

INVASION ECOLOGY OF THE PLAGUE SKINK (*LAMPROPHOLIS
DELICATA*) IN HAWAII

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Chapter 1

The Plague Skink (*Lampropholis delicata*) in Hawaii

1.1 Invasion Biology

The spread of invasive species is a global problem that has extensive biological (Clavero Pineda and Garca-Berthou, 2005; Mack et al., 2000) and economic costs (Pimentel, 2011; Olson et al., 2006). Of approximately 948 listed endangered species in the United States, as of 2005, 45% were considered at risk of extinction primarily due to interactions with invasive species (Pimentel et al., 2005). Globally, 28% of ICUN threatened species are listed as at risk due to invasive species (Bellard et al., 2016*b*) and contributed to 58% of all IUCN listed extinctions (Bellard et al., 2016*a*). There is now a substantial body of research aimed at elucidating impacts and predicting invasions across diverse areas of the globe which is focused on assessing the risk and damage to native ecosystems and on stemming the spread of and environmental problems caused by new invasive taxa.

Ecologists often use the term invasive to describe the ability of a species to spread rapidly in a novel habitat (Richardson et al., 2000) while others, such as policy makers, use the term to denote having an economic or biological impact (Occhipinti-Ambrogi and Galil, 2004). However, no correlation has been shown between the ability to spread and ecological impacts in an introduced range (Ricciardi and Cohen, 2007). Yet it is clear that species with negative impacts that readily undergo range expansion are of great concern for ecosystem integrity.

Island ecosystems are especially vulnerable to impacts of invasive species (Blackburn et al., 2004). Fewer competitors and favorable climates interacting with high levels of endemism

and constricted land mass can result in higher risk of extinction of native fauna due to introduction of non-native species. Hawaii is the most geographically isolated land mass in the world. Consequently, natural colonization events are historically rare and many of those lineages that did manage to arrive and become established in the Hawaiian Islands underwent rapid adaptive and facultative radiations, such as birds (Freed et al., 1987; Pratt et al., 2009), flowering plants (Helenurm and Ganders, 1985; Witter and Carr, 1988; Givnish et al., 2009), land snails (Holland and Cowie, 2009), *Drosophila* (Kambysellis et al., 1995), damselflies (Jordan et al., 2003), spiders (Gillespie, 2004), and other arthropods (Eldredge and Miller, 1995; Roderick and Gillespie, 1998; Rubinoff and Schmitz, 2010; Medeiros and Gillespie, 2011). Isolation can also result in absences in the faunal assemblages; ants, termites, amphibians, land reptiles, and mammals (with exception of a bat) did not colonize the Hawaiian islands naturally (Tomich, 1986; Ziegler, 2002). However, these groups contain taxa included among the most invasive species worldwide. The devastating losses attributed to invasive predators (e.g. ants and mammals) have been scientifically characterized in Hawaii, due to their rapid and direct impacts on endemic taxa.

Although research efforts have focused on determining and curbing impacts of introduced species in Hawaii, some taxonomic groups have been overlooked. At least 43 introductions of herpetofauna have been recorded in Hawaii with 27 currently established (Oliver and Shaw, 1953; Hunsaker and Breese, 1967; McKeown, 1996; Van Kleeck, 2016), all of which are considered injurious by the Department of Forestry and Wildlife (HAR §13–124, 2014). However, only recently have any environmental impacts been addressed, and for only three species: the coqui and greenhouse frogs, *Eleutherodactylus coqui*, *Eleutherodactylus planirostris* (Kraus et al., 1999; Beard and Pitt, 2006; Beard, 2007) and the Jackson’s chameleon *Trioceros jacksonii xantholophus* (Holland et al., 2010; Kraus and Preston, 2012; Chiaverano and Holland, 2014; Van Kleeck et al., 2015). These are more conspicuous species in the sense that although coqui frogs are relatively small and cryptic, they are social and produce loud calls, attain high population densities, and therefore are considered a nuisance, while Jacksons chameleons are larger, charismatic, popular in the pet trade, and diurnal. However, little if any scientific attention has been focused on the other two dozen widespread predatory invasive reptile and amphibian species in Hawaii.

Reptiles are particularly effective invasive species due to characteristics such as high reproductive rates and rapid population growth. Often reptiles are generalist predators able to utilize locally abundant resources with small body size, cryptic morphologies leading to a lack of detection and accidental transport (Pitt et al., 2005). The two most common avenues of reptile introductions into nonnative areas are through the pet trade and cargo shipments with lizards being most commonly introduced and successfully established group (Kraus, 2003).

Pitt et al. (2005) suggest that the best way manage invasive reptiles and prevent their spread is through research, especially when basic biology and ecology of the species are unknown.

The notion that fundamental ecological data are required for formulation of effective management and control strategy, and yet are often lacking, is echoed throughout the invasive species literature (Simberloff et al., 2005). In this study, my objective was to provide critical, relevant ecological data for the plague skink, *Lampropholis delicata*, an uncharacterized, cryptic, predatory invasive lizard that is widespread in Hawaii at both broad and local geographic scales by modeling the ecological niche and by examining exploited prey in the diet, selectivity, and biological impacts, respectively.

1.2 Genetics and Introduction History

The plague skink (*L. delicata*), also known as the delicate skink, metallic skink, and rainbow skink, is a medium sized lizard in the family Scincidae, native to the Eastern part of Australia and Tasmania. This species has been introduced to three island systems across the Pacific: Lord Howe Island, New Zealand, and Hawaii (Baker, 1976; Peace, 2004; Chapple et al., 2013a). The plague skink is considered one of the most successful reptilian invaders across the Pacific (Lever, 2003), having large population sizes in and adverse impacts across Lord Howe Island and New Zealand (Peace, 2004; Hutchinson et al., 2005).

Lampropholis delicata was accidentally introduced in Hawaii through cargo transport around 1900 (Baker, 1976, 1979; Chapple et al., 2013a). This species was originally misidentified as the moth skink (*Lygosoma noctua*), and later erroneously recorded as the metallic skink (*Lygosoma metallicum*) (Hunsaker and Breese, 1967). The latter species has never been documented in the Hawaiian Islands and all museum specimens attributed to this species examined were *L. delicata* (Baker, 1979).

Greer (1974) identified museum specimens from Hawaii as belonging to the Southeastern Queensland clade of the species-complex. Subsequent molecular evidence supports the Southeastern Queensland origin (Mather, 1989; Chapple et al., 2013a). Only a single haplotype is known to occur in Hawaii originating from a single source population in the Northern suburbs of Brisbane, Australia (Chapple et al., 2013a), suggesting that a single introduction occurred first on Oahu and secondarily spread to all the main Hawaiian islands by 1978 (Baker, 1979).

The entire species-complex was first described by Greer (1974) and more recently further characterized by a molecular study across the entire range of *L. delicata* (Chapple et al., 2011). This study showed nine different clades that span the eastern coast of Australia, separated by extensive areas of unsuitable, dry habitat (Chapple et al., 2011) restricting dispersal and gene flow. This type of species-complex is common among lizards (e.g. Vanzolini and Williams, 1970; Morando et al., 2007; Leach et al., 2009) and other reptiles (e.g. Wüster et al., 1996; Rodriguez-Robles and De Jess-Escobar, 2000; Starkey et al., 2003).

Following introduction into the Hawaiian islands, *L. delicata* quickly displaced the moth skink on Oahu (Hunsaker and Breese, 1967). By 1979, *L. delicata* could be found from 0-1,760 meters in elevation representing the high-altitude record for reptiles in the state (Baker, 1979). *Lampropholis delicata* was also implicated in the extirpation of another non-native skink in Hawaii, the Pacific lizard (*Emoia impar*).

1.3 Natural History

Some of the basic biology of *L. delicata* is known from its native range where it has been studied in part due to its large geographic range which spans 26 degrees of latitude from Northern Queensland to Southern Tasmania (Wilson and Swan, 2013). This skink is a ground dwelling species that utilizes leaf litter (Twigg and Fox, 1991; Howard et al., 2003) and occurs in many different habitat types such as forests, urban areas, scrub, and farmland (Gill and Whitaker, 2001). Although some reports suggest that they feed opportunistically on invertebrates (Wilson and Swan, 2013; Cogger, 2014; Lunney et al., 1989), no studies on the diet of *L. delicata* have been published to address this in any portion of its range (Chapple et al., 2015).

Lampropholis delicata has a relatively high fecundity and is oviparous (Cheetham et al., 2011). The age at first reproduction is unclear, but likely occurs within the first year during the subsequent breeding season, with males reaching sexual maturity at around 35 mm snout-vent length (SVL) and females at 39 mm SVL (Joss and Minard, 1985; Greer, 1989). In Hawaii, females can lay 2-7 eggs per clutch with clutch size increasing with body size (Baker, 1979) which is comparable to the 2-6 eggs per clutch reported in their native range (Joss and Minard, 1985). The breeding season ranges from September to February in its native Australian range (Joss and Minard, 1985; Clerke and Alford, 1993), while egg masses and gravid females have been collected in June and July in Hawaii suggesting the breeding season has shifted (and possibly inverted) or extended in the Northern Hemisphere (pers obs). Clerke and Alford (1993) indicate solar radiation as a mechanism for female reproductive activity timing supporting this possibility. Individual females reproduce once per breeding season in the southern portion of their native range (Joss and Minard, 1985), however up to three clutches per year were observed in a Sydney population (Ehmann and Strahan, 1992). This likely constitutes a latitudinal gradient with increasing number of clutches moving closer to the equator (Shine, 1983; Peace, 2004) making it highly likely that there are multiple clutches per year in Hawaii.

Lampropholis delicata is a communal nester with multiple females laying eggs in a single location (Chapple et al., 2015; Cheetham et al., 2011). Females deposit eggs and then abandon

the nesting site with eggs taking about 31 days to hatch in warm temperatures (Forsman and Shine, 1995) but slowing to around 55 days in cold conditions without additional mortality (Downes and Shine, 1999). Communal nest sizes can reach over 70 eggs in their native range (Cheetham et al., 2011) suggesting a minimum of 10 different females using the same nest site, and over 200 in Lorde Howe Island (Chapple et al., 2015) with similarly sized nests found in Hawaii (>100 eggs). This indicates that *L. delicata* may reach higher densities across its introduced range.

1.4 Objectives

The goal of this thesis was to characterize some ecologically important aspects of the invasion biology of *L. delicata* in Hawaii. Despite predatory feeding ecology, invasive lizard species in Hawaii have been largely overlooked, and their impacts unknown, possibly influenced by their small size and cryptic nature. Additionally, many of the squamates introduced in Hawaii are incorrectly viewed by the public as being native (pers obs), further obscuring the impacts of these species. The first chapter of the thesis examined the background of this invasion. The overall focus of the following chapters was on the broad geographic ecology of *L. delicata* by constructing Ecological Niche Models (ENMs) for Hawaii and then narrowing in on the impacts at the habitat scale, including analysis of diet choice at multiple sites in Hawaii.

In the second chapter, broad scale ecological theory of climate matching for predicting invasion success was addressed. Since the invasion history of *L. delicata* is well characterized, the exact location of the source population for all of Hawaii is known, which allows for examination of climate matching hypotheses at multiple, hierarchical levels. The multiple spatial scales of modeling allow for the effect of realized niches of clades and entire species complexes for invasions to be analyzed when effectively controlling for genetic diversity. This study also explores the predictive ability of a native range on an invasive species distribution using these three different spatial scales. The results of the second chapter suggest that both the climate matching hypothesis and predictive ability for *L. delicata* in Hawaii are discounted and the implications of this for invasive niche models, as well as more broadly for invasion biology are discussed.

In the third chapter, we look at the local scale impacts of *L. delicata* in the introduced range of Hawaii. We first examine differences in diet and available prey across sites on the island of Oahu. This was then compared to the diet of the native range providing the first comprehensive comparative investigation of diet for *L. delicata*. Although *L. delicata* has been categorized as a generalist feeder, we examined this assumption by investigating the exploited prey taxa across native and non-native forest sites in Hawaii to determine impacts

on vulnerable groups. This large number of endemic fauna concentrated in certain orders can be of conservation concern if a generalist predator feeds on that particular group preferentially or even at its natural availability. In this chapter, we highlighted potential impacts that a cryptic, overlooked invasive species may be having on the micro-fauna in its introduced range.

Finally, I concluded with a discussion and summary of the contribution to our understanding of the invasion of Hawaii by *L. delicata* made by this study, highlighting potential future directions and priorities for research and management. The implications of the results presented for other studies of invasive herpetofauna are also discussed for the Hawaiian islands, the Pacific, and globally. The hope is that this study can lay the foundation for further comparative work for invasive herpetofauna and the present methods which can be applied for other biological invasions in Hawaii.

Chapter 2

Exploring the climate matching hypothesis using Ecological Niche Models for the invasive plague skink (*Lampropholis delicata*) in Hawaii

2.1 Introduction

Ecological niche models (ENMs) are a popular tool used for a variety of purposes in ecology and conservation such as mapping the geographic extent of species (Apps et al., 2004; Mieszkowska et al., 2013), determining potential suitable habitat for threatened and endangered species (Menon et al., 2010; Adhikari et al., 2012), and investigating the spread of invasive species (Peterson, 2003; Murray et al., 2015). Regardless of purpose, ENMs use the association of environmental variables and geographic space occupied by a species to map the potential suitable range of a species (Franklin et al., 2009; Peterson et al., 2011). The models can then be used to predict across geographic or temporal space to answer the ecological question of interest. This study attempts to characterize the ecological drivers of an invasive species in a novel geographic area and falls under the umbrella of invasive ecological niche models (iENMs).

ENM building follows a set process that can be broken down into four main phases: data collection, model construction, model evaluation, and model projection (Figure 2.1). In the data collection phase, the presence locations of a species are obtained through surveys or museum collections and environmental variables in geographic space are compiled. This includes an optional data processing step to reduce the number of environmental covariates for the model.

For this study, we obtained environment data from BioClim, a set of 19 environmental variables in GIS layers that are often used in ENMs. BioClim variables are highly correlated, with many of the variables being subsets or combinations of each other. Common practices to remove extra covariates for the model are evaluating likelihood estimates (AICc, etc.), conducting Principal Component Analysis (PCA), sequentially dropping highly correlated variables, selecting based on focal species biology, or determining importance or contribution to the model (Peterson et al., 2011). The literature is unclear on best practices for model reduction when projecting into novel areas or time periods and is often ignored in reviews of modeling approaches (Austin, 2007). However, PCA has the advantage of retaining large portions of the variation of climate variables in only a few principal components (Hijmans et al., 2005) with the only drawback being conclusions on individual variables contribution to the model being obscured (McCormack et al., 2010).

In the model construction phase, a modeling algorithm is applied to the data with appropriate parameters. In this study, we use the machine learning algorithm Maxent which models presence only data compared to a background in geographic space (pseudo-absences). This is a popular method for constructing ENMs, performing equally as well or better than other niche models (Phillips et al., 2006; Elith et al., 2006). Machine learning algorithms, including Maxent, can correctly predict occurrences at low sample size reaching 90% of maximal accuracy at a sample size of ten and approaching maximum at fifty (Stockwell and Peterson, 2002; Pearson et al., 2007). The Maxent algorithm compares the probability densities of geographically associated environmental covariates for presence points to the background probability distributions of these covariates (Elith et al., 2011). The algorithm fits a model using six different features of varying complexity: linear, quadratic, products, hinge, threshold, and categorical. It then maximizes entropy by minimizing the difference between the two probability distributions while constraining the features of the model to reflect average value for the covariates (Phillips et al., 2006). The resulting probability distribution for presences can then be used to give continuous probability estimates of the species occurring across geographic space. Thresholds for binary predictions can then be determined based on certain criteria.

In the model evaluation stage, data is withheld when constructing the model and used to assess the performance of the model. Statistics on the model's ability to correctly classify presences from psuedo-absence points taken from the background are then calculated. The

area under the curve (AUC) of the receiver operator characteristic (ROC) is used to evaluate the ability to classify over a continuous probability spectrum (see Methods). Models that show appropriate ability during the evaluation stage can then be used for the primary purpose of a study. For our purpose, we conduct a model projection phase and apply the model to a new geographic region. We then assess the model’s predictive ability using the AUC statistic on the continuous probability predictions and create binary predictions to further assess the performance of the model in the novel area.

ENMs get their name because fundamentally the model is determining the broad geographic niche of a species (also called Grinnellian niche: see James et al., 1984). Three parameters determine a species persisting in a geographic area. The area must have favorable biotic factors that allow the species to have positive population growth (**B**), favorable abiotic conditions (**A**), and finally the species must have had the ability to disperse to that area (**M**). This can be visualized in geographic space using the Biotic-Abiotic-Movement (**BAM**) framework (Soberon and Peterson, 2005; Figure 2.2). The effect of biotic factors in an area are extremely complex and often density dependant not only on the modeled species but also other species that directly or indirectly interact with the modeled species. This complexity makes **B** impossible to include in models except for only the most simplistic of cases (Huisman and Weissing, 2001). Furthermore, theoretically these interactions are important only for small scale niche differentiation but become unimportant at large geographic scales where the influence of broad abiotic factors becomes dominant (Tilman, 1982; Pearson and Dawson, 2003; Peterson et al., 2011). For these two reasons, complexity and scale, the biotic factors (**B**) are not included in ENM modeling.

When constructing a niche model, the goal is usually to either characterize the exact species distribution for which the term Species Distribution Model (SDM) is applicable or to map the potential niche of a species, ENM (Peterson and Soberón, 2012). The area of overlap of **A** and **M** (Figure 2.3a) results in the occupied geographic area (G_o) which is what SDMs desire to approximate. The area outside of **M** but inside **A** is the invadable geographic area (G_i). ENMs typically desire to map the combined $G_o + G_i$ in order to approximate the potential niche of a species, which is equal to **A** in the absence of **B**. In this study and others which attempt to project models into a new geographic region, the potential niche of the species is what is desired and therefore should be what is modeled.

Exactly what is being modeled depends on the scenario that the species is under. A scenario in which the abiotic factors fully constrain the species because it has had the ability to disperse to all areas of **A** and beyond (Figure 2.3b) will model both G_o and **A** and the potential niche accurately since all three are equal. If dispersal is limited, the classic **AM** model scenario (Figure 2.3a) is applicable and the resulting model approximates closer to **A** and the potential niche than to G_o . The more similar G_i is to G_o , the closer the model approximates **A**, and

the more different they are, the closer it approximates G_o (Saupe et al., 2012). In both of these cases, there are unsuitable abiotic areas that the species encounters but cannot occupy allowing for the model to discriminate suitable abiotic conditions from unsuitable. However, if a species is fully constrained by dispersal and \mathbf{M} is contained within \mathbf{A} (Figure 2.3c) the species never encounters unsuitable habitat and the model will perform no better than random because it is unable to discriminate. Similarly, if the suitable abiotic and dispersal area are approximately equal (Figure 2.3d) then the same problem will arise and the model performs poorly (Saupe et al., 2012).

ENMs are ideally constructed within the geographic area that the species has encountered (Barve et al., 2011). Including large areas beyond this would potentially create large suitable but unoccupied areas (G_i) and reduce the accuracy of the model (Phillips et al., 2006; Owens et al., 2013). The most common way ENMs achieve this is by limiting the geographic scope for model construction to within a set distance from known presence points for which it is reasonable to assume dispersal has occurred for the species (Godsoe, 2010).

