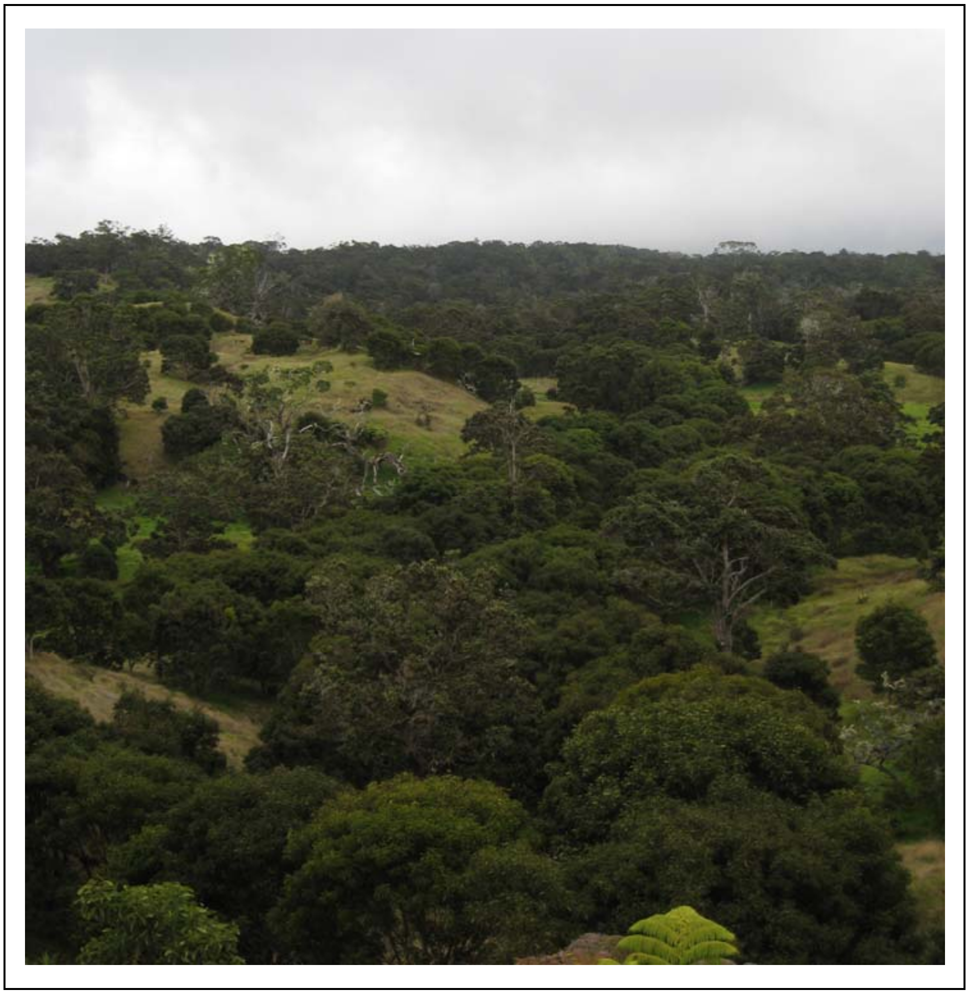
An Assessment of Non-native Plant Species Distribution at Hakalau Forest National Wildlife Refuge



An assessment of non-native plant species distribution at Hakalau Forest National Wildlife Refuge

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Introduction

Much of the science, theory, and concern around the global redistribution of plant species originated from observation and study of Islands (MacArthur and Wilson 1967, Mack and Lonsdale 2002). Many islands are repeatedly exposed to invasive species from trade, tourism, and agriculture (Van Driesche and Van Driesche 2004), and a variety of resource availability (Denslow 2003) and competition scenarios (Elton 1958, Durand and Goldstein 2001) may make islands susceptible to invasion. There is little doubt that invasion has significant impact on islands, and that the ecosystems of Hawaii are possibly more impacted by invasion than any other in the United States.

Considerable effort is dedicated to understanding and mitigating the establishment of invasive species in Hawaii. Preeminent invasive species science comes from investigation on the Islands (Vitousek et al. 1987), and government and non-government agency cooperation have put Hawaii at the forefront of prevention, early detection, control, and public education (www.HEAR.org). While stories of success exist, intense propagule pressure and multiple pathways of invasion overwhelm these efforts and incidence of invasion continues to occur. Impacts are most severe at lower elevations and near urban centers where much of the native flora has been completely displaced, but invasive species also exist at higher elevation sites that are federally protected (Kitayama and Mueller-Dombois 1995).

Hakalau Forest National Wildlife Refuge's goal of protecting endangered native bird and plant species is challenged by non-native species. The upper elevations have a disturbance history of anthropogenic-induced fire and cattle grazing that resulted in persistent abandoned pasture dominated by non-native grass species (Scowcroft and Jeffrey 1999, D'Antonio 2000). Feral pigs (*Sus scrofa*) also disturb regions of the Refuge by rooting and destroying vegetation (Aplet et al. 1991). Finally, a lack of control of non-native species, considerable human disturbance, and maintenance of wild pigs as game species in the matrix of state-managed land surrounding the Refuge provides a source of invasion that counteracts efforts by the Refuge to keep invasion in check.

The Refuge maintains an aggressive invasive species management program. They have fenced out pigs from many sections at considerable cost and labor. In both fenced and unfenced areas snares attempt to locally eradicate pigs. Staff target non-native plant species with manual and chemical treatments, and control of non-native plants may be furthered by a forest restoration project program. Refuge staff hypothesize that replacing pasture with native forest will shade and eliminate the non-native grass species (Scowcroft and Jeffrey 1999). Thousands of native koa seedlings have been planted to restore native forest and habitat for endangered bird species with hours and hours of staff and volunteer time.

The National Invasive Species Program of the National Wildlife Refuge System has recognized this work and the impact of invasive species at Hakalau Forest National Wildlife Refuge. They provided support for a volunteer mapping program, and, in the fall of 2007, a plot-based inventory of non-native and native vegetation. This inventory was designed to:

-provide an unbiased characterization of plant invasion across the Refuge
-help understand the distribution of specific non-native plant species
-evaluate co-occurrence of native and non-native plant species
-evaluate components of the control efforts
-develop recommendations for further management, inventory, and monitoring

For the purposes of this report we refer to non-native and invasive species interchangeable as species that are of concern for the Refuge.

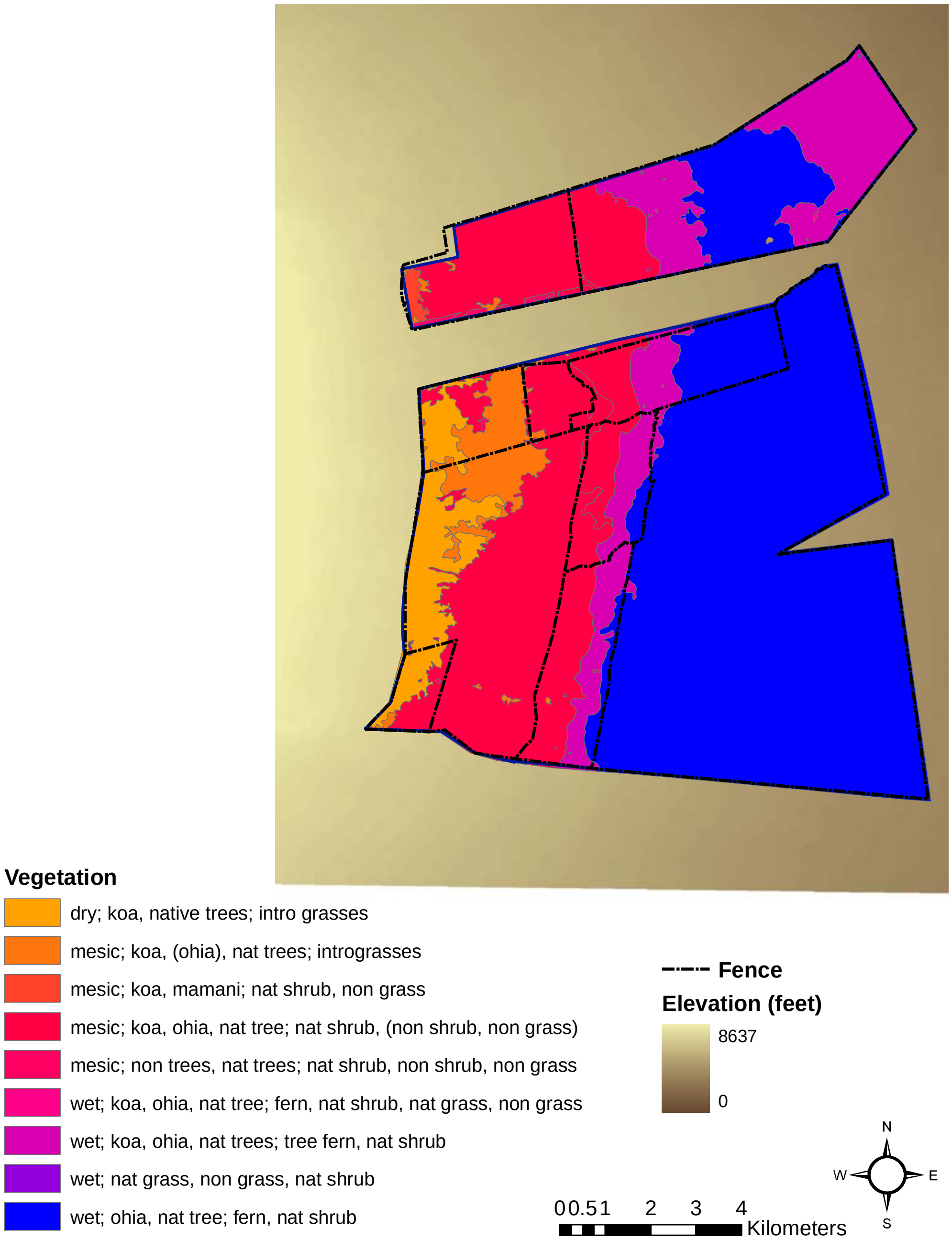


Figure 1. Principal vegetation types at Hakalau Forest National Wildlife Refuge.

Methods

Sampling was directed by a stratified-random design. Initial stratification was done according to a vegetation map (Fig. 1), but after Refuge staff suggested the map was out of date, a sentiment generally confirmed by visits to randomly chosen locations, we included an elevation stratification that also provided that basis for analysis (Table 1). After each of two rounds of sampling we constructed species-accumulation curves and models of non-native species distribution and focused sampling on previously selected plots in strata that seemed to be undersampled and have high non-native plant diversity. This process insures that the most useful information was obtained for the sampling effort.

Some additional plots were placed to coincide with avian monitoring stations (4 plots), at random distances on a gulch in the Pua Akala unit of the Refuge to evaluate transport along these features (6 plots), and additional plots were selected from the initial strata in the Pua Akala unit in an attempt to evaluate control of English holly (*Ilex aquafolia*) and blackberry (*Rubus argutus*).

