dem
0.916
4160.125
landcover
1 5 9 14 19 25 30 35
soil
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Laupala_makaio
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
Without variable
With only variable
With all variables
0.0 0.2 0.4 0.6 0.8 1.0 1.2 1.4 1.6 1.8 2.0 2.2 2.4 2.6
regularized training gain

L. makaweli

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bio15
9
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bio2
75
96
bio4
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1768
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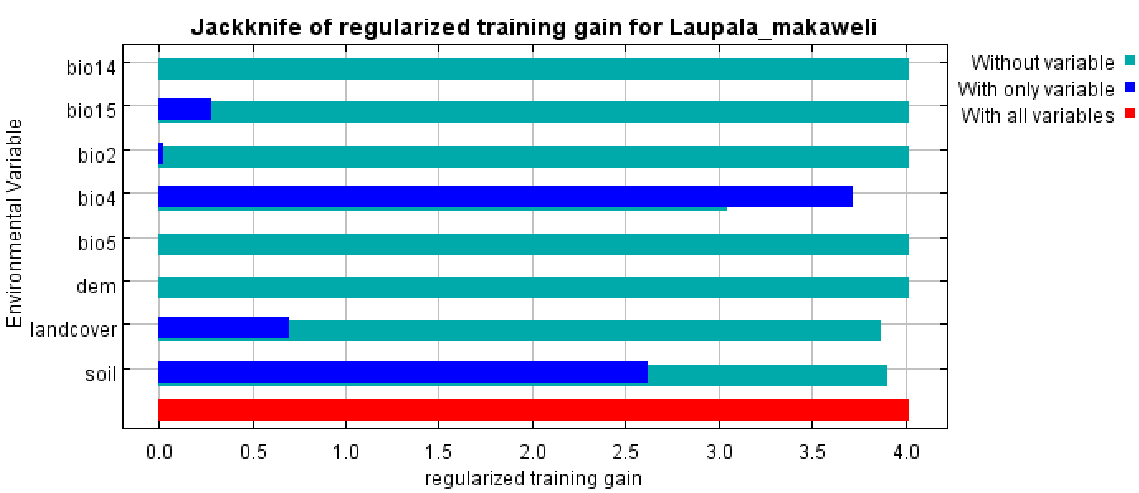
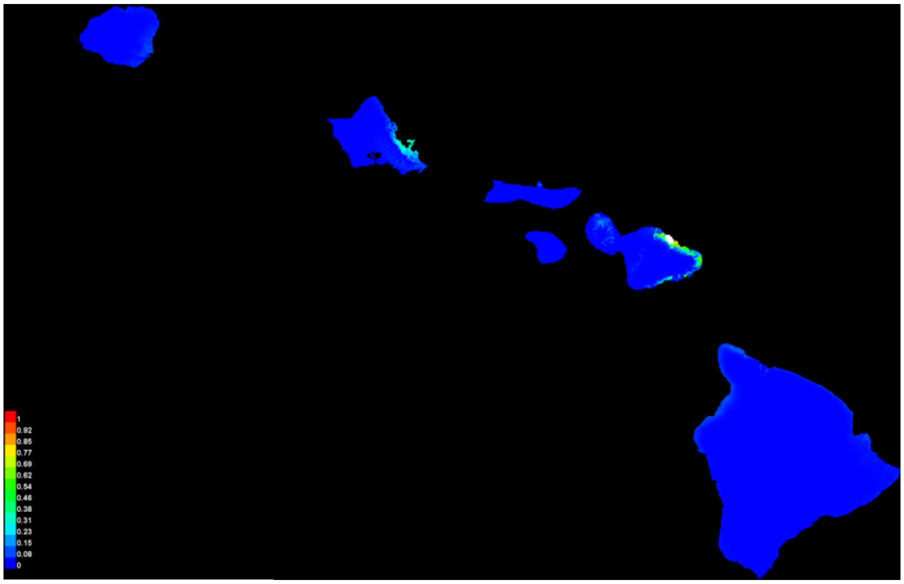
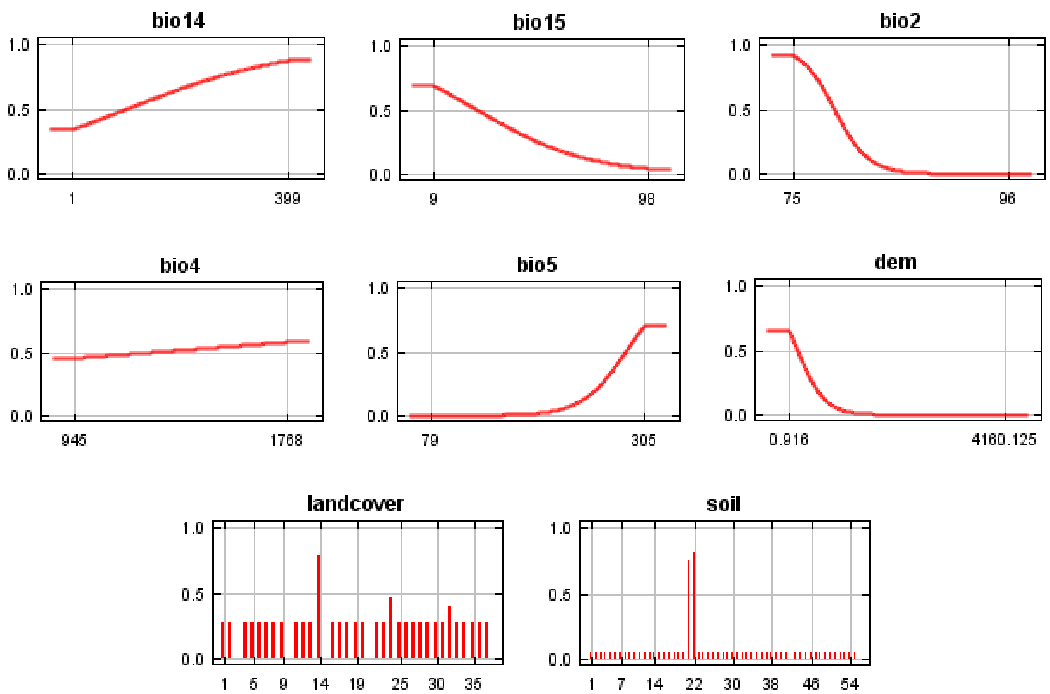
79
305
dem
0.916
4160.125
landcover
1 5 9 14 19 25 30 35
soil
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Laupala_makaweli
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
Without variable
With only variable
With all variables
0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0
regularized training gain

L. media

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bio2
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bio4
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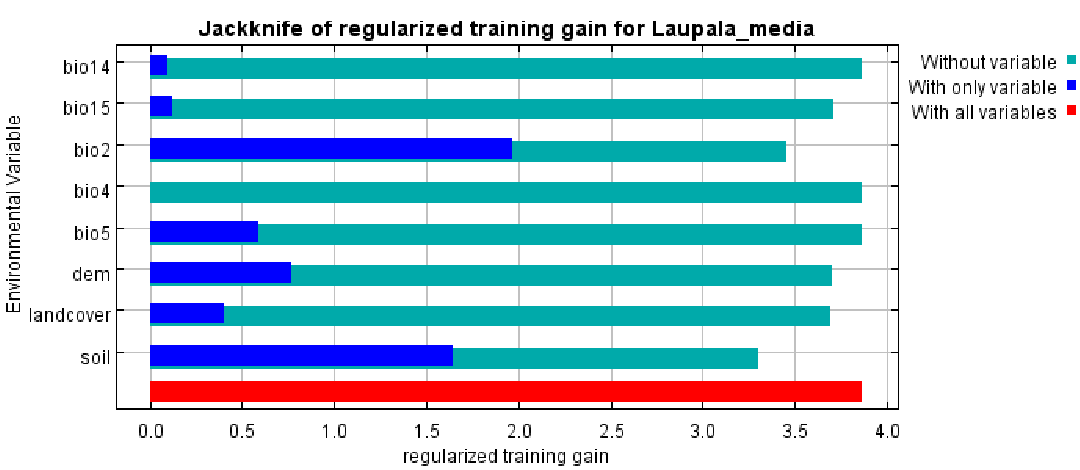
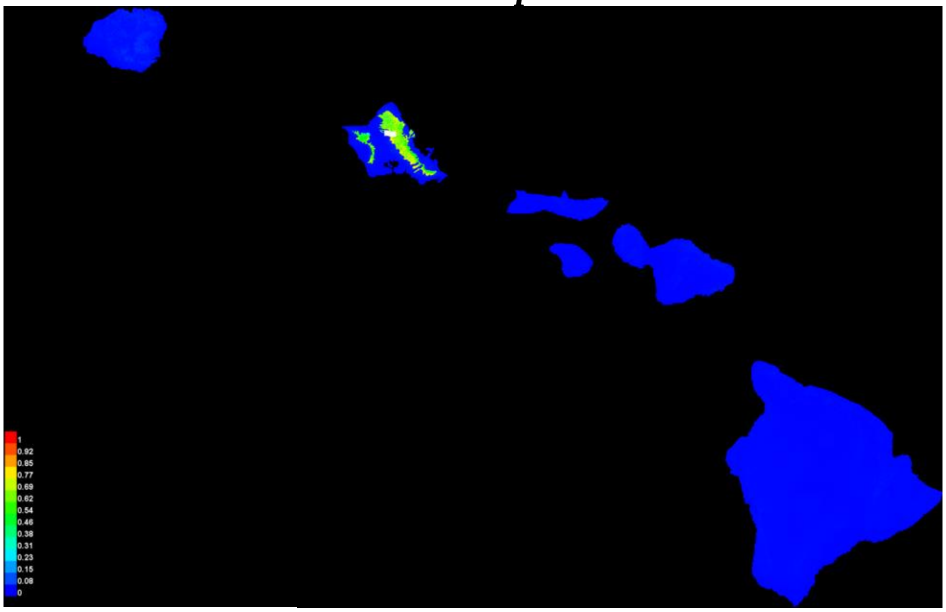
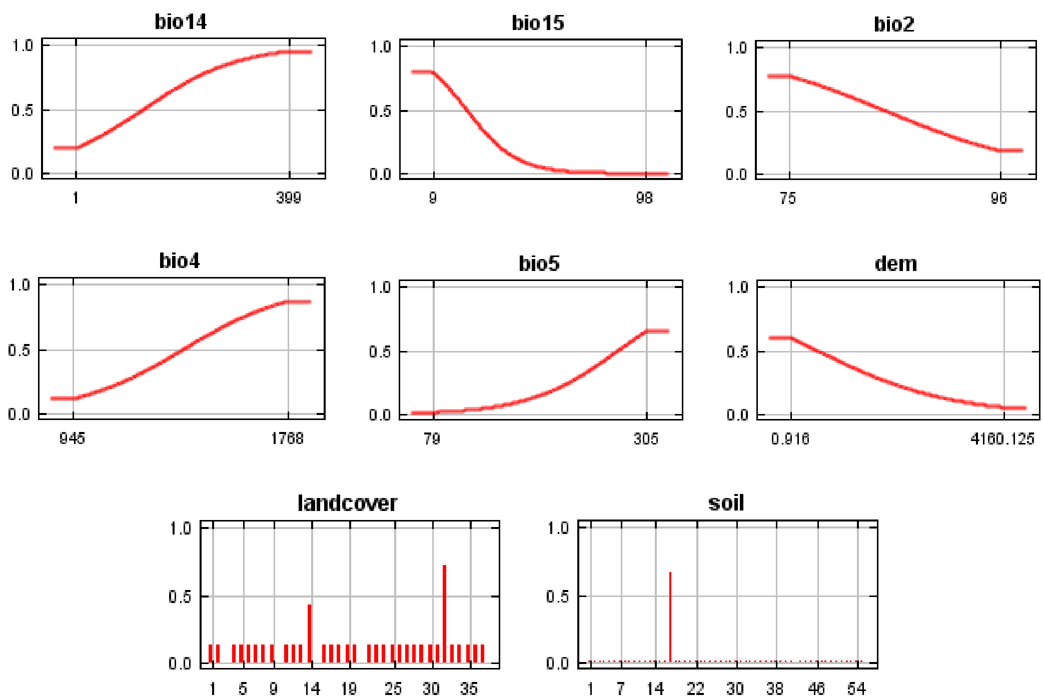
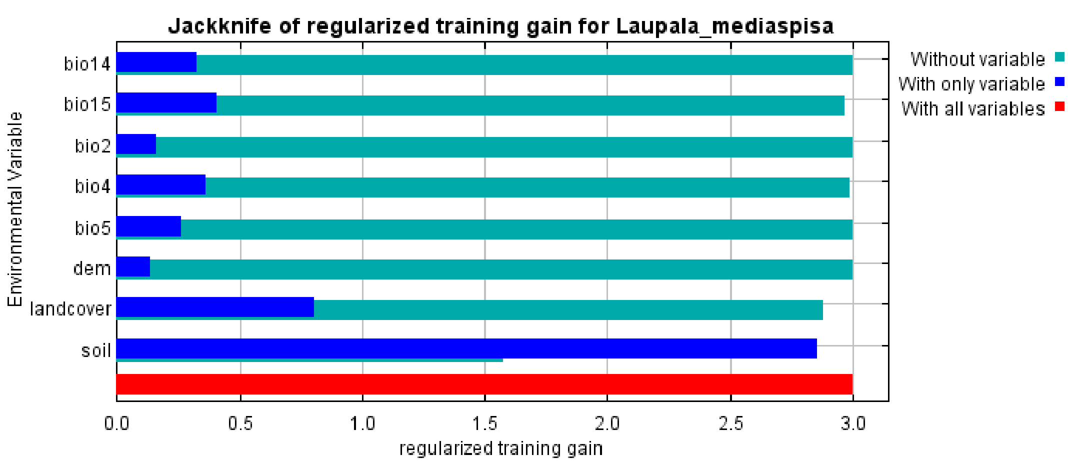
305
dem
0.916
4160.125
landcover
1 5 9 14 19 25 30 35
soil
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Laupala_media
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0
regularized training gain
Without variable
With only variable
With all variables