Often niche models are constructed for applications relating to invasive species (iENMs). One of the major assumptions of ecological niche models is that the species is at equilibrium with the environment (Elith and Leathwick, 2009), allowing for sufficient time to be limited by abiotic conditions. Often this is not the case for invasive species (Vclavk and Meentemeyer, 2009), especially incipient ones. If the invasive species is still expanding its range, then the lack of presences cannot be attributed to environmental constraints but rather lack of dispersal time. This leads to an artificial fully dispersal limited model (Figure 3c) with poor model performance. In this study, the invasive range will be used for model testing rather than construction. In this case, we may see an over prediction of presences if there has been insufficient time for adequate dispersal to all suitable environmental areas.

The plague skink, *L. delicata*, is a scincid lizard native to the Eastern coast of Australia. It was introduced in Hawaii around 1900 and has become established across all the major islands via the plant trade (see Chapter 1). This human mediated transport and over 100 years since establishment should indicate that the problems generally associated with iENMs are not a factor in this system. Instead, *L. delicata* appears to be at equilibrium in Hawaii, appearing from sea level to the highest reported elevation of any reptile or amphibian in the islands (Baker, 1979; Chapple et al., 2013a).

There are five classic predictors of invasion success. The first two, high fecundity and vagility, deal with the ability of the species to spread quickly upon establishment. *L. delicata* exhibits rapid maturation and produces multiple large clutches per year in communal nests while exhibiting exploratory behavior paired with human mediated dispersal (see Chapter 1) therefore satisfying the first two predictors. The latter three, high behavioral and phenotypic

diversity, high genetic diversity, and climate matching, deal with the species' ability to handle a different geographic area. Both behavioral and phenotypic diversity and genetic diversity relate to the ability to respond to a novel set of conditions while climate matching requires the environmental similarity of the new area to be the driver of success. *L. delicata* has low genetic diversity in Hawaii arising from a single point introduction from suburban Brisbane, Australia (Chapple et al., 2013a; Chapter 1). This leaves only plasticity and climate matching as potential predictors for invasion success in Hawaii. There is some evidence that behavioral plasticity in *L. delicata* may have aided dispersal to Hawaii (Moule et al., 2016; Chapple et al., 2013b). However, determining if this behavior is the sole predictor for persistence and growth in the novel area requires the climate matching hypothesis to be tested.

Formally, the climate matching hypothesis posits that similar environmental conditions in the native range to those in the introduced range of a species leads to the species being successful and ultimately invasive. *L. delicata* in Hawaii is derived from a known source population (Chapple et al., 2013a). To determine if the invasive population is climate matching directly with the range of the source population, we compared the climate variables of the introduced range with those of the source range at multiple geographic scales. The diversity of ecomorphs exhibited across the entire native range (Greer, 1974; Chapter 1) may mean that adequately mapping the potential niche of *L. delicata* in Hawaii requires constricting the model geographically to the clade level rather than the small geographic area of the specific haplotype. Constricting the model to a smaller geographic range than the one realized by entire species may artificially constrict the occupied area (G_o) leading to a model that does not adequately cover all the possible suitable abiotic area and leads to poor model projection. Therefore the entire range model must also be constructed to evaluate the climate matching hypothesis throughout the different population levels that correspond to the invasion history of *L. delicata*.

Niche models were created in Maxent at three geographic scales, suburban Brisbane, south-east Queensland, and all of eastern Australia and Tasmania, which correspond to the three population spatial scales: the introduced haplotype, clade, and entire species native range (see Chapple et al., 2013a; Chapter 1). Eco-morphs in a species complex exhibit markedly different morphology and are associated with different habitats (Langerhans et al., 2006; Wegener et al., 2014). Therefore the expectation is that the model constructed around the source population will be most predictive if climate matching is occurring. However, the small geographic range of the source population may not encompass all the suitable habitat types realized for the *L. delicata* eco-morph found in Hawaii and therefore not adequately map the potential niche. In this scenario, we would expect the Queensland model to predict more accurately in Hawaii. However, it may be the case that each eco-morph is competitively excluding the others resulting in a realized niche much smaller than what would be observed in absence of the others. This would be a situation where biotic interactions **B** are occurring at

the geographic scale. The entire range of the species-complex would then be necessary to map the potential niche of *L. delicata*. In this situation, the entire range model would perform best during projection.

This study allows for the examination of how population scales reflect the potential niche of a species and its spread to novel habitat. Climate matching is often supposed in invasion biology but many studies have shown niche shifts and niche expansion. Here, the use of a large diverse species-complex with well recorded genetic structure and introduction history allows for the examination of this hypothesis in the unique natural laboratory of Hawaii (Chapter 1). The multi-level spatial scales of the native range allow for the examination of the ecological theory underpinning the models and how that affects projections into novel space, a well known difficulty of ENMs (Peterson et al., 2007; Phillips, 2008).

2.2 Methods

2.2.1 Data Collection

Nineteen BioClim variables were obtained from WordClim database with raster cells at 30 arcsecond ($\sim 1km^2$) resolution for eastern Australia, Tasmania (native range), and the main Hawaiian Island archipelago (introduced range). Variable reduction is necessary when attempting to fit a broadly applicable ENM (Peterson et al., 2007). A PCA was performed on a random sample of one million raster cells within a 50km area around all presence points in Australia and New Zealand in the native range, and 21,000 cells in Hawaii. The ratio of native range and Hawaii raster cells was proportional to the total land area for the respective ranges and included in order to account for variable relationships in model construction and projection phases. The sample points were restricted to limit the models to realistic dispersal areas ($50km^2$) for *L. delicata* (Figure 2.7). The first three components from the PCA were chosen to avoid overfitting. These three components made up 85.0%, 12.6%, and 1.8% of the variation in the covariates with all remaining components below 0.3% (Loadings in Table 2.1).

The models were constrained to encompass only the realistic potential dispersal range for *L. delicata* (M; see Introduction). Background points used for the PCA and Maxent model were restricted geographically to within 50km of a recorded locality for *L. delicata*, a reasonable assumption for a small exploratory lizard (see Chapter 1). This included the entire land mass of the main Hawaiian islands due to their small geographic size and therefore no constraint was imposed on the islands.

Location data was retrieved from VertNet for both the native Australian range and the introduced Hawaiian range. The locality data for the native range was subsetted as either

full native range encompassing all entries for Eastern Australia and Tasmania, Queensland clade encompassing the Southeastern Queensland territory based on Chapple et al. (2013a) (27.90°S to 25.25°S and 151.00°E to 153.60°E), or the Brisbane haplotype encompassing northern suburban Brisbane (27.05°S to 25.55°S and 151.00°E to 153.60°E) (Chapple et al., 2013a, see Figure 7). The total number of *L. delicata* entries with known GPS locations was 6,231 individuals. When constructing ENMs, only one unique presence point per cell is allowed to avoid both sampling bias and errors of independence. This resulted in a total of 1,652 presence records for the full native range, 199 for the Queensland clade range, and 71 for the Brisbane haplotype range.

2.2.2 Model Construction and Evaluation

Maxent models were constructed in R (Ver. 3.2.2) using the *dismo* package with Maxent version 3.3.3k. The models for the three native range distributions were assessed using a k-fold jackknife procedure, withholding 20% of the presence points. This type of jackknife assigns the presence points randomly into five groups and sequentially withholds one group for model testing while using the other four for model training resulting in five model runs. The Brisbane model constrained maximum number of replicates due to the small size of the testing set (only 14 withheld with five k-fold groups).

When attempting to judge the ability of a model to correctly classify certain objects into the correct categories, a confusion matrix (or error matrix) can be constructed to evaluate true positives (a), false positives (b), false negatives (c), and true negatives (d) (Figure 4). In the case of an ENM, positives correspond with presences and negatives with absences and these are used to construct the evaluative statistics.

$$Sensitivity = \frac{a}{a + c} \tag{2.1}$$

$$Specificity = \frac{d}{b + d} \tag{2.2}$$

For each jackknife replicate, the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) curve was calculated. This value indicates how well the model discriminates presences and absences over a continuum of thresholds. The ROC curve also indicates how quickly the sensitivity increases as the specificity decreases (See Figures 2.8-2.10). Sensitivity measures the proportion of validation presences that are accurately classified by the model (Eq. 2.1). Specificity is the proportion of validation absences that are correctly classified as such by the model (Eq. 2.2). Once an ROC curve is obtained, the integral gives the

AUC. Possible values for AUC range from 0 to 1 with a value of 0.5 being no better than random, 0.5-0.7 a poor model, 0.7-0.9 a moderate model, and >0.9 a good model (Hosmer and Lemeshow, 2000). Models with average AUCs >0.7 were considered adequate for projecting onto the introduced range in Hawaii. Because the standard error measurements from resampling are unstable at such low replicates, error was not included formally or informally (Liu et al., 2005).

2.2.3 Model Projection

To predict potential ecological niches in Hawaii, the same three native geographic scale models were bootstrapped for 100 replicates using all the presence localities. Each model run was then projected on to Hawaii and the probability of presence for *L. delicata* for each 1 km² cell in the introduced range in Hawaii was determined based on the PC transformed environmental covariates.

$$Overall Accuracy = \frac{a + d}{n} \quad (2.3)$$

The True Skill Statistic (TSS)(E.q. 2.4) was then calculated for each bootstrap replicate to evaluate the predictive ability of the resulting models. This statistic ranges from -1 to 1, and can be thought of as the difference between the hit rate, H, and the false alarm rate, F, $TSS = H - F$. TSS can be useful in interpretation of a model distinguishing between yes and no cases, and allows one to examine whether forecasting events such as climate phenomena or presence of an invasive species in a particular habitat, and particularly a rare event, more often leads to an increase in false outcomes or not. The term discriminant is sometimes used and refers to the statistic measuring the discrimination between yes and no cases. In this sense, it is also related to the relative operating characteristic (ROC).

$$TSS = Sensitivity + Specificity - 1 = H - F = \frac{ad - bc}{(a + c)(b + d)} \quad (2.4)$$

The TSS can be useful when comparing the performance of distribution models since it takes into account errors of two fundamental types, of commission, Type I errors (b), and of omission, Type II errors (c), something that a pure overall accuracy calculation (Eq. 2.3) does not. A rare species can have a high overall accuracy, or hit rate, due to the large number of true absences predicted (d) overwhelming the statistic (Figure 2.4). Likewise a common, widespread species may also have high accuracy score due to correspondingly high presence.

To assess the continuous predictive values given for each cell in Maxent, these values had to be converted to binomial presence-absence predictions using a threshold that maximized

both sensitivity (Eq. 2.1) and specificity (Eq. 2.2). TSS was calculated using these binary predictions by adding the sensitivity and specificity and subtracting one. The equation is as follows:

Using the threshold that produces the maximum TSS, pseudo-absences were generated in Hawaii to calculate the TSS for each model run. A total of 500 psuedo-absence points were used for each run to create an approximate prevalence of 0.176. Extremely low prevalence (<0.05) increases the variance in TSS calculations due to large variability in the sensitivity of the model and extremely high prevalence also increases the variability by affecting specificity similarly (Allouche et al., 2006). Additionally, both TSS and AUC decrease as prevalence increases. The effect becomes pronounced as prevalence moves higher than 0.40 (Allouche et al., 2006). As a rule of thumb, models with a TSS over 0.5 have been shown to be accurate in predicting presences (Liu et al., 2011). Both AUC and TSS were compared among the three range models using one-way ANOVAs. We used Tukey’s post hoc tests to evaluate the differences shown by the bootstrap method.

For each bootstrap replicate, we calculated both the threshold determined to maximize TSS and the threshold at which sensitivity reaches 90%. The latter was included since it is unaffected by prevalence (Allouche et al., 2006) and does not take into account absence predictions. Since it is unclear how well *L. delicata* has been sampled throughout Hawaii, specificity measures may be inaccurate. Low variation and high threshold values for both TSS and 90% sensitivity threshold would indicate precise and accurate models (Ruetz and Leynaud, 2015). One-way ANOVAs were performed to evaluate difference in thresholds among the three geographic scale models of predictions in Hawaii. We then applied Tukey’s post hoc test on the 90% sensitivity threshold statistic. The maximum TSS threshold was excluded from post hoc tests due to nonsignificance of the ANOVA. Within a single geographic model, the thresholds set for maximum TSS and sensitivity were compared using a Student’s t-test to evaluate the degree to which balancing specificity affected the binary prediction threshold.

2.3 Results

2.3.1 Model Construction and Evaluation

The PCA transformed rasters used in the model indicate differences in PC combinations across the native range of Australia (Figure 2.5). The constrained background used for the models show similar levels of difference across the range with a gradient of PC1 with higher scores in the north and lower in the south (but high in Tasmania) and higher values along the coast (Figure 2.7). The distribution of covariates were similar in the Queensland and Brisbane model, with these being a subset of the larger full range distribution (Figure 2.14).

The k-folded jackknife replicate model runs showed that both the Queensland clade and the full native range model performed well in predicting the withheld presence points showing AUCs of 0.856 (SD = 0.014) and 0.797 (SD = 0.009) respectively. However, the Brisbane model's AUC fell into the poor category with a high standard deviation (AUC = 0.573, SD = 0.093). The ROC curves indicate that the Queensland model increases in sensitivity at the fastest rate approaching 1 at a specificity of 0.65 (Figure 2.9). The full range model has a more gradual increase in sensitivity as specificity decreases (Figure 2.10). The ROC for the Brisbane model reflects the poor AUC with the majority falling very close to the diagonal line and within one standard deviation indicating the performance of a random model (Figure 2.8).

Each of the three trained models showed different trends in how the PCs affected the models. For the Queensland clade model, PC1 showed both the highest percent contribution and percent importance, 71.1% and 77.7% respectively, followed by PC2 with 22.4% and 11.8%, and finally PC3 with 6.4% and 10.6% (Table 2.2 and 2.3). The full range model had similar results but PC1 and PC2 shared almost equal contribution, 42.5% and 38.4%, with a slightly larger difference in percent contribution. The relationship inverted with the Brisbane model. PC3 showed the largest contribute at 60.7% while PC2 and PC3 were around 20% (Table 2.2). However, PC1 showed very little importance at only 3.6% compared to almost 50% for both PC2 and PC3 (Table 2.3).

2.3.2 Model Prediction

When projected onto the PCA transformation of Hawaii and averaged across the 100 bootstrapped replicates, the two best performing models based on AUC in the evaluation phase, full range and Queensland, had similar spread in the predicted likelihood of presences in Hawaii but with the Queensland model predicting some areas with even higher probability of presence (Full range: 18% to 48%; Queensland: 18% to 60%). However, these two models predicted the almost inverse of each other for the areas where *L. delicata* would be present (Figures 2.11 and 2.12). The poorly evaluated Brisbane model predicts a similar area of presences of *L. delicata* as the Queensland model but with even higher probabilities in certain areas (Brisbane: 27% to 72%; Figure 2.13).

The performance statistics for the prediction maps show similar trends with the Queensland model performing better on predictions of presences compared to the full model. The Brisbane model performed variably for each of the statistics and had larger standard deviations. The average TSS values from the bootstrap runs for each model were significantly different than each other (ANOVA: $F_{2, 297} = 100.3$, $p < 0.0001$) with the full range model being almost half of the Brisbane and Queensland models (Figure 2.18). All were close to zero, however, with

none above 0.152. A similar trend appears in the AUC calculated for the projections with both Queensland and Brisbane having a larger average (ANOVA: $F_{2,297} = 168$, $p < 0.0001$) but with Brisbane slightly higher than Queensland (Tukey's HSD: $p < 0.001$) (Figure 2.17). These all fell close to an AUC of 0.5 representing poor models with the full model actually slightly below that mark.

The probability threshold analysis revealed that the TSS threshold was the same for all three models (ANOVA: $F_{2,297} = 2.36$, $p = 0.096$) at an overall average of 0.26 (Figure 15). The thresholds determined for the 90% sensitivity were lower except for the Brisbane model which had a similar threshold for both (Full Range t-test: $t = -17.5$, $p < .0001$; Queensland t-test: $t = -4.52$, $p < .0001$; Brisbane t-test: $t = -0.526$, $p = 0.597$). There was a marked difference among the three models for the 90% sensitivity binary threshold (ANOVA: $F_{2,297} = 78.36$, $p < 0.0001$) with the full range model approaching zero (Figure 2.16: 0.0197) and the Queensland model around 0.18. The Brisbane model threshold showed an almost uniform distribution across all probabilities (0.0033 to 0.786) indicating highly variable model performance (Figure 2.16).

2.4 Discussion

The climate matching hypothesis is not supported by any of the geographic range models that were produced for *L. delicata*. All of the three models projected into Hawaii had low TSS scores and low maximum TSS thresholds which have been shown to be inaccurate for predicting species distributions (Ruetz and Leynaud, 2015). The reason for such poor performance when predicting into Hawaii appears to be the shift in ecological variables in the Hawaiian archipelago compared to those encountered by *L. delicata* in Australia and Tasmania. PC1 was a major contributor to both the Queensland and full range model but the distribution of this covariate is almost completely distinct from the distributions for the three native ranges (Figure 2.14) causing the model to poorly estimate probability densities in this region of PC1.

The Brisbane model failed to perform well in the evaluation phase likely because the background was restricted to a small environmentally homogeneous areas. This ended up creating a situation similar to Figure 2d where the modeled dispersal range (**M**) has been reduced to an area that is approximately the same as the favorable abiotic area (**A**) which does not allow the model to discern any difference between the background and the suitable area. Better performance in the projection phase for all statistics compared to the other two range models is an artifact of having less contribution coming from PC1. The inability of the Brisbane model to predict the distribution of *L. delicata* within its own native range area but still outperform the other two models further indicates the poor ability of all of these models to predict when projected into Hawaii.

Invasive ENMs are often difficult to construct because they require that the potential niche of a species be properly modeled. Fully modeling the potential niche can only occur when all possible areas that contain suitable habitat for that species have been encountered as in the fully abiotic constrained **AM** model (Figure 2.3b). *L. delicata* experiences the case where human dispersal allows it to encounter completely new areas of environmental space from what it has ever encountered in its native range. Regardless of the model, if projected into an area of which the majority is in the invadable geographic range (G_i) of that species but is dissimilar to the occupied area (G_o), the model will be unable to adequately describe the potential niche and predict the distribution poorly. The results of this study show that *L. delicata* is experiencing an extreme of such a situation and any attempt to use native range environmental data would inadequately describe the potential niche of *L. delicata*.

The use of novel environmental niche space by invaders is termed niche shift or niche expansion. A niche shift describes a species that has completely changed the environmental covariates that it is associated with, while a niche expansion occurs when the original realized niche is expanded upon. Often niche shifts and expansion occur in invasive systems as a species is encountering a novel habitat or is released from biotic limitations such as predation or interspecific competition. In *L. delicata*'s case in Hawaii, it is unclear which of these two processes is occurring since very little of the native range environmental space occurs in Hawaii. Since the environmental space of Hawaii is not found in Australia, we cannot determine if *L. delicata* would fill that potential niche in the native habitat if it were present. Regardless of whether a niche shift or expansion has occurred for *L. delicata* in Hawaii, because of the little environmental overlap, it would have been impossible to predict the occurrence of these processes from the native range. Additionally, the invasion into Lord Howe island and New Zealand (Chapter 1) would not have led to predictions of niche shift or expansion as *L. delicata* in these areas are occupying niche space almost 100% similar to the niche space they occupy in their native range (Tingley et al., 2016). The unique environmental conditions present in Hawaii may prove modeling most invasive species with ENMs difficult. An analysis of all invasive herpetofauna in Hawaii may indicate that the sheer number of open niches makes any attempt to predict success impossible from ENMs alone.