At each location we sampled with a 168-m^2 circular, multi-scale vegetation plot modified from the National Forest Service Inventory and Analysis Program (Fig 2; Barnett et al. 2007). Species composition, cover, the average height of each species, and cover of abiotic variables (lichen, litter, moss, poop, rock, soil, standing duff, water, and wood) were recorded to the nearest 1% in each of three 1-m^2 subplots. We also collected species composition in the entire 7.32 m radius circular plot (168-m^2).

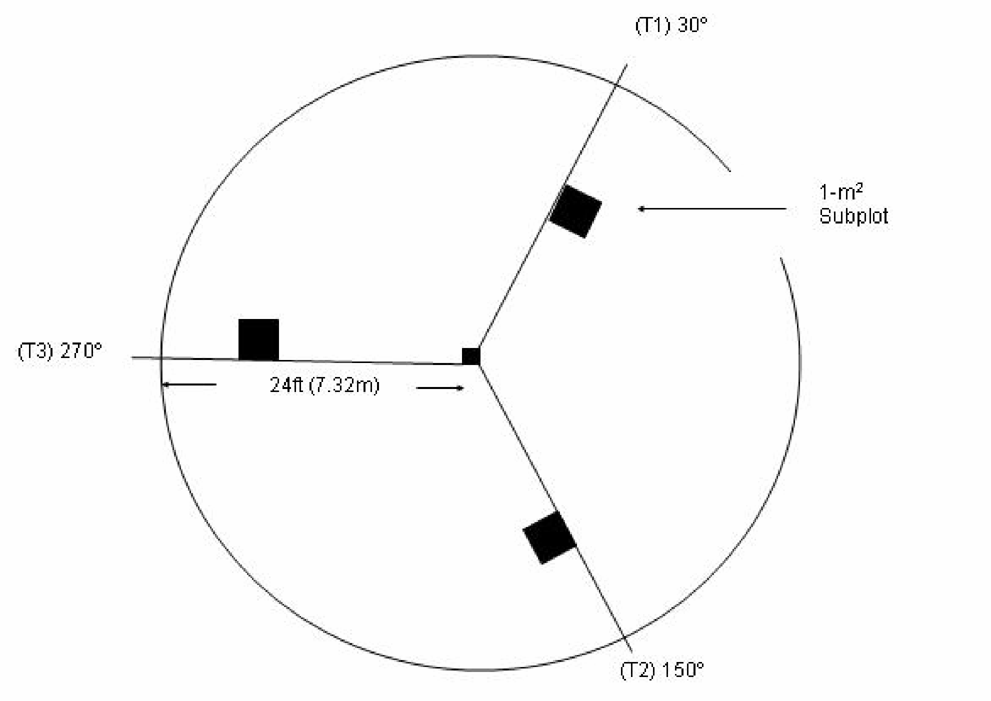


Figure 2. The multi-scale plot design, modified from the Forest Inventory and Analysis Program, used to sample native and non-native vegetation.

Soil samples were collected at each plot. Soils were collected in the center of the plot and at the inside corner of each 1-m^2 subplots and analyzed for texture and carbon and nitrogen content (texture - % sand, silt, and clay; inorganic C, organic C, total C, and total N). Ancillary data including slope degree and slope aspect were recorded at the location. Other variables including the distance to road, distance to water, LANDSAT remote sensing information (including NDVI and tasselcap (bright, green, wet)), and the slope, aspect, and elevation from a Digital Elevation Model (DEM) were attributed to each plot during analysis.

The sampling locations were recorded but not permanently marked on the ground. Each plot can be roughly geo-referenced with associated UTM coordinates to place repeat measurements generally 2 to 5 m from the original plot. Repeat sampling should include a search of the area surrounding each plot to account for extant species of concern that the plot may have missed.

Unknown species were collected and/or photographed and subsequently identified by botanists. Data was consolidated in a Microsoft Access database, analyzed with in a Geographic Information System (ESRI 2002) and the S Plus and Systat statistical packages.

STATISTICAL ANALYSIS

Patterns of Invasion

With repeated random draws of plots, we used species-accumulation curves to look at the contribution of plots to the total number of native and non-native species found by elevation. By fitting a curve to the sampled data, we were able to estimate species richness as if sampling intensity had been equal across elevation zones (36 plots). We evaluated relationships between species richness with primary environmental gradients (e.g. elevation, canopy cover) using simple and multiple linear regression, and evaluated species overlap between elevation zones.

Non-native plant species modeling

Managers must consider entire landscapes, not point locations. Spatial models attempt to describe a variable of interest across an entire landscape based on information gleaned from point-specific sampling. Some models included only plot-based data (variables such as non-native species richness could only be estimated in plots); some incorporated the plot and mapping data. The same independent variables (slope, elevation, aspect (0-180 degrees transformation to make the variable linear and approximate degrees from the south and east slopes), distance to road, distance to water, relative vegetation type moisture, and LANDSAT bands 1, 2, 3, 4, 5, 7, NDVI, tassel cap bright, green, and wet) were used for each model and log transformed to approximate assumptions of normality when appropriate. Independent variables were assessed for collinearity.

•Trend Surface Models. Working with plot-based data increased our ability to model the variability of non-native plant species. We used multiple regression analysis (Reich and Davis 1998) to evaluate coarse-scale variability with a stepwise procedure to select the independent variables to include in the regression models. We then modeled the error (i.e., residuals) from the regression model with a binary regression tree (De'ath and Fabricius 2000), and avoided over-fitting the model with a 10-fold cross-validation procedure to identify the tree size that minimized the total deviance associated with the tree. We generated grids using model parameter estimates from the regression model. Passing the appropriate independent variables through the regression tree created another grid representing the error in the regression model. A sum of the two grids amounted to the final surface (Reich et al. 2004).

•Maxent. We also estimated species distributions with maximum entropy (Maxent, version 2.3.18; http://www.cs.princeton.edu/~schapire/maxent/; Phillips et al. 2006). Using positive locations and continuous environmental variables, maxent attempts to estimate distributions by finding the distribution of maximum entropy (or closest to uniform) under the constraint that the expected value of the features under the distribution matches the empirical average (Phillips et al. 2006).

•Logistic regression is a type of general linear model (GLM) appropriate for data with a binary distribution such as species presence or absence. Logistic regression used a logit link function that assumed a binomial distribution. Variables were selected using a stepwise procedure for GLM in S-plus. The probability surface was generated using the predictor variable raster layers with the statistical output from S-plus. The resulting cell values were in the logit scale and were therefore back-transformed to the original scale of the probability surface using:

$$p = \frac{e^{(LP)}}{1 + e^{(LP)}}$$

where *p* is the probability and LP is the linear predictor. Percent deviance (D^2, similar to an R^2 value) was used to evaluate the model percent deviance explained and measure discrimination were calculated. Percent deviance explained was calculated as

$$Percentdeviance = \frac{NullDev - \mathrm{Re}\,sDev}{NullDev} X100$$

where NullDev is the null deviance of the evaluation data and ResDev is the residual deviance of the evaluation data in relation to probabilities predicted by the model. This measurement is of overall goodness of fit of the model to the known observations.

The Maxent model has the ability to predict species occurrence with presence-only data and small datasets. Maxent estimates a species distribution by finding the probability distribution of maximum entropy, or that is closes to uniform, subject to constraints of incomplete data about the actual distribution of the species (Phillips et al. 2006). Maxent models are evaluated by the area under the curve (AUC) of the receiver operatic characteristic. This statistic can not be directly compared to the logistic regression D^2.

RESULTS

Plot Sampling

In the plot-based survey, we identified a total of 112 species in 76 plots (Fig. 3). The Refuge lists 45 (Appendix 2) of these as non-native plant species. Kikuyugrass (*Pennisetum clandestinum*), kikuyugrass occurred with the highest frequency (51 plots). Other species occurring with high frequency include sweet vernalgrass (*Anthoxanthum odoratum,* 48 plots), common rush (*Juncus effuses*, 45 plots), common velvetgrass (*Holcus lanatus*, 44 plots), and weeping grass (*Ehrharta stipoides* 43 plots). Thirteen non-native species occurred on only one plot (Appendix 2).

Fifteen non-native species only occurred in the largest plot (Fig. 2) and do not have cover values (Appendix 2). Of the 30 non-native species occurring in subplots kikuyugrass had the highest average percent cover, followed by weeping grass (Appendix 2).

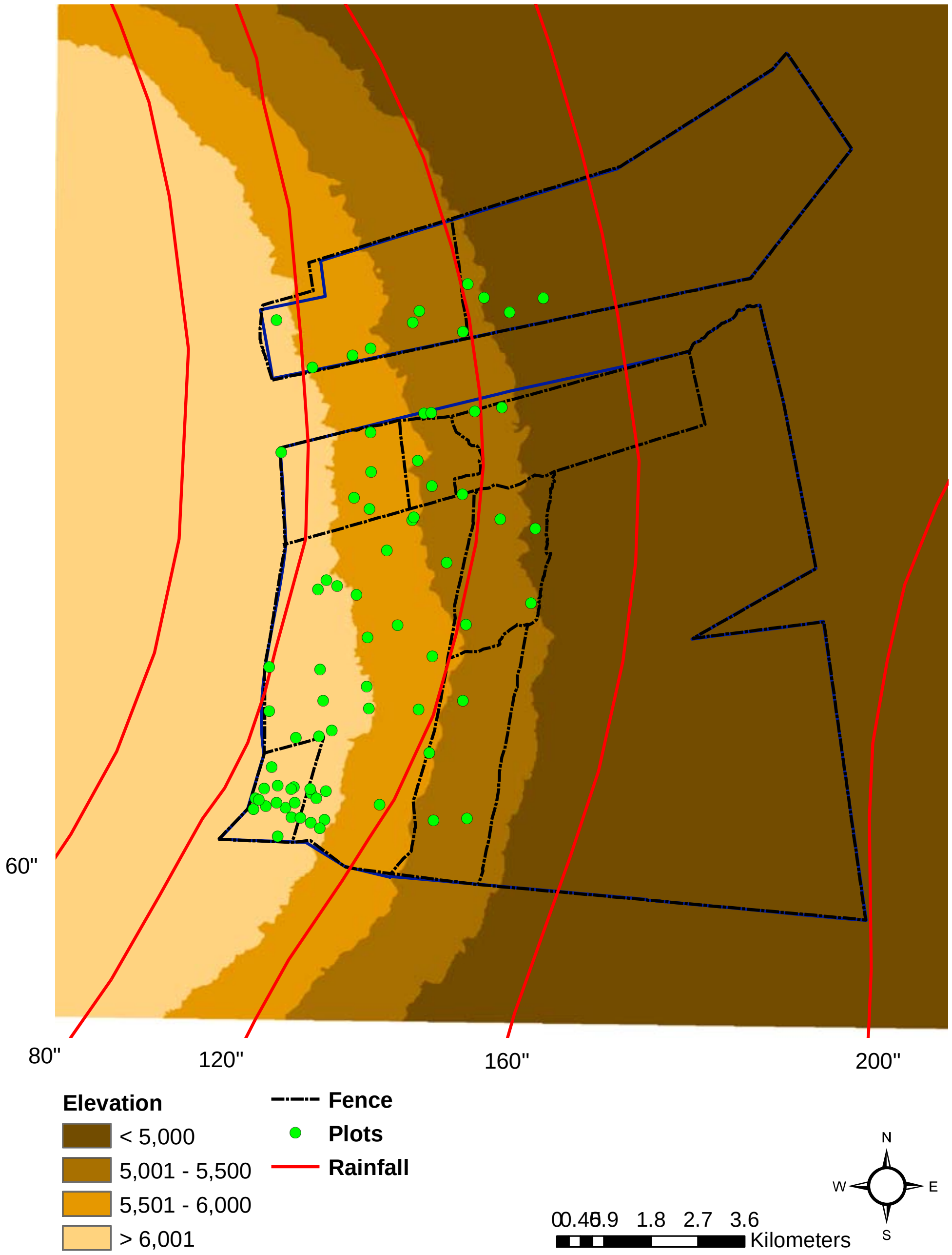


Figure 3. The distribution of sampling plot and elevation zones.