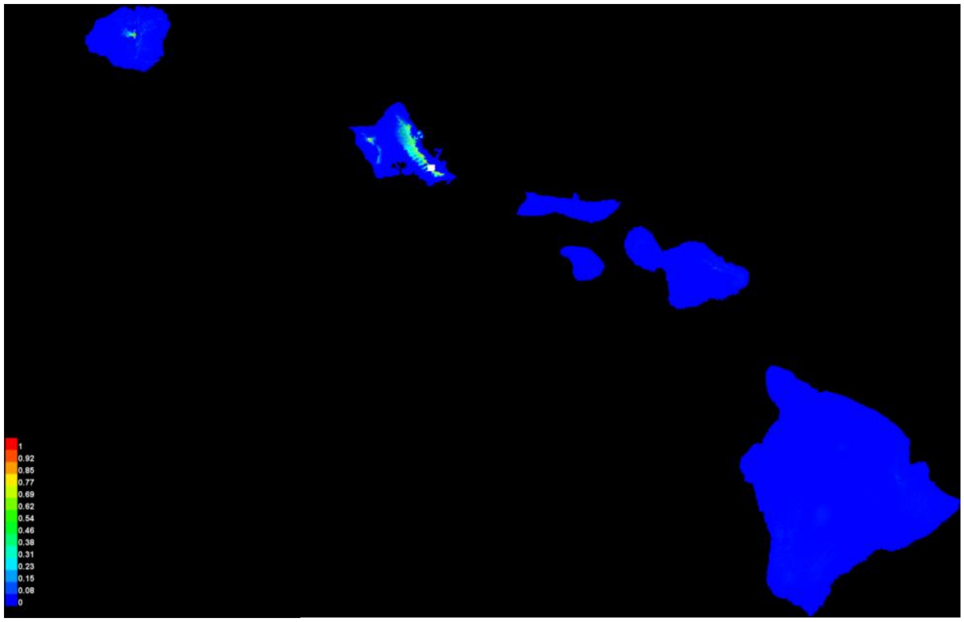
L. mediaspisa

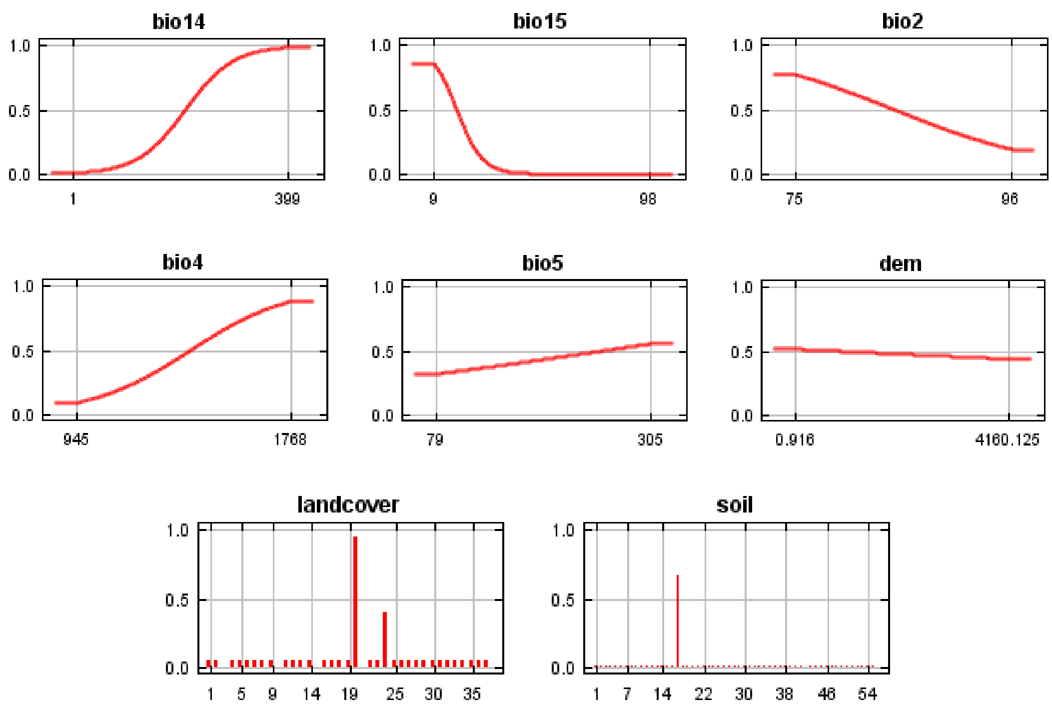






L. melewiki

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bio4
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dem
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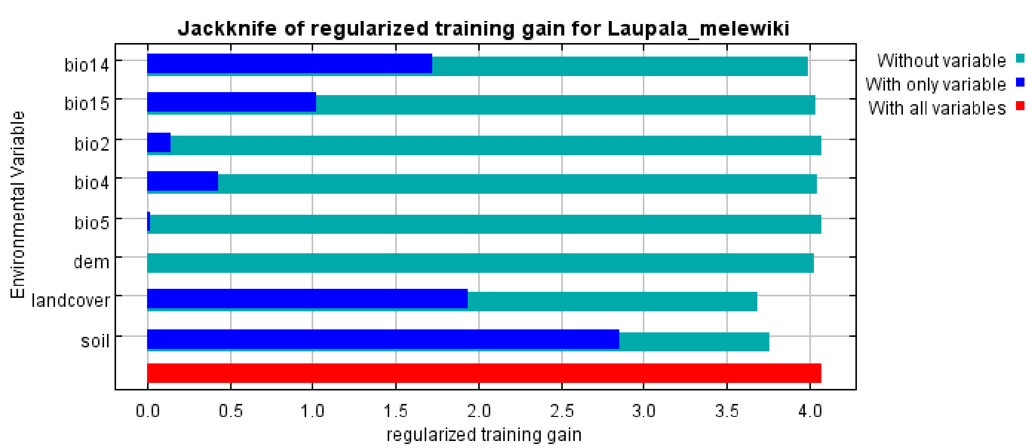
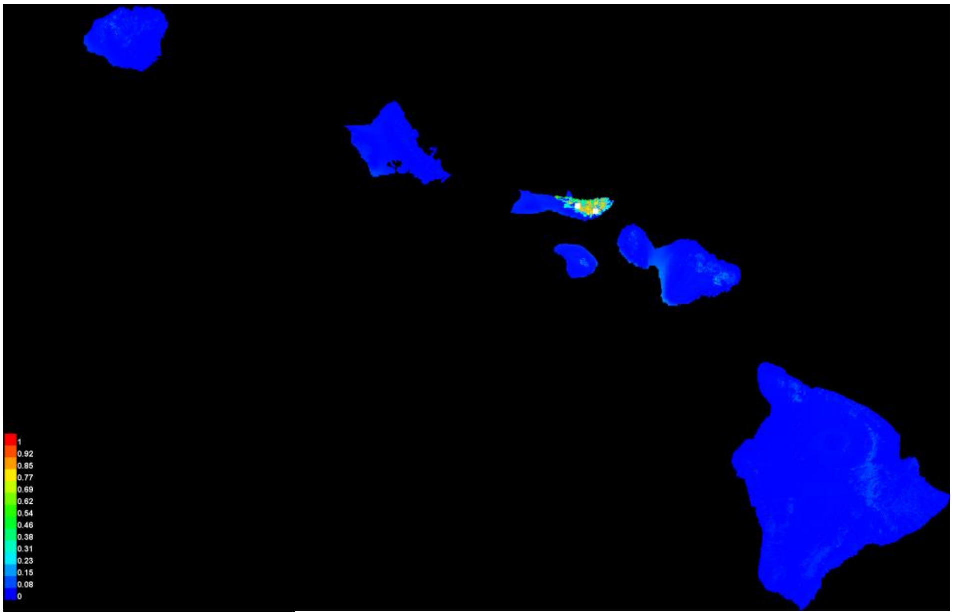
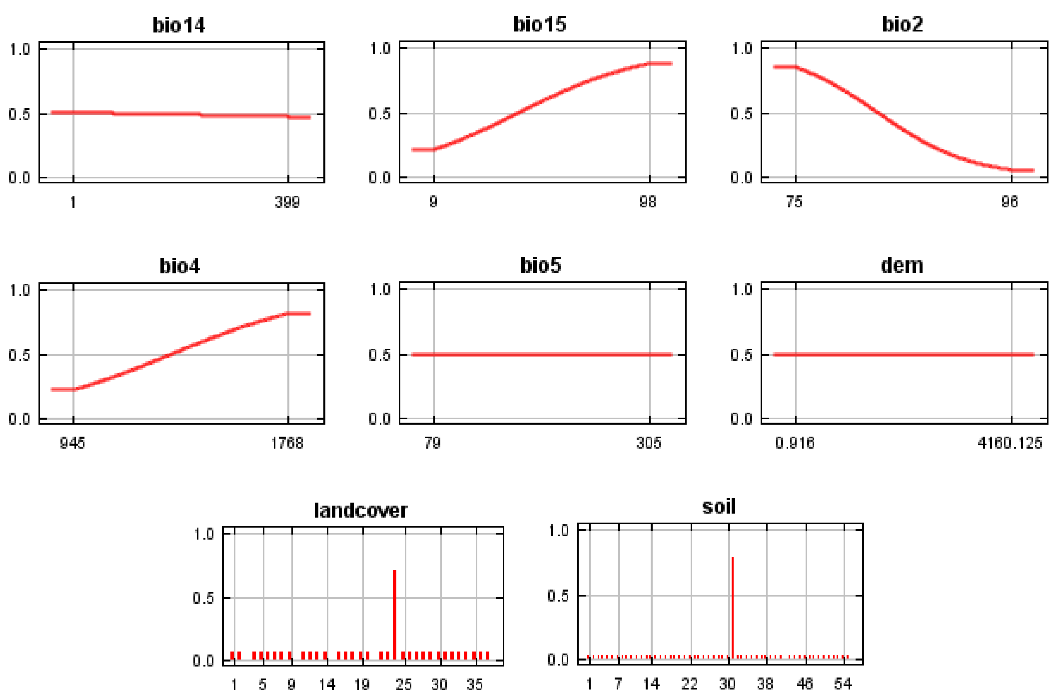
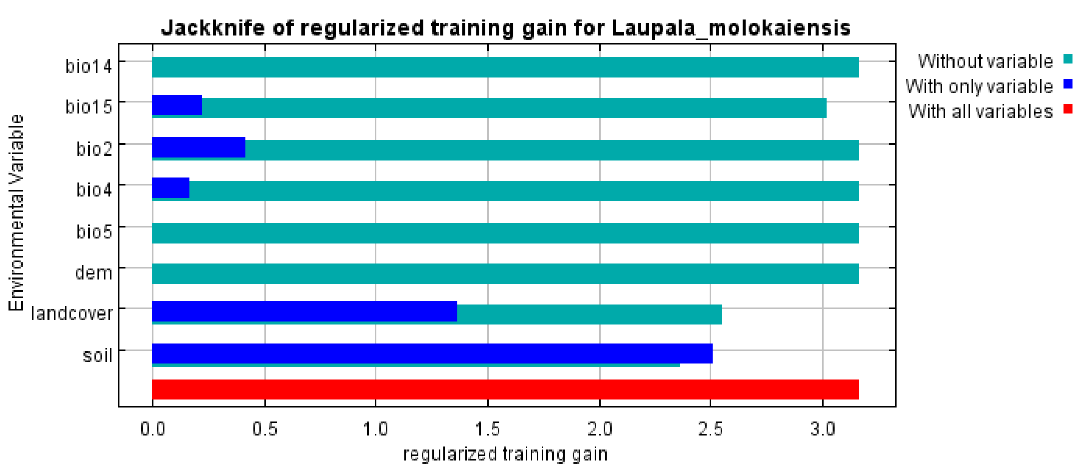
4160.125
landcover
1 5 9 14 19 25 30 35
soil
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Laupala_melewiki
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
Without variable
With only variable
With all variables
0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0
regularized training gain