This study also offers insights into some of the pitfalls of scale when constructing ENMs. Our large full range model and smaller Queensland model gave very different probability maps when projected into Hawaii. Conclusions based on one of the model's maps would likely directly conflict with conclusions based on the other. For instance, if someone was looking to determine suitable areas in Hawaii for the introduction and spread of *L. delicata*, the Queensland built projection map would lead to the conclusion that Hawaii would be quite resistant, with only high probability of occurrence located at upper elevation away from population centers where introduction of human mediated dispersers would arise. If the researcher's purpose was to estimate impacts of the invasive skink, the two models would

conflict on how *L. delicata* is occupying native habitat sites especially in those high elevation sites with distinct environmental patterns (Figures 2.11 and 2.12).

Ruling out the climate matching hypothesis for the invasion success of *L. delicata* in Hawaii leaves only the idea that phenotypic or behavioral plasticity is the key to success of this species in a novel habitat. The correlation of the spread of *L. delicata* and the decrease in abundance of the moth skink (*Lygosama noctua*) (Hunsaker and Breese, 1967) suggests that *L. delicata* has a competitive advantage and is not merely filling empty niche space. Plasticity being the only predictor of invasion success makes determining those species that will be successful difficult because usually differences in phenotype and behavior get associated with genetic underpinnings rather than responses to environment. The phenotypic change of *Anolis* lizards introduced to small islands in the Caribbean was first attributed to genetic responses (Losos et al., 1997), however subsequent laboratory experiments showed that environmental responses caused the observed differences in phenotype (Losos et al., 2000). The fact that the best predictor of success for invasive species is their ability to be invasive elsewhere suggests that the cryptic nature of plasticity rather than genetic diversity or climate matching could ultimately be responsible for invasion success.

As many before it, this study reinforced the difficulties of modeling iENMs. It suggests that these tools are not particularly useful for predicting invasion success in isolated island systems with distinct environments. Additionally, any attempt to model the species distribution (SDM) in Hawaii for *L. delicata* should only use the introduced range of the species considering the lack of overlap of environmental habitat between Australia and Hawaii and the effects this has on the niche models. Furthermore, the potential niche of a species often may be much larger than the native range suggests, but it is impossible to model the potential niche if the species and model do not encounter all possible suitable niche space. Expansion of this study to all invasive herpetofauna or vertebrates may show trends in novel niche use, especially if a gradient of species with similar to dissimilar environmental native ranges can be tested. However, in this case, we see that climate matching is not occurring and may be only relevant in systems where plasticity and genetic diversity are not present.

2.5 Figures and Tables

Table 2.1: Loadings for the first three Principal Components (PCs). Loading values greater than 0.1 are shown in bold font.

BioClim Variable	PC1	PC2	PC3
BIO1 = Annual Mean Temperature	0.005	0.005	-0.135
BIO2 = Mean Diurnal Range (Mean of monthly max temp - min temp)	-0.013	0.001	-0.009
BIO3 = Isothermality (BIO2/BIO7) (*100)	0.005	-0.002	0.001
BIO4 = Temperature Seasonality (standard deviation *100)	-0.941	0.329	0.034
BIO5 = Max Temperature of Warmest Month	-0.014	0.007	-0.102
BIO6 = Min Temperature of Coldest Month	0.024	-0.003	-0.095
BIO7 = Temperature Annual Range (BIO5-BIO6)	-0.039	0.010	-0.007
BIO8 = Mean Temperature of Wettest Quarter	-0.005	0.022	-0.232
BIO9 = Mean Temperature of Driest Quarter	0.015	-0.012	-0.027
BIO10 = Mean Temperature of Warmest Quarter	-0.006	0.009	-0.125
BIO11 = Mean Temperature of Coldest Quarter	0.018	0.000	-0.127
BIO12 = Annual Precipitation	0.291	0.825	0.189
BIO13 = Precipitation of Wettest Month	0.040	0.109	-0.140
BIO14 = Precipitation of Driest Month	0.010	0.036	0.072
BIO15 = Precipitation Seasonality (Coefficient of Variation)	0.002	-0.003	-0.084
BIO16 = Precipitation of Wettest Quarter	0.109	0.300	-0.402
BIO17 = Precipitation of Driest Quarter	0.043	0.138	0.268
BIO18 = Precipitation of Warmest Quarter	0.052	0.254	-0.561
BIO19 = Precipitation of Coldest Quarter	0.089	0.155	0.509

Table 2.2: Percent contribution of the three Principal Components (PCs) averaged across the jackknife replicates (n=5) for each training model dataset. This indicates the percentage that each variable contributed to training the models. Each variable coefficient modification that results in a gain in the probability of prediction of presence locations in the model is counted and then converted to a percentage after model training. This can be misleading especially with highly correlated variables since it depends on the path that the machine learning algorithm takes. However this is less of an issue with PC variables.

	Brisbane	Queensland	Full Native Range
PC1	17.6	71.1	42.5
PC2	21.7	22.4	38.4
PC3	60.7	6.4	19.1

Table 2.3: Permutation importance of the three Principal Components (PCs) averaged across the jackknife replicates ($n=5$) for each training model dataset. This percentage measure is calculated by the decrease in AUC score that occurs when the values for each variable of the training data are permuted among both presences and pseudo-absences. This is done independently for each variable in the model and is normalized to obtain the percentages. These values only depend on the final Maxent model and are unaffected by the path the algorithm takes.

	Brisbane	Queensland	Full Native Range
PC1	3.6	77.7	47.2
PC2	49.6	11.8	33.4
PC3	46.8	10.6	19.4

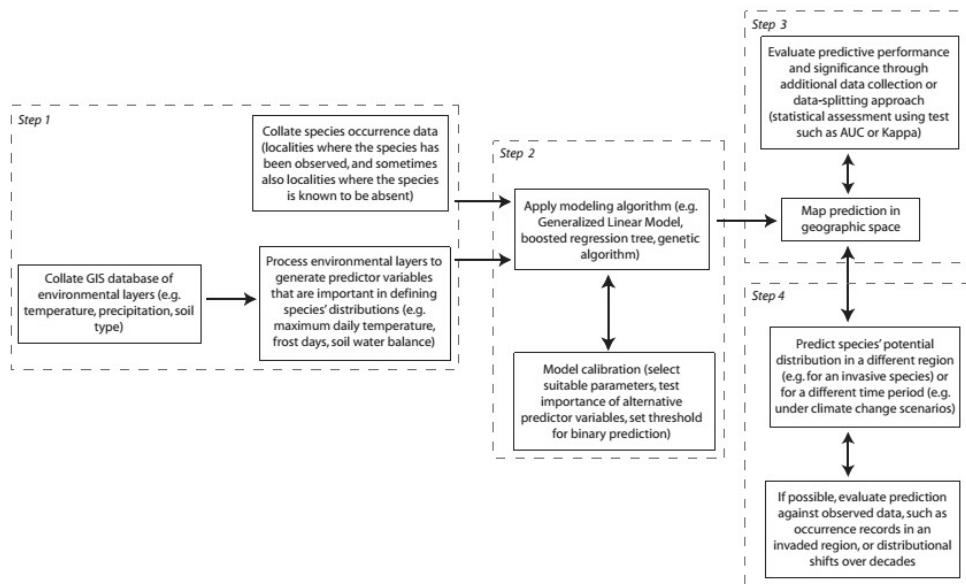


Figure 2.1: Steps in the Ecological Niche Modeling process. Step 1: Data Collection. Step 2: Model Construction. Step 3: Model Evaluation. Step 4: Model Projection (Peterson et al., 2011).

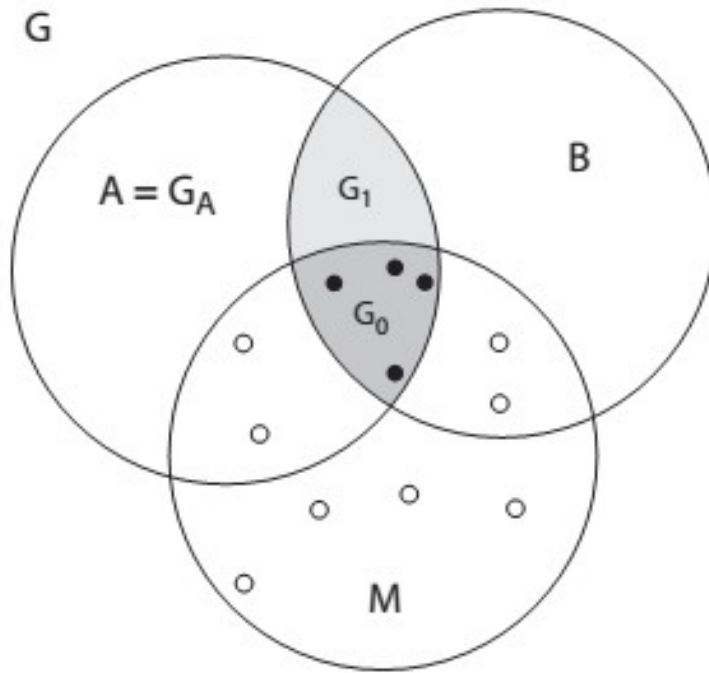


Figure 2.2: BAM model framework. This displays the geographic space (G) in which the ecological model is developed. A species is limited in space based on the three factors presented. These are: the given area in which the biotic interactions are favorable to the species (B), the area where favorable combinations of abiotic factors are favorable (A), and the geographic space into which the species is able to disperse (M). Open circles are species absences and closed circles are presences. G_i is the potential invadable range of the species and G_o is the occupied range. (Peterson et al., 2011)

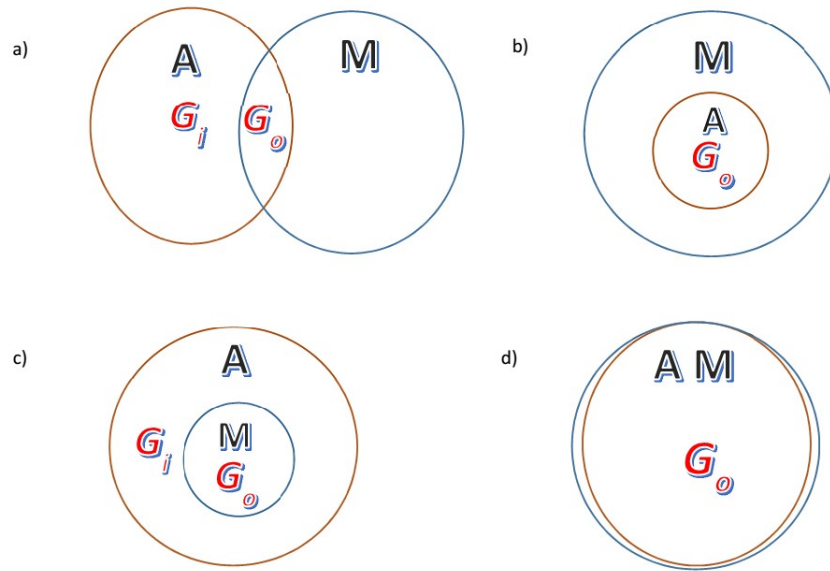


Figure 2.3: Four possible AM scenarios when constructing ENMs. a) The classic model in which the abiotic (**A**) and dispersal area (**M**) overlap partially and there are clear areas of invadable (G_i) and occupied (G_o) geographic space. b) A model where the species is fully constrained by abiotic factors (**A**) resulting in only occupied geographic area (G_o) and no potential invadable area (G_i). c) Species is fully constrained by dispersal leading to both invadable (G_i) and occupied (G_o) geographic space but the species never encounters unsuitable abiotic conditions. d) Suitable abiotic factors (**A**) and dispersal area (**M**) of the species overlap completely leading to only occupied (G_o) geographic space and no invadable (G_i) or unsuitable abiotic area in the model.

		Validation data set	
		Presence	Absence
Model	Presence	a	b
	Absence	c	d

Figure 2.4: A confusion matrix showing the possible outcomes of a binary prediction model. In the ENM framework, the validation set is either withheld presences for testing or known presences in areas of projection (from Allouche et al., 2006).

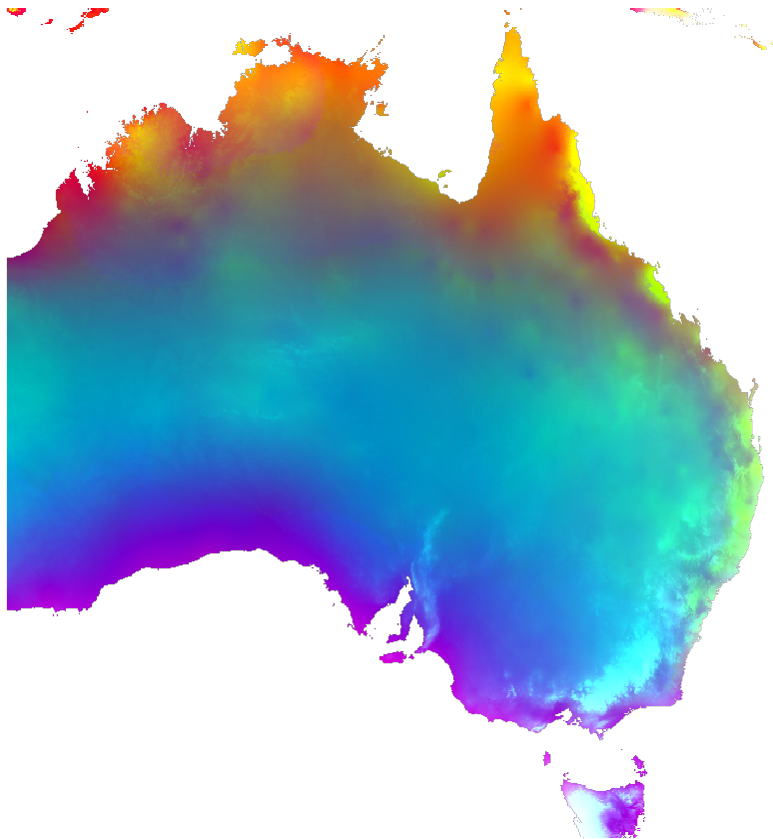


Figure 2.5: Red Green Blue (RGB) plot of the three Principal Components across Australia. PC1 is represented by the red spectrum (85.0% of variation), PC2 by the green (12.6%), and PC3 by the blue (1.8%).

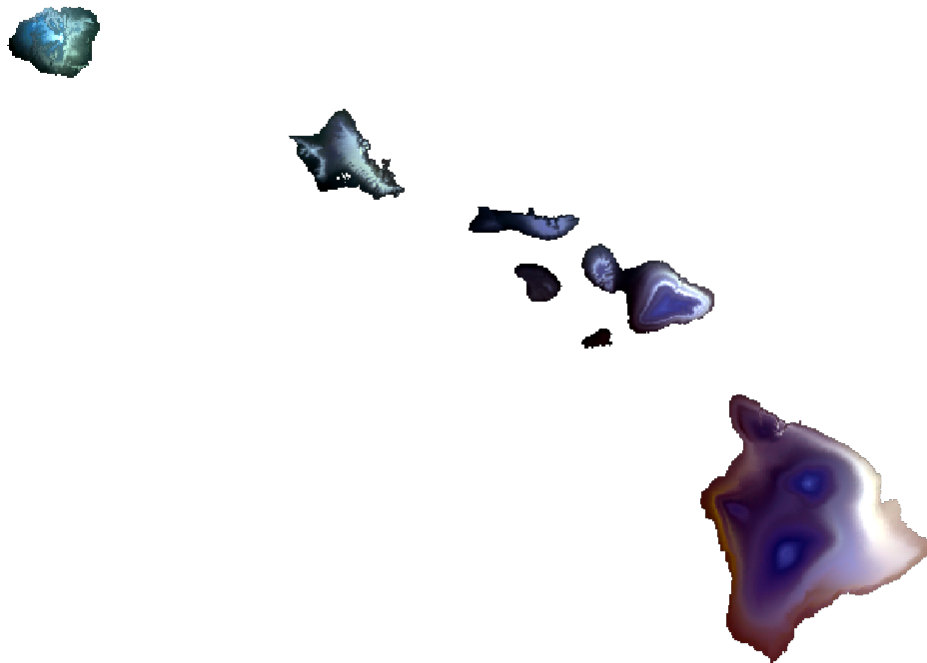


Figure 2.6: Red Green Blue (RGB) plot of the three Principal Components across Hawaii. PC1 is represented by the red spectrum (85.0% of variation), PC2 by the green (12.6%), and PC3 by the blue (1.8%).

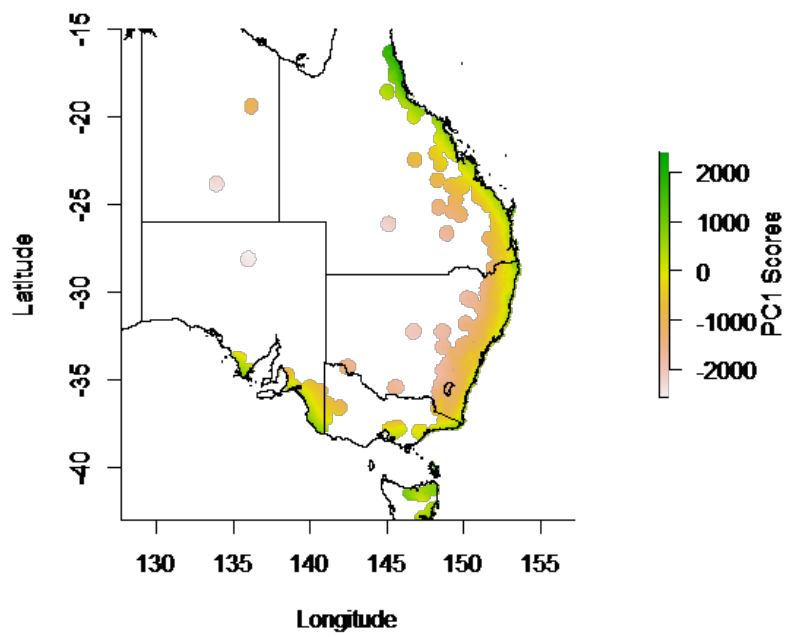


Figure 2.7: Plot of PC1 restricted to within $50km^2$ of a presence point of *L. delicata* across the full native range. This was the background used for the construction of Maxent models.

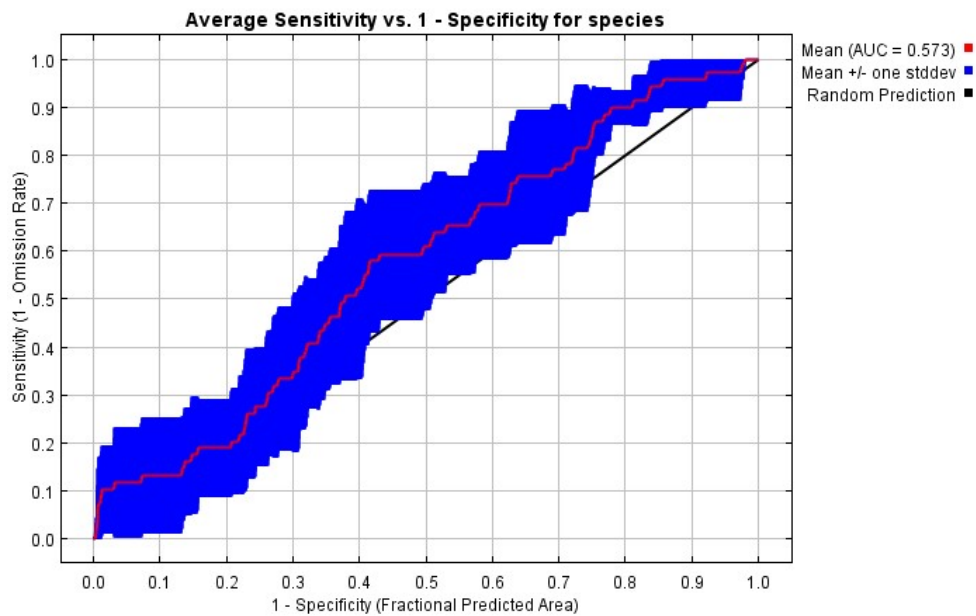


Figure 2.8: Receiver Operator Characteristic (ROC) curve for the Brisbane trained models based on jackknife cross validation ($n=5$) with output given by Maxent (Ver. 3.2.2). The shaded blue area representing one standard deviation shows high overlap with black random prediction line suggesting a poor model and supported by the low mean AUC (0.573).