While the sampling effort was not equitable across the elevation zones (Table 1), we found the highest cumulative non-native species between 5000 and 5500 feet, but on average, plots across all elevations had a similar number of non-native plant species.

Table 1. Distribution and estimated richness of native and non-native plant species at Hakalau Forest National Wildlife Refuge, standard error of mean appears in parentheses where appropriate.

Elevation (feet)	Number of Plots	Non-native Species Richness	Estimated Non-native Species Richness	Native Species Richness	Estimated Native Species Richness	Mean Non-native Species/Plot	Mean Native Species/Plot	Unique Non-native species
< 5000	4	11	21	35	62	5 (0.87)	23 (1.89)	1
5001 – 5500	17	34	40	36	44	6 (0.93)	12 (1.54)	10
5501 – 6000	19	19	21	16	18	6 (0.69)	7 (1.73)	1
> 6001	36	31	31	39	39	7 (0.44)	6 (0.72)	9

Table 2. Percent cover, coefficient of variation, and richness at 1-m^2 of non-native plant species at Hakalau Forest National Wildlife Refuge; standard error of the mean appears in parentheses where appropriate.

Elevation (feet)	Plots	% Cover of Non-native Species	CV Non-native % Cover	% Cover of Native Species	CV Native % Cover	1-m^2 Native Richness	CV 1-m^2 Native Richness	1-m^2 Non-native Richness	CV 1-m^2 Non-native Richness
< 5000	4	7.6 (5.3)	1.396	92.4 (5.3)	0.115	4 (0.63)	0.53	1 (0.22)	1.15
5001 - 5500	17	42.2 (9.6)	0.939	57 (9.9)	0.71	2 (0.42)	0.63	2 (0.36)	0.74
5501 - 6000	19	72.5 (8.1)	0.49	27.4 (8.1)	1.29	1 (0.25)	0.89	2 (0.38)	0.43
> 6001	36	75.4 (3.9)	0.312	21.6 (3.7)	1.05	1 (0.18)	0.98	3 (0.21)	0.43

Table 3. Jaccard’s coefficients of regional species pool overlap.

	5000	5000-5500	5500-6000	6000
5000	1			
5000-5500	0.30	1		
5500-6000	0.42	0.50	1	
6000	0.22	0.46	0.45	1

Species Accumulation Curves

We used species-accumulation curves to compare invasion across elevation while controlling for unequal sample intensity (Fig. 4). Statistically extended curves suggested we would have found the greatest number of non-native plant species between 5000 and 5500 feet if 36 plots had been sampled in each elevation zone, and the greatest diversity of native species below 5000 feet with 36 plots (Table 1).

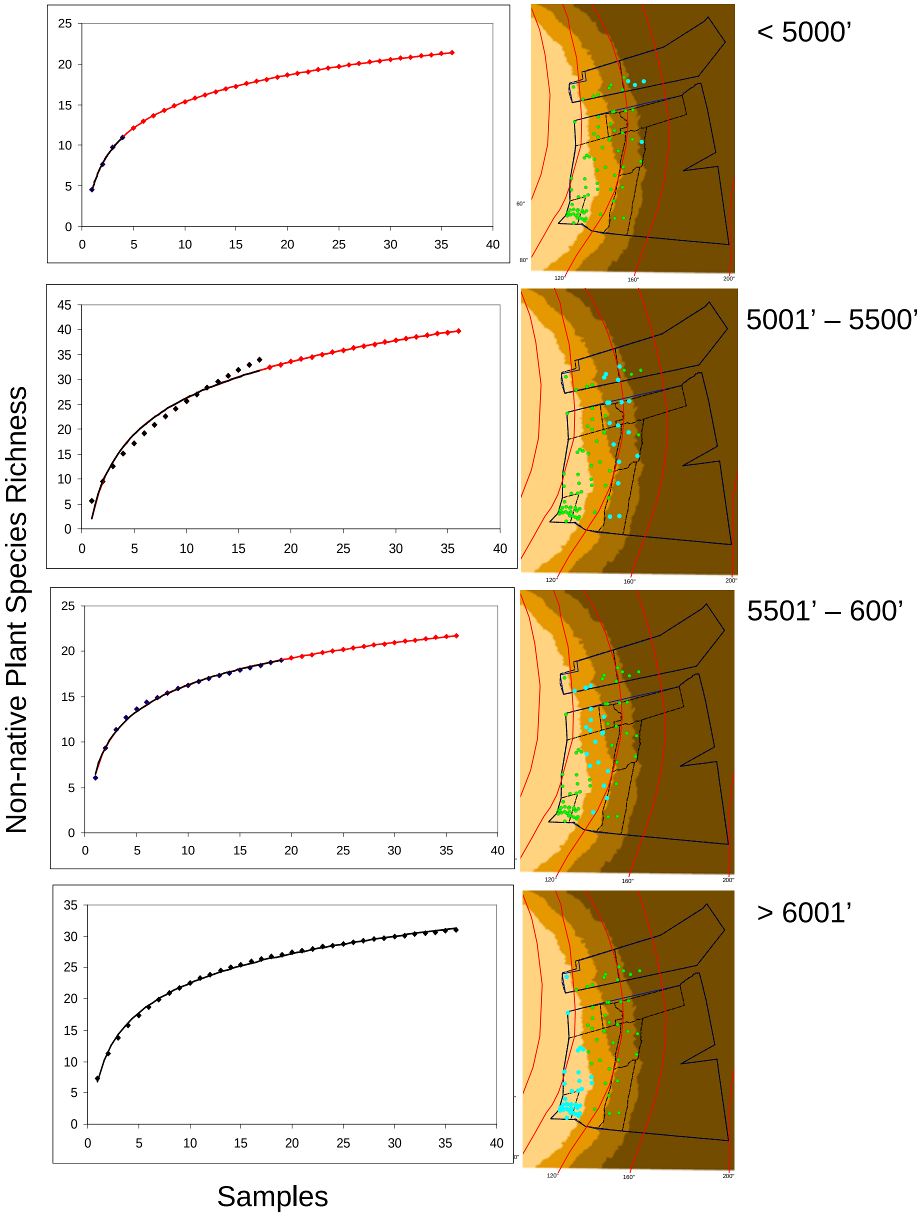


Figure 4. Species-accumulation curves and fit curves (in red).

Patterns of Invasion

Non-native species richness and cover both demonstrated a positive and significant linear relationship with elevation (Fig. 5) and a negative and significant relationship with canopy cover (Fig. 6). Native plant species richness and cover demonstrated opposite relationships with elevation (Fig. 7). Non-native plant species richness and cover decreased with increases in native plant species richness and cover (Fig. 8). We were able to increase our ability to describe patterns of non-native plant species richness and cover when we used all available independent variables (Fig. 9).

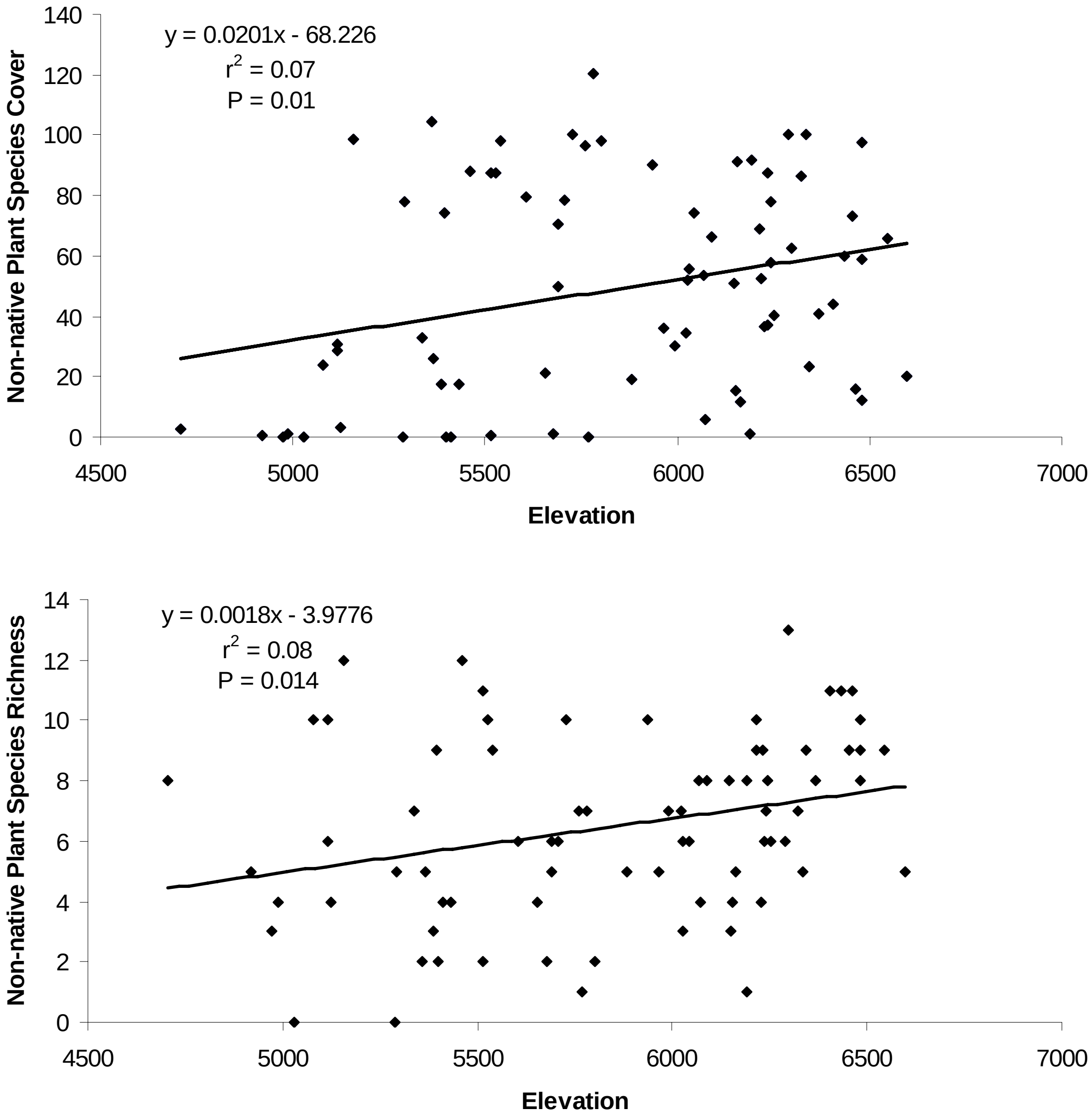


Figure 5. Comparisons of plot non-native plant species richness and cover with elevation.