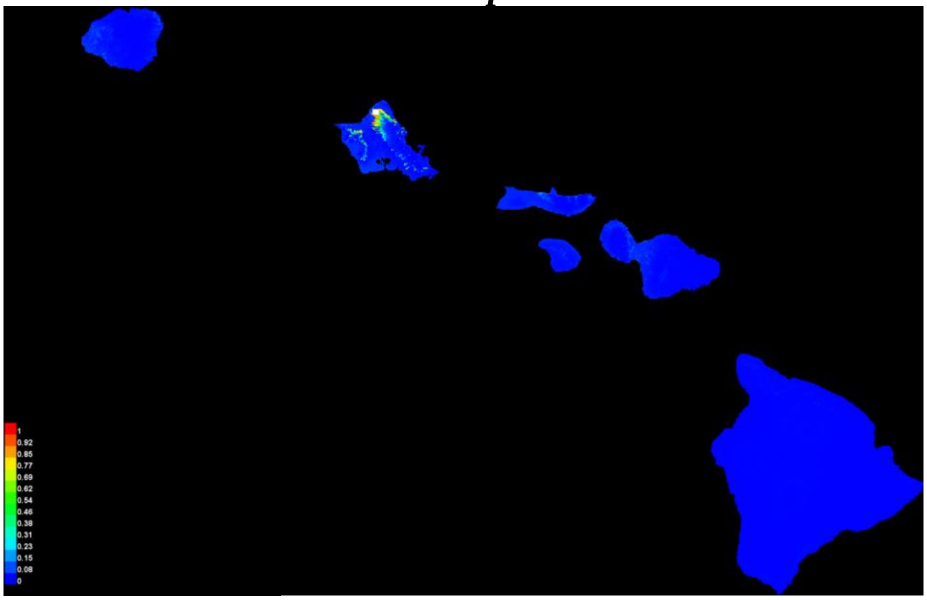
L. molokaiensis

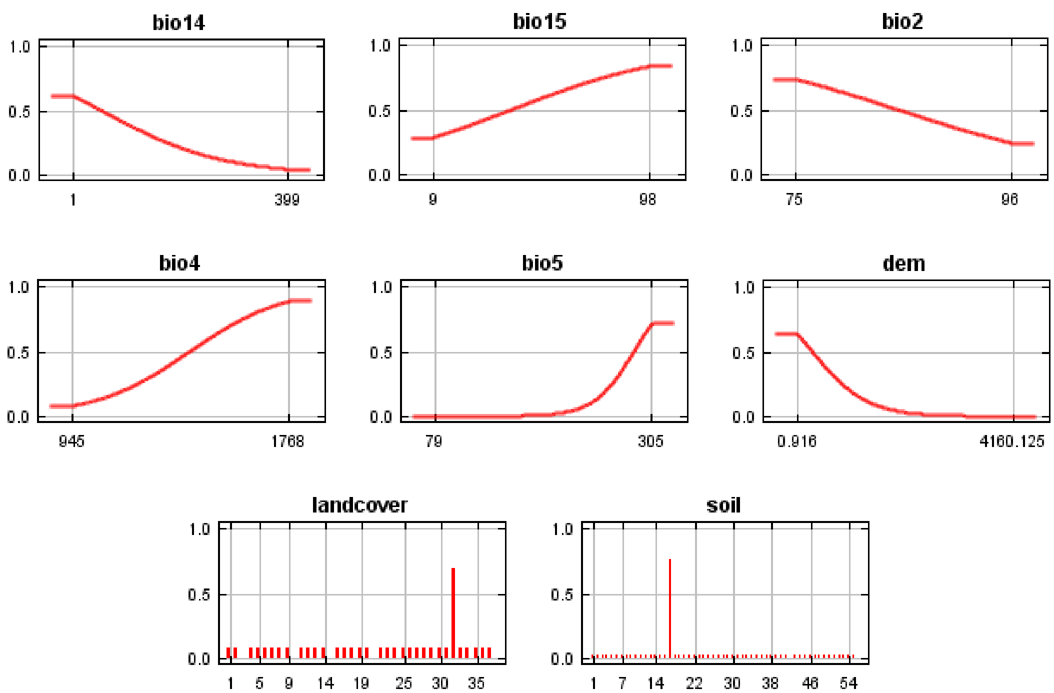


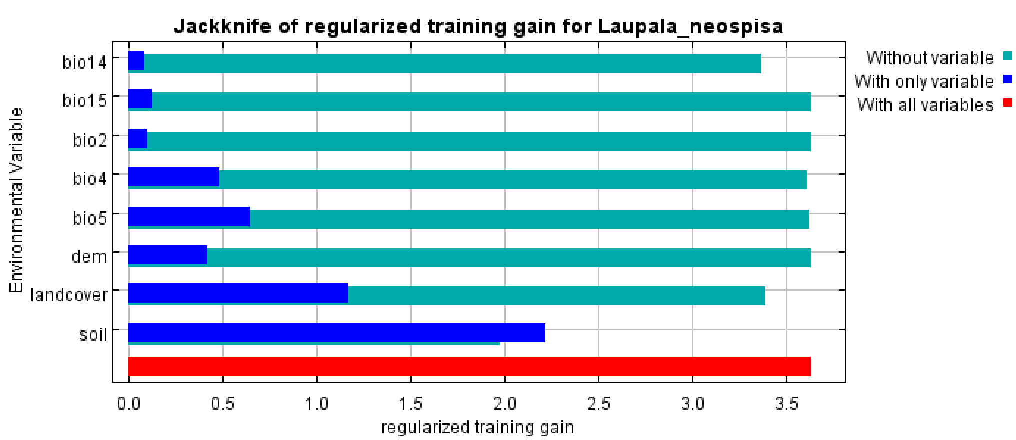




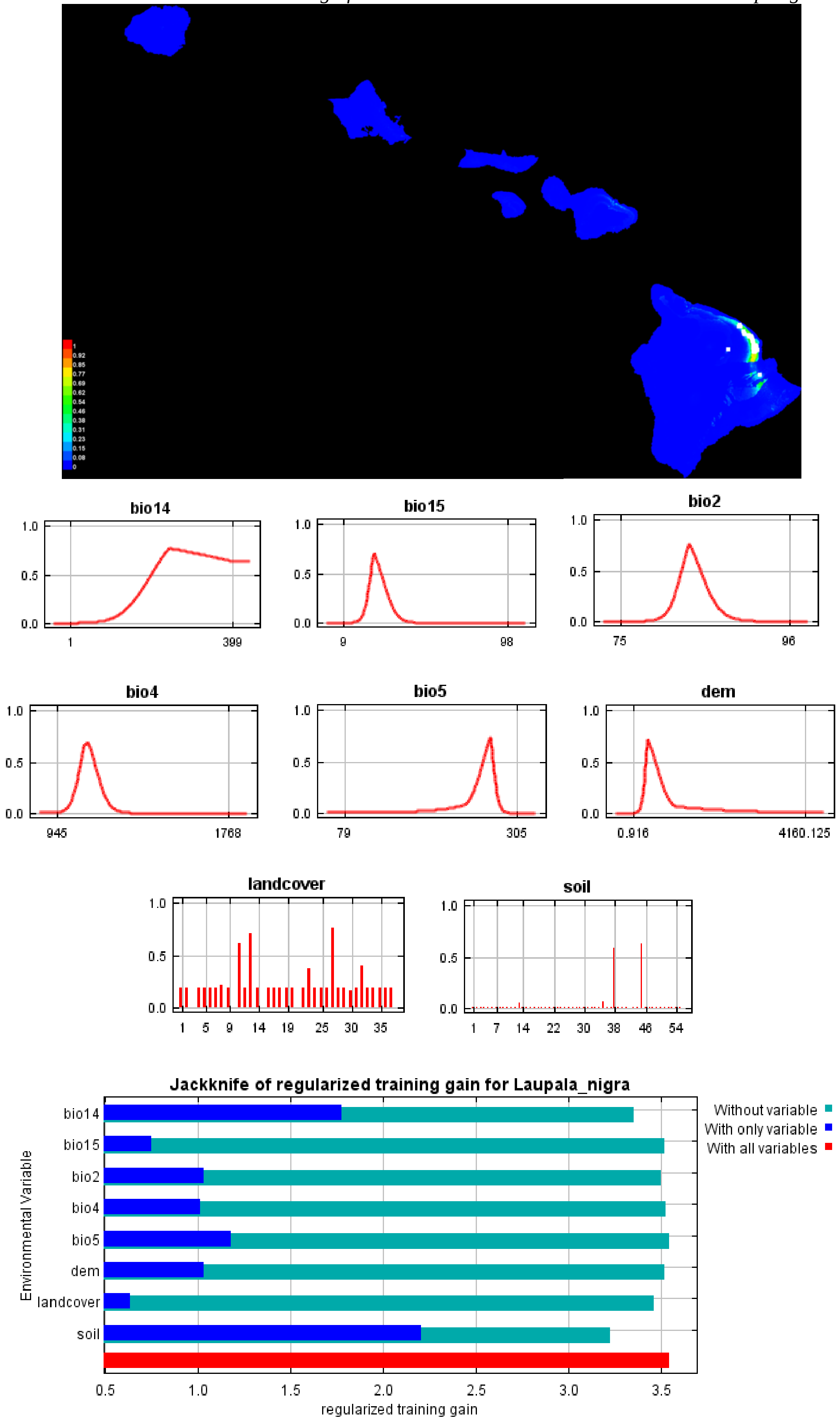
L. neospisa







L. nigra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bio4
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1768
bio5
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305
dem
0.916
4160.125
landcover
soil
Jackknife of regularized training gain for Laupala_nigra
Environmental Variable
bio14
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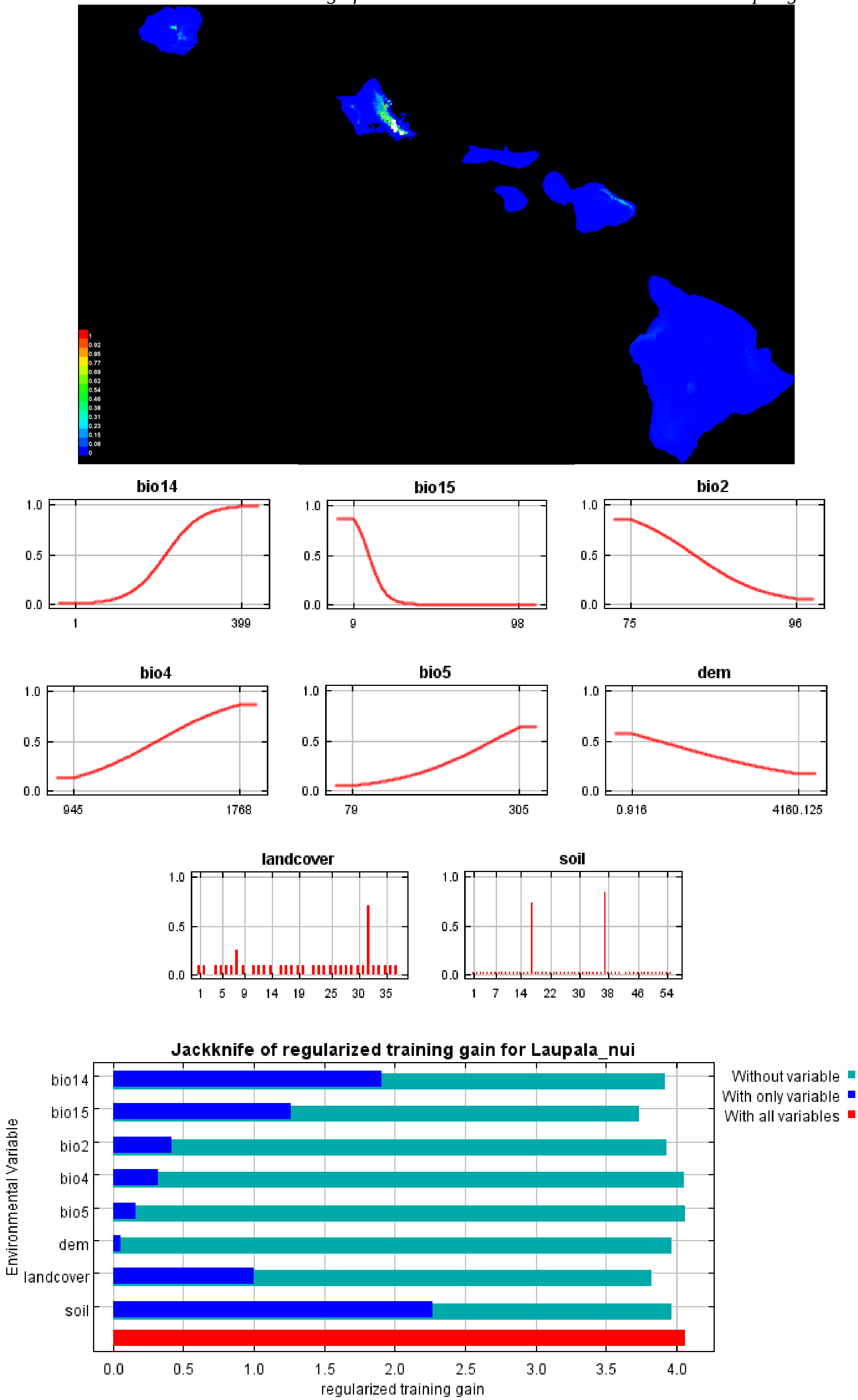
bio2
bio4
bio5
dem
landcover
soil
regularized training gain
Without variable
With only variable
With all variables

L. nui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bio2
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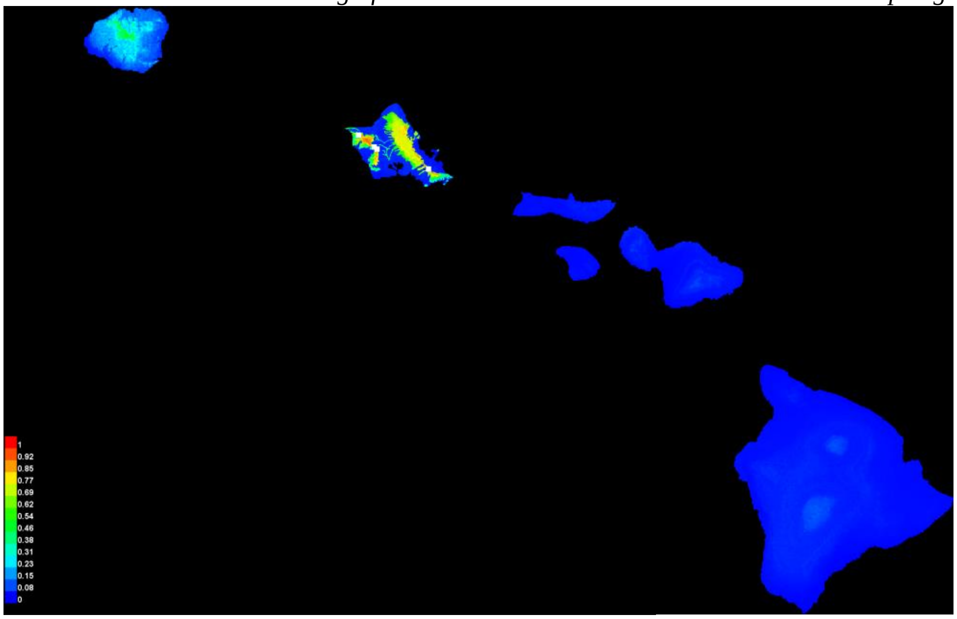
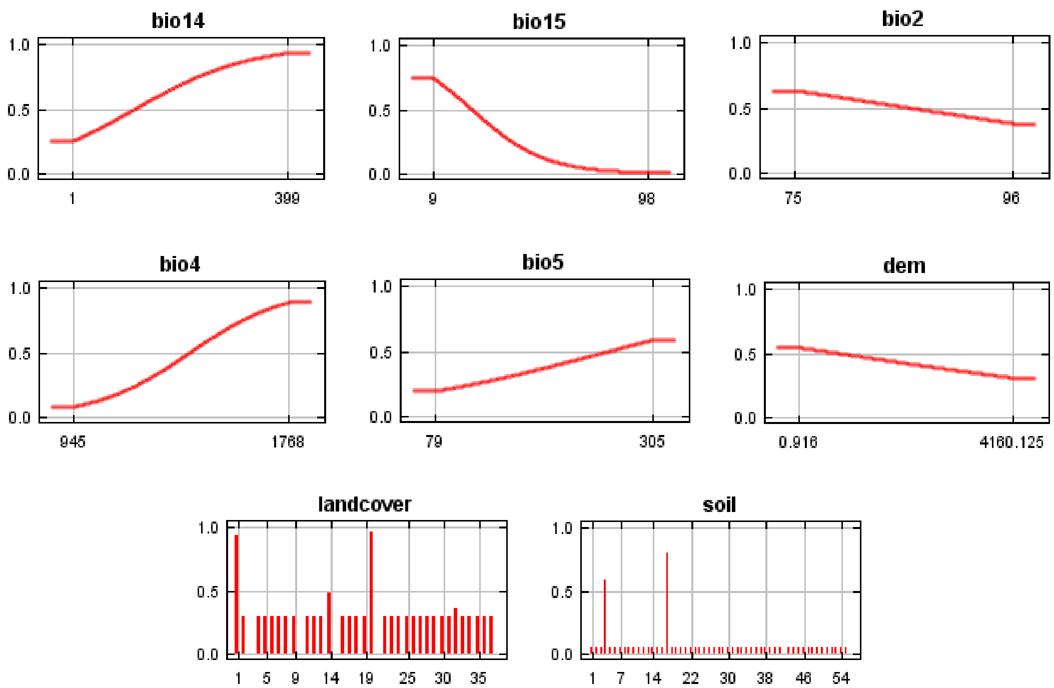
bio4
945
1768
bio5
79
305
dem
0.916
4160.125
landcover
1 5 9 14 19 25 30 35
soil
1 7 14 22 30 38 46 54
Jackknife of regularized training gain for Laupala_nui
Without variable
With only variable
With all variables
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0
regularized training gain

L. oahuensis

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bio15
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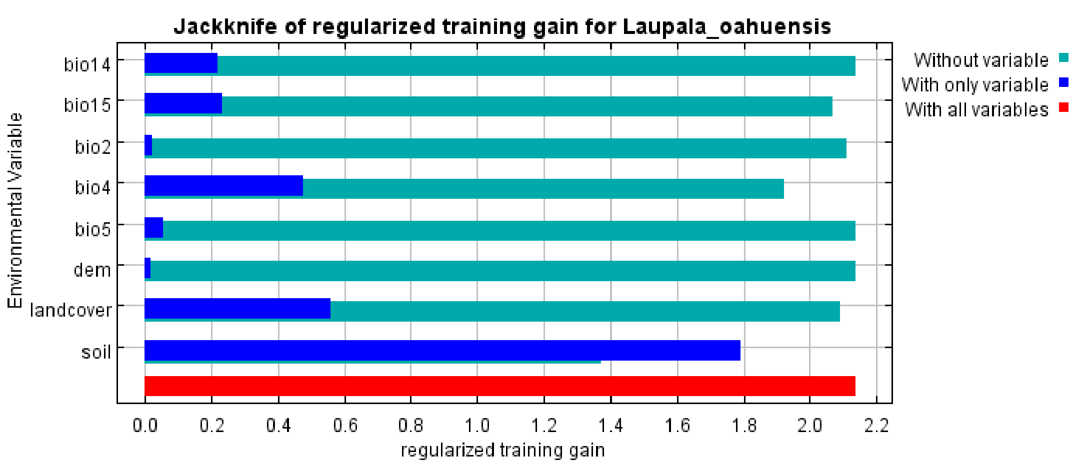
98
bio2
1.0
0.5
0.0
75
96
bio4
1.0
0.5
0.0
945
1768
bio5
1.0
0.5
0.0
79
305
dem
1.0
0.5
0.0
0.916
4160.125
landcover
1.0
0.5
0.0
1 5 9 14 19 25 30 35
soil
1.0
0.5
0.0
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Laupala_oahuensis
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
Without variable
With only variable
With all variables
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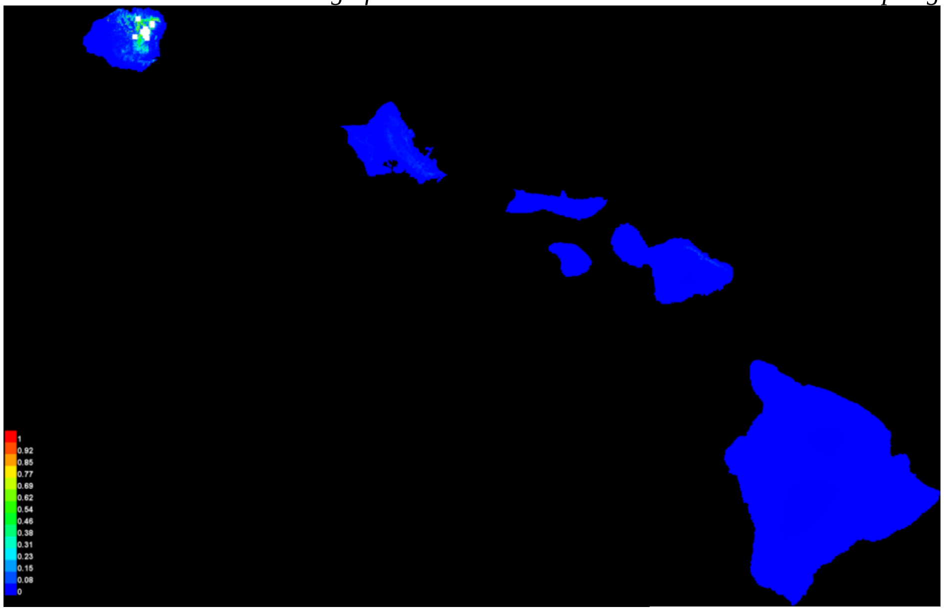
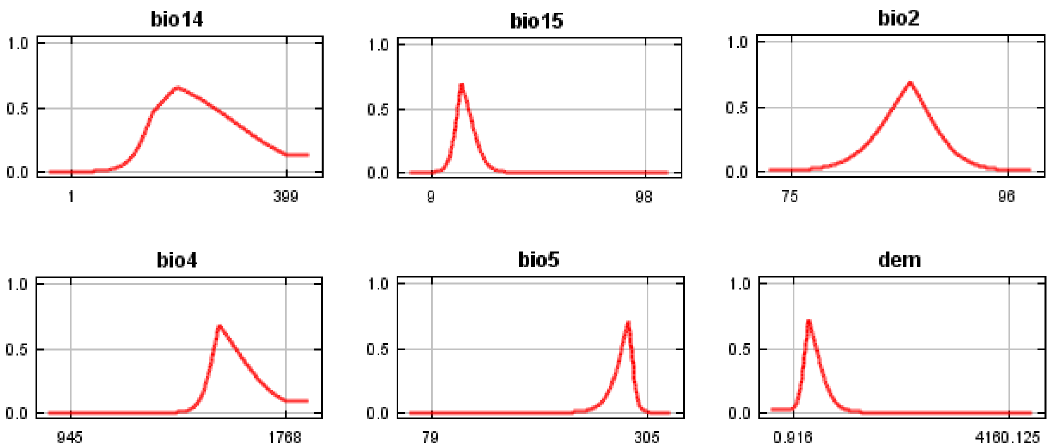
regularized training gain