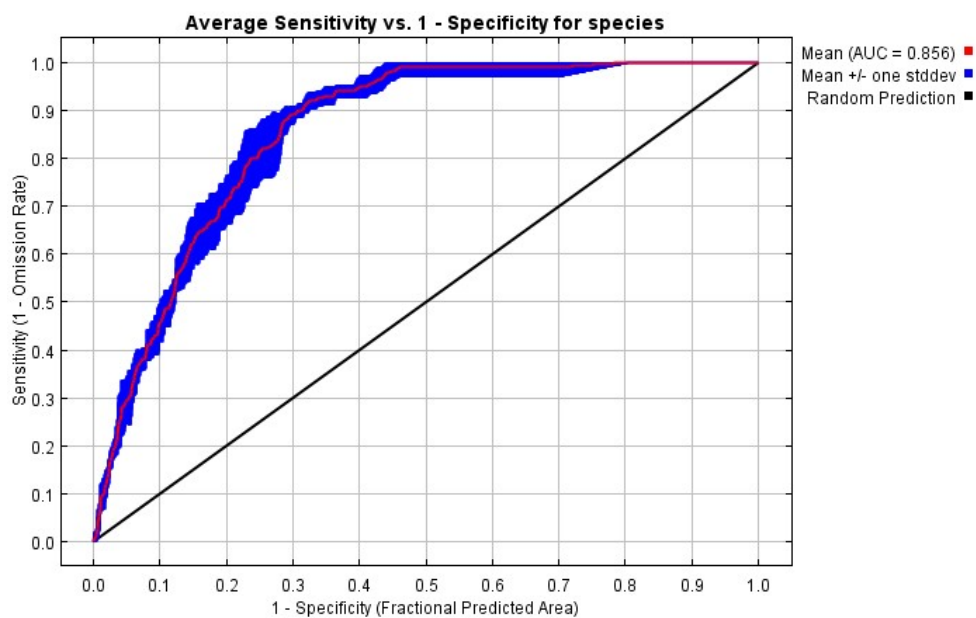


Figure 2.9: Receiver Operator Characteristic (ROC) curve for the Queensland trained models based on jackknife cross validation ($n=5$) with output given by Maxent (Ver. 3.2.2). The small standard deviation represented by the shaded blue area and the steep curve that quickly approaches maximum sensitivity at a relatively high specificity suggests a model that performs well as indicated by the mean AUC (0.856).

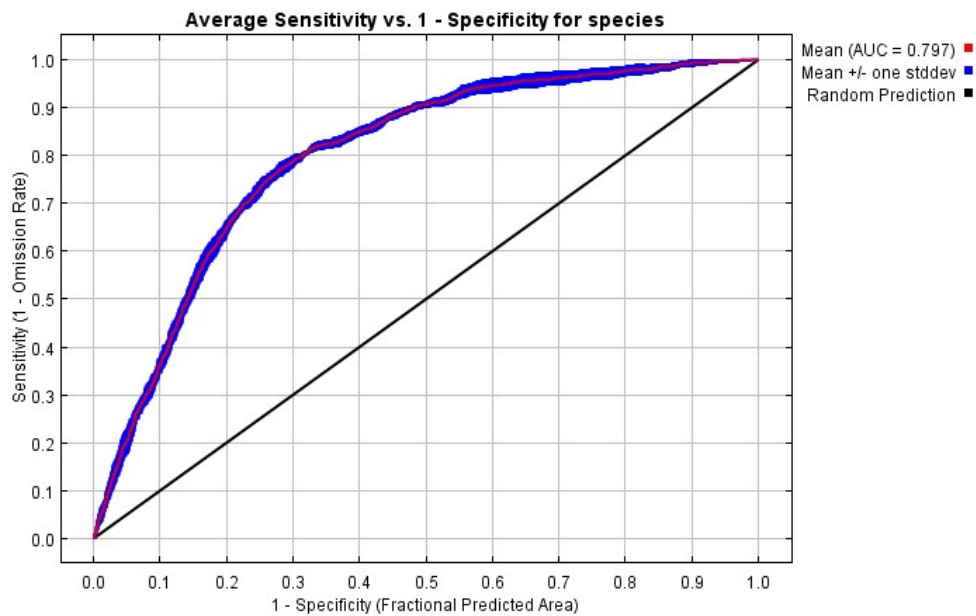


Figure 2.10: Receiver Operator Characteristic (ROC) curve for the full native range trained models based on jackknife cross validation ($n=5$) with output given by Maxent (Ver. 3.2.2). The very small standard deviation indicated by the narrow shaded blue area shows consistent model performance. The more gradual curve and maximum sensitivity not being reached until a very low specificity suggests this is a moderate performing model which is reflected in the mean AUC (0.797).

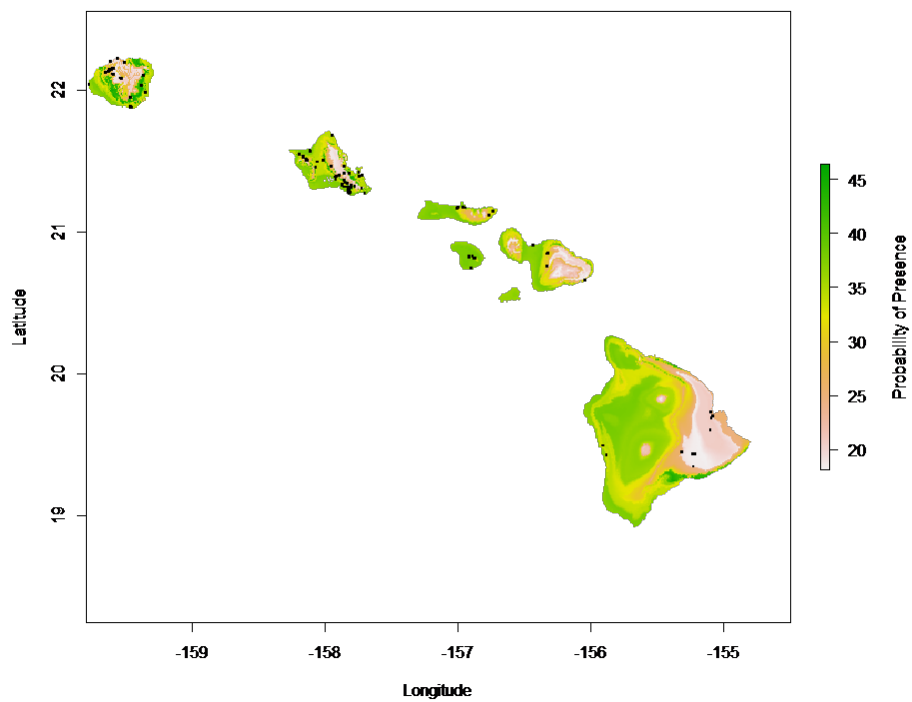


Figure 2.11: Full native range model projected onto a map of the Hawaiian Islands. The probability of presences of *Lampropholis delicata* is shown in percent, ranging from around 20-45%. Black circles represent presence records for this invasive lizard in Hawaii.

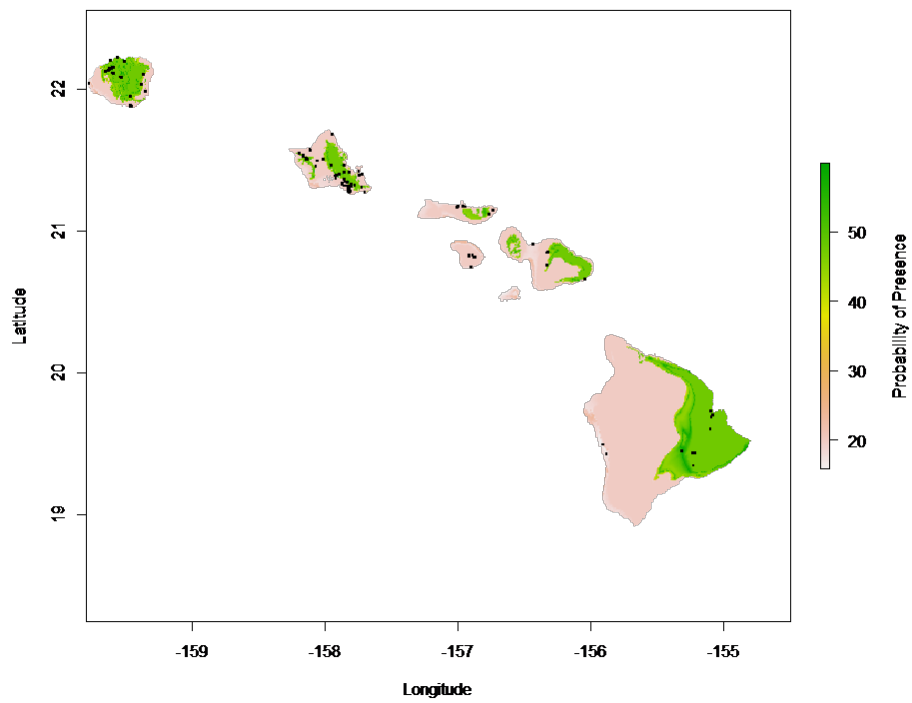


Figure 2.12: Queensland clade range model projected onto a map of the Hawaiian Islands. The probability of presences of *Lampropholis delicata* is shown in percent, ranging from around 20-60%. Black circles represent presence records for this invasive lizard in Hawaii. The areas of high prediction for this model appear to be the inverse of the full range model.

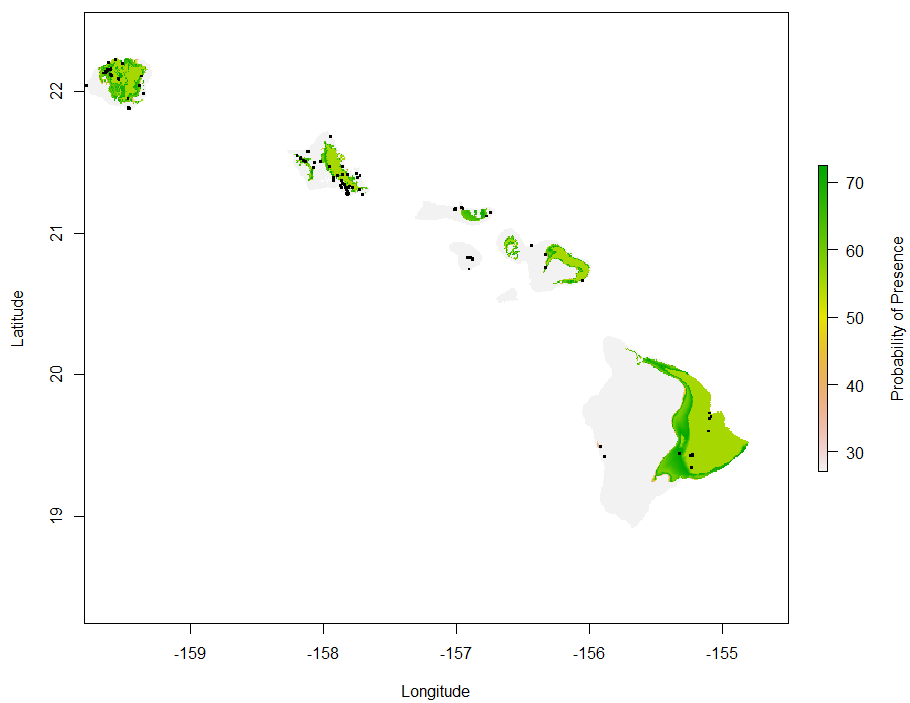


Figure 2.13: Brisbane haplotype range model projected onto a map of the Hawaiian Islands. The probability of presences of *Lampropholis delicata* is shown in percent, ranging from around 25-72%. Black circles represent presence records for this invasive lizard in Hawaii. This prediction map shows a similar trend as the Queensland model.

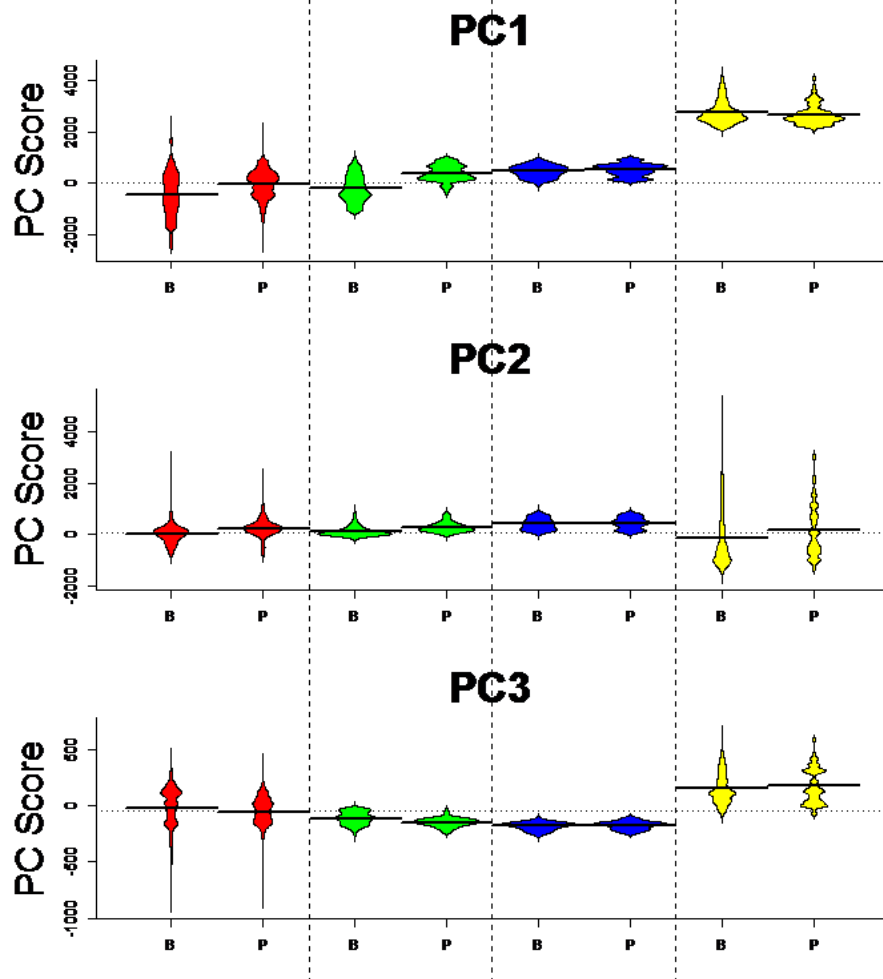


Figure 2.14: Bean plots showing the distribution of background (B) and presence points (P) for the three native range scales and Hawaii. Red represents the full model, green represents Queensland, blue represents Brisbane, and yellow represents Hawaii. Solid lines indicate means for each sample. The dashed line indicates overall mean. The width of the bean plots represents the number of values at that PC score.

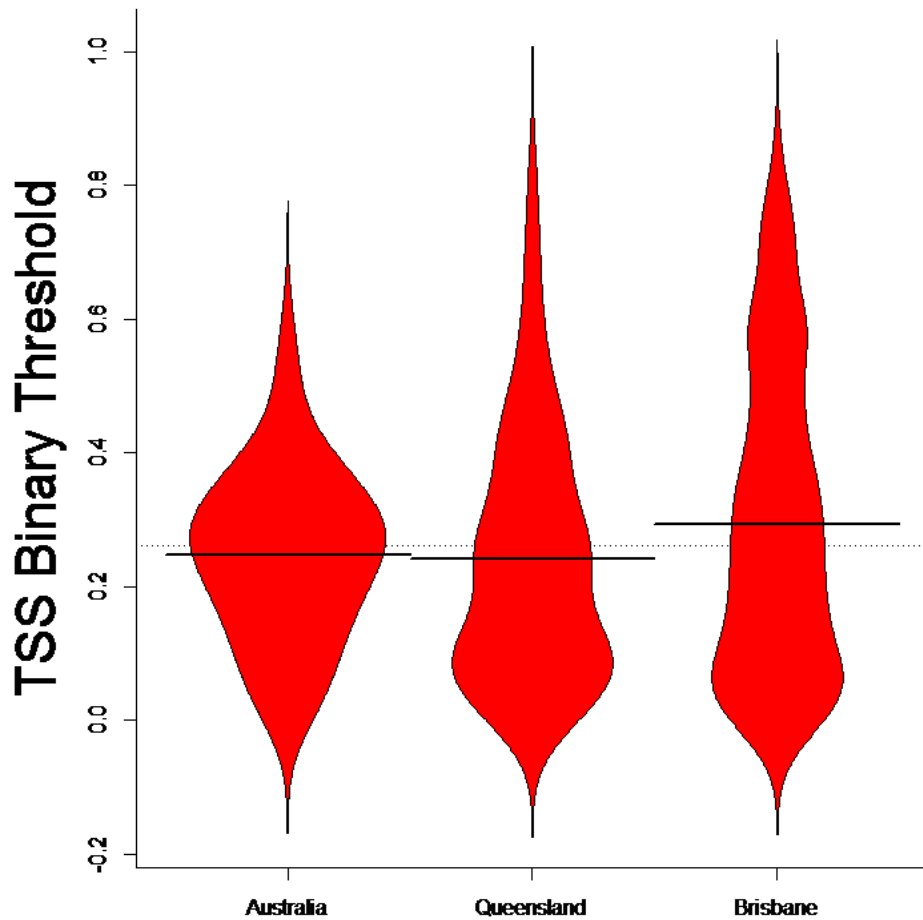


Figure 2.15: Bean plots of the probability thresholds for binary predictions of presences and absences. The thresholds were calculated to give the highest True Skill Statistic (TSS) for each Maxent model projection in Hawaii over the 100 bootstrap replicates. Solid lines indicate means for each sample. The dashed line indicates overall mean. The width of the bean plots represents the number of observations at that threshold. Similar mean thresholds resulted for each of the models (ANOVA: $F_{2,297} = 2.36$, $p = 0.096$) with slightly increased variance in the Queensland and Brisbane models.