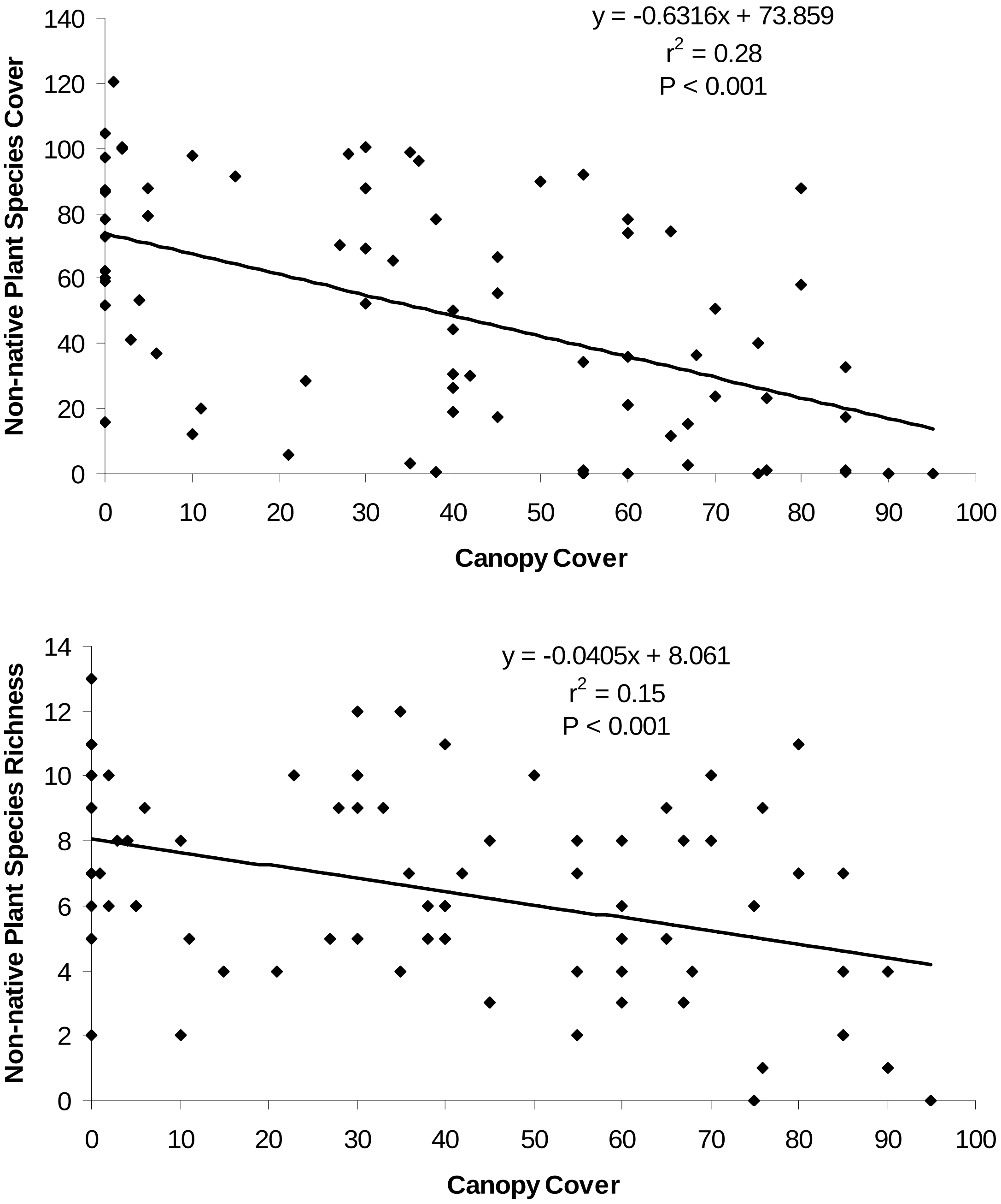
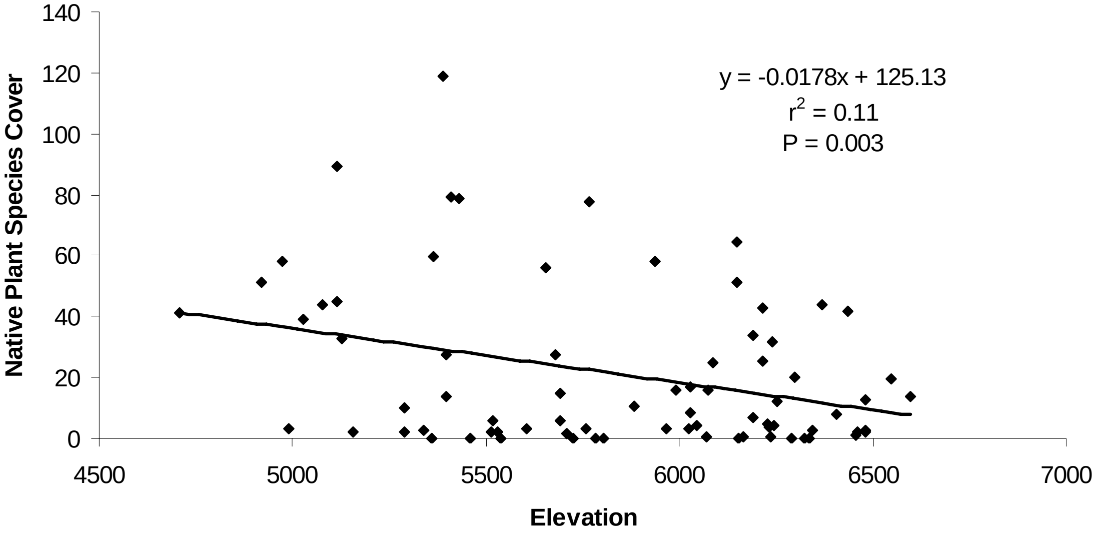


Figure 6. Comparisons of non-native plant species richness and cover with forest canopy cover.



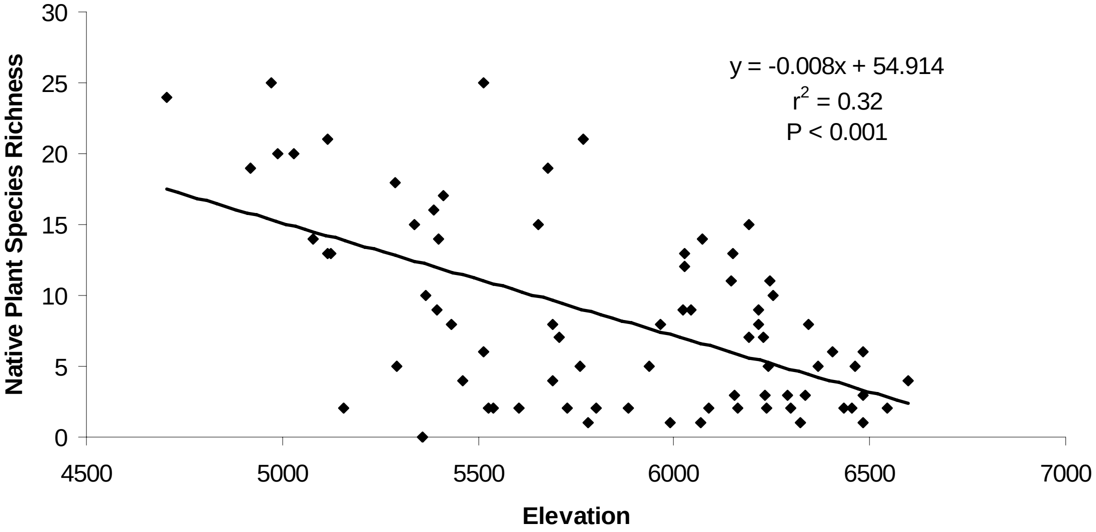


Figure 7. Comparisons of native plant species richness and cover with elevation.

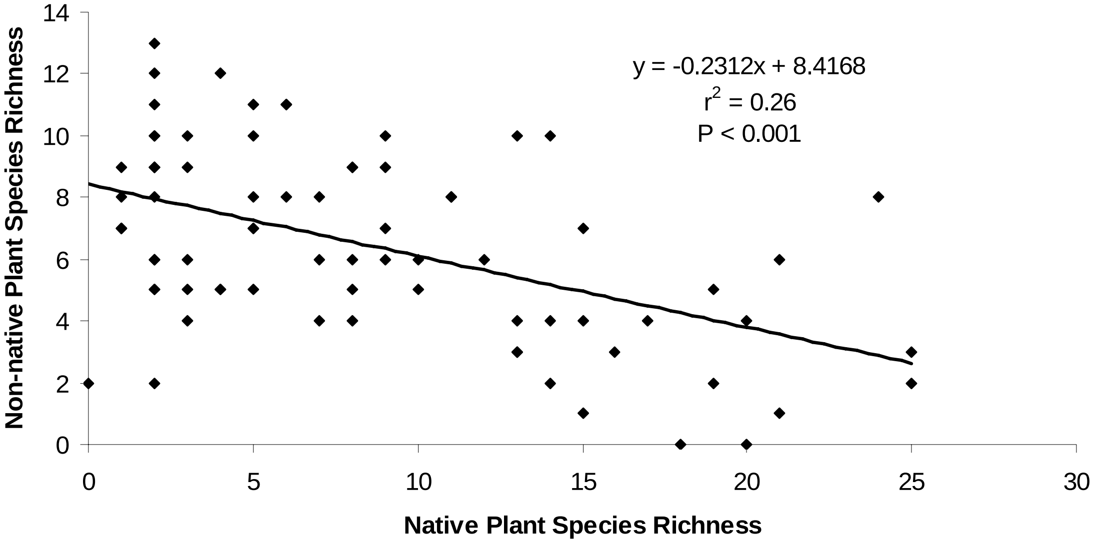


Figure 8. Comparisons of plot non-native and native plant species richness.