L. olohena

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bio4
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bio5
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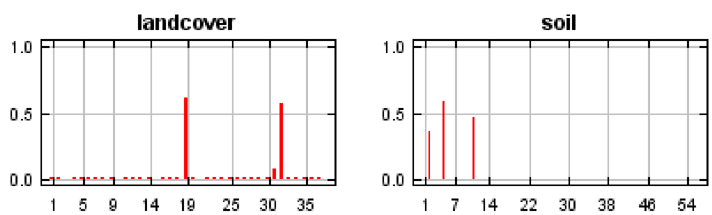
305
dem
0.916
4160.125


landcover
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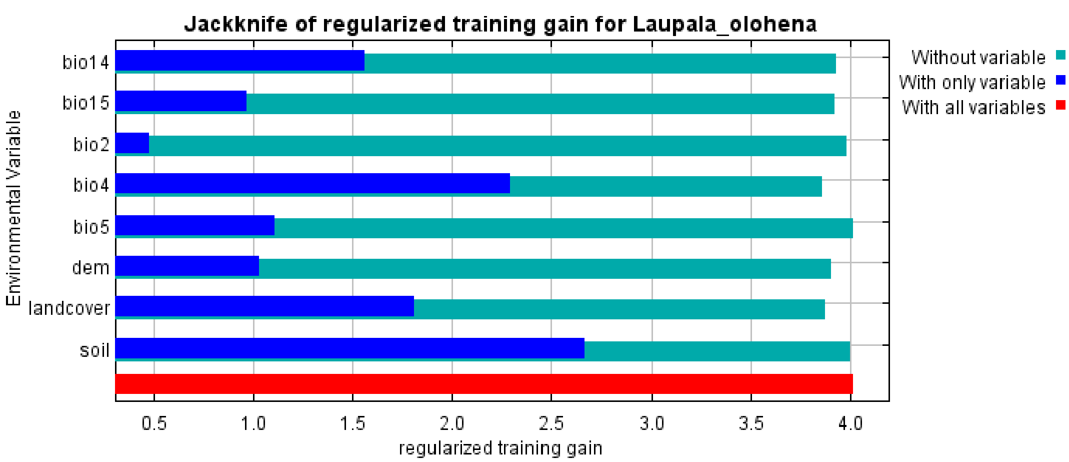
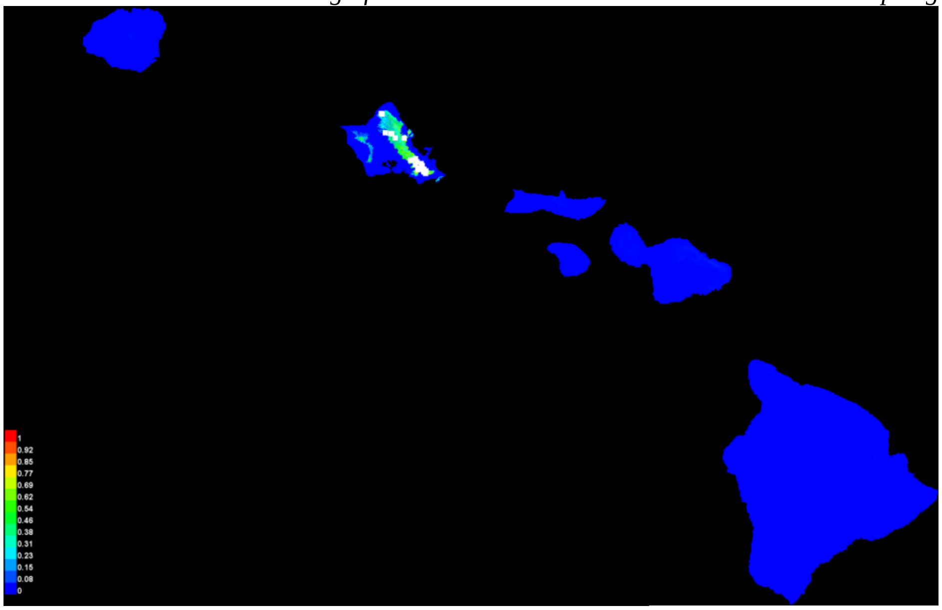
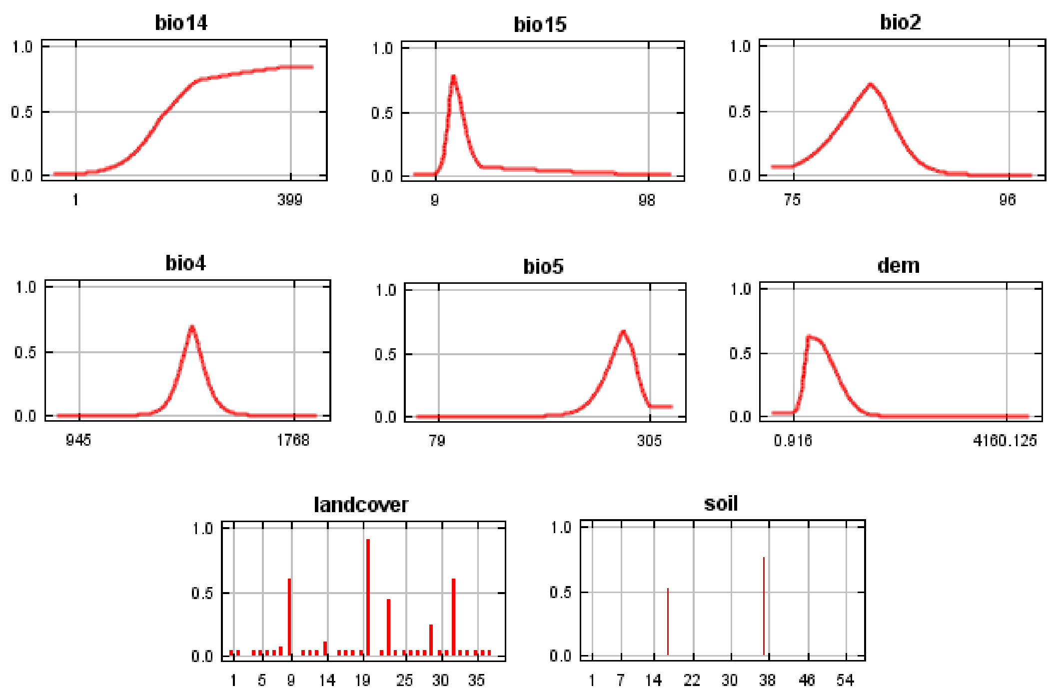
0.5
0.0
1 5 9 14 19 25 30 35
soil
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Laupala_olohena
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0
regularized training gain
Without variable
With only variable
With all variables

L. pacifica




bio14
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bio15
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bio2
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bio4
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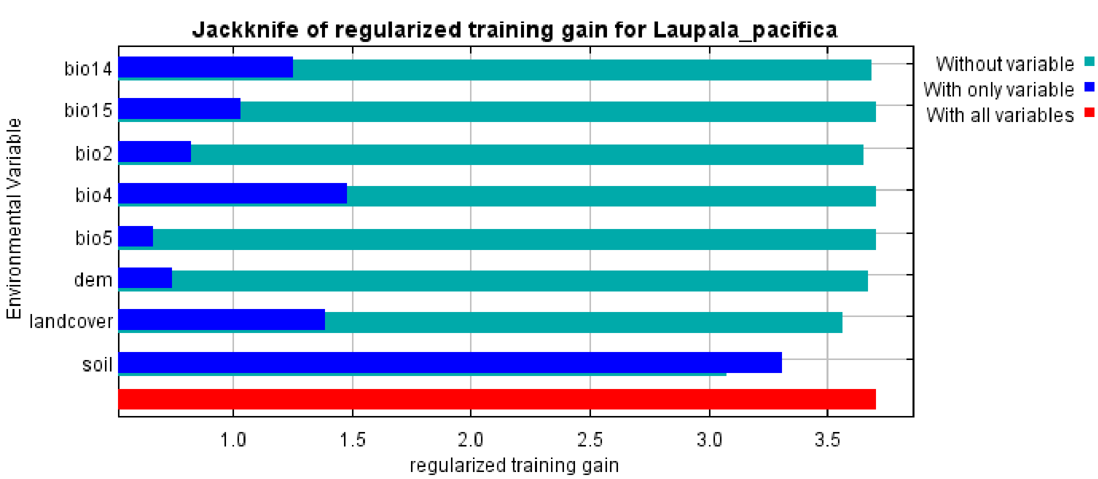
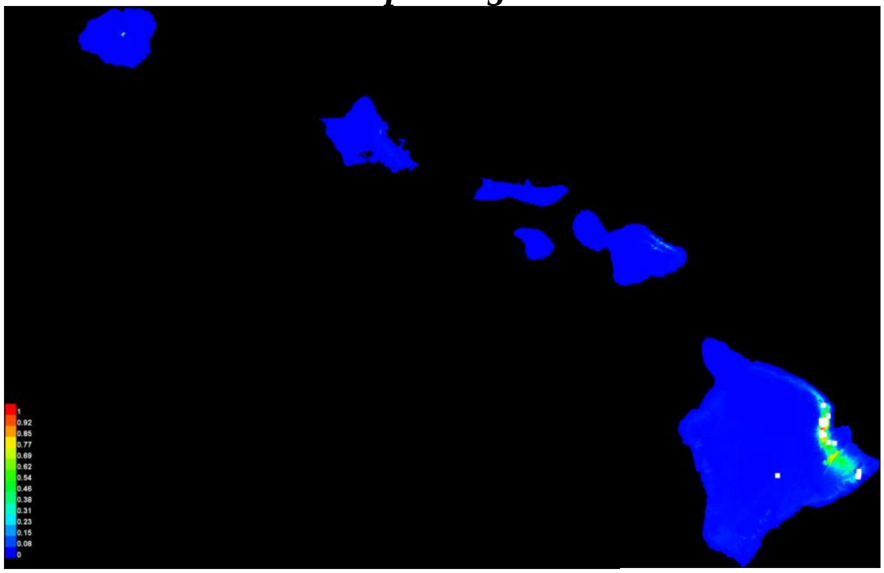
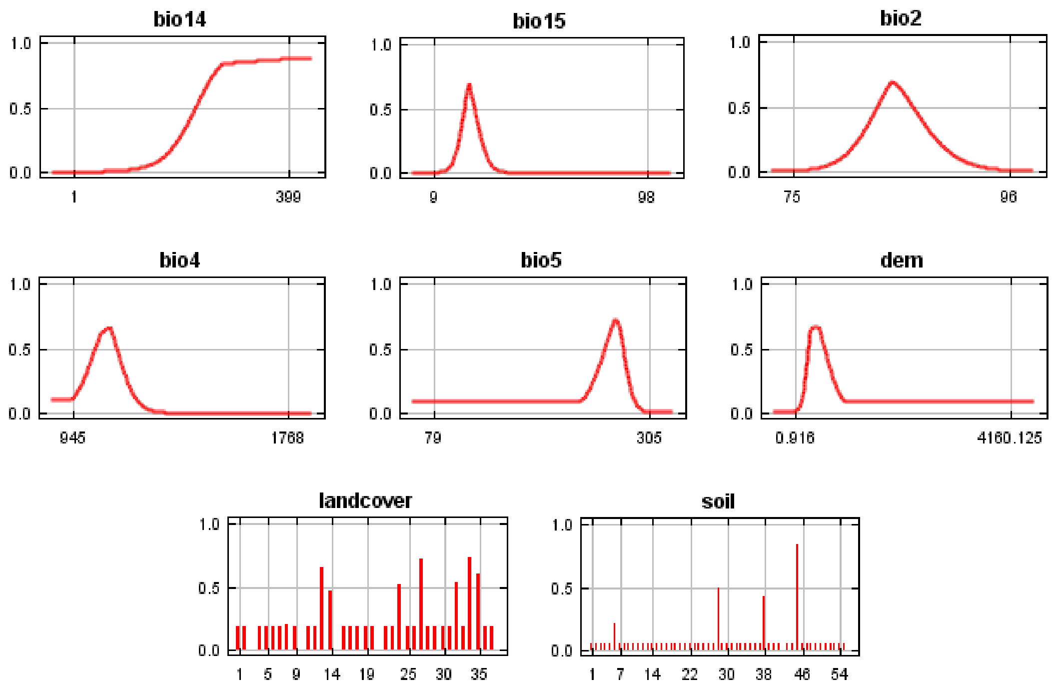
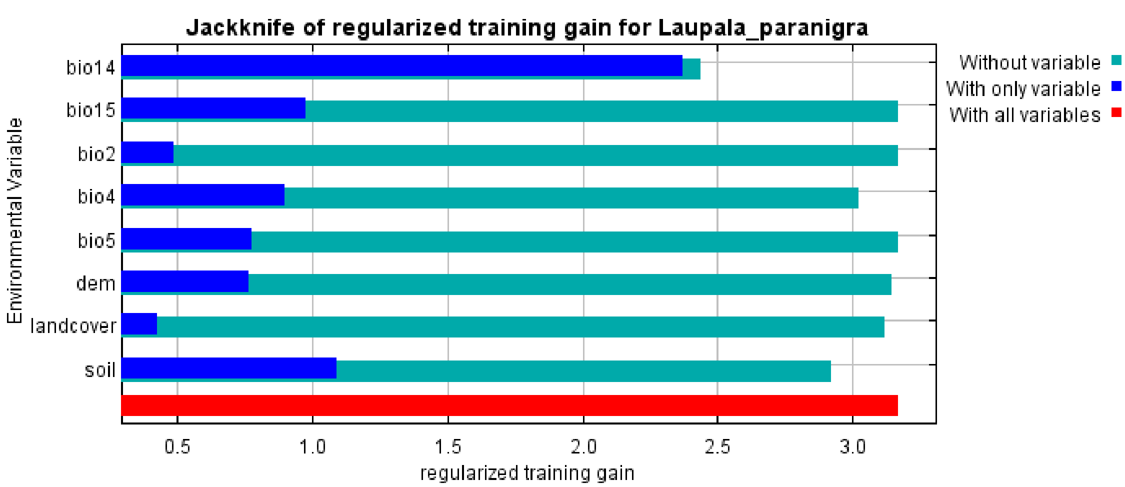
305
dem
0.916
4160.125
landcover
1 5 9 14 19 25 30 35
soil
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Laupala_pacifica
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
1.0 1.5 2.0 2.5 3.0 3.5
regularized training gain
Without variable
With only variable
With all variables