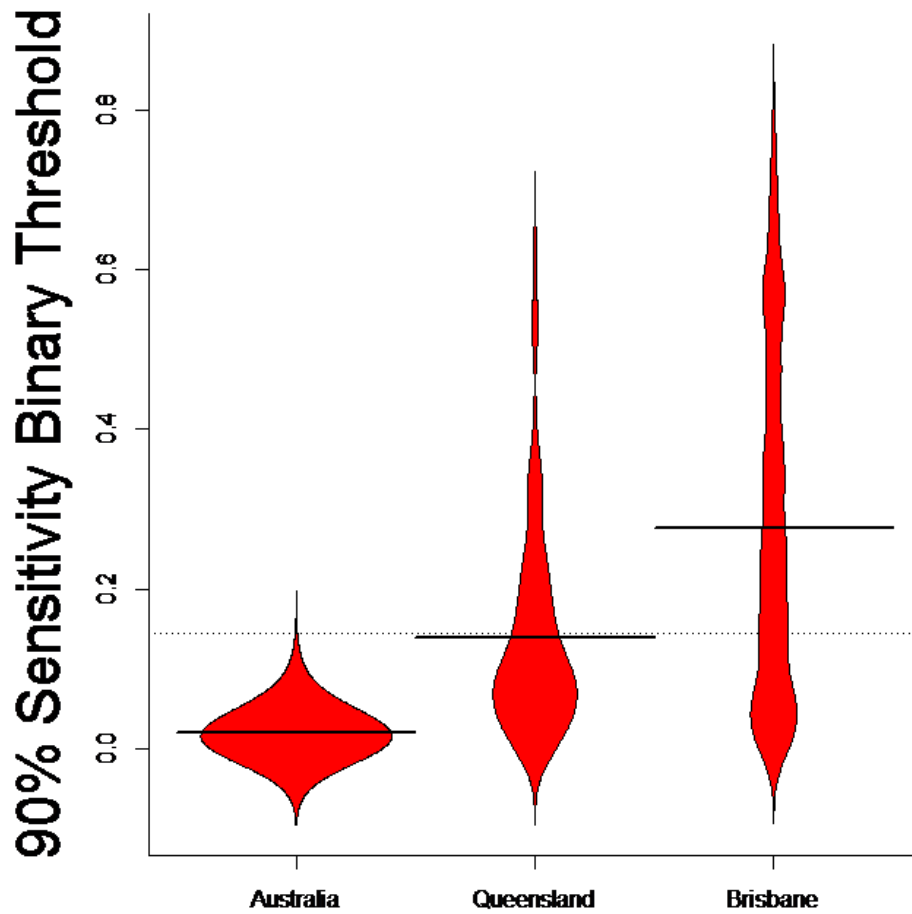


Figure 2.16: Bean plots of the probability thresholds for binary predictions of presences and absences when sensitivity equals 90%. Thresholds were calculated for 100 bootstrap replicates from the Maxent projections in Hawaii. Solid lines indicate means for each sample. The dashed line indicates overall mean. The width of the bean plots represents the number of observations at that threshold. Mean thresholds increase from the full native range models up to the Brisbane haplotype models (ANOVA: $F_{2,297} = 78.36$, $p < 0.0001$) with increasing variance.

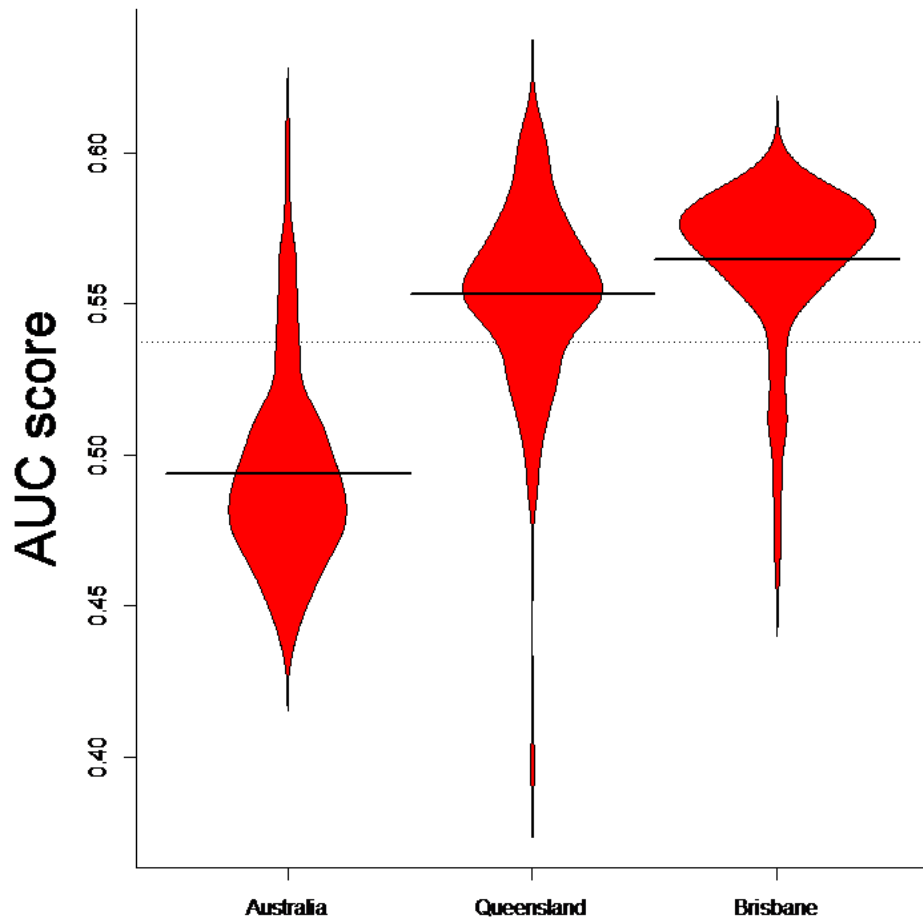


Figure 2.17: Bean plots of AUC scores for the 100 bootstrap replicates from Maxent projections in Hawaii. Solid lines indicate means for each sample. The dashed line indicates overall mean. The width of the bean plots represents the number of observations at that AUC. The mean for the full range model fell below the random 0.50 mark. Both the Queensland and Brisbane models had higher average AUCs (ANOVA: $F_{2,297} = 168$, $p < 0.0001$) with Brisbane slightly higher than Queensland (Tukey's HSD: $p < 0.001$). However, none of these values were above 0.6 and are considered poor predictive models.

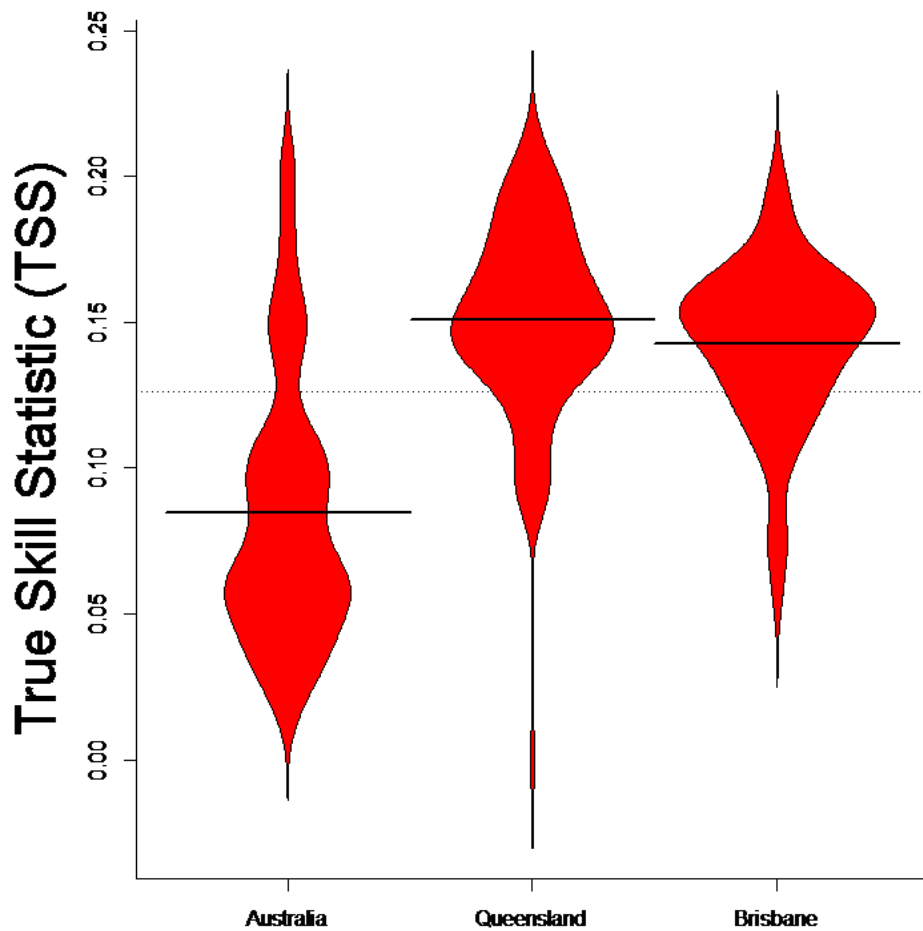


Figure 2.18: Bean plots of TSS scores for the 100 bootstrap replicates from Maxent projections in Hawaii. Solid lines indicate means for each sample. The dashed line indicates overall mean. The width of the bean plots represents the number observations at that TSS. All models showed low mean TSS scores (<0.20) with the full range model's mean approximately half that of the Queensland and Brisbane model (ANOVA: $F_{2, 297} = 100.3$, $p < 0.0001$). Every replicate run for all three models failed to approach the 0.5 benchmark TSS score for a good predictive model.

Chapter 3

Feeding ecology, preference, and impacts of the invasive plague skink (*Lampropholis delicata*) on Oahu

3.1 Introduction

The plague skink, *Lampropholis delicata*, is one of the many invasive herpetofaunal taxa in Hawaii whose ecological impacts have not been studied. Despite also being introduced to both New Zealand and Lord Howe Island, no analyses of diet have been performed in any of the invaded regions for this species (Chapple et al., 2015). In its native range, *L. delicata* has been described as an opportunistic predator (Wilson and Swan, 2013; Cogger, 2014), commonly employing a mixed foraging strategy of sit and wait and ambush predation (Rawlinson, 1971; Howard et al., 2003). Closely related members of *L. delicata* in the Scincidae family all showed arthropod based diets. Only one study presents diet information for this species specifically, finding 17 different orders in the stomach in the native range (Lunney et al., 1989).

Hawaii is well-known for a number of endemic radiations of arthropods. Across all major terrestrial arthropod orders greater than 97% endemism occurs for native species except for chewing lice (9%) and mites (91%) (Ziegler, 2002; Nishida, 2002). The exception for these two orders likely stems from relatively frequent transportation by migratory birds. There are over

5,500 described native arthropod species across the Hawaiian Islands (Nishida, 2002). Because of few natural colonizers, adaptive radiation occurred for many orders including: Araneae, Isopoda, Diptera, Odonata, Hemiptera, Orthoptera, and Lepidoptera (Roderick and Gillespie, 1998). This has led to the evolution of many endemic genera and families in these orders with unique ecologies across the islands.

The endemic arthropod community in Hawaii, as with the Hawaiian vertebrate lineages, is also known for what is missing. Only half of all insect orders are found in the islands with as little as 15% of the worldwide total for insect families. This biogeographic phenomenon is known as a disharmonic distribution, where community composition is unbalanced relative to continents. This natural phenomenon occurs across lineages in archipelagos that have strong geographic filters to colonization such as geographic isolation (e.g. Cox and Moore, 2005). Biotic disharmony in native taxa finds its extreme in Hawaii due to the islands being the most isolated group on earth (Gillespie and Roderick, 2002). Noticeably absent from the Hawaiian native fauna are cockroaches, termites, and ants (Ziegler, 2002). This disharmony also led to a tendency to evolve flightlessness in the Hawaiian insect taxa with ten out of the eleven winged orders that colonized Hawaii evolving flightless forms (Howarth, 1990). Flightlessness occurs in mainland taxa, but in the absence of selection pressures from a complete community it can lead to a native species being less able to avoid predation. This often becomes apparent when exploited by an introduced predator that has not coevolved in this ecosystem.

A lack of native vertebrate mesopredators in the leaf litter assemblages in the Hawaiian islands meant that many of these taxa likely evolved in the absence of strong predation selective pressure. The absence of evolutionary history with a certain predator type results in greater vulnerability of endemic taxa (Kats and Ferrer, 2003). Likely, the extinct rail lineage of Hawaii, of which 11 species occurred prehistorically (Boyer, 2008), would have been the primary consumers of leaf litter arthropods (Ziegler, 2002). The mode of foraging employed by rails is much different than scincid lizard actively foraging from within the litter (Lunney et al., 1989; Wapstra and Swain, 1996). The Guam rail (*Gallirallus owstoni*) and the Laysan rail (*Porzana palmeri*) used an ambush method from above the litter in order to capture arthropods (Baldwin, 1947; Jenkins, 1979). The introduction of rats by early Polynesians likely replaced the rails as the primary vertebrate predator on leaf litter arthropods. Around this time, three species of skinks were also introduced by Polynesians that could have impacted the community. The rapid replacement of these skinks upon the introduction of *L. delicata* suggest both that *L. delicata* is a better competitor in this microhabitat and that they are utilizing the food resources differentially than the introduced rats.

The unique geography of the Hawaiian islands resulted in a diverse set of endemic habitats that ranged from sea level to the top of Mauna Kea at an elevation of 4,205 meters. The islands of Hawaii arose from the ocean sequentially through volcanic activity followed by

erosion that created ridges and valleys isolated from each other. This separation combined with extreme rainfall gradients has driven the speciation across taxa and resulted in unique arthropod communities found within distinct native habitats (Simon, 1987). However, much of this native habitat in Hawaii has decreased for a number of reasons including agriculture (Dye, 1994; Blackmore and Vitousek, 2006), logging (Jenkins, 1983), and invasive species of both plants and animals (Huenneke and Vitousek, 1990; Nogueira-Filho et al., 2009). Today much of the native habitat that is left is found in mid (above 600m) and higher elevation areas of the islands, isolated from regular human perturbation and development. Although *L. delicata* is known to thrive in urban habitats, it is also found in other areas provided there is sufficient leaf litter and open basking sites. Occurrence records and reports from Baker (1979) show that in Hawaii *L. delicata* can be found both in lower disturbed nonnative habitats and in higher elevation native refugia. With the high elevation record of all reptiles, not just skinks, *L. delicata* has been able to invade native areas inaccessible even to the earlier introduced skink species.

For this reason, many endemic terrestrial arthropods that persist in native habitats may be especially vulnerable to *L. delicata*. In many of these native sites, rodents are controlled to protect nesting native forest birds and endemic tree snails. This has led to higher observed densities of *L. delicata* (pers. obs.) but the effects of such high densities remain unknown. The lack of formal knowledge on the breadth and preference in the diet of *L. delicata* both in its native range and in Hawaii leaves a large gap in knowledge for this overlooked invasive species.

The feeding ecology of any species is influenced by morphology. For small lizards, limb length and head shape affect the type of prey consumed. Limb length influences the agility and speed utilized to catch prey (Miles, 1994), and head shape influences the ability to grasp and consume prey (Kohlsdorf et al., 2008). Head size in particular has been shown to vary with differences in diet for a variety of lizard species (Herrel et al., 2001, 2006; Costa et al., 2008). The correlation of diet with morphological differences suggests that population differences in diet for a small lizard such as *L. delicata* may be confounded by differences in morphology.

Therefore, in this study, we first tested the hypothesis that there are differences in the diet of *L. delicata* across sites in Hawaii arising from differences in arthropod abundances in nonnative versus native sites. We then tested the confounding of morphology by assessing differences in limb length and head size among these sites. The last hypothesis tested is that *L. delicata* is preferentially consuming certain taxa, when controlling for arthropod proportions compared to the available leaf litter arthropod community. As a generalist predator, we expect to see differences in exploited prey if there are differences in arthropod communities in the leaf litter at sites. We also expected many orders to be represented in the diet with very few eaten preferentially and similarly very few avoided. Finally, to address predation by *L. delicata* on

native arthropod fauna across habitats in Hawaii, we identified known endemic taxa in the gut contents and highlighted orders with high representation in the native Hawaiian terrestrial arthropod fauna.

3.2 Methods

3.2.1 Study Locations

Three locations across the island of Oahu were chosen as study sites to investigate the feeding ecology of *L. delicata* in its invasive range. The first two, Pahole Natural Area Reserve and Puu Hapapa, are mid-elevation native mesic forests in the Waianae mountain range (731 m and 853 m elevation). The Pahole study area is located within a protected natural reserve which has a mean annual temperature of 20.4°C and rainfall of 231 cm. The habitat within the site is mixed native forest with mainly the dominate native trees ohia (*Metrosideros polymorpha*), koa (*Acacia koa*), alaa (*Pouteria sanwicensis*) and aulu (*Pisonia sandwicensis*) scattered with nonnative christmasberry (*Shinus terebinthifolia*), and guava (*Psidium guajava*) among others. The Puu Hapapa study site had similar annual weather with a mean temperature of 20.1°C and 272 cm of rainfall. The habitat is a similar mixed native site with an additional small native tree, mamaki (*Pipturus albidus*), and the same nonnative assemblage but with a higher proportion of guava. The third site, Tantalus, is a nonnative forest area in the Koolau range adjacent to residential area. This plot has a similar mean annual temperature of 21.1°C and slightly more rainfall at 402 cm. The habitat in the study area consists of a mix of nonnative plants, such as christmasberry, guava, fiddlewood (*Citharexylum spinosum*), avocado (*Persea americana*), and cinnamon (*Cinnamomum verum*), with a few scattered native trees such as ohia and koa. At each site, a 0.25 ha plot was sampled for available arthropods and individuals of *L. delicata*.

3.2.2 Animal Sampling

At each of the three sites, Puu Hapapa, Tantalus, and Pahole, we captured adults of *L. delicata* by hand or pitfall trap. Populations at Puu Hapapa and Pahole were of sufficient densities that hand trapping was the only method required. Low densities at Tantalus required pitfalls to capture eleven of the fourteen individuals used in this study. The pitfall traps used were steel cans with a diameter of 157 mm and 178 mm in depth. They were placed flush to the ground in areas of high skink activity with mesh drift fences one meter in length. Traps were checked every four hours and left open only during the morning and afternoon to ensure that food eaten was properly assessed.

Individuals were then brought to the lab and euthanized according to State of Hawaii Department of Agriculture injurious species regulations, and in accordance with IACUC Protocol 21-2184. Each individual was measured, sexed, and had the stomach removed for gut content analysis. All identifiable arthropod fragments were counted and the minimum, or most conservative number of individuals possible, was used for each arthropod count (e.g., three elytra for a given species would be counted as two individuals). Individuals with no stomach contents were removed from analysis leaving 14 individuals from Tantalus and Puu Hapapa, and 18 individuals from Pahole. The total number of identified arthropods across these 46 skinks was 237.

3.2.3 Environmental Sampling

Invertebrates were collected using two methods: pitfall traps and leaf litter collection from the three sites: Tantalus, Pahole, and Puu Hapapa on the island of Oahu. Each site was visited multiple times from May 2013 until September 2014. The visits were spread across the wet and dry seasons to account for natural fluctuations in the arthropod community.

Five pitfall traps per visit were set up at random locations within each study site. Each trap had a diameter of 9 cm and the bottom was filled with 50 mL propylene glycol. The traps were left for seven days and then collected to assess arthropods over an extended time frame. Once collected, arthropods were taken to the lab and identified to the lowest taxonomic level possible. All individuals identified to order were used in this study. Both Puu Hapapa and Pahole sites were sampled on six occasions for a sample size of 28 and 30 respectively. The two missing samples from Puu Hapapa were washed out by heavy rain. The Tantalus site was sampled on three occasions with a total of 11 pitfalls recovered with multiple losses due to feral pig damage. In spite of the trap losses, the total number of arthropods identified in pitfall traps was 31,237.

To collect arthropods in leaf litter, a 0.3 m by 0.3 m quadrat was randomly placed in five locations at each site, and all leaf litter contained in that sample was removed. These five samples were then pooled in a large container and thoroughly mixed. Two liters of the mixed leaf litter were then removed and brought to the lab. Arthropods were extracted from the leaf litter using a Berlese funnel trap. We identified each arthropod to the lowest possible taxonomic level. Overall, sixteen pooled leaf litter samples were used in this study accounting for 1,731 total arthropods. The Puu Hapapa site had seven collections, Pahole had six collections, and Tantalus had three collections.