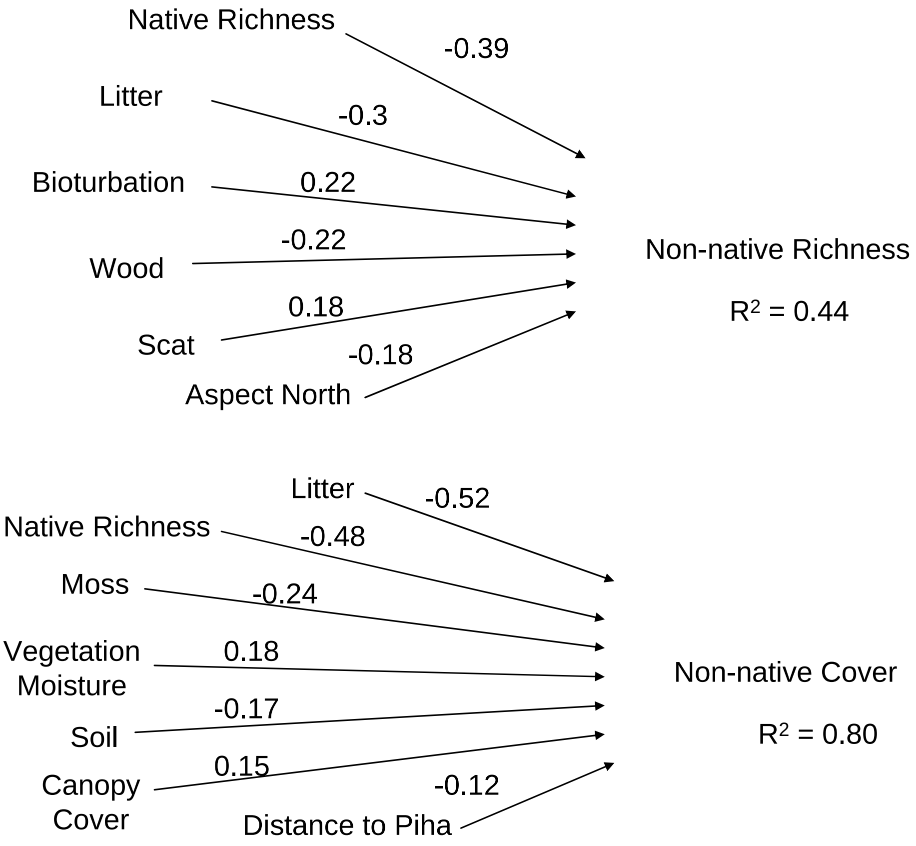


Figure 9. Multiple linear regression standardized regression coefficients attempt to describe patterns of non-native plant species richness and cover.

Spatial Models

Species-specific models were created for species of concern for control. While the ability of the models to predict distribution can not be compared, the environmental variables and the relative strength of each variable in the model can be compared (Appendix 1). In some cases we were not able to create models for some species when we did not have enough data for those models. Many of the models were influenced by vegetation moisture, a numeric variable we created as a surrogate for precipitation, elevation, and in some cases variables that might indicate disturbance such as animal tracks, bioturbation, and bare soil (Appendix 1).

Models of non-native plant species richness and cover provide insight to hotspots of non-native plant species and some of the variables associated with distribution. The non-native plant species richness model ($R^2 = 0.5$, $P < 0.001$) was directed by the aspect degrees away from east, elevation, and distance from the Piha section. Non-native plant species cover ($R^2 = 0.62$, $P < 0.001$) was associated with elevation, distance from the Piha section, and slope (Table 4). The models were both improved by the explanation of fine-scale variability with regression trees.

Table 4. Non-native plant species richness and cover model standardized correlation coefficients from Hakalau Forest National Wildlife Refuge.

Non-native Plant Species Richness		Non-native Plant Species Cover	
Independent Variable	Standardized Correlation Coefficient	Independent Variable	Standardized Correlation Coefficient
aspect east	0.22	elevation	0.01
elevation	0.44	Piha distance	-0.002
Piha distance	-0.25	slope	0.4

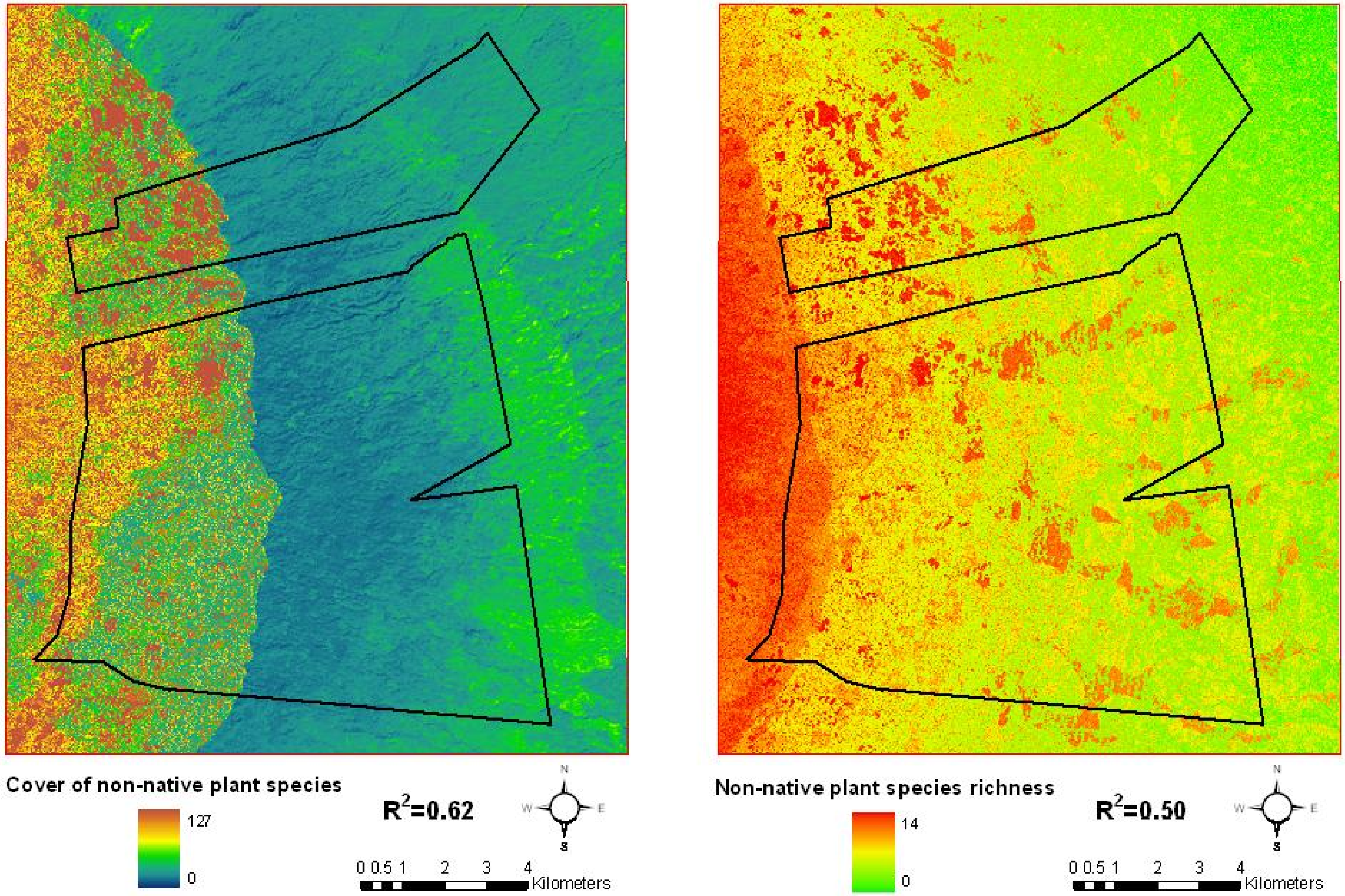


Figure 10. Models of non-native plant species richness and cover.

DISCUSSION

Disturbance seems to drive invasion at the Refuge. Historical logging, fire and grazing (Scowcroft and Jeffrey 1999) removed forest and altered species composition that is now maintained by persistent and dominant non-native grass species (Denslow et al. 2006). In addition to the non-native grass diversity at higher elevation, many species distributions seem to benefit from the disturbed pasture (Appendix 3), but while the historical, large-scale disturbance drives the prominent patterns of invasion it may not tell the complete story. Select non-native plant species have established at lower elevations and seem to be surviving in the largely intact native forest.

General Patterns of Invasion

Non-native plant species distributions across the elevation gradient generally confirm Refuge assumptions about patters of invasion and correspond to patters at larger scales. Generally, the upper parts of the Refuge, dominated by grassland and patches of forest, supported greater non-native plant species richness and abundance than the lower elevation forest (Fig. 5). Similarly, found greater incidence of invasion in higher elevation montane forest was found in nearby Hawaii Volcanoes National Park, and Kitayama and Mueller-Dombois (D'Antonio et al. 2000, Kitayama and Mueller-Dombois 1995) found considerable invasion at high elevations, minimal invasion in largely undisturbed forest at middle elevations, and significant invasion at lower, coastal locations on the island of Maui. Because elevation remains constant it provides a way to understand patterns of invasion but may not drive patterns of invasion.

Local and regional elevation patterns of invasion are likely better explained by associations with areas that are accessible and disturbed by humans. Coastal regions have a long history of agriculture and other human impacts (Van Driesche and Van Driesche 2004). Middle elevations tend to be characterized by steep topography and abundant precipitation (at least on windward sides of the Island of Hawaii) that create the dense forests (Mack and D'Antonio 1998) found at lower elevations of the Refuge and that tend to be less accessible and less disturbed. Across the Island, gentle terrain and reduced moisture made subalpine environments more accessible to historical logging and conversion to pasture (Pejchar and Press 2006). In the slice of this regional gradient within the Refuge boundary we documented more disturbance at higher elevations (Fig. 5) indicating that while elevation may describe gradients of invasion (D'Antonio et al. 2000), disturbance of native vegetation may be more directly related to patterns of non-native plant species establishment.

The negative relationship of non-native plant species richness and cover to canopy cover (Fig. 6) highlights the role of disturbance in the success of invasive plant species establishment at the Refuge. Typical explanations of the disturbance-invasion relationship include pulses of resources such as space, water, and nutrients that become available as previously established flora is reduced or removed (Mack and D'Antonio 1998). An observational study affords us little power to evaluate these factors at Hakalau National Wildlife Refuge, but trends do suggest that light may be factor. That punching holes in the canopy and removing native vegetation provides opportunity for invasion only offers evidence to support existing theories (Denslow et al. 1990). The substantial koa reforestation project aims to counteract disturbance by nudging succession towards a closed canopy that should result in a reduced non-native plant species presence (Fig. 11; Hughes and Vitousek 1993).