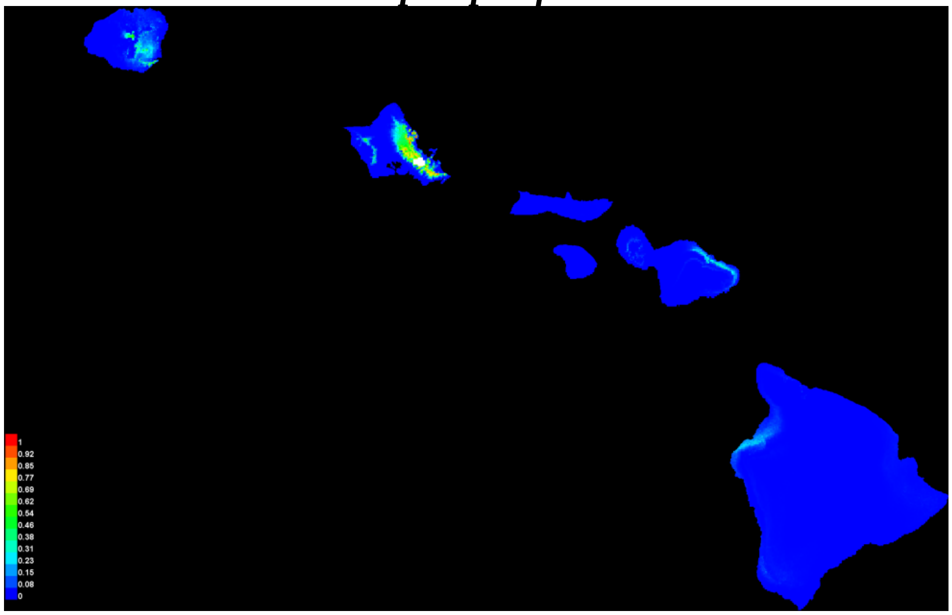
L. paranigra

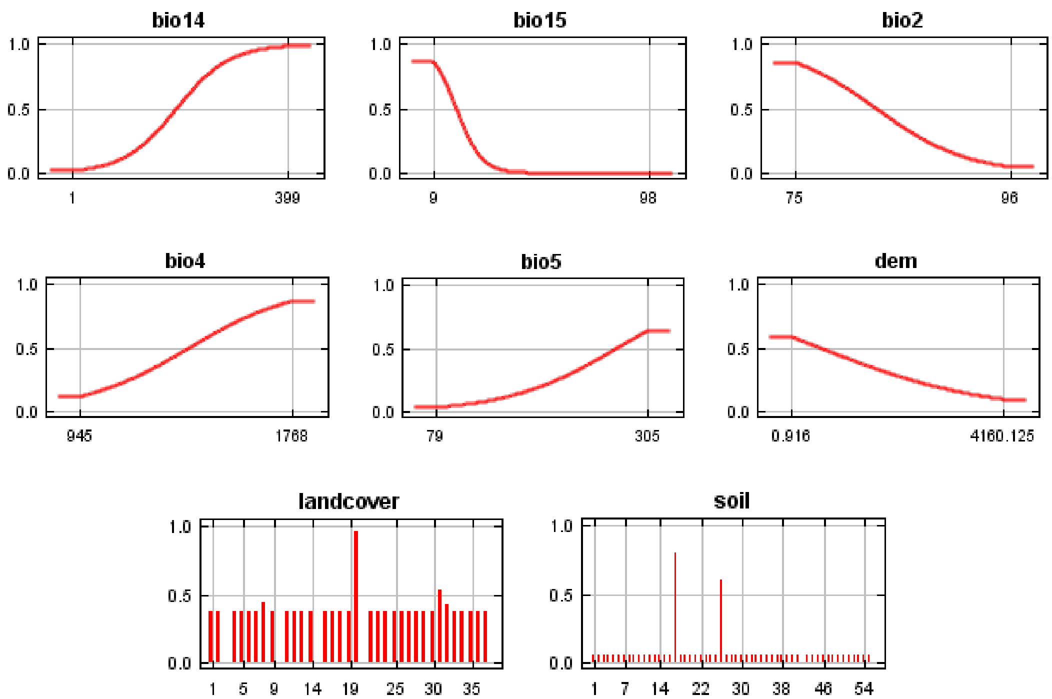


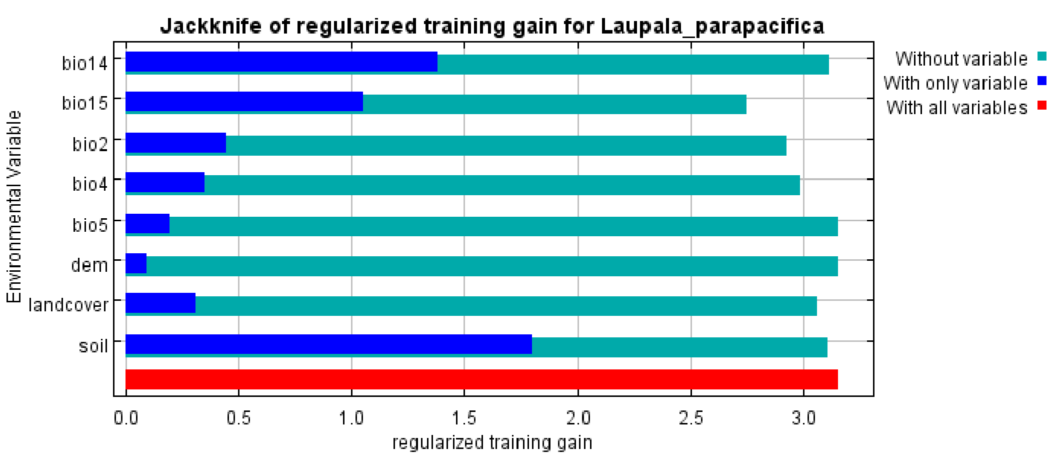

bio14
bio15
bio2
bio4
bio5
dem
landcover
soil


Jackknife of regularized training gain for Laupala_paranigra
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
Without variable
With only variable
With all variables
regularized training gain

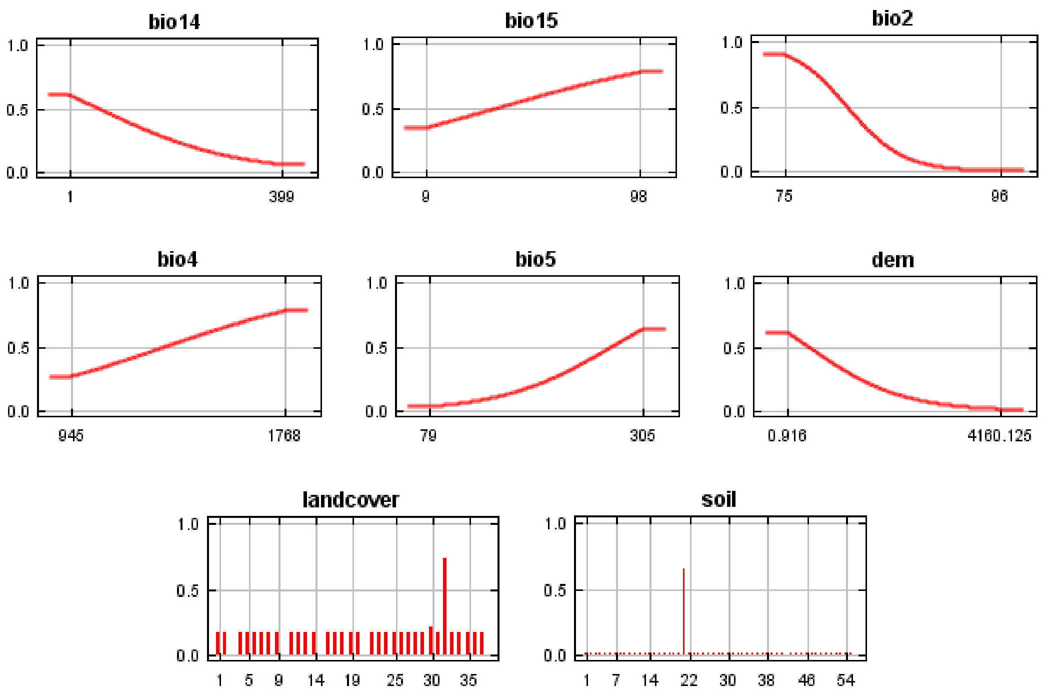
L. parapacifica

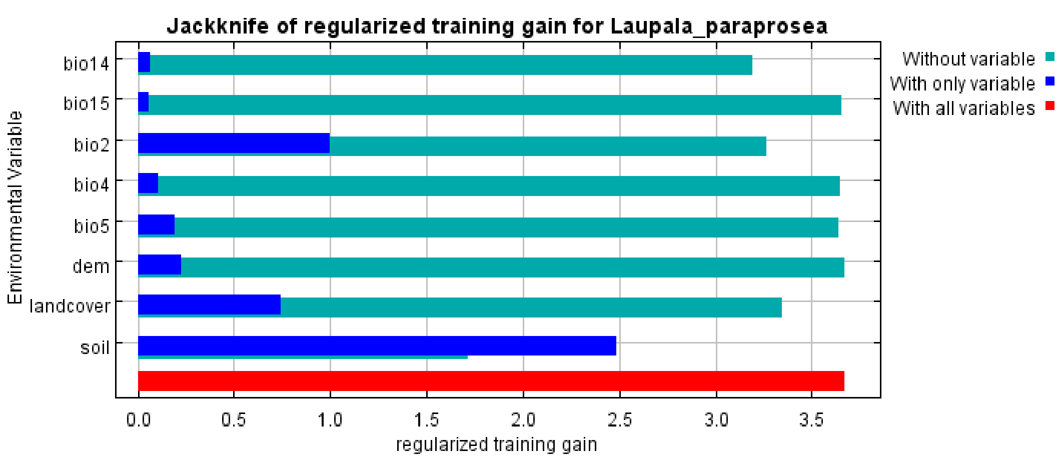




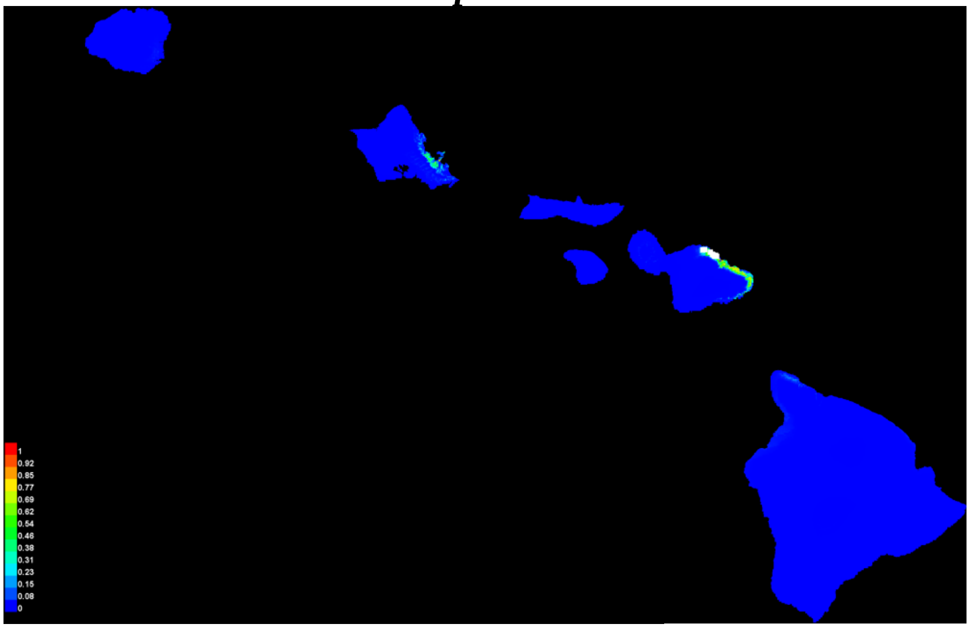


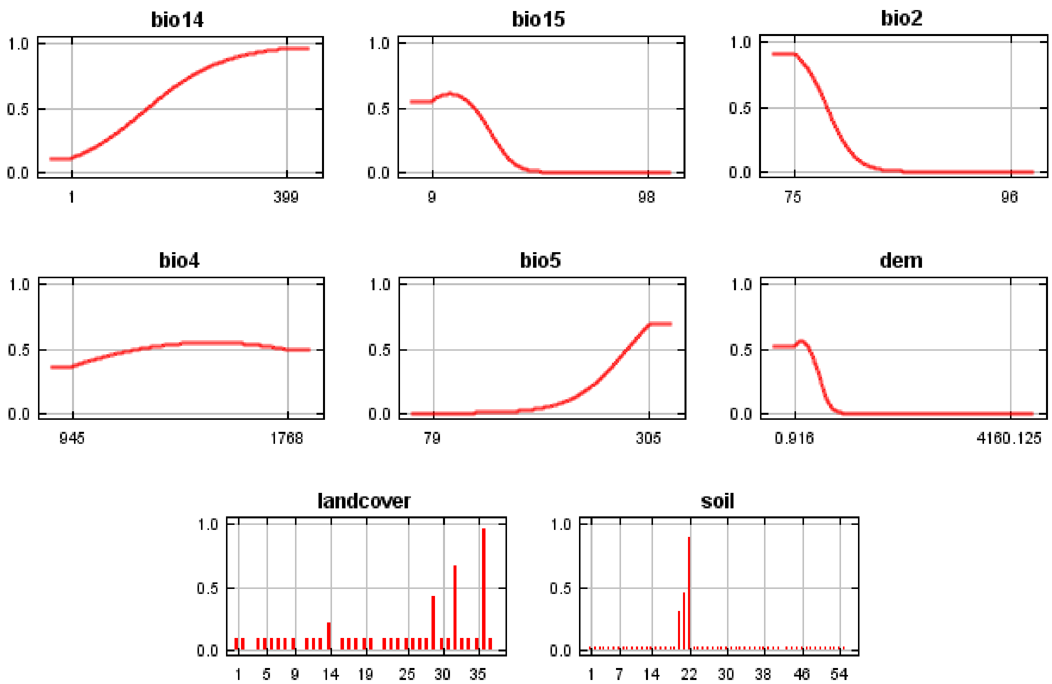
L. paraprosea





L. prosea


1
0.92
0.85
0.77
0.69
0.62
0.54
0.46
0.38
0.31
0.23
0.15
0.08
0


bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
1.0
0.5
0.0
1
399
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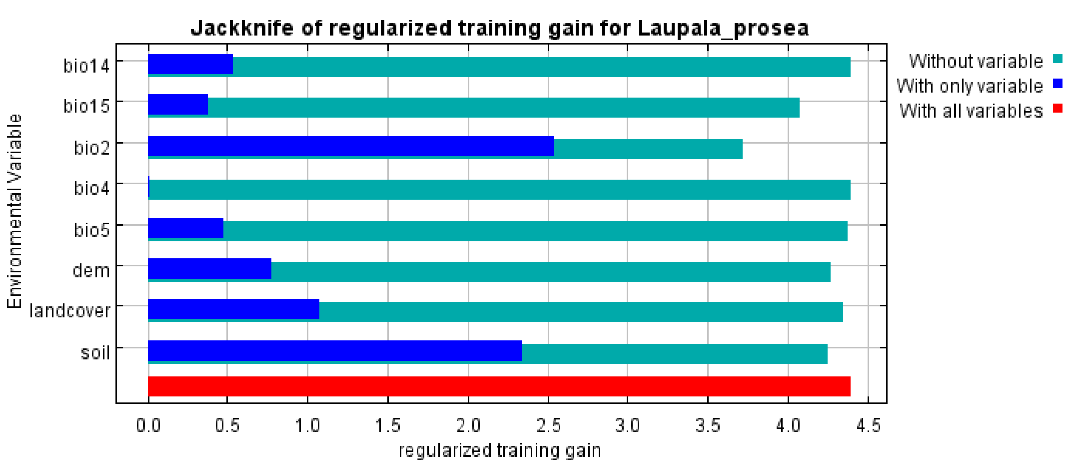
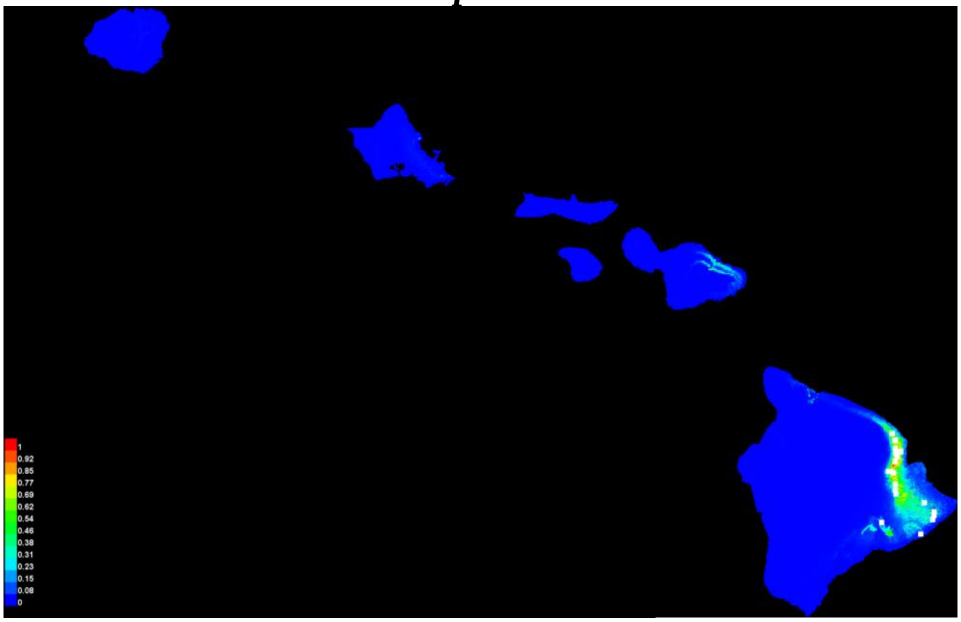
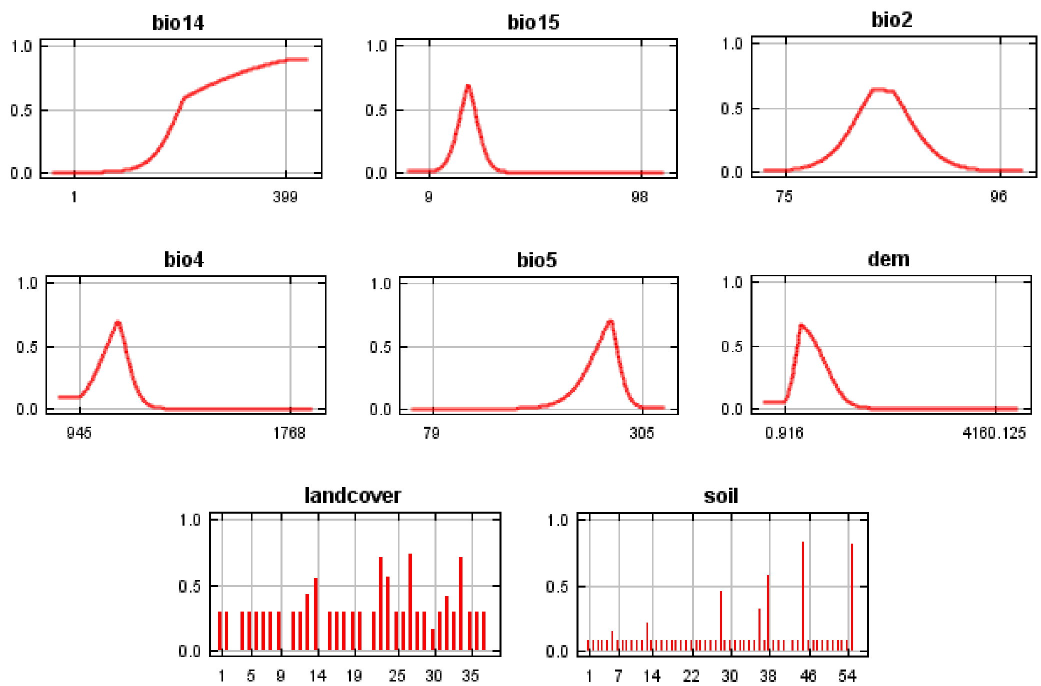
98
75
96
945
1768
79
305
0.916
4160.125
1 5 9 14 19 25 30 35
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Laupala_prosea
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
Without variable
With only variable
With all variables
0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0 4.5
regularized training gain