3.2.4 Site Difference

We examined whether differences in diet occur among sites in order to determine whether *L. delicata* is consuming prey resources differently across Oahu. All arthropods from the gut analysis of stomach contents of *L. delicata* were grouped at the order level within each site. A Pearson’s chi-square test was performed to assess the association between the three sites and the proportion of orders consumed. All orders with less than five individuals in the diet for all sites were removed before this analysis was performed (Table 3.2).

Differences in abundance of available prey at each site were analyzed to determine whether food resource availability differed across Oahu; if not, available prey could be pooled. This was done both for leaf litter and pitfall sampling approaches to determine if differences could be detected. All arthropods for a given order were pooled within each site. For both of the sampling methods, a Pearson’s chi-square test was performed to identify an association between the three sites and orders of prey available. All orders with less than 5 individuals across all sites were omitted for this analysis (Table 3.3, Table 3.4). However, all orders in the pitfall analysis were of sufficient sample size to be included in the chi-squared test.

3.2.5 Body Measurements

All skinks captured were measured using standard head and limb characters for lizards. Head measurements included head width, head length, interocular width, internare width, and ocular-nare distance. We measured forelimbs and hindlimbs separately. Forelimb measurements were humerus length, radia-ulna length, and longest carpus length. Hindlimb measurements were femur length, tibia-fibula length, and longest tarsus length. All morphological measurements were corrected for snout-vent length using the Leonart and Thorpe method (Eq. 3.1) to control for different allometries among populations (Thorpe, 1975; Leonart et al., 2000). This method was shown to effectively control for variation due to size compared to other methods of correction (Reist, 1985) and was preferable when allometries varied among groups (Reist, 1986). This has been shown to be effective in invasive reptiles in Hawaii where a population’s morphology may be affected differently in response to environmental factors (Van Kleeck et al., 2015).

$$Y^* = Y_i \left(\frac{SVL_m}{SVL_i} \right)^b \quad (3.1)$$

The within group size corrected head shape variables were log transformed and a principal component analysis was performed (PCA) to reduce the variables to one axis. The first

principal component consisted of 69% of the variation and represents a positive combination of all measurements. A two-way ANOVA for the three sites and two sexes with an interaction term was performed on the first principal component.

The within group corrected limb length variables were combined to get total relative forelimb length and total relative hindlimb length. The total relative lengths were each log transformed and separate two way ANOVAs were performed. Both used the site and sex variables as main terms, as well as the interaction term.

3.2.6 Preference Index

Both the available and exploited arthropod prey were separated by site in order to assess the preference exhibited for each by *L. delicata*. Within each site, the terms in Table 3.1 were calculated. This was repeated for both sampling methods, pitfall and leaf litter. We calculated the foraging ratio (w_i) which is the proportion of available prey that are consumed for a particular arthropod order present in the diet of *L. delicata* at the three sites (Eq. 3.2; from Manly et al., 2002). This equation pools data from all individuals in the population and does not include variation between individuals per se. Confidence intervals for this measure were constructed by first calculating the variance of w_i (Eq. 3.3). This measure incorporates the variation among individuals to accurately estimate the population variance (Manly et al., 2002). Since w_i has an approximately normal distribution, the z statistic with a Bonferroni correction for the number of confidence intervals was constructed within each site (I) (Eq. 3.4) .

$$\hat{w}_i = \frac{(U_{i+}/U_{++})}{\pi_i} \quad (3.2)$$

$$var(\hat{w}_i) = \left(\frac{\sum_{j=1}^n (\frac{U_{ij}}{\pi_i} - \hat{w}_i U_{+j})^2}{(n-1)} \right) \left(\frac{n}{U_{++}^2} \right) \quad (3.3)$$

$$\hat{w}_i \pm Z_{(\alpha/2I)} se(\hat{w}_i) \quad (3.4)$$

The confidence intervals were used to indicate which orders were being avoided ($w_i < 1$), consumed at the same proportion as the available ($w_i = 1$), and consumed at a higher proportion than available ($w_i > 1$). This was then compared for each site and between sampling methods.

3.3 Results

3.3.1 Site Differences

The results of the Pearson's chi-square tests for differences in diet among sites showed that *L. delicata* is consuming arthropod orders at different proportions across Oahu ($\chi^2_{18} = 80.3$, $p < 0.00001$; Table 3.2). These differences were driven by the two native sites, Puu Hapapa and Pahole, consuming higher than expected spiders, no springtails, and lower than expected true bugs. *L. delicata* at Pahole consumed more flies than expected and at Tantalus was differentiated by consuming less spiders, more springtails, and greater than expected hymenopterans (Table 3.2).

The Pearson's chi-square for the available prey to *L. delicata* in the environment based on leaf litter sampling showed a difference among sites in the proportions present ($\chi^2_{24} = 550.73$, $p < 0.00001$; Table 3.3). These difference were driven by the Pahole site having more than expected Acari, Hymenoptera, and Gastropoda and lower than expected values for the rest of the orders, with the exception of approximately even values for Araneae. Puu Hapapa showed a reverse trend with Acari, Hymenoptera, and Gastropoda having lower than expected proportions and the rest of the groups above expected with the exception of even values for Orthopterans. Tantalus had higher than expected proportions for Acari, Gastropoda, and Hemiptera. The rest were approximately even with the expected distributions except for low proportions of Hymenopterans and Amphipods (Table 3.3).

The pitfall traps also showed a difference in available prey in the environment ($\chi^2_{36} = 3983.6$, $p < 0.00001$; Table 3.4). Both Tantalus and Puu Hapapa showed higher than expected counts for Amphipoda, Chilopoda, Collembola, Diplopoda and Isopoda with lower counts in Acari, Diptera, and Thysanoptera. Tantalus also had higher than expected counts in Araneae but low totals in Hemiptera and Lepidoptera. Pahole showed the reverse trend of Puu Hapapa again with high counts in Acari, Dermaptera, Diptera, Lepidoptera, Psocodea, and Thysanoptera compared to lower than expected counts in Amphipoda, Chilopoda, Collembola, Diplopoda, Hemiptera, Isopoda, and Orthoptera. Puu Hapapa was unique in the high counts of Coleopterans and Hemipterans but low counts of individuals of Orthoptera and Araneae. Only Pahole showed any Blattodea present. The counts observed for gastropods were very close to the expected for all three sites (Table 3.4).

3.3.2 Body Measurements

Comparisons of the within group size corrected head measures showed no interaction between sex and site differences nor did the comparison show an effect of site on the first principal component (Table 3.5). However, there was an effect of sex on head shape owing to sexual dimorphism. Similar results were obtained for the two limb measurements with both forelimb and hindlimb showing no effect of the interaction of sex and site nor site alone. Both forelimb and hindlimb also showed a significant effect of sex (Table 3.6; Table 3.7).

3.3.3 Preference Index

The preference index calculations showed a number of trends across orders, sampling types and sites (Figure 3.1). Over sixteen different orders were consumed by *L. delicata* in Hawaii. *L. delicata* positively selected for spiders in all sites regardless of the sampling method of available prey. Similarly, the centipedes were preyed on with positive selection with the exception of the leaf litter Tantalus cell which showed proportional consumption. At both the native sites, Pahole and Puu Hapapa, amphipods were negatively selected against regardless of sample method. Tantalus indicated equal or positive selection of Amphipoda. Dipterans were predated at an equal proportion to their availability for all sites when looking at the pitfall sampling method, which was able to adequately sample these flying insects. Hemipterans were consumed either equally to their environmental proportion or positively selected for in all cases except for the Tantalus leaf litter. Lepidopterans were consumed at the proportion that they were encountered except for positive selection at Puu Hapapa for the pitfall method. Hymenopterans were dominated by ant counts in both the diet and the environment. These showed positive selection at the Tantalus site, where ants were common in the diet and were absent or avoided at Pahole and Puu Hapapa respectively. The last major taxa with high observed numbers were the Isopods which showed the most variability across sampling methods and sites. The Isopods showed similar absolute proportions in the diet (Table 3.2) but were variable in the environmental counts based on site and sampling method (Table 3.3; Table 3.4).

Absences of orders in the gut contents appeared during the analysis of preference index. Members of Collembola, Diplopoda, Dermaptera, and Orthoptera were all only found in the stomach contents at one of the sites (Figure 3.1). Individuals of Collembola were found in the diet at Tantalus which showed the lowest counts compared to the expected in the environment for leaf litter. Sampling at Puu Hapapa showed the most Collembola for both methods but these did not appear in the diet. Dermapterans only appeared in the diet at Tantalus despite being plentiful at Pahole in the pitfall sampling. Diplopods only showed up in the diet at

Pahole which had the lowest observed versus expected counts for both leaf litter and pitfall methods. Only a single individual orthopteran was documented at Puu Hapapa despite being plentiful at Tantulus.

3.4 Discussion

As was expected, *L. delicata* in Hawaii did show differences in exploited prey across sites and this corresponded to differences in available prey in this species' habitat, the forest floor and leaf litter. Therefore impacts are likely to be heterogeneous across not only Oahu, but also the rest of the Hawaiian Islands. Lack of differences in morphology in both head shape and limb length among sites suggests that diet differences are not driven by difference in feeding mode or ability to capture certain prey. Likewise selective forces driving changes in functional morphology may not have exerted sufficient evolutionary pressure to result in measurable differences among sites. *L. delicata* has been established on Oahu for over 100 years (see Chapter 1) and this should be a sufficient amount of time for a founder population to diverge if strong selection forces on predation ability were encountered across sites (Van Kleeck et al., 2015). Therefore, the differences in exploited prey by *L. delicata* in this study are likely behavioral shifts such as functional responses or an artifact of the differences in availability of prey among the three sites. In addition, nutritional factors, ease of digestion, ability to catch prey, and presence of toxins as chemical defense may also play roles leading to differences between available versus exploited prey.

The findings of this study support previous suggestions that *L. delicata* is a generalist predator. Sixteen total arthropod orders were found in the stomach of skinks collected in Hawaii, a comparable number to the seventeen recorded by Lunney et al. (1989) in Australia. Only Chilopoda and Araneae were consumed at a higher proportion than they were available for almost all method and site combinations, and no other taxa present in the environment were avoided to this degree. Prey taxa present in the diet at only one site were also rare in the available prey stock. For example, only a single individual skink preyed on Collembola and Diplopoda. This is expected under a Type III functional response curve (Holling, 1959) where rare prey are only consumed opportunistically as they are encountered but at a diminished level to availability due to prey switching. Often stomach contents would be filled with a single taxon. This could lead to a Type III response by limiting opportunities to encounter rare prey while unsatiated.

The two native sites with very similar habitat composition, Pahole and Puu Hapapa, exhibited opposite trends in the proportion of available prey in the environment for each order. This suggests that there is not a specific native terrestrial arthropod community makeup for mixed

mesic forests on Oahu. However, the agreement observed in the preference indices suggests that *L. delicata* selected, avoided, or proportionally exploited the arthropod communities in the same way at both sites (Figure 3.1). The nonnative site, Tantalus, showed uniqueness from both of the native sites but aligned closer to Puu Hapapa for orders of available prey. However, lack of avoidance of any prey order in the diet at Tantalus coupled with the largest breadth in orders consumed suggests that they are utilizing arthropods differently in this nonnative site. The lack of rare species or less vulnerable endemic taxa at these locations could result in this more generalist diet.

The preference for spiders across all three study sites is alarming in terms of conservation status for native spiders in Hawaii. Of the known endemic radiations of spider families, Lycosidae (Gertsch, 1973), Theridiidae (Gillespie and Rivera, 2007), Linyphiidae (Hormiga et al., 2003), Philodromidae (Gillespie et al., 1998), Oonopidae (Suman, 1965), Salticidae (Arnedo and Gillespie, 2006), Thomisidae (Garb, 1999), and Tetragnathidae (Gillespie et al., 1997), only Philodromidae was not represented in the gut contents of *L. delicata*. Although these individuals in the gut samples were not identified as being native species except for the tetragnathids and the oonopids (Table 3.9), the generalist nature shown by *L. delicata* suggests that all members of these orders that occupy the leaf litter at some life stage are vulnerable to predation by *L. delicata*.

The positive selection for centipedes also is a cause for concern. The chilopods are known for their cosmopolitan distribution even at the species level. In Hawaii, there is a similar trend but there exists at least six endemic species (Zaparoli and Shelley, 2000; Shelley, 2000; Bonato et al., 2004). These endemic centipedes are all small in size at less than 10 mm, making them similar in length to those found in the diet of *L. delicata*. This group is understudied in Hawaii and globally which makes evaluation of diversity and thus the impacts of the plague skink difficult to assess. The preferential consumption of these species by a widespread invasive lizard suggests that the centipedes in Hawaii are especially vulnerable and further study of this group as suggested by Zaparoli and Shelley (2000) should be conducted as soon as possible to investigate this diversity before it is lost.

The relatively small size of prey consumed by *L. delicata*, usually less than one centimeter in total body length, led to a significant proportion of the diet consisting of juvenile and subadult prey individuals. At least twelve juvenile individuals were present in the diet (Orders: Leptidoptera, Araneae, Hemiptera, and Orthoptera) representing 5% of the entire diet. The presence of juveniles in the diet suggests that the impact of *L. delicata* may not be restricted to only diminutive adult arthropods that occur in the leaf litter. Removal of individuals that have not yet had the opportunity to reproduce could have devastating demographic impacts on arthropod as well as gastropod populations that overlap in habitat with the plague skink. In addition, insular island lineages tend to have reduced fecundity and reproductive

output relative to continental sister taxa, and are thus often incapable of maintaining viable population sizes in the face of invasive predators. And to compound all of these concerns, native spiders, insects and centipedes in the size class favored by skinks (<1.0 cm) are poorly described due to their small size, and therefore their conservation status is largely unknown.

Identifying native arthropods is difficult since there is an absence of information about many groups throughout the islands. Positive identification often requires a specialist for a particular group in Hawaii. This difficulty coupled with the many juvenile individuals collected in the study made it impossible to fully determine the amount of native arthropods in the diet or environment. However, based on the individuals that were positively identified as native, *L. delicata* consumed 4.4% native arthropods across all sites at a minimum (see Table 3.8). This is critical information because we know that *L. delicata* is distributed across Hawaii and at high elevation native sites (Baker 1979; see Chapter 1). Even if this minimum estimate was accurate (i.e. none of the unidentified species from families with high endemism are truly native), this still constitutes a large overall effect on the native arthropod community. Lever (2003) reports extraordinarily high densities of *L. delicata* in the invasive New Zealand range and similarly Baker (1979) estimated a density of 300-400 in 100 m^2 a suburban park on Oahu. We did see fairly dense populations especially at our native sites with ongoing rodent control programs but not to the extreme documented by Baker. However, even at reasonable density estimates, the take on native arthropods is substantial. Unfortunately, the conservation status of the majority of native terrestrial arthropods in general is unknown (Gagne, 1982) due in part to the large degree of taxonomic ignorance (Howarth, 1990) and thus likely underestimated (Redak, 2000) making it difficult to determine the potential impact of *L. delicata* on biodiversity for this community.

This is the first study to quantify and formally document the generalist predatory behavior of *L. delicata* and the first to document the predation on native arthropods in its invasive range. Perhaps unsurprisingly as they are documented as generalist predators, skinks are consuming small (<1.0cm length) invertebrate prey across a variety of native and nonnative forest types. But even in forests that are considered nonnative, new species of endemic micro-invertebrates are still being described (Kawahara and Rubinoff, 2012), and should therefore not be dismissed as unimportant areas for conservation and management of invasive taxa. The microfauna of Hawaii are especially vulnerable because many of these taxa are understudied or unknown. Therefore there is also a high likelihood that the effects of skinks on arthropod biodiversity have been occurring over decades, and long before we were aware of its establishment. This study indicates that the vast majority of diminutive invertebrates in the leaf litter are potential prey and that the presence of the invasive *L. delicata* in native understories should not be overlooked, and that targeted control efforts for this voracious invasive lizard are warranted.

3.5 Figures and Tables

Table 3.1: List of terms used for calculating the preference index and confidence intervals (Eq. 3.2, 3.3, and 3.4).

Term	Definition
A_i	Number of available resource units (prey) in category i
A_+	Total amount of available resource units (number of prey)
U_{i+}	A_i/A_+ Proportion of available resources unit (proportion of prey) in category i
U_{++}	Total number of used resource units (prey consumed)
π_i	Number of used resource units (prey consumed) in category i of sample
U_{+j}	Number of used resource units (prey consumed) by animal j in the sample
U_{ij}	Number of used resource units (prey consumed) by animal j in category i in the sample
w_i	Proportion of available resource units (prey) in category i that are used (consumed)

Table 3.2: Counts of arthropods in the stomach contents of *L. delicata* grouped by order for the three study sites. Expected counts from Pearson's chi square in parentheses.

Order	Tantalus	Pahole	Puu Hapapa
Acari	1	-	1
Amphipoda	13 (9.5)	4 (6.5)	7 (13)
Araneae	10 (21.1)	21 (14.3)	22 (17.6)
Blattodea	-	-	1
Chilopoda	2 (2.8)	2 (1.9)	3 (2.3)
Coleoptera	2 (3.5)	3 (2.4)	4 (3.0)
Collembola	19 (7.5)	- (5.1)	- (6.3)
Dermaptera	1	-	-
Diplopoda	-	4	-
Diptera	3 (8.3)	11 (5.7)	7 (7.0)
Hemiptera	2 (4.8)	3 (3.2)	7 (4.0)
Hymenoptera	17 (7.2)	- (4.8)	1 (6.0)
Isopoda	18 (19.5)	13 (13.2)	18 (16.3)
Lepidoptera	1 (2.8)	2 (2.3)	4 (2.3)
Orthoptera	-	-	1
Phasmatodea	-	-	-
Psocodea	-	-	-
Pseudoscorpiones	1	-	-
Unknown	-	-	-
Totals	89	65	75

Table 3.3: Counts of arthropods (and Gastropoda) from leaf litter collections grouped by order (or class) for the three study sites. Expected counts from Pearson's chi square in parentheses.

Order (or Class)	Tantalus	Pahole	Puu Hapapa
Acari	37 (29.5)	184 (105.1)	10 (96.3)
Amphipoda	10 (28.0)	114 (99.7)	95 (91.3)
Araneae	2 (4.0)	14 (14.1)	15 (12.9)
Blattodea	-	-	-
Chilopoda	1 (1.8)	1 (6.4)	12 (5.8)
Coleoptera	4 (2.3)	4 (8.2)	10 (7.5)
Collembola	2 (5.6)	9 (20.0)	33 (18.4)
Dermaptera	1	1	2
Diplopoda	1 (3.7)	4 (13.2)	24 (12.1)
Diptera	1	3	1
Gastropoda	43 (15.9)	48 (56.4)	33 (51.7)
Hemiptera	12 (4.5)	3 (15.9)	20 (14.6)
Hymenoptera	4 (24.9)	168 (88.7)	23 (81.3)
Isopoda	70 (65.7)	124 (233.9)	320 (214.4)
Lepidoptera	3 (5.11)	9 (18.2)	28 (16.7)
Orthoptera	4 (0.89)	- (3.2)	3 (2.9)
Psocodea	-	1	1
Thysanoptera	-	2	1
Unknown	-	14	-
Totals	194	704	634

Table 3.4: Counts of arthropods (and Gastropoda) from pitfall traps grouped by order (or class) for the three study sites. Expected counts from Pearsons chi square in parentheses.