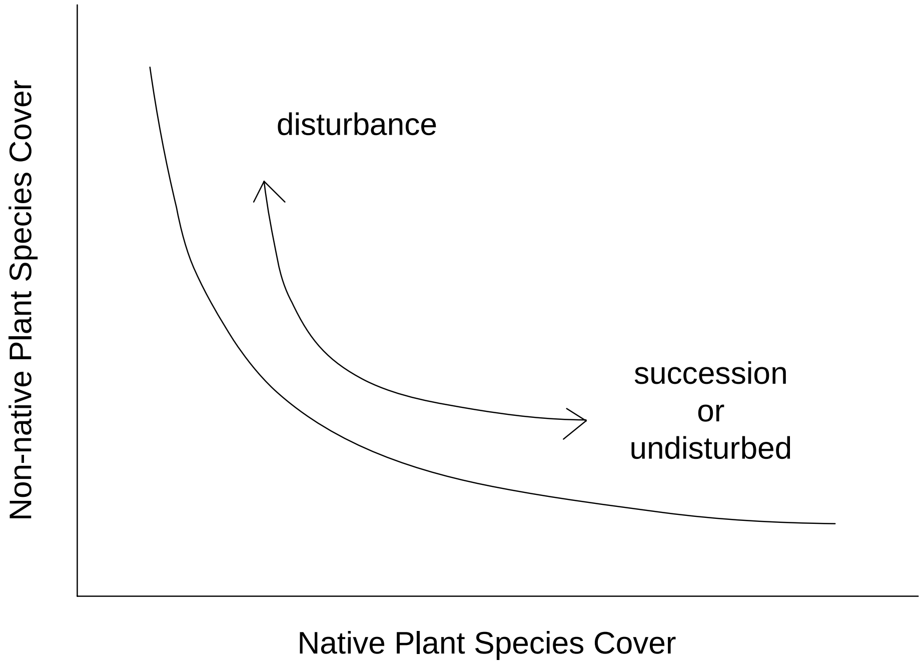


Figure 11. Conceptual diagram of native and non-native plant species cover on a disturbance-succession continuum.

But, is it working, really?

It could be inferred that encouraging succession is a good strategy. Our data suggest that non-native plant species don't do as well under dense canopy or in coexistence with abundant native vegetation. We found a negative relationship between native and non-native plant species richness (Fig. 8), and curves of non-native plant species cover against native plant species cover mimicked our theoretical understanding of the system (Fig. 11 and 12). Because our work can only imply correlation and not causation, the snapshot in time described by these curves presents a 'chicken and the egg' problem: do non-native plant species invade locations with low native cover, or does invasion result in native cover reductions? It is more likely that disturbance provides an opportunity for invasion because (1) the general association of invasion with disturbed areas on the Refuge and across the Hawaiian Islands, (2) the long history of land use suggests that non-natives plant species and a source of seeds that could invade lower elevations has existed on the Refuge since the middle of the 19th century (Drake 1998, Scowcroft and Jeffrey 1999), and (3) lower elevation plots demonstrated significantly less non-native plant species cover (Fig. 5).

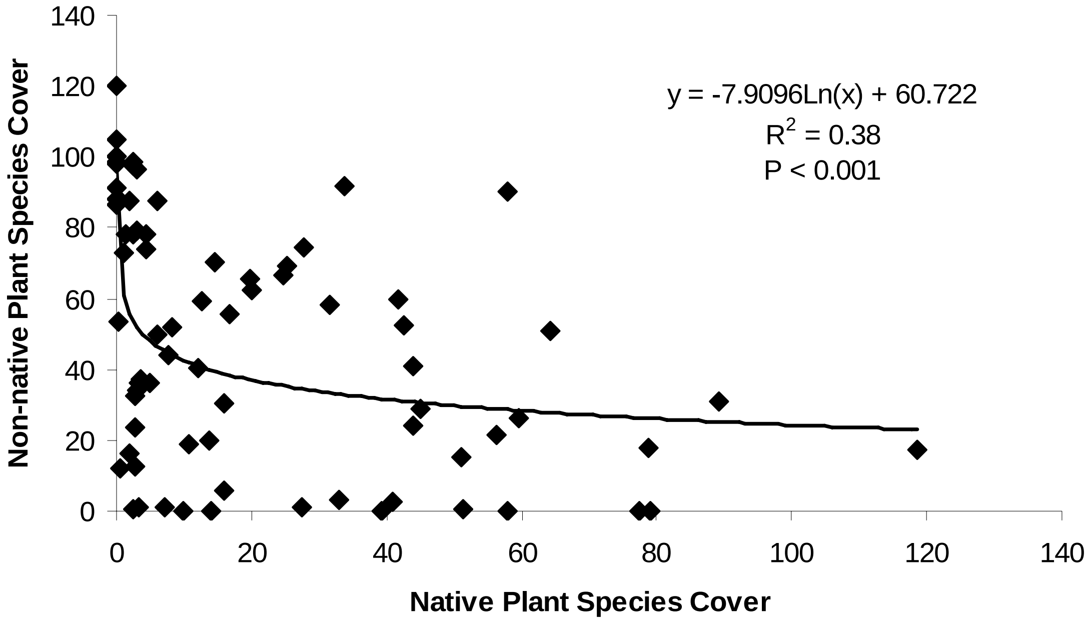


Figure 12. The relationship of non-native plant species cover to native cover helps define the importance of disturbance in plant species invasion.

Controlling non-native plant species may be more complicated than growing koa forest. Numerous examples exist of non-native plant species altering disturbance regimes (D'Antonio and Vitousek 1992), or entering transitional states by changing functional groups or structure of a system (Denslow and Hughes 2004). The non-native grasses that dominate the pasture may already represent an altered or transitional state (Mack and D'Antonio 1998), but restoration techniques (Scowcroft and Jeffrey 1999) may overcome limitations to establishment of tree seedlings in a landscape dominated by non-native grass species (Hughes and Vitousek 1993, Denslow et al. 2006). But, new forests in transition will likely grow as mosaics and even the canopy of an established koa forest does not have a dense canopy. The light that will reach the understory under both scenarios may allow the persistence of non-native plant species. Only time or further investigation will tell if succession will reduce non-native plant species or if the presence of these species has caused some kind of altered trajectory in patterns of succession (Asner and Beatty 1996, Denslow and Johnson 2006).

Finding a Way at Lower Elevations

Non-native plant species do exist in the lower elevation koa and ohia forests; richness and cover decrease but is not reduced altogether (Fig. 5). All four of the lowest elevation plots (<5000 feet) were invaded, and species accumulation projections suggest that non-native plant species richness at these elevations might be comparable to incidence at higher elevations (Fig. 4, Table 1). The difference is that non-native species don’t dominate the landscape at lower elevations (Table 2).

Disturbance, like the presence of non-native plant species, is less pervasive at lower elevations. Feral pigs cause small-scale, patchy and significant disturbance to forests across Hawaii (Katahira et al. 1993) and the Refuge (Van Driesche and Van Driesche 2004). Pigs were first introduced to Hawaii by Polynesian settlers and were continuously supplemented by European stock. Spatz and Muller-Dombois (Spatz and Mueller-Dombois 1975) and many others (Ralph and Maxwell 1984, Drake and Pratt 2001) recorded impacts on soil and a ‘greatly enlarged component of introduced species in communities with a former high percentage of native species.’

Propagules that take advantage of low elevation disturbance most likely originate from higher elevations, possibly transported by wind, water, human foot traffic down bird monitoring transects, or pigs moving from upper elevations and the State of Hawaii managed Piha section. The resulting regional species pool (<5000 feet) is not unique; only one of the non-native species found below 5000 feet was unique to this study (Table 1). Overlap with other elevations was greatest with non-native species found between 5500 and 6000 (Table 3) that demonstrated low non-native diversity, but the greatest percent cover (Table 2). But, these non-native plant species are marginalized and patchy at low elevations: percent cover and alpha diversity (richness in 1-m^2 plot) are low and variable (Table 2), and there is some evidence that percent cover of non-native plant species is higher in areas of less litter and more bioturbation ($R^2 = 0.45$, $P = 0.06$) when we increase sample size to 12 plots below 5300 feet (sample size is too small with 4 plots below 5000 feet). Non-native plant species seem to exploit small-scale, high-frequency disturbances (Drake and Pratt 2001), and given the behavior of a similar suite of species at higher elevations, might dominate any large-scale disturbance to occur at lower elevations.

Once a regional species pool is established non-native plant species may persist by exploiting temporally and spatially sporadic available resources. Banana poka (*Passiflora mollissima*) survives shade by sending tree-climbing runners to the canopy, and then it waits (LaRosa 1992). In a nearby forest, Drake (Drake 1998) found that despite 95% native cover and 99% native seed rain, 67% of the seed bank consisted of non-native plant seeds; another way to wait. And waiting is a good strategy. Tree fall gaps allow light to the forest floor and provide nurse logs for the establishment of new species (Denslow 1987, Denslow et al. 1990). Similarly, senescing palm fronds from tree ferns (*Cibotium spp.*) can open smaller gaps and also destroy native vegetation and tree seedlings (Drake and Pratt 2001), and substrate instability (Mack and D'Antonio 1998) and erosion disturb vegetation in deep gullies that are prominent on the Refuge (Van Driesche and Van Driesche 2004). The unique and isolated evolution left Hawaii’s native flora with few r-selected species capable colonizing these disturbances (Herben 2005), and in Hawaii non-native plant species seem to be superior competitors for the resources made available (D'Antonio et al. 2001, Durand and Goldstein 2001, Theoharides and Dukes 2007). Our conceptual understanding of invasion at the Refuge seems to be accurate only at large scales and for invasions that dominate the landscape (Fig. 11). Consideration of invasion should be altered to include smaller-scale disturbances that facilitate patchy invasion. After inoculation intact native forests are generally not immune to invasion (Denslow 2003).

Species

Species identity matters in invasion biology. Some species wreak havoc on natural systems while others seem to be additive, existing at low levels that do not disrupt native species or processes. Most detrimental invasive plant species undergo a lag phase, existing at low, background numbers and densities for some time before spreading across the landscape (Hobbs and Humphries 1995). While further inventory and monitoring should maintain a landscape-scale focus that accounts for all non-native plant species, limited resources and distributions mean that the inclusion of control on new species should be targeted and educated. The difficulty of differentiating between relatively harmless invasive species and the next big invader is one of the difficulties of management.

Numerous resources exist to prioritize invasive plant species in Hawaii. The Hawaii Ecosystem at Risk (www.hear.org), Hawaii Invasive Species Council (http://www.hawaiiinvasivespecies.org/hisc/) and others provide substantial information about invasive species management, science, locations, and control. A ranking system developed by Pacific Island Ecosystem at Risk (http://www.hear.org/pier/wra.htm) provides detailed information about species, risk assessments and scores that define risk of particular species (Appendix 2).

A species-specific approach that compares percent cover of species can provide an estimate of the prevalence of non-native plant species found in this inventory, and perhaps help identify species to be targeted for control (Appendix 2; Huston 2004, Crall et al. 2006). The high scores of alsike clover and kikuyugrass reflects pervasiveness (Appendix 2). Depending on the threat to valued natural resources and processes (spatial and biological), a dominant species may not be one worth attempting to control. Most species had low percent cover and may currently be a lower priority as they are not taking up a lot of space or resources. Conversely, species with relatively low frequency and ranking score (e.g. Madagascar ragwort (*Senecio madagascariensis*)) might be worth prioritizing for control. These species seem to have limited distribution across the landscape but may be a good target for early control. They should be continuously evaluated and monitored as they may have the ability to spread and have a significant impact on native plant species.