L. pruna

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0.0
1
399
bio15
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bio2
75
96
bio4
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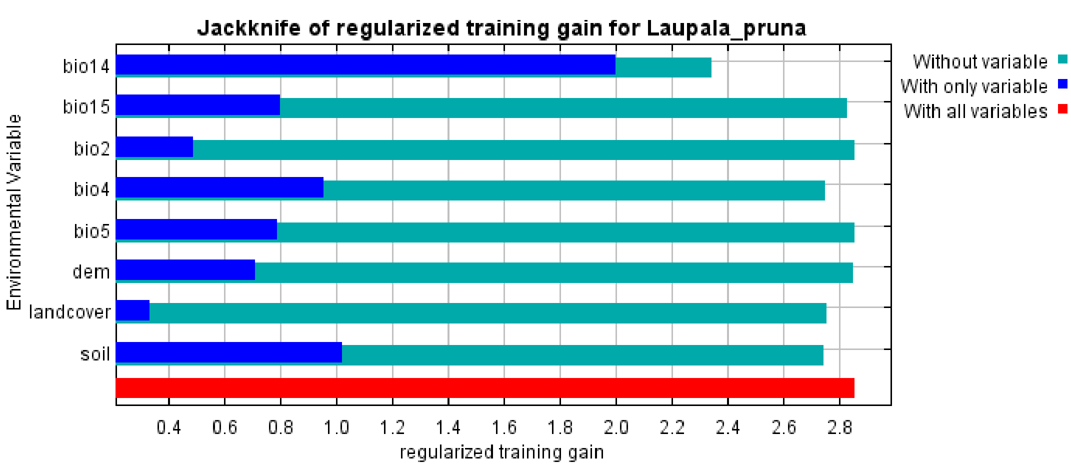
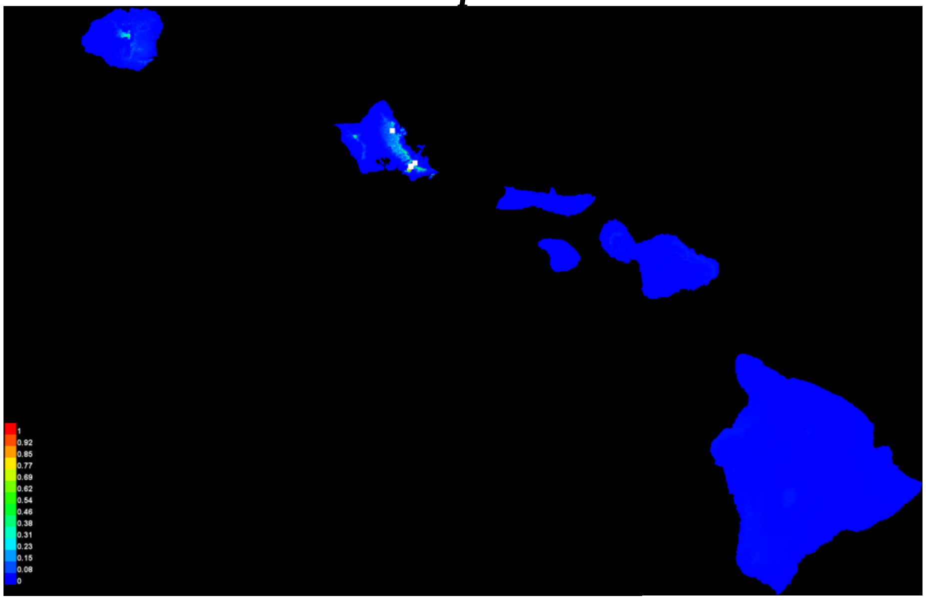
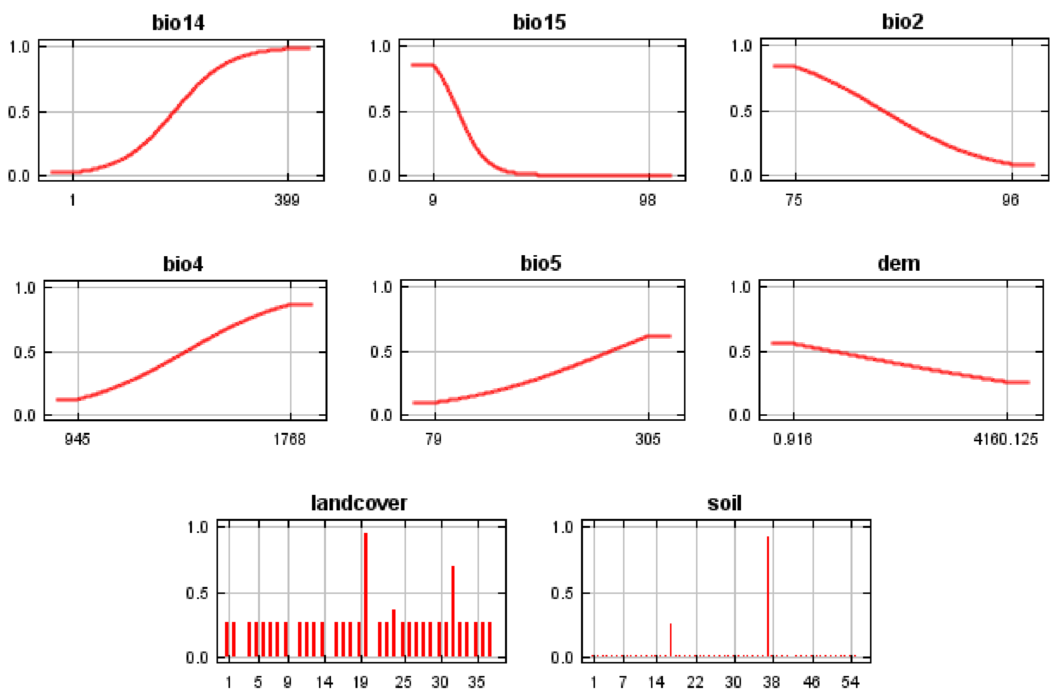
1768
bio5
79
305
dem
0.916
4160.125
landcover
1 5 9 14 19 25 30 35
soil
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Laupala_pruna
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
0.4 0.6 0.8 1.0 1.2 1.4 1.6 1.8 2.0 2.2 2.4 2.6 2.8
regularized training gain
Without variable
With only variable
With all variables

L. spisa




bio14
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0.0
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399
bio15
9
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bio2
75
96
bio4
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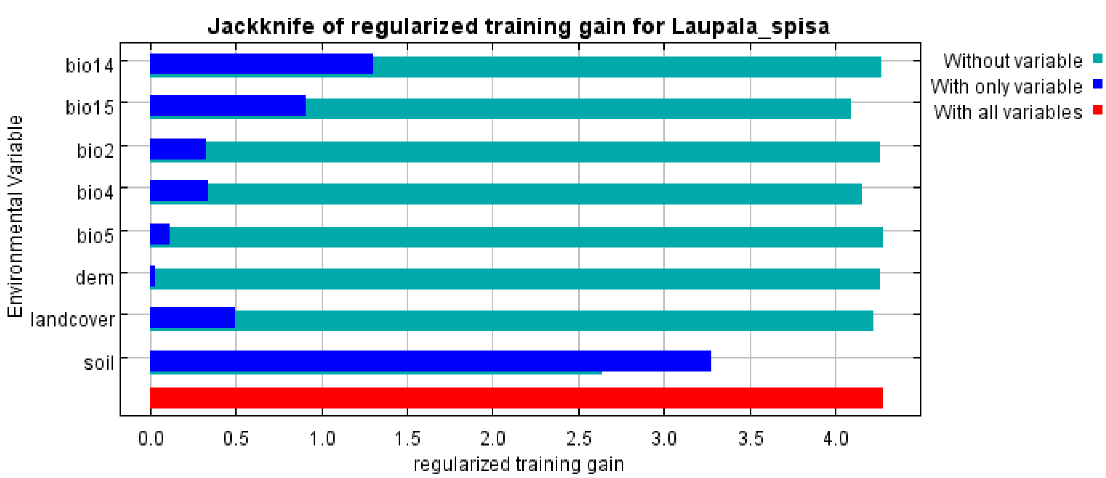
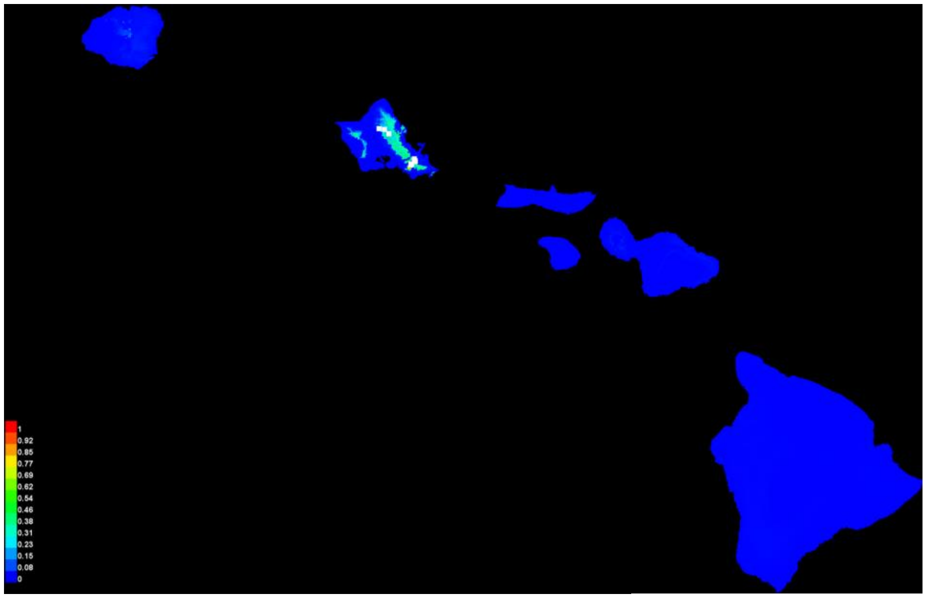
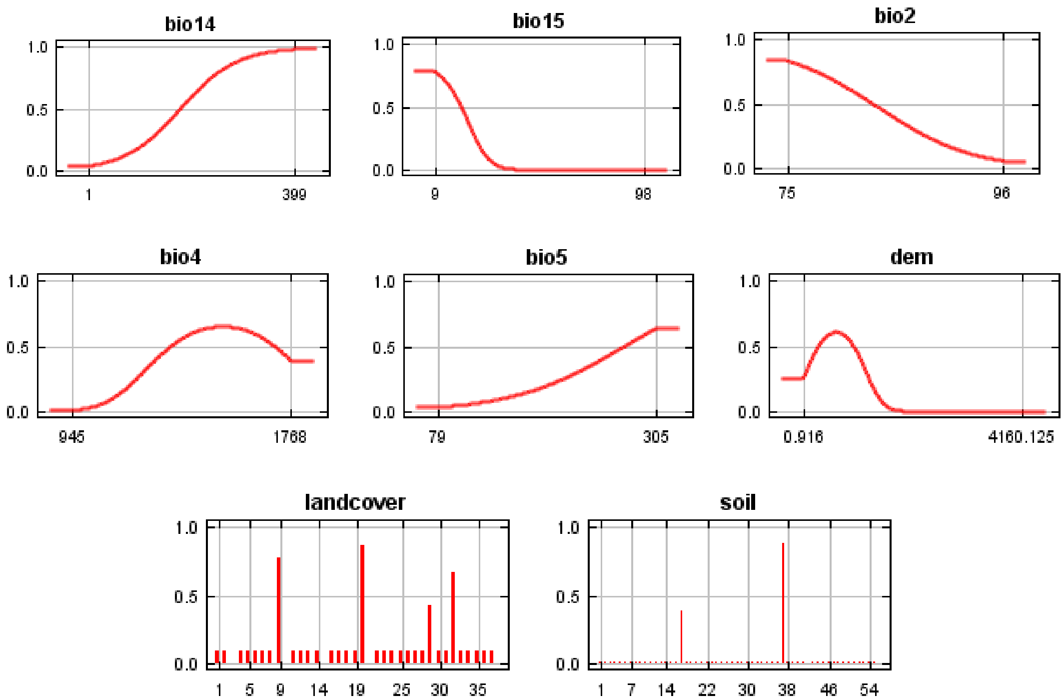
bio5
79
305
dem
0.916
4160.125
landcover
1 5 9 14 19 25 30 35
soil
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Laupala_spisa
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
Without variable
With only variable
With all variables
0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0
regularized training gain

L. tantalis

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bio15
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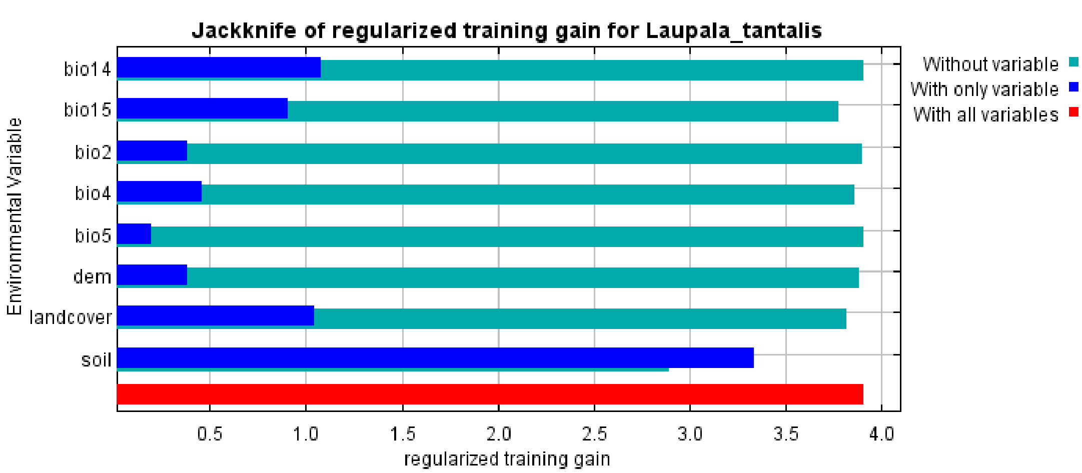
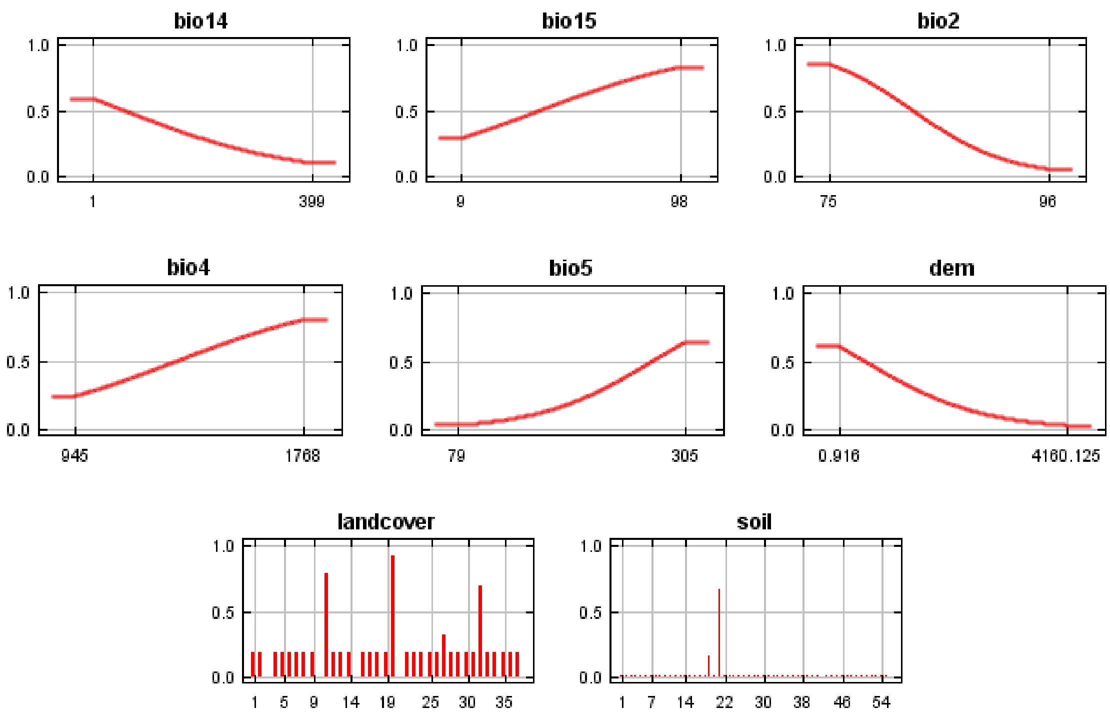
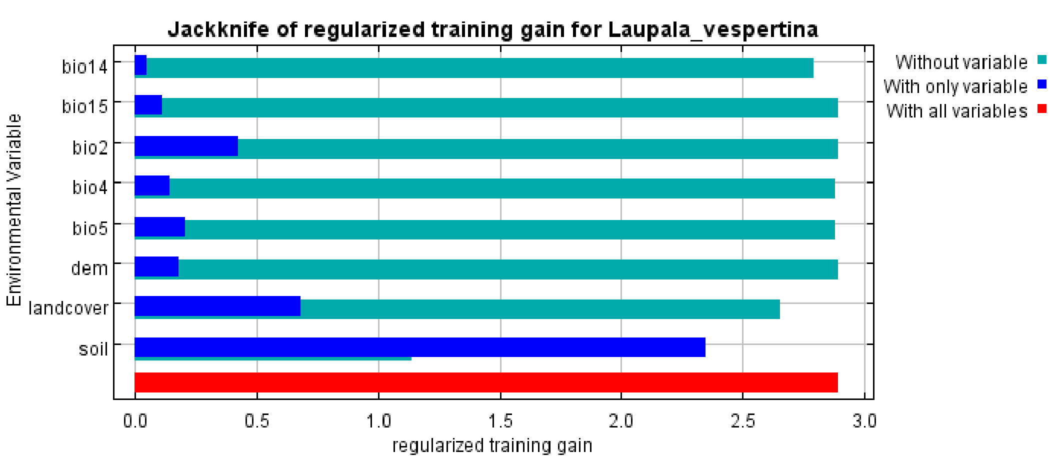
9
98
bio2
1.0
0.5
0.0
75
96
bio4
1.0
0.5
0.0
945
1768
bio5
1.0
0.5
0.0
79
305
dem
1.0
0.5
0.0
0.916
4160.125
landcover
1.0
0.5
0.0
1 5 9 14 19 25 30 35
soil
1.0
0.5
0.0
1 7 14 22 30 38 46 54