Order (or Class)	Tantalus	Pahole	Puu Hapapa
Acari	38 (84.5)	515 (390.6)	187 (264.8)
Amphipoda	531 (368.1)	1274 (1700.8)	1417 (1153.1)
Araneae	161 (116.0)	576 (535.8)	278 (363.3)
Blattodea	- (3.7)	32 (16.9)	- (36.5)
Chilopoda	6 (2.1)	2 (9.5)	10 (6.4)
Coleoptera	38 (235.3)	1171 (1087.4)	851 (737.3)
Collembola	328 (276.1)	1128 (1275.8)	961 (865.0)
Dermaptera	34 (40.8)	305 (188.4)	18 (127.8)
Diplopoda	108 (13.4)	2 (61.8)	115 (41.9)
Diptera	108 (384.1)	2261 (1774.7)	993 (1203.2)
Gastropoda	344 (376.0)	1770 (1737.2)	1177 (1177.8)
Hemiptera	78 (114.6)	327 (529.5)	598 (359.0)
Hymenoptera	273 (244.7)	1163 (1130.7)	706 (766.6)
Isopoda	464 (339.6)	1397 (1569.4)	1112 (1064.0)
Lepidoptera	34 (55.4)	320 (256.0)	131 (173.6)
Orthoptera	318 (45.1)	2 (208.5)	75 (141.4)
Psocodea	- (17.8)	122 (82.3)	34 (55.8)
Thysanoptera	14 (40.2)	330 (185.8)	8 (126.0)
Unknown	-	2	-
Totals	2,769	12,797	8,675

Table 3.5: ANOVA table of the first principal component representing size corrected head shape based on site and sex differences with the interaction. Only the effect of sex was significant (in bold and starred).

	DF	F-value	P-value
Site	2	0.0074	0.993
Sex	1	4.3880	0.040 *
Interaction	2	0.012034	0.815
Error	75		

Table 3.6: ANOVA table of the size corrected and log transformed forelimb length based on site and sex differences with the interaction. Only the effect of sex was significant (in bold and starred).

	DF	F-value	P-value
Site	1	0.21	0.6507
Sex	1	14.1	0.00037 *
Interaction	1	0.093	0.7612
Error	64		

Table 3.7: ANOVA table of the size corrected and log transformed hindlimb length based on site and sex differences with the interaction. Only the effect of sex was significant (in bold and starred).

	DF	F-value	P-value
Site	1	0.68	0.41
Sex	1	4.87	0.031 *
Interaction	1	0.68	0.41
Error	64		

Table 3.8: Individual native arthropod taxa found in the stomach of *L. delicata* at each site.

	Tantalus	Pahole	Puu Hapapa
Araneae: Tetragnathidae	-	-	1
Araneae: Oonipidae	2	-	-
Hemiptera: Delphacidae	-	1	5
Pseudoscorpiones	1	-	-

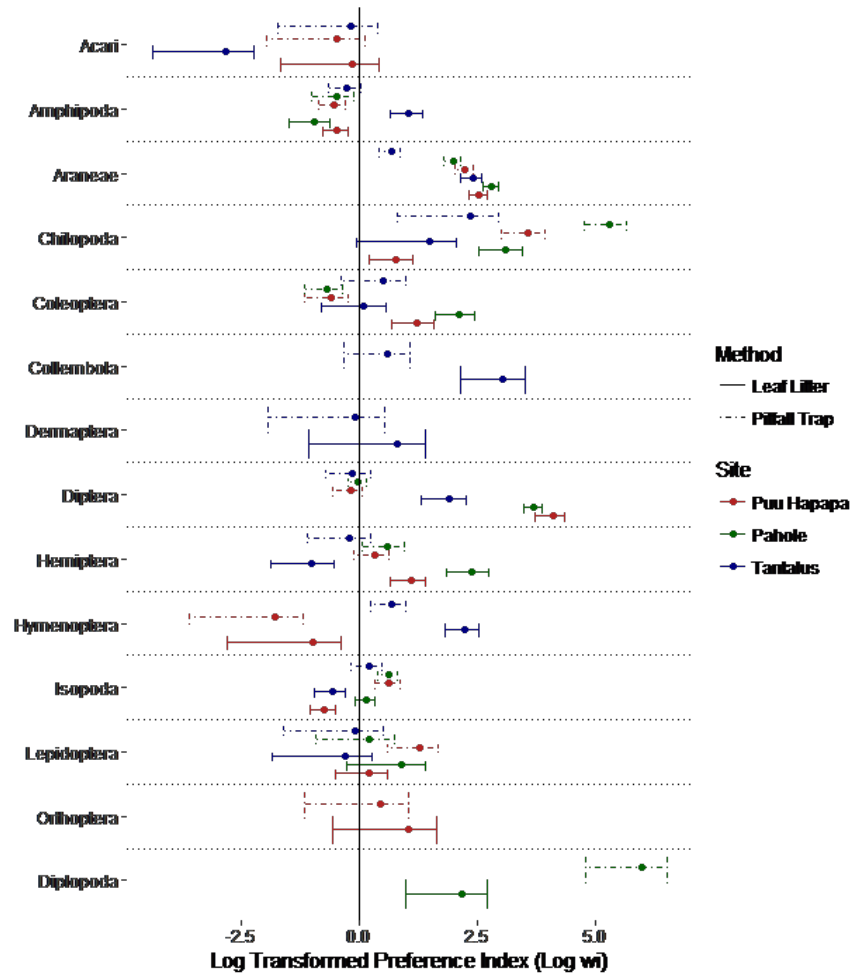


Figure 3.1: Log transformed preference index (w_i) with confidence intervals for all orders separated by the three sites and two methods. Solid lines represent values calculated from leaf litter sampling of available arthropods, and dashed lines represent pitfall trap values. The sites are distinguished by color: Puu Hapapa (red), Pahole (green), and Tantalus (blue). The zero vertical line represents no preference.

Chapter 4

Conclusions

4.1 Nature of the invasion of *Lampropholis delicata* in Hawaii

The plague skink, *Lampropholis delicata*, has been a successful invader in the Hawaiian islands over the past one hundred years. The second chapter of this thesis shows that the success is not from matching a similar ecological niche as in their native ranges, but from utilizing an novel environment outside from anything they experience in Australia. This led to poor predictive ecological niche models regardless of the geographic scope used from the native range. The low genetic diversity in Hawaii arising from the single introduction event suggests that behavioral and phenotypic diversity are the important driver of this success in Hawaii.

The investigation of diet specialization of *L. delicata* in the third chapter of this thesis indicates that the plague skink is a generalist feeder that is able to exploit many taxa of both introduced and endemic prey. This supports behavioral flexibility being an important component of success for *L. delicata* in Hawaii. The potential presence of a functional response to available prey further indicates that this invasive lizard is able to adjust to a new and changing habitat.

4.2 Management Implications

This study indicates that *L. delicata* is not food limited in Hawaii and has the potential to consume prey regardless of location. The generalist diet of this lizard means that the abundance of the plague skink is not regulated by the density of one or two important prey items.

Therefore, no significant population regulation occurs unless the entire arthropod community is impacted. Curbing the effects of this invasive species will require control efforts that remove individuals from the wild to prevent further expansion and population growth. The use of native and introduced arthropod prey items suggests that expansion and growth of populations in upper elevation native habitat can be facilitated by populations in disturbed and introduced habitats. As it is unlikely that complete eradication of a small and cryptic lizard would be feasible, the most effective management strategy would be continuous effort removal at vulnerable and important native habitat sites. This could be employed alongside current removal efforts of other invasive species such as Jackson's chameleons *Trioceros jacksonii xantholophus* and rats *Rattus rattus*.

The management and control of the plague skink in Hawaii is further warranted because of the increased fecundity that *L. delicata* experiences in its introduced range. The more mild seasonality in Hawaii compared to the native Australia range suggests that the trend toward multiple clutches per year likely occurs in Hawaii and is a major contributor to their success. Paired with a lack of competitors in the leaf litter microhabitat and few major predators, this increased fecundity is likely responsible for the high densities observed at some sites in Hawaii. Additionally, in areas where invasive rats are controlled, the densities can become alarmingly high (pers. obs.). These rats are likely the major predator of eggs, juveniles, and possibly adults at these sites limiting population sizes. Therefore any management action that reduces the density of rats should also incorporate a control regiment for *L. delicata* to prevent their population growth as well.

The consumption of native arthropods and the selection for vulnerable endemic taxa suggests that the presence of *L. delicata* in Hawaii is detrimental to the native community. The cryptic nature of this invasive lizard means that it is often overlooked and the diminutive size of its prey allows for its impact to be underestimated. However, our lack of a complete understanding of the native arthropod community of the leaf litter and the unique predation pressure that *L. delicata* creates for this community means that control of this invasive species is necessary.

4.3 Future Studies

Much is still unknown concerning the biology of *L. delicata* in Hawaii. In order to accurately assess population growth rates and the necessary levels of control, an understanding of the reproduction rate of *L. delicata* in Hawaii is needed. A systematic survey of time to first reproduction and number of clutches per year would allow for accurate estimates of population growth parameters. Baker (1979) laid the groundwork for these studies with a thorough

examination of clutch size across Hawaii. Additionally, modeling the potential range and future expansion of *L. delicata* in Hawaii using similar ENM methods but based on current distribution in the islands would help realize vulnerable areas for this invasive lizard. A survey of presence localities across all the major islands would be necessary for the accurate completion of this research. Currently, coverage is only sufficient for Oahu and Kauai.

The endemic arthropod community in Hawaii is known for its high endemism with over 5000 described endemic terrestrial arthropod species (Miller and Eldredge, 1996). However, there are many more undescribed species (Howarth, 1990) with many of these being diminutive and uncharismatic fauna. An assessment of the native arthropod species present in the leaf litter community at sites where *L. delicata* is present would help quantify the impact that this lizard is having.

Finally, in order to adequately control *L. delicata* in Hawaii, feasibility studies need to be performed to identify the most effective removal efforts. The tendency to communally nest in crevices with higher than ambient humidity levels may allow for the use of artificial nest boxes to remove whole clutches from the habitat. This could be paired with removal of adults using drift fences and pitfall traps similar to those employed by this study. However, until these efforts are explored in a systematic study and paired with knowledge of reproductive rates in Hawaii, it is unclear how effective the removal efforts will be. Regardless of the next steps taken, it is clear that the invasiveness of the plague skink in Hawaii should not be ignored.

Bibliography

- Adhikari, D., S. K. Barik, and K. Upadhaya. 2012. Habitat distribution modelling for reintroduction of *Ilex khasiana* Purk., a critically endangered tree species of northeastern India. *Ecological Engineering* **40**:37–43.
- Allouche, O., A. Tsoar, and R. Kadmon. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of applied ecology* **43**:1223–1232.
- Apps, C. D., B. N. McLellan, J. G. Woods, and M. F. Proctor. 2004. Estimating grizzly bear distribution and abundance relative to habitat and human influence. *Journal of Wildlife Management* **68**:138–152.
- Arnedo, M. A., and R. G. Gillespie. 2006. Species diversification patterns in the Polynesian jumping spider genus *Havaika* Prószyński, 2001 (Araneae, Salticidae). *Molecular phylogenetics and evolution* **41**:472–495.
- Austin, M. 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecological modelling* **200**:1–19.
- Baker, J. K. 1979. The rainbow skink, *Lampropholis delicata*, in Hawaii. *Pacific Science* **33**:207–212.
- Baker, K. 1976. The occurrence and ecological significance of metallic skinks on the islands of Hawai'i and Kaua'i. *Proceedings of Natural Science, Hawaii Volcanoes National Parks* **1**:11–17.
- Baldwin, P. H. 1947. The life history of the Laysan Rail. *The Condor* **49**:14–21.
- Barve, N., V. Barve, A. Jiménez-Valverde, A. Lira-Noriega, S. P. Maher, A. T. Peterson, J. Soberón, and F. Villalobos. 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecological Modelling* **222**:1810–1819.
- Beard, K. H. 2007. Diet of the invasive frog, *Eleutherodactylus coqui*, in Hawaii. *Copeia* **2007**:281–291.

- Beard, K. H., and W. C. Pitt. 2006. Potential predators of an invasive frog (*Eleutherodactylus coqui*) in Hawaiian forests. *Journal of Tropical Ecology* **22**:345–347.
- Bellard, C., P. Cassey, and T. M. Blackburn. 2016*a*. Alien species as a driver of recent extinctions. *Biology letters* **12**:20150623.
- Bellard, C., P. Genovesi, and J. M. Jeschke. 2016*b*. Global patterns in threats to vertebrates by biological invasions. *Proc. R. Soc. B* **283**:20152454.
- Blackburn, T. M., P. Cassey, R. P. Duncan, K. L. Evans, and K. J. Gaston. 2004. Avian Extinction and Mammalian Introductions on Oceanic Islands. *Science* **305**:1955–1958.
- Blackmore, M., and P. M. Vitousek. 2006. Cattle Grazing, Forest Loss, and Fuel Loading in a Dry Forest Ecosystem at Pu'u Wa'a Wa'a Ranch, Hawai'i. *Biotropica* **32**:625–632.
- Bonato, L., D. Foddai, A. Minelli, and R. Shelley. 2004. The centipede order Geophilomorpha in the Hawaiian Islands (Chilopoda). *Bishop Museum Occasional Papers* **78**:13–32.
- Boyer, A. G. 2008. Extinction patterns in the avifauna of the Hawaiian islands: Hawaiian avian extinctions. *Diversity and Distributions* **14**:509–517.
- Chapple, D. G., C. J. Hoskin, S. N. Chapple, and M. B. Thompson. 2011. Phylogeographic divergence in the widespread delicate skink (*Lampropholis delicata*) corresponds to dry habitat barriers in eastern Australia. *BMC Evolutionary Biology* **11**:1–18.
- Chapple, D. G., K. A. Miller, K. Chaplin, L. Barnett, M. B. Thompson, and R. D. Bray. 2015. Biology of the invasive delicate skink (*Lampropholis delicata*) on Lord Howe Island. *Australian Journal of Zoology* **62**:498–506.
- Chapple, D. G., K. A. Miller, F. Kraus, and M. B. Thompson. 2013*a*. Divergent introduction histories among invasive populations of the delicate skink (*Lampropholis delicata*): has the importance of genetic admixture in the success of biological invasions been overemphasized? *Diversity and Distributions* **19**:134–146.
- Chapple, D. G., A. H. Whitaker, S. N. Chapple, K. A. Miller, and M. B. Thompson. 2013*b*. Biosecurity interceptions of an invasive lizard: origin of stowaways and human-assisted spread within New Zealand. *Evolutionary applications* **6**:324–339.
- Cheetham, E., J. S. Doody, B. Stewart, and P. Harlow. 2011. Embryonic mortality as a cost of communal nesting in the delicate skink. *Journal of Zoology* **283**:234–242.
- Chiaverano, L. M., and B. S. Holland. 2014. Impact of an invasive predatory lizard on the endangered Hawaiian tree snail *Achatinella mustelina*: a threat assessment. *Endangered Species Research* **24**:115–123.

- Clavero Pineda, M., and E. Garca-Berthou. 2005. Invasive species are a leading cause of animal extinctions. *Trends in Ecology and Evolution* **20**:110.
- Clerke, R. B., and R. A. Alford. 1993. Reproductive biology of four species of tropical Australian lizards and comments on the factors regulating lizard reproductive cycles. *Journal of Herpetology* **27**:400–406.
- Cogger, H. 2014. *Reptiles and amphibians of Australia*. Csiro Publishing, Sydney, Australia.
- Costa, G. C., L. J. Vitt, E. R. Pianka, D. O. Mesquita, and G. R. Colli. 2008. Optimal foraging constrains macroecological patterns: body size and dietary niche breadth in lizards. *Global Ecology and Biogeography* **17**:670–677.
- Cox, C. B., and P. D. Moore. 2005. *Biogeography: An Ecological and Evolutionary Approach* (6th edn). 7th edition. Blackwell Publishing, Oxford, UK.
- Downes, S. J., and R. Shine. 1999. Do incubation-induced changes in a lizard's phenotype influence its vulnerability to predators? *Oecologia* **120**:9–18.
- Dye, T. 1994. Population trends in Hawaii before 1778. *The Hawaiian Journal of History* **28**:1–20.
- Ehmann, H., and R. Strahan. 1992. *Encyclopedia of Australian animals: reptiles*. Angus & Robertson, Sydney, Australia.
- Eldredge, L. G., and S. E. Miller. 1995. How many species are there in Hawaii. *Bishop Museum Occasional Papers* **41**:3–18.
- Elith, J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**:129–151.
- Elith, J., and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* **40**:677–697.
- Elith, J., S. J. Phillips, T. Hastie, M. Dudk, Y. E. Chee, and C. J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and distributions* **17**:43–57.
- Forsman, A., and R. Shine. 1995. Parallel geographic variation in body shape and reproductive life history within the Australian scincid lizard *Lampropholis delicata*. *Functional Ecology* **9**:818–828.
- Franklin, J., K. E. Wejnert, S. A. Hathaway, C. J. Rochester, and R. N. Fisher. 2009. Effect of species rarity on the accuracy of species distribution models for reptiles and amphibians in southern California. *Diversity and Distributions* **15**:167–177.

- Freed, L. A., S. Conant, and R. C. Fleischer. 1987. Evolutionary ecology and radiation of Hawaiian passerine birds. *Trends in Ecology & Evolution* **2**:196–203.
- Gagne, W. C. 1982. Working towards an assessment of the conservation status of Hawaii's endemic arthropods, with an emphasis on the moths or lepidoptera. *Proc. 4th Conf. Nat. Sci. Hawaii* pages 63–72.
- Garb, J. E. 1999. An adaptive radiation of Hawaiian Thomisidae: Biogeographic and genetic evidence. *Journal of Arachnology* **27**:71–78.
- Gertsch, W. J. 1973. The cavernicolous fauna of Hawaiian lava tubes, 3. Araneae (spiders). *Pacific Insects* **15**:163–180.
- Gill, B. J., and A. H. Whitaker. 2001. *New Zealand frogs & reptiles*. David Bateman, Auckland.
- Gillespie, R. 2004. Community assembly through adaptive radiation in Hawaiian spiders. *Science* **303**:356–359.
- Gillespie, R. G., H. B. Croom, and G. L. Hasty. 1997. Phylogenetic relationships and adaptive shifts among major clades of Tetragnatha spiders (Araneae: Tetragnathidae) in Hawai'i. *Pacific Science* **51**:280–394.
- Gillespie, R. G., M. A. Rivera, and J. E. Garb, 1998. Sun, surf and spiders: taxonomy and phylogeography of Hawaiian Araneae. Pages 41–51 *in* 17th European Colloquium of Arachnology. British Arachnological Society, Burnham Beeches, Bucks, Edinburgh. Citeseer.
- Gillespie, R. G., and M. A. J. Rivera. 2007. Free-living spiders of the genus *Ariamnes* (Araneae, Theridiidae) in Hawaii. *Journal of Arachnology* **35**:11–37.
- Gillespie, R. G., and G. K. Roderick. 2002. Arthropods on islands: colonization, speciation, and conservation. *Annual review of entomology* **47**:595–632.
- Givnish, T. J., K. C. Millam, A. R. Mast, T. B. Paterson, T. J. Theim, A. L. Hipp, J. M. Henss, J. F. Smith, K. R. Wood, and K. J. Sytsma. 2009. Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proceedings of the Royal Society of London B: Biological Sciences* **276**:407–416.
- Godsoe, W. 2010. I can't define the niche but I know it when I see it: a formal link between statistical theory and the ecological niche. *Oikos* **119**:53–60.
- Greer, A. E. 1974. The genetic relationships of the Scincid lizard genus *Leiopisma* and its relatives. *Australian Journal of Zoology* **22**:1–67.
- Greer, A. E. 1989. *The biology and evolution of Australian lizards*. Surrey Beatty and Sons, Chipping Norton, N.S.W., Australia.