Recent investigations have demonstrated that no model is better suited in every situation (Evangelista et al. in press). It may be that the Maxent model is more appropriate for modeling the distribution of species that are either new to an area or do not occupy the extent of the potential range. Logistic regression benefits from the incorporation of both present and absent data (in this case plots that did not include the species in question), but is complicated by the fact that absence at snapshot in time does not guarantee a species can't survive under the environmental constraints at that location. In either case, the models are perhaps best interpreted as the potential distribution of the species based on where it was found in the survey. The models are not actual maps of occurrence, and each model has a probability range associated, higher numbers (brighter colors) indicate areas where the species is more likely to occur across the landscape.

Invasive Plant Species Control

A thorough evaluation of the efficacy of control is beyond the scope of this data, and more specifically, the design of the inventory. An ideal test of control would include sampling prior to control, monitoring of those sites, and comparison to sites both invaded and free of the target species. With accurate and current maps of control, comparisons of this data could be made but would be complicated by the temporal nature of control and compromised by inadequate sample size and design. Perhaps maps of occurrence, cover, and dominance of each species as measured in plots will provide some insight on resent control efforts.

Despite the preponderance of literature on the impact of pigs on Hawaiian vegetation and soil, we were not able to detect a difference in plant species richness (P = 0.1) or cover (P = 0.2) in comparisons of Refuge management units with and without pigs. The patchy nature of pig disturbance reduces the odds of recording such evidence in a randomly placed 168-m^2 plot. We did see evidence of pig disturbance, especially at lower elevations of Maualua Nui (units 9, 11) and Honohina (unit 3) near the Piha section. Fences were compromised along the Honohina-Piha boundary, we encountered pigs near the Nauhi cabin, and had pigs running through a plot in the forest below the cabin.

We found considerable plant species invasion around the Pua Akala cabin. The gully that passes nearby also seemed to be invaded and provided a chance to see if it played a role in dispersal of non-native plant species to lower elevations of the Refuge, and to see if the cabin-associated disturbance or the State of Hawaii land up the gully was the seed source. We sample four plots at random distance below the cabin in the gully and two plots above the cabin in the same gully. The sample size is small and we have no replicates to statistically comment about gully transport, but it does seem like richness is greater at higher elevations and that the gully is not facilitating extraordinary non-native establishment at lower elevations (Fig. 13).

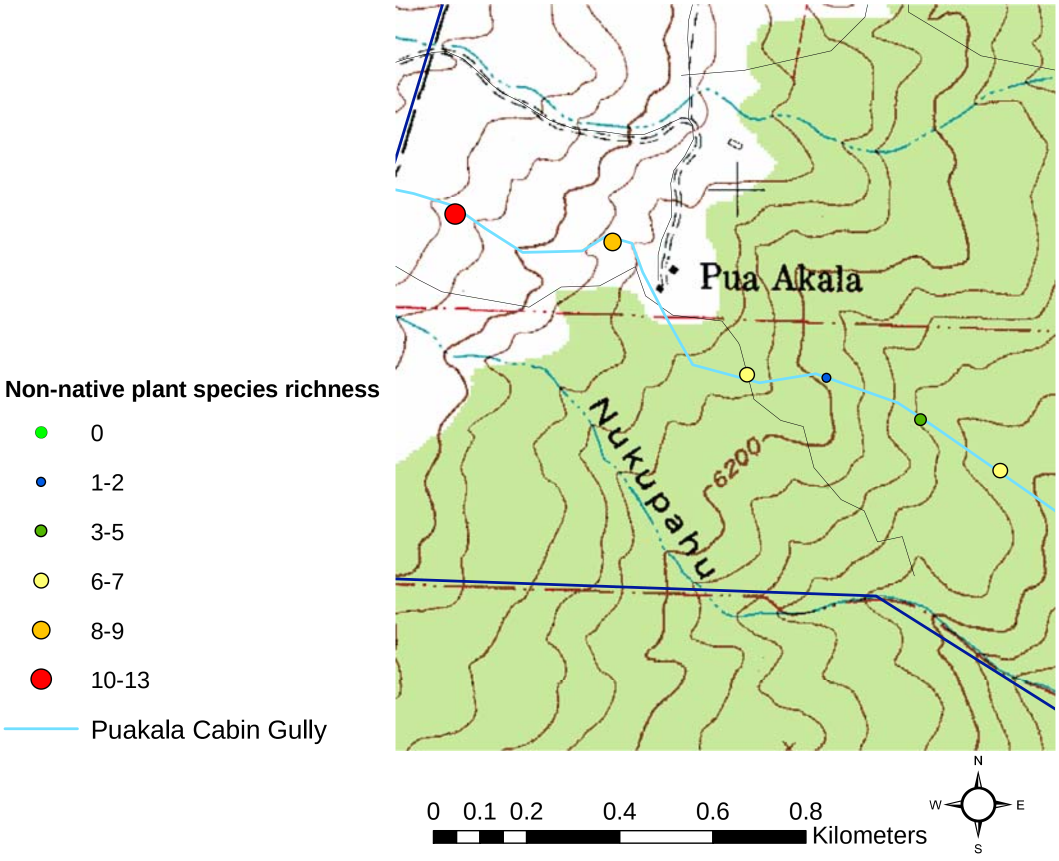


Figure 13. Non-native plant species distribution on a gully near the Pua Akala cabin.

CONCLUSIONS AND RECOMMENDATIONS

Pasture Reforestation

In addition to the habitat benefits to endangered native plants and bird species, this work provided evidence that increasing native forest canopy cover reduces incidence of non-native plant species. A monitoring project could be established to directly address the success of reforestation goals. Networks of plots bisecting the gradient (Stohlgren et al. 1998, Stohlgren et al. 2000) from pasture-forest mosaic-forest would better evaluate success and assess the possibility that extant invasive species initiated alternate trajectories that may disrupt anticipated patterns of succession (Asner and Beatty 1996, Denslow et al. 2006).

Forest Invasion

A considerable portion of the Refuge is covered by koa and ohia forest with steep topography, significant rainfall, and dense vegetation that makes travel expensive, difficult, and challenges detection and control of non-native plant species. Our results highlight accessible management 'dials' that might make the invasion situation more tractable and help contain non-native plant species distribution:

1. Minimize disturbance at low elevations. Plots of mean native plant species cover against mean non-native cover at demonstrate that thresholds may exist (Fig. 12). Reducing native cover below 20% generally results in an exponential increase in non-native cover values above 40%. Discerning meaningful patterns can be difficult with only four plots, so to examine thresholds at the crucial, low-elevation forests we increased the elevation to 5300 feet (increasing the low elevation analysis window by 300 feet) and the number of plots to twelve. Lower elevations are more sensitive. Non-native cover increases when native cover drops below just 40%, but logarithmic increases in non-native cover are less aggressive and initiate at only 20% (Fig. 13). Perhaps correlations could be developed that direct the management of pig populations to decrease the frequency and distribution of patches of disturbance that reduce native cover below 40%. Control could focus on patches of natural disturbance that significantly reduce native cover because non-native plant species seem to congregate in these areas.

Similarly, any large scale-disturbance of native vegetation should be monitored and prioritized for control.

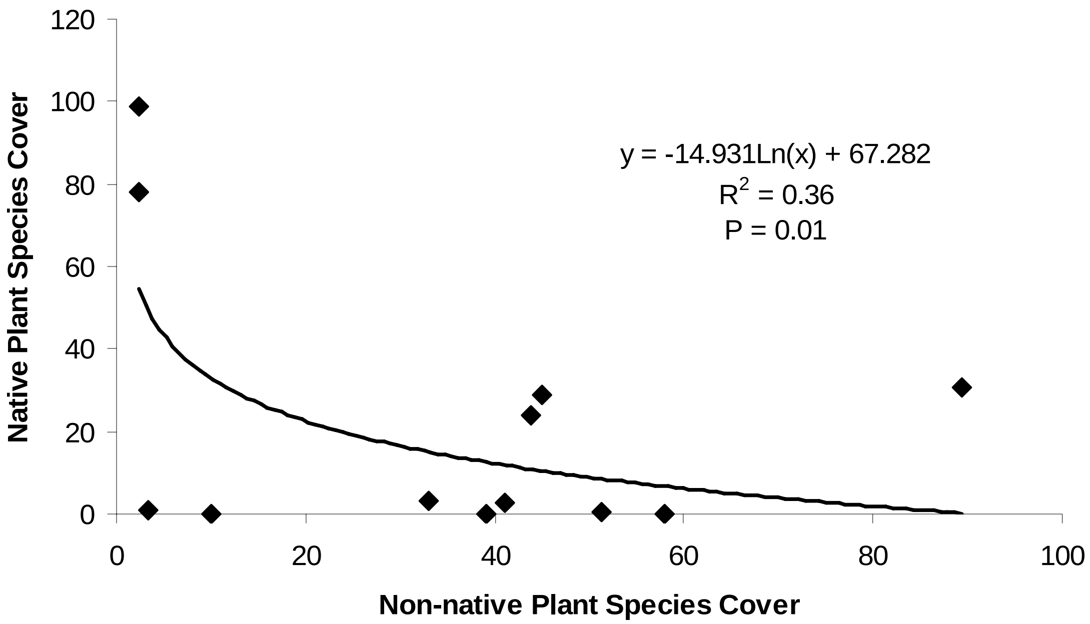


Figure 14. Comparison of native and non-native plant species cover at low elevations might provide some indication of disturbance thresholds.

2. Manage low elevation regional species pool. The established low elevation non-native plant species likely exist in isolated foci from which they capitalize on resource pulses (Denslow 2007). Efforts to control some of these populations with the goal of reducing the abundance and distribution of these isolated sources should decrease further spread. Further inventory to detect other non-native plant species that we project exist at lower elevations (Fig. 4, Table 1) and to detect and locally eradicate other new arrivals will help control the regional species pool (Mack and Lonsdale 2002). Focus on high risk species that can survive in forested habitats (Appendix 3), models of species distributions, and hotspots of non-native plant species diversity should help direct early detection efforts.

3. Reduce propagule pressure and establishment at low elevations. Numerous non-native plant species practice phorsey, they rely on other animals to transport seed. It may be that human traffic conducting inventory of plants (this study), bird monitoring (annually), and fence building act as vectors. *Erharta stipulides* was found below 5000' and likely arrived by shoelace; protocol should be developed to minimize seed transport (www.hear.org). Pigs may also act as vectors. Increased propagule pressure bolsters existing populations and diversity that is likely to further overwhelm native populations and increase chances that available resources will be monopolized by non-native plant species. Smart, iterative sampling (Stohlgren et al. in prep), and techniques that combine plots and survey reminiscent of rare plant surveys (Barnett et al. 2007) should facilitate early detection and subsequent containment of non-native plant species new to the low elevation regional species pool.