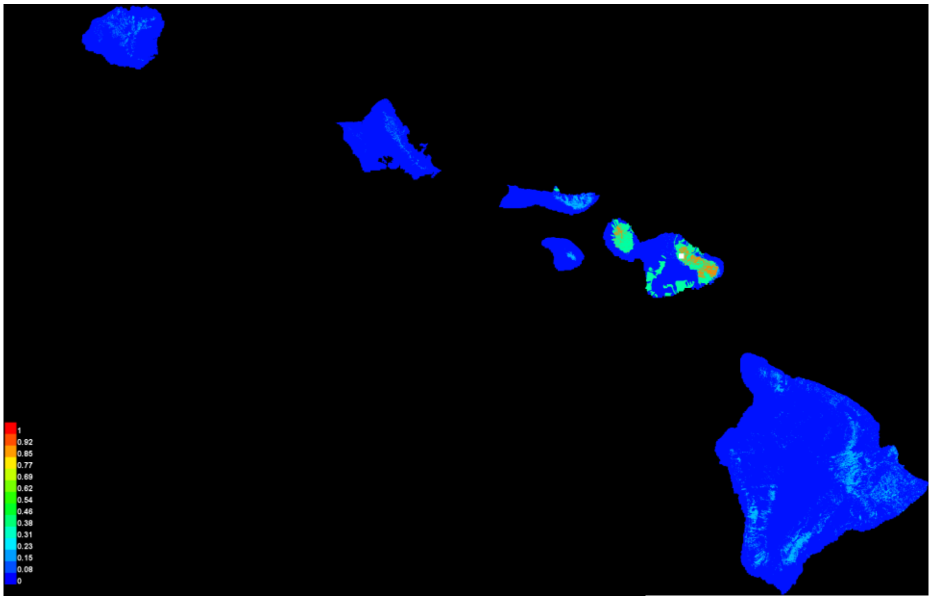

Jackknife of regularized training gain for Laupala_tantalis
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
Without variable
With only variable
With all variables
0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0
regularized training gain

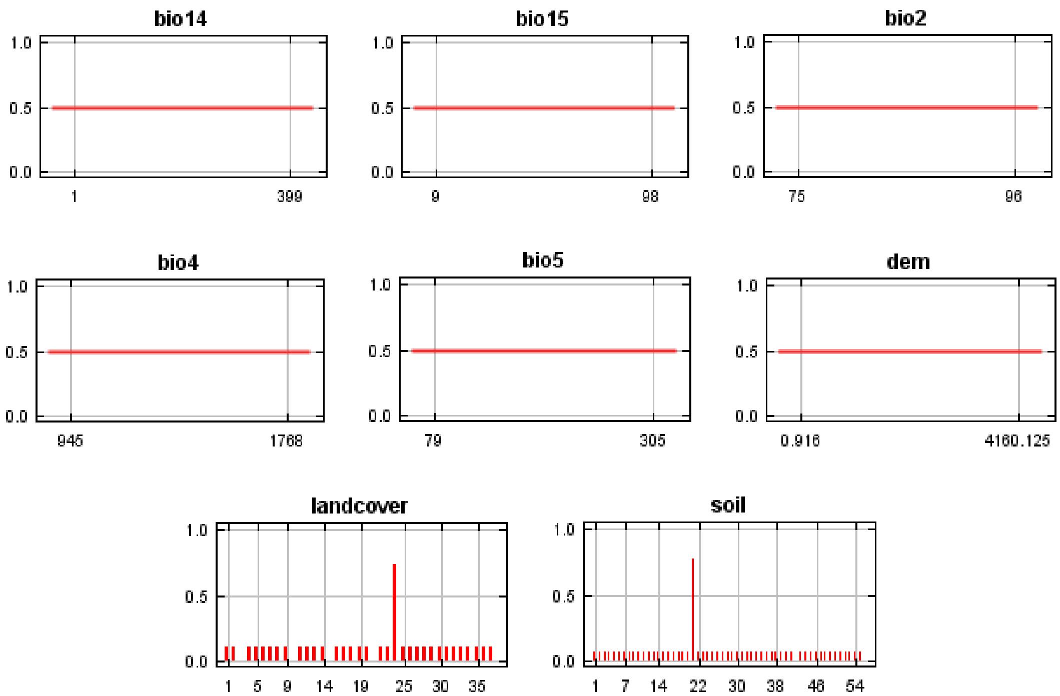
L. vespertina





L. waikemoi




bio14
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0.5
0.0
1
399
bio15
9
98
bio2
75
96
bio4
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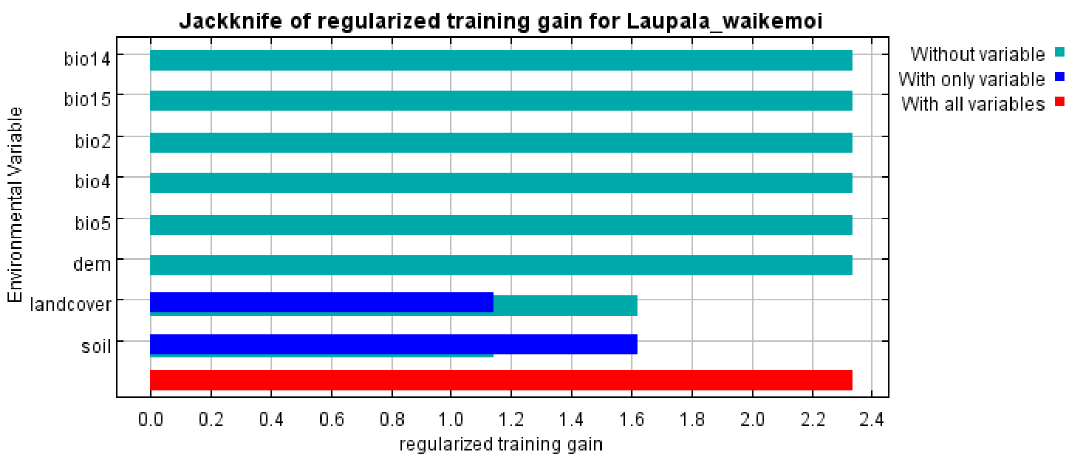
1768
bio5
79
305
dem
0.916
4160.125
landcover
1 5 9 14 19 25 30 35
soil
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Laupala_waikemoi
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
Without variable
With only variable
With all variables
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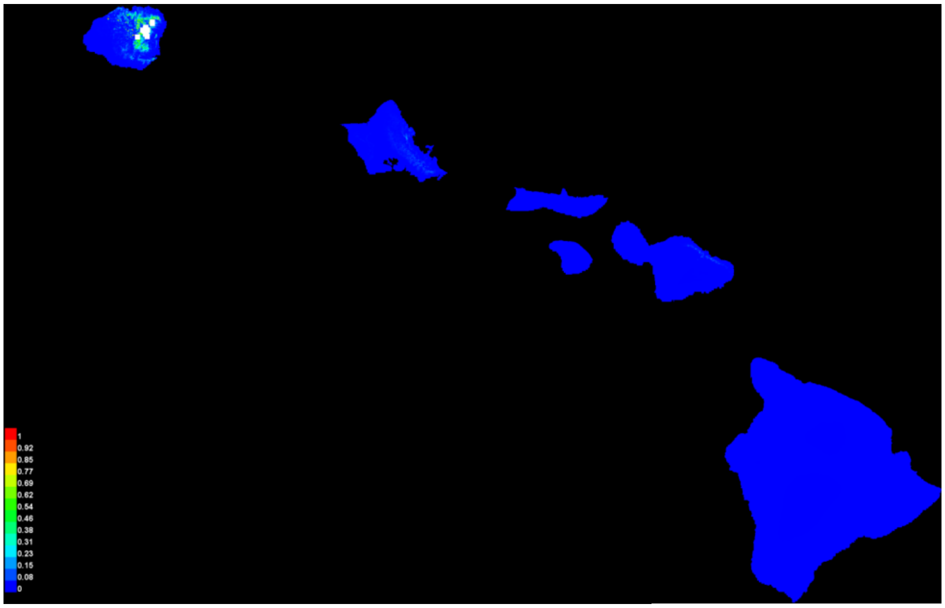
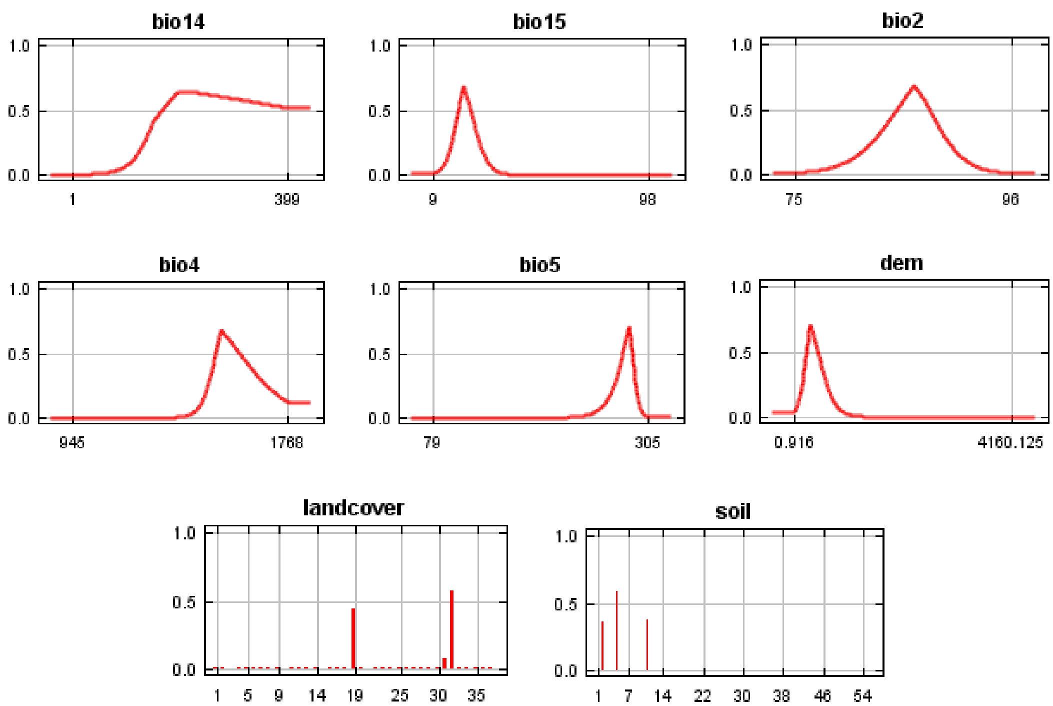
regularized training gain

L. wailua

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1
399
bio15
9
98
bio2
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96
bio4
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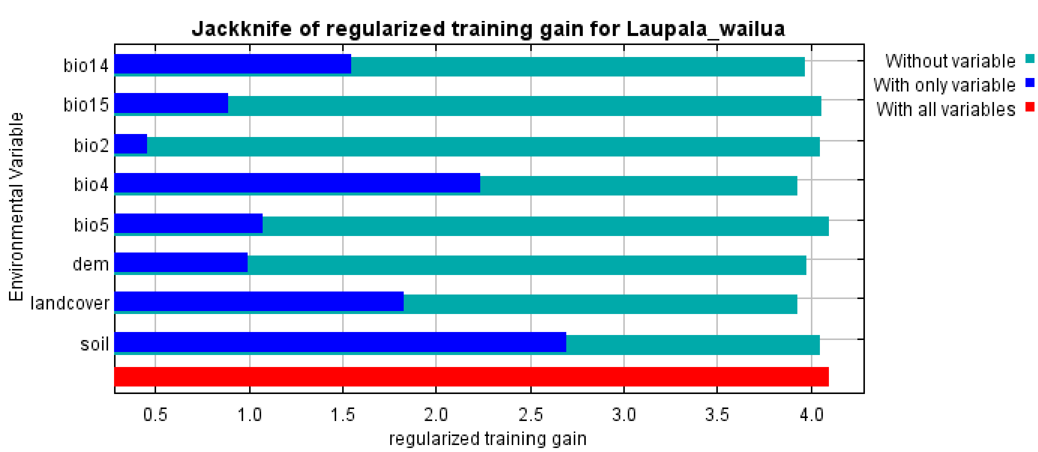
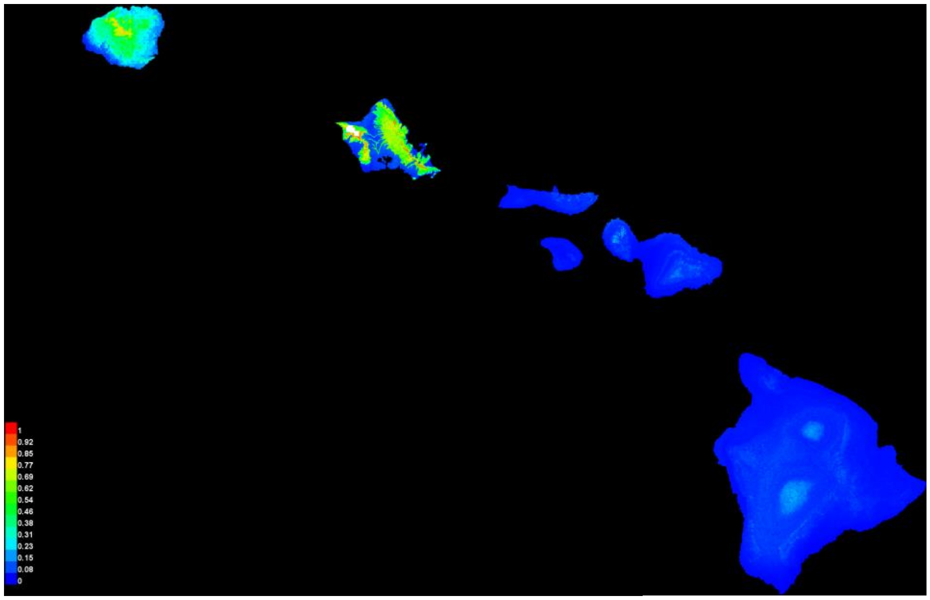
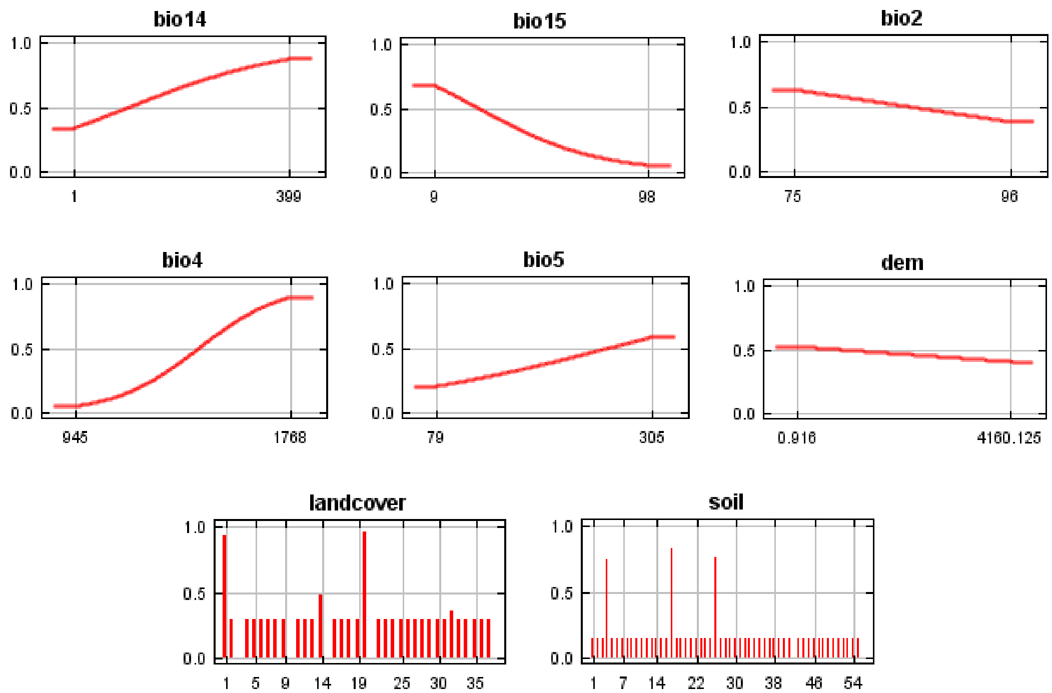
bio5
79
305
dem
0.916
4160.125
landcover
1 5 9 14 19 25 30 35
soil
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Laupala_wailua
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
Without variable
With only variable
With all variables
0.5 1.0 1.5 2.0 2.5 3.0 3.5 4.0
regularized training gain