- HAR §13–124, 2014. List of Species of Injurious Wildlife in Hawaii. State of Hawaii, Division of Forestry and Wildlife.
- Helenurm, K., and F. R. Ganders. 1985. Adaptive radiation and genetic differentiation in Hawaiian *Bidens*. *Evolution* **39**:753–765.
- Herrel, A., R. V. Damme, B. Vanhooydonck, and F. D. Vree. 2001. The implications of bite performance for diet in two species of lacertid lizards. *Canadian Journal of Zoology* **79**:662–670.
- Herrel, A., R. Joachim, B. Vanhooydonck, and D. J. Irschick. 2006. Ecological consequences of ontogenetic changes in head shape and bite performance in the Jamaican lizard *Anolis lineatopus*. *Biological Journal of the Linnean Society* **89**:443–454.
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International journal of climatology* **25**:1965–1978.
- Holland, B. S., and R. H. Cowie. 2009. Land Snail Models in Island Biogeography: A Tale of Two Snails. *American Malacological Bulletin* **27**:59–68.
- Holland, B. S., S. L. Montgomery, and V. Costello. 2010. A reptilian smoking gun: first record of invasive Jacksons chameleon (*Chamaeleo jacksonii*) predation on native Hawaiian species. *Biodiversity and conservation* **19**:1437–1441.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist* **91**:385–398.
- Hormiga, G., M. Arnedo, and R. G. Gillespie. 2003. Speciation on a conveyor belt: sequential colonization of the Hawaiian Islands by Orsonwelles spiders (Araneae, Linyphiidae). *Systematic Biology* **52**:70–88.
- Hosmer, D. W., and S. Lemeshow. 2000. *Applied logistic regression*. Wiley, New York.
- Howard, R., I. Williamson, and P. Mather. 2003. Structural Aspects of Microhabitat Selection by the Skink *Lampropholis delicata*. *Journal of Herpetology* **37**:613–617.
- Howarth, F. G. 1990. Hawaiian terrestrial arthropods: an overview. *Bishop Museum Occasional Papers* **30**:4–26.
- Hueneke, L. F., and P. M. Vitousek. 1990. Seedling and clonal recruitment of the invasive tree *Psidium cattleianum*: Implications for management of native Hawaiian forests. *Biological Conservation* **53**:199–211.
- Huisman, J., and F. J. Weissing. 2001. Fundamental unpredictability in multispecies competition. *The American Naturalist* **157**:488–494.

- Hunsaker, D. I., and P. Breese. 1967. Herpetofauna of the Hawaiian islands. *Pacific Science* **21**:423–428.
- Hutchinson, M. N., M. B. Thompson, and J. R. Stewart. 2005. *Lampropholis delicata* (delicate skink, rainbow skink). Introduction. *Herpetological Review* **36**:450–451.
- James, F. C., R. F. Johnston, N. O. Wamer, G. J. Niemi, and W. J. Boecklen. 1984. The Grinnellian niche of the wood thrush. *American Naturalist* **124**:17–47.
- Jenkins, I. 1983. Hawaiian furniture and Hawaii's cabinetmakers, 1820-1940. Published for the Daughters of Hawaii by Editions Ltd, Honolulu, Hawaii.
- Jenkins, J. M. 1979. Natural history of the Guam Rail. *The Condor* **81**:404–408.
- Jordan, S., C. Simon, and D. Polhemus. 2003. Molecular systematics and adaptive radiation of Hawaii's endemic damselfly genus *Megalagrion* (Odonata: Coenagrionidae). *Systematic Biology* **52**:89–109.
- Joss, J. M. P., and J. A. Minard. 1985. On the reproductive cycles of *Lampropholis guichenoti* and *L. delicata* (Squamata: Scincidae) in the Sydney region. *Australian journal of zoology* **33**:699–704.
- Kambysellis, M. P., K.-F. Ho, E. M. Craddock, F. Piano, M. Parisi, and J. Cohen. 1995. Pattern of ecological shifts in the diversification of Hawaiian *Drosophila* inferred from a molecular phylogeny. *Current Biology* **5**:1129–1139.
- Kats, L. B., and R. P. Ferrer. 2003. Alien predators and amphibian declines: review of two decades of science and the transition to conservation. *Diversity and Distributions* **9**:99–110.
- Kawahara, A., and D. Rubinoff. 2012. Three new species of Fancy Case caterpillars from threatened forests of Hawaii (Lepidoptera, Cosmopterigidae, Hyposmocoma). *ZooKeys* **170**:1–20.
- Kohlsdorf, T., M. Grizante, C. Navas, and A. Herrel. 2008. Head shape evolution in Tropidurinae lizards: does locomotion constrain diet? *Journal of evolutionary biology* **21**:781–790.
- Kraus, F., 2003. Invasion pathways for terrestrial vertebrates. Chapter 4, pages 68–92 in G. M. Ruiz and J. T. Carlton, editors. *Invasive species: vectors and management strategies*. Island Press, Washington, DC.
- Kraus, F., E. W. Campbell, A. Allison, and T. Pratt. 1999. Eleutherodactylus frog introduction to Hawaii. *Herpetological Review* **30**:21–25.
- Kraus, F., and D. Preston. 2012. Diet of the Invasive Lizard *Chamaeleo jacksonii* (Squamata: Chamaeleonidae) at a Wet-Forest Site in Hawaii. *Pacific Science* **66**:397–404.

- Langerhans, R. B., J. H. Knouft, and J. B. Losos. 2006. Shared and unique features of diversification in Greater Antillean Anolis ecomorphs. *Evolution* **60**:362–369.
- Leach, A. D., M. S. Koo, C. L. Spencer, T. J. Papenfuss, R. N. Fisher, and J. A. McGuire. 2009. Quantifying ecological, morphological, and genetic variation to delimit species in the coast horned lizard species complex (*Phrynosoma*). *Proceedings of the National Academy of Sciences* **106**:12418–12423.
- Lever, C. 2003. *Naturalized reptiles and amphibians of the world*. Oxford University Press, Oxford.
- Liu, C., P. M. Berry, T. P. Dawson, and R. G. Pearson. 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* **28**:385–393.
- Liu, C., M. White, and G. Newell. 2011. Measuring and comparing the accuracy of species distribution models with presence-absence data. *Ecography* **34**:232–243.
- Lleonart, J., J. Salat, and G. J. Torres. 2000. Removing Allometric Effects of Body Size in Morphological Analysis. *Journal of Theoretical Biology* **205**:85–93.
- Losos, J., K. Warheit, and T. Schoener. 1997. Adaptive differentiation following experimental island colonization in Anolis lizards. *Nature* **387**:70–73.
- Losos, J. B., D. A. Creer, D. Glossip, R. Goellner, A. Hampton, G. Roberts, N. Haskell, P. Taylor, and J. Ettling. 2000. Evolutionary implications of phenotypic plasticity in the hindlimb of the lizard *Anolis sagrei*. *Evolution* **54**:301–305.
- Lunney, D., E. Ashby, J. Grigg, and M. O'Connell. 1989. Diets of Scincid Lizards *Lampropholis guichenoti* (Dumeril and Bibron) and *Lampropholis delicata* (De Vis) in Mumbulla State Forest on the South Coast of New South Wales. *Wildlife Research* **16**:307.
- Mack, R. N., D. Simberloff, W. Mark Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological applications* **10**:689–710.
- Manly, B. F. L., L. McDonald, D. Thomas, T. L. McDonald, and W. P. Erickson. 2002. *Resource selection by animals: statistical design and analysis for field studies*. Springer Science & Business Media.
- Mather, P. B. 1989. A Comparison of the Normal Habitats of Skinks of 3 Electrophoretically Distinguishable Forms of *Lampropholis-declivata* (Lacertilia, Scincidae) in South-Eastern-Queensland. *Wildlife Research* **16**:159–165.
- McCormack, J. E., A. J. Zellmer, and L. L. Knowles. 2010. Does niche divergence accompany allopatric divergence in *Aphelocoma* jays as predicted under ecological speciation?: insights from tests with niche models. *Evolution* **64**:1231–1244.

- McKeown, S. 1996. A field guide to reptiles and amphibians in the Hawaiian Islands. Diamond Head Publishing, Honolulu, Hawaii.
- Medeiros, M. J., and R. G. Gillespie. 2011. Biogeography and the evolution of flightlessness in a radiation of Hawaiian moths (Xyloryctidae: Thyrocopa). *Journal of biogeography* **38**:101–111.
- Menon, S., B. I. Choudhury, M. L. Khan, and A. T. Peterson. 2010. Ecological niche modeling and local knowledge predict new populations of *Gymnocladus assamicus* a critically endangered tree species. *Endangered Species Research* **11**:175–181.
- Mieszkowska, N., G. Milligan, M. T. Burrows, R. Freckleton, and M. Spencer. 2013. Dynamic species distribution models from categorical survey data. *Journal of animal ecology* **82**:1215–1226.
- Miles, D., 1994. Covariation between morphology and locomotory performance in sceloporine lizards. Pages 207–235 . Princeton University Press, Princeton.
- Miller, S., and L. Eldredge. 1996. Numbers of Hawaiian species: supplement 1. Bishop Museum Occasional Papers **45**:8–17.
- Morando, M., L. J. Avila, C. R. Turner, and J. W. Sites. 2007. Molecular evidence for a species complex in the patagonian lizard *Liolaemus bibronii* and phylogeography of the closely related *Liolaemus gracilis* (Squamata: Liolaemini). *Molecular phylogenetics and evolution* **43**:952–973.
- Moule, H., M. Michelangeli, M. Thompson, and D. Chapple. 2016. The influence of urbanization on the behaviour of an Australian lizard and the presence of an activity–exploratory behavioural syndrome. *Journal of Zoology* **298**:103–111.
- Murray, R. G., V. D. Popescu, W. J. Palen, and P. Govindarajulu. 2015. Relative performance of ecological niche and occupancy models for predicting invasions by patchily-distributed species. *Biological Invasions* **17**:2691–2706.
- Nishida, G. M., editor. 2002. Hawaiian terrestrial arthropod checklist. 4th edition. Bishop Museum, Honolulu, Hawaii.
- Nogueira-Filho, S. L. G., S. S. C. Nogueira, and J. M. V. Fragoso. 2009. Ecological impacts of feral pigs in the Hawaiian Islands. *Biodiversity and Conservation* **18**:3677–3683.
- Occhipinti-Ambrogi, A., and B. S. Galil. 2004. A uniform terminology on bioinvasions: a chimera or an operative tool? *Marine pollution bulletin* **49**:688–694.
- Oliver, J. A., and C. E. Shaw. 1953. The amphibians and reptiles of the Hawaiian Islands. *Zoologica* **38**:65–95.

- Olson, L. J., et al. 2006. The economics of terrestrial invasive species: a review of the literature. *Agricultural and Resource Economics Review* **35**:178.
- Owens, H. L., L. P. Campbell, L. L. Dornak, E. E. Saupe, N. Barve, J. Sobern, K. Ingenloff, A. Lira-Noriega, C. M. Hensz, C. E. Myers, and others. 2013. Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Ecological Modelling* **263**:10–18.
- Peace, J. E., 2004. Distribution, habitat use, breeding and behavioural ecology of rainbow skinks (*Lampropholis delicata*) in New Zealand. Master's thesis, University of Auckland, New Zealand.
- Pearson, R. G., and T. P. Dawson. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global ecology and biogeography* **12**:361–371.
- Pearson, R. G., C. J. Raxworthy, M. Nakamura, and A. Townsend Peterson. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of biogeography* **34**:102–117.
- Peterson, A. T. 2003. Predicting the geography of species invasions via ecological niche modeling. *The quarterly review of biology* **78**:419–433.
- Peterson, A. T., M. Papes, and M. Eaton. 2007. Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. *Ecography* **30**:550–560.
- Peterson, A. T., and J. Soberón. 2012. Integrating fundamental concepts of ecology, biogeography, and sampling into effective ecological niche modeling and species distribution modeling. *Plant Biosystems—An International Journal Dealing with all Aspects of Plant Biology* **146**:789–796.
- Peterson, A. T., J. Soberón, R. G. Pearson, R. P. Anderson, E. Martínez-Meyer, M. Nakamura, and M. B. Araújo. 2011. *Ecological Niches and Geographic Distributions* (MPB-49). Princeton University Press, Princeton, NJ.
- Phillips, S. J. 2008. Transferability, sample selection bias and background data in presence-only modeling: a response to Peterson et al.(2007). *Ecography* **31**:272–278.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological modelling* **190**:231–259.
- Pimentel, D. 2011. *Biological invasions: economic and environmental costs of alien plant, animal, and microbe species*. 2nd edition. CRC Press, Boca Raton, FL.

- Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological economics* **52**:273–288.
- Pitt, W., D. Vice, and M. Pitzler. 2005. Challenges of invasive reptiles and amphibians. *Wildlife Damage Management Conferences – Proceedings* **11**:112–119.
- Pratt, T. K., C. T. Atkinson, P. C. Banko, J. Jacobi, and B. L. Woodworth, editors. 2009. *Conservation biology of Hawaiian forest birds: implications for island avifauna*. Yale University Press, New Haven.
- Rawlinson, P. A., 1971. Reptiles of Victoria. Pages 11–36 *in* V. Arnold, editor. *Victorian Yearbook*, volume 85. Government Printer, Melbourne, Victoria, Australia.
- Redak, R. A. 2000. Arthropods and multispecies habitat conservation plans: are we missing something? *Environmental Management* **26**:S97–S107.
- Reist, J. D. 1985. An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. *Canadian Journal of Zoology* **63**:1429–1439.
- Reist, J. D. 1986. An empirical evaluation of coefficients used in residual and allometric adjustment of size covariation. *Canadian Journal of Zoology* **64**:1363–1368.
- Ricciardi, A., and J. Cohen. 2007. The invasiveness of an introduced species does not predict its impact. *Biological Invasions* **9**:309–315.
- Richardson, D. M., P. Pyek, M. Rejmnek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and distributions* **6**:93–107.
- Roderick, G. K., and R. G. Gillespie. 1998. Speciation and phylogeography of Hawaiian terrestrial arthropods. *Molecular Ecology* **7**:519–531.
- Rodriguez-Robles, J. A., and J. M. De Jess-Escobar. 2000. Molecular systematics of New World gopher, bull, and pinesnakes (*Pituophis*: Colubridae), a transcontinental species complex. *Molecular phylogenetics and evolution* **14**:35–50.
- Rubinoff, D., and P. Schmitz. 2010. Multiple aquatic invasions by an endemic, terrestrial Hawaiian moth radiation. *Proceedings of the National Academy of Sciences* **107**:5903–5906.
- Ruete, A., and G. C. Leynaud, 2015. Goal-oriented evaluation of species distribution models accuracy and precision: True Skill Statistic profile and uncertainty maps. Technical report, PeerJ PrePrints.

- Saupe, E. E., V. Barve, C. E. Myers, J. Sobern, N. Barve, C. M. Hensz, A. T. Peterson, H. L. Owens, and A. Lira-Noriega. 2012. Variation in niche and distribution model performance: the need for a priori assessment of key causal factors. *Ecological Modelling* **237**:11–22.
- Shelley, R. 2000. The centipede order Scolopendromorpha in the Hawaiian islands (Chilopoda). *Bishop Museum Occasional Papers* **64**:39–48.
- Shine, R. 1983. Reptilian viviparity in cold climates: testing the assumptions of an evolutionary hypothesis. *Oecologia* **57**:397–405.
- Simberloff, D., I. M. Parker, and P. N. Windle. 2005. Introduced species policy, management, and future research needs. *Frontiers in Ecology and the Environment* **3**:12–20.
- Simon, C. 1987. Hawaiian evolutionary biology: an introduction. *Trends in ecology & evolution* **2**:175–178.
- Soberon, J., and A. T. Peterson. 2005. Interpretation of Models of Fundamental Ecological Niches and Species Distributional Areas. *Biodiversity Informatics* **2**.
- Starkey, D. E., H. B. Shaffer, R. L. Burke, M. R. Forstner, J. B. Iverson, F. J. Janzen, A. G. Rhodin, and G. R. Ultsch. 2003. Molecular systematics, phylogeography, and the effects of Pleistocene glaciation in the painted turtle (*Chrysemys picta*) complex. *Evolution* **57**:119–128.
- Stockwell, D. R., and A. T. Peterson. 2002. Effects of sample size on accuracy of species distribution models. *Ecological modelling* **148**:1–13.
- Suman, T. W. 1965. Spiders of the family Oonopidae in Hawaii. *Pacific Insects* **7**:225–242.
- Thorpe, R. S. 1975. Quantitative handling of characters useful in snake systematics with particular reference to intraspecific variation in the ringed snake *Natrix natrix* (L.). *Biological Journal of the Linnean Society* **7**:27–43.
- Tilman, D. 1982. *Resource competition and community structure* (MPB-17). Princeton university press, Princeton, NJ.
- Tingley, R., M. B. Thompson, S. Hartley, and D. G. Chapple. 2016. Patterns of niche filling and expansion across the invaded ranges of an Australian lizard. *Ecography* **39**:270–280.
- Tomich, P. 1986. *Mammals in Hawaii: a synopsis and national bibliography*. 2nd edition. Bishop Museum Press, Honolulu, Hawaii.
- Twigg, L. E., and B. J. Fox. 1991. Recolonization of regenerating open forest by terrestrial lizards following sand mining. *Australian Journal of Ecology* **16**:137–148.

- Van Kleeck, M. J., 2016. The title of the work. Ph.D. thesis, University of Hawaii, Manoa, Honolulu, Hawaii.
- Van Kleeck, M. J., L. M. Chiaverano, and B. S. Holland. 2015. Prey-associated head-size variation in an invasive lizard in the Hawaiian Islands. *Biological Journal of the Linnean Society* **116**:626–636.
- Vanzolini, P. E., and E. E. Williams. 1970. South American anoles: the geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae). *Arquivos de Zoologia* **19**:1–176.
- Vclavk, T., and R. K. Meentemeyer. 2009. Invasive species distribution modeling (iSDM): Are absence data and dispersal constraints needed to predict actual distributions? *Ecological Modelling* **220**:3248–3258.
- Wapstra, E., and R. Swain. 1996. Feeding Ecology of the Tasmanian Spotted Skink, *Niveoscincus ocellatus* (Squamata: Scincidae). *Australian Journal of Zoology* **44**:205.
- Wegener, J. E., G. E. Gartner, and J. B. Losos. 2014. Lizard scales in an adaptive radiation: variation in scale number follows climatic and structural habitat diversity in Anolis lizards. *Biological Journal of the Linnean Society* **113**:570–579.
- Wilson, S., and G. Swan. 2013. Complete guide to reptiles of Australia. 4 edition. New Holland, Sydney, Australia.
- Witter, M. S., and G. D. Carr. 1988. Adaptive radiation and genetic differentiation in the Hawaiian silversword alliance (Compositae: Madiinae). *Evolution* **42**:1278–1287.
- Wüster, W., R. S. Thorpe, G. Puerto, and BBBSP. 1996. Systematics of the *Bothrops atrox* Complex (Reptilia: Serpentes: Viperidae) in Brazil: A Multiv Ariate Analysis. *Herpetologica* pages 263–271.
- Zaparoli, M., and R. Shelley. 2000. The centipede order Lithobiomorpha in the Hawaiian Islands (Chilopoda). I. The epigean fauna. *Bishop Museum Occasional Papers* **63**:35–49.
- Ziegler, A. C. 2002. Hawaiian natural history, ecology, and evolution. University of Hawai'i Press, Honolulu.