P. kaalensis

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0.0
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399
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98
bio2
1.0
0.5
0.0
75
96
bio4
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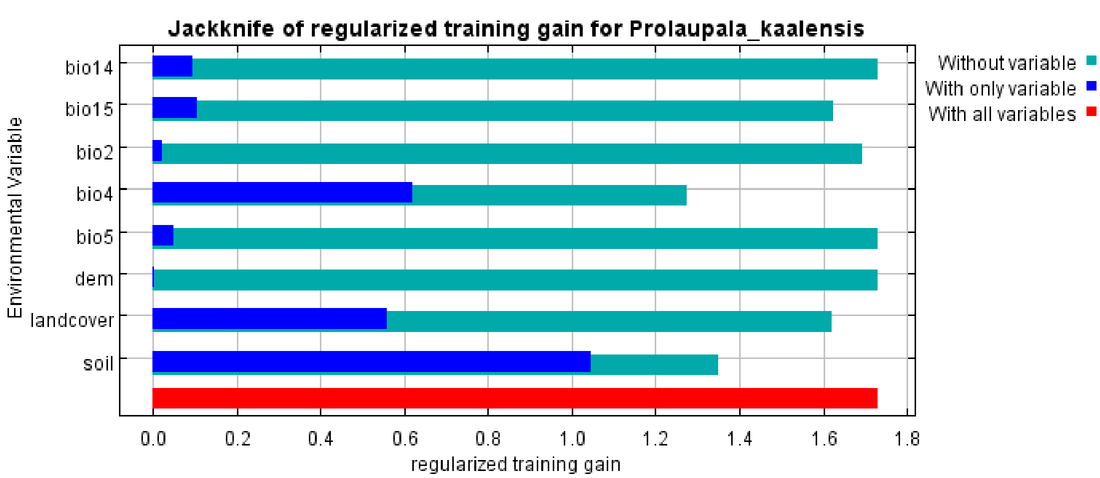
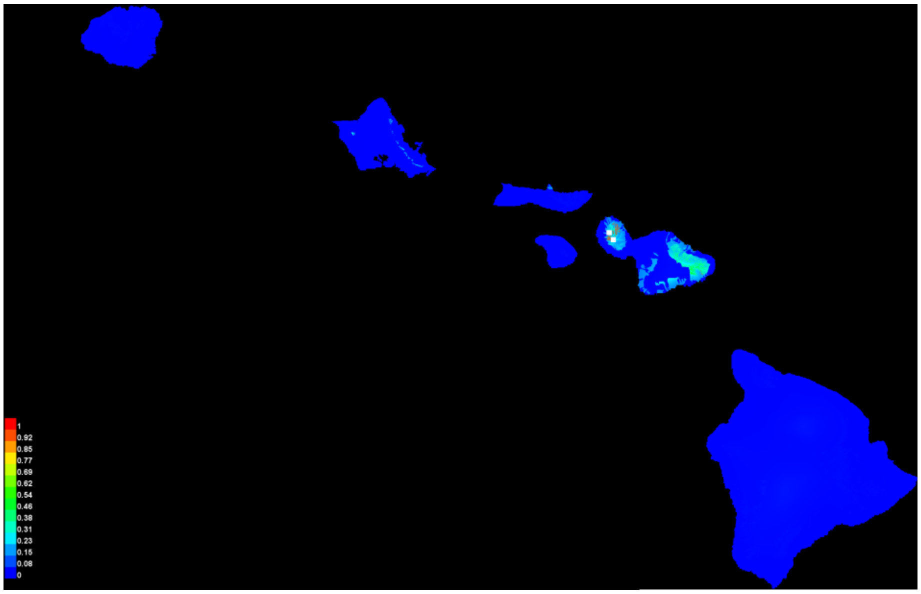
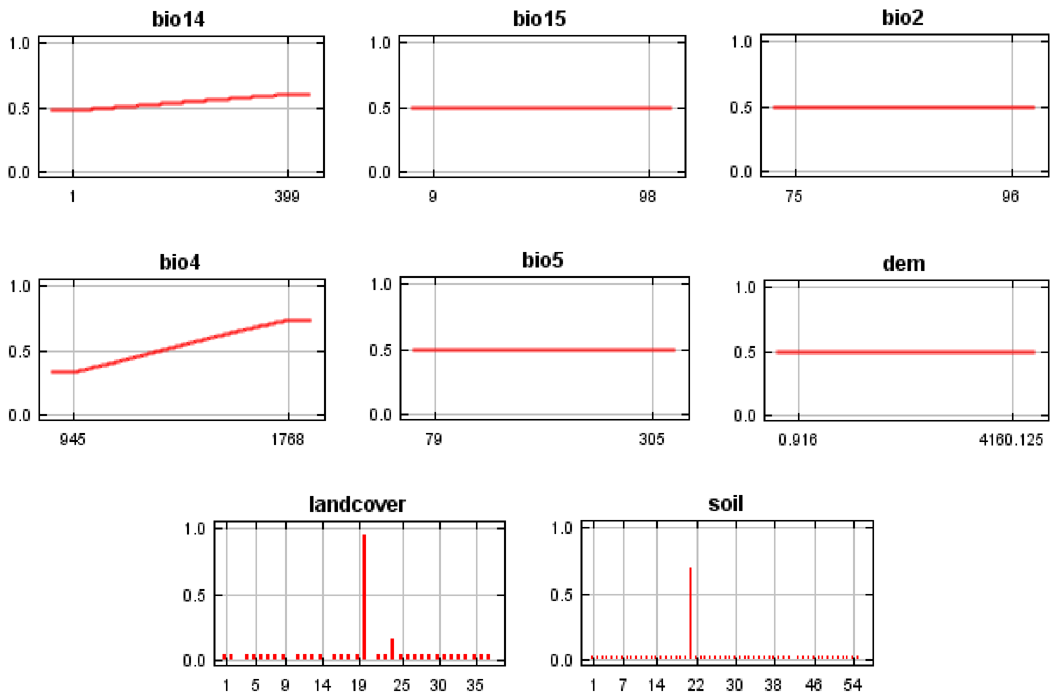
0.5
0.0
945
1768
bio5
1.0
0.5
0.0
79
305
dem
1.0
0.5
0.0
0.916
4160.125
landcover
1.0
0.5
0.0
1 5 9 14 19 25 30 35
soil
1.0
0.5
0.0
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Prolaupala_kaalensis
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
Without variable
With only variable
With all variables
0.0 0.2 0.4 0.6 0.8 1.0 1.2 1.4 1.6 1.8
regularized training gain

P. kukui




bio14
1.0
0.5
0.0
1
399
bio15
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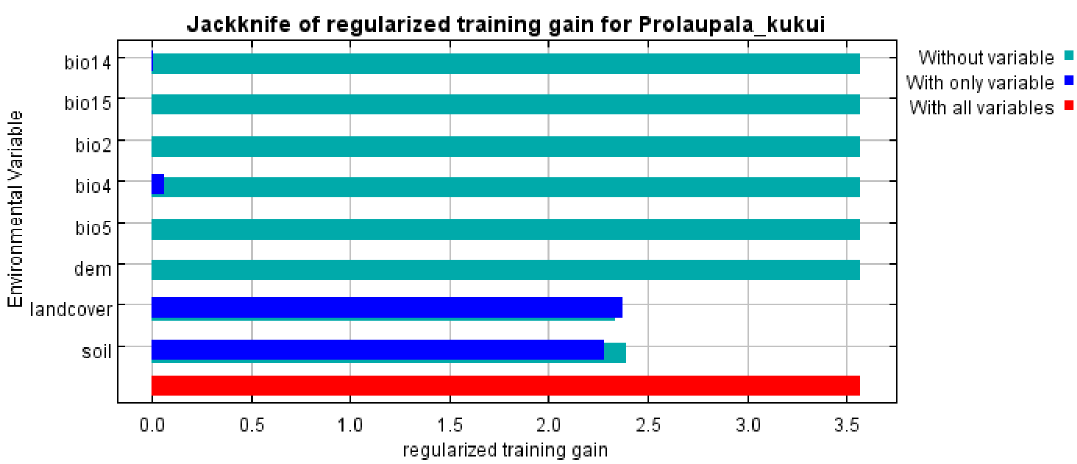
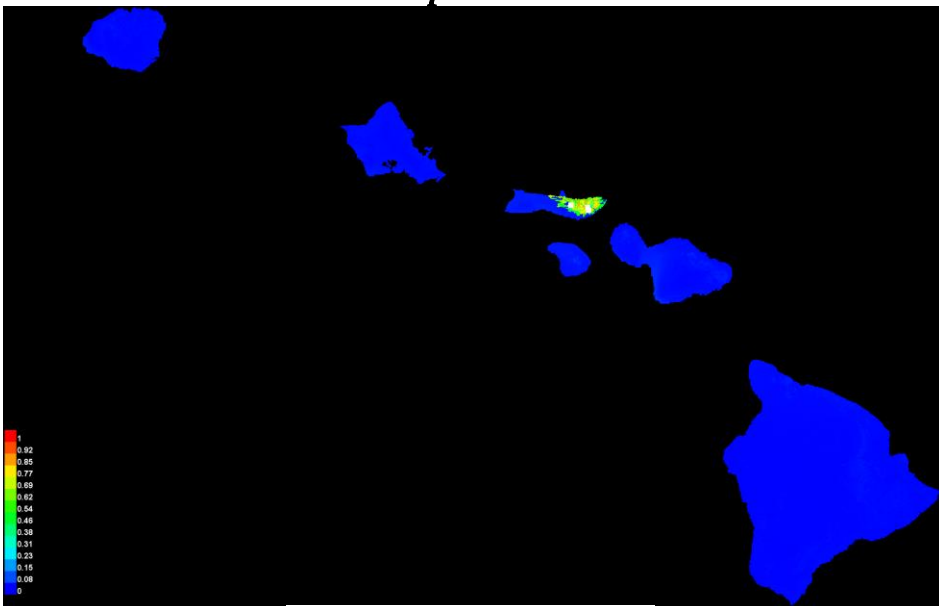
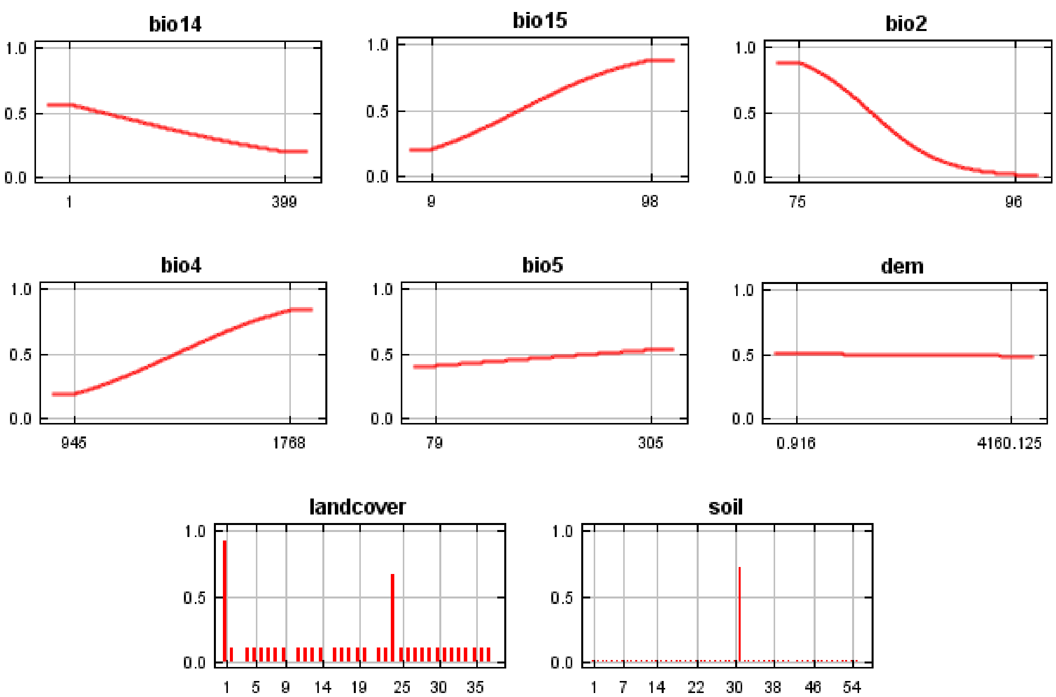
bio2
75
96
bio4
945
1768
bio5
79
305
dem
0.916
4160.125
landcover
1 5 9 14 19 25 30 35
soil
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Prolaupala_kukui
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
0.0 0.5 1.0 1.5 2.0 2.5 3.0 3.5
regularized training gain
Without variable
With only variable
With all variables

P. perkinsi




bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
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0.5
0.0
1
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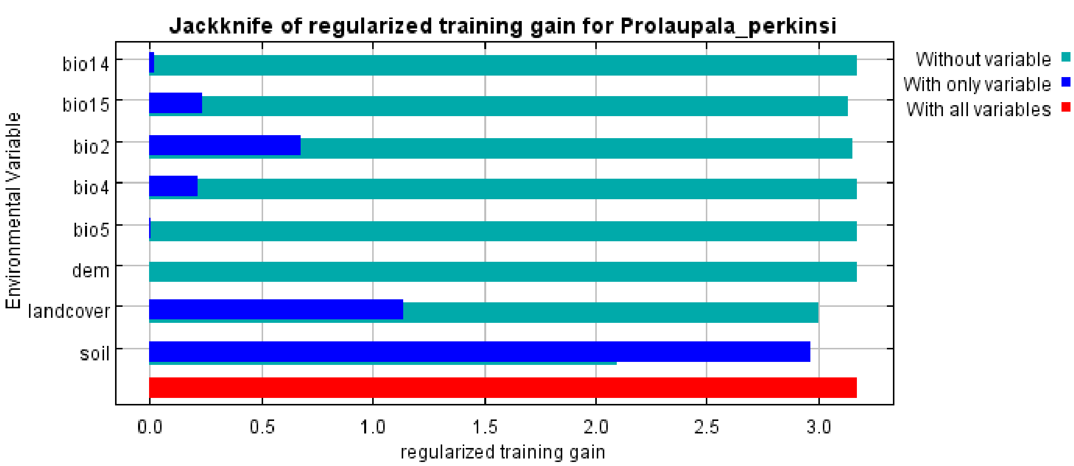
1768
79
305
0.916
4160.125
1 5 9 14 19 25 30 35
1 7 14 22 30 38 46 54


Jackknife of regularized training gain for Prolaupala_perkinsi
Environmental Variable
bio14
bio15
bio2
bio4
bio5
dem
landcover
soil
Without variable
With only variable
With all variables
0.0 0.5 1.0 1.5 2.0 2.5 3.0
regularized training gain