4. Continue pig management. Existing eradication and fencing help minimize invasion at lower elevations. Efforts to fund compete fencing of low elevations of the Refuge should be a priority. Currently the higher elevation and more disturbed parts of the Refuge are fenced and pig free. The vulnerable, less disturbed lower elevations that are surrounded by high incidence of invasion are not fenced and might be better suited for protection than the highly disturbed higher elevations that are currently pig free. It is entirely possible that pigs migrate on and off the Refuge at low elevations and carry with them an entirely different suite of species than what was found in this inventory. Past studies have shown that the removal of pigs from Hawaiin forests does not insure reductions of non-native plants (Anderson et al. 1992). Pigs assist with establishment and then species find ways to persist and exploit disturbance.

5. Monitor control. Efficacy of control could be easily addressed with a set of plots placed in areas prior to control, monitored at intervals after control and compared to other control plots. The plots used in the inventory described provide a means to evaluate non-target impacts such as native mortality and disturbance (Barnett et al. 2007); that might provide opportunity for non-native invasion.

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Appendix 1. Non-native plant species HEAR ranking, percent cover, and coefficient of variation of percent cover for all plots.

NRCS code	Species	Score	Percent Cover	CV
pecl2	*Pennisetum clandestinum*, kikuyugrass	18	24.2 (3.56)	1.3
Ehst[1]	*Ehrharta stipoides*, weeping grass		10.9 (2.24)	1.8
anod	*Anthoxanthum odoratum*, sweet vernalgrass		8.3 (1.66)	1.8
Juef[1]	*Juncus effusus*, common rush		4.57 (1.74)	3.3
hola	*Holcus lanatus*, common velvetgrass	15	4 (1)	2.2
agal3	*Agrostis alba*, redtop		2.6 (1.22)	4
fuma	*Fuchsia magellanica*, hardy fuchsia		1.4 (0.73)	4.5
Mist[1]	*Microlaena stipoides*, weeping grass		1.37 (0.54)	3.4
ruar2[1]	*Rubus argutus*, sawtooth blackberry	22	1.26 (0.72)	5
Axaf[1]	*Axonopus affinis*, common carpetgrass	16	1.10 (0.52)	4.2
ruac3	*Rumex acetosella*, common sheep sorrel		1.01 (0.35)	3.1
loja	*Lonicera japonica*, japanese honeysuckle	12	0.73 (0.68)	8.1
hyra3	*Hypochaeris radicata*, hairy catsear		0.42 (0.15)	3
loul	*Lotus uliginosus*, big trefoil		0.28 (0.2)	6.3
erbr	*Eragrostis brownei*, cuming`s lovegrass		0.25 (0.14)	5
uleu	*Ulex europaeus*, common gorse	20	0.24 (0.12)	4.4
pamo5[1]	*Passiflora mollissima*, banana passionflower		0.14 (0.1)	6.2
popu5	*Polygonum punctatum*, dotted smartweed		0.12 (0.1)	7.6
hybo3	*Hydrocotyle bowlesiodes*		0.07 (0.07)	8.7
sema15	*Senecio madagascariensis*, madagascar ragwort	23	0.07 (0.07)	8.7
padi3	*Paspalum dilatatum*, dallisgrass	12	0.06 (0.05)	7.1
Jute[1]	*Juncus tenuis*, poverty rush		0.04 (0.03)	6.2
trre3	*Trifolium repens*, white clover		0.04 (0.03)	7.4
drco2	*Drymaria cordata*, whitesnow		0.03 (0.03)	8.7
ilaq80	*Ilex aquifolium*, english holly		0.03 (0.02)	5.6
vepl2	*Veronica plebia*, island speedwell		0.02 (0.02)	8.7
dagl	*Dactylis glomerata*, orchardgrass	2	0.01 (0.01)	8.7
hypa6[1]	*Hypericum parvulum*, sierra madre st. johnswort	12	0.01 (0.01)	8.7
prvu	*Prunella vulgaris*, common selfheal		0.01 (0.01)	8.7
rola	*Rosa laevigata*, cherokee rose		0.01 (0.01)	8.7
buma80	*Buddleja madagascariensis*, smokebush	7	0	
chle80	*Chrysanthemum leucanthemum*, oxeye daisy		0	

civu	*Cirsium vulgare*, bull thistle		0
cola6	*Corynocarpus laevigatus*		0
euro2	*Eucalyptus robusta*, swampmahogany	3	0
geca5	*Geranium carolinianum*, carolina geranium		0
geho5	*Geranium homeanum*, australasian geranium		0
mepo3	*Medicago polymorpha*, burclover		0
nami2	*Nasturtium microphyllum*, onerow yellowcress		0
oxco	*Oxalis corniculata*, creeping woodsorrel		0
phda5	*Photinia davidiana*, chinese photinia	-2	0
rare3[1]	*Ranunculus repens*, creeping buttercup		0
rucr	*Rumex crispus*, curly dock	16	0
vese[1]	*Veronica serpyllifolia*, thymeleaf speedwell		0
zaae	*Zantedeschia aethiopica*, calla lily	13	0

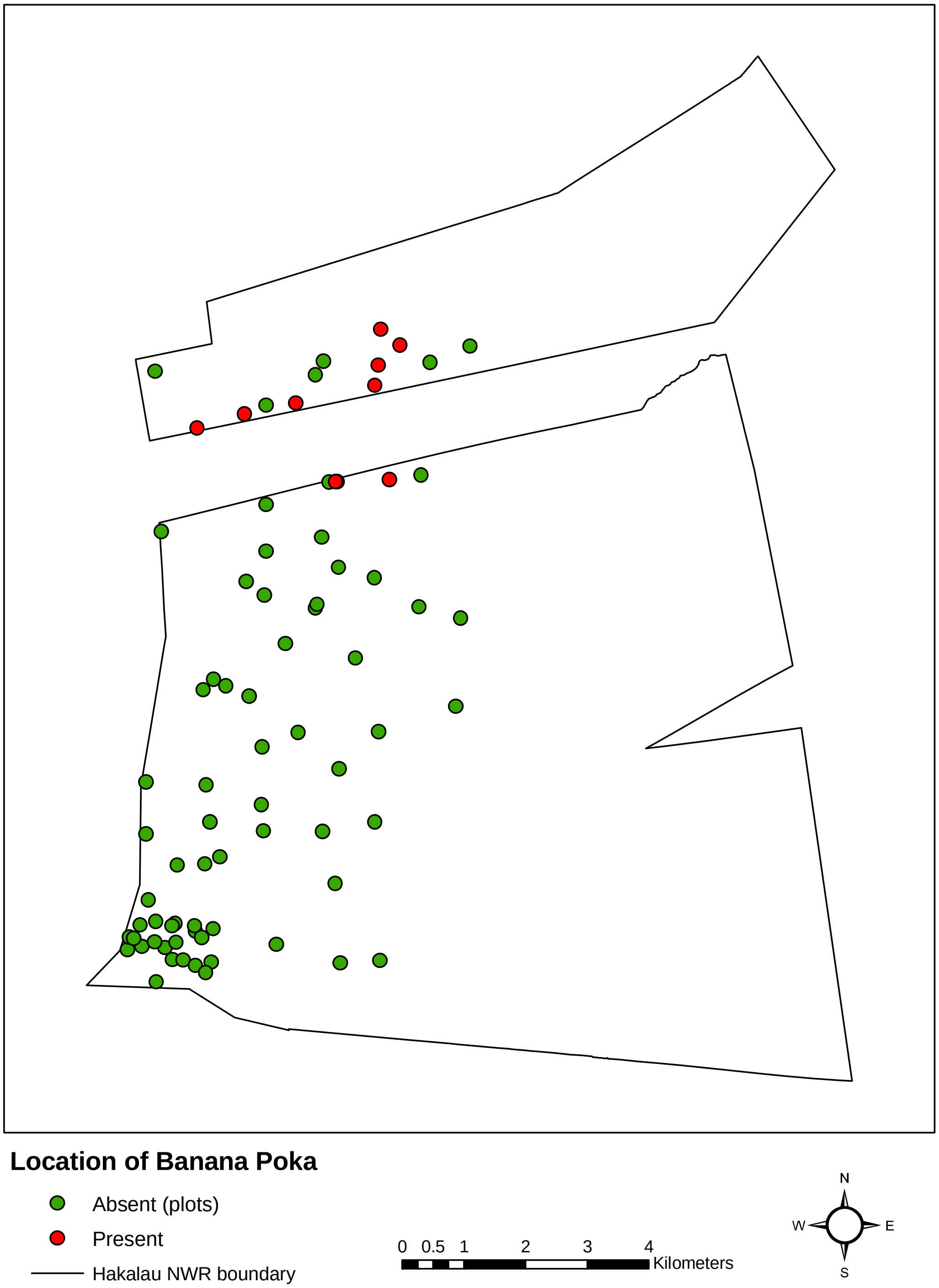
Appendix 2. Non-native plant species typical habitat, means of dispersal and association with pig disturbance.

NRCS Code	Species	Habitat	Dispersal	Pig Disturbance
agal3	*Agrostis alba*, redtop			
anod	*Anthoxanthum odoratum*, sweet vernalgrass	open, dry, disturbed, pastures, disturbed in wet forests	seed, wind, water, animals	
axaf[1]	*Axonopus affinis*, common carpetgrass	wet pastures, disturbed wet forest	seed	
buma80	*Buddleja madagascariensis*, smokebush	mesic	bird dispersed fruit	
chle80	*Chrysanthemum leucanthemum*, oxeye daisy			
civu	*Cirsium vulgare*, bull thistle			
cola6	*Corynocarpus laevigatus*	mesic	seed by birds and pigs	
dagl	*Dactylis glomerata*, orchardgrass	heathland, forests, disturbed sites, pastures, roads, trails	seed, wind, water, animals	
drco2	*Drymaria cordata*, whitesnow	pastures, shaded moist sites,	seed, rooting from nodes	
ehst[1]	*Ehrharta stipoides*, weeping grass	openings in wet forest, other moist shaded sites	seed	yes
erbr	*Eragrostis brownei*, cuming`s lovegrass	pastures, openings in wet forest	seed	
euro2	*Eucalyptus robusta*, swampmahogany			
fuma	*Fuchsia magellanica*, hardy fuchsia	mesic to wet forest	seed, maybe birds	
geca5	*Geranium carolinianum*, carolina geranium			
geho5	*Geranium homeanum*, australasian geranium			
hola	*Holcus lanatus*, common velvetgrass	wet, disturbed areas, pastures, grasslands	seed	no
hybo3	*Hydrocotyle bowlesiodes*			
hypa6[1]	*Hypericum parvulum*, sierra madre st. johnswort			
hyra3	*Hypochaeris radicata*,	wet disturbed sites,	seed, wind	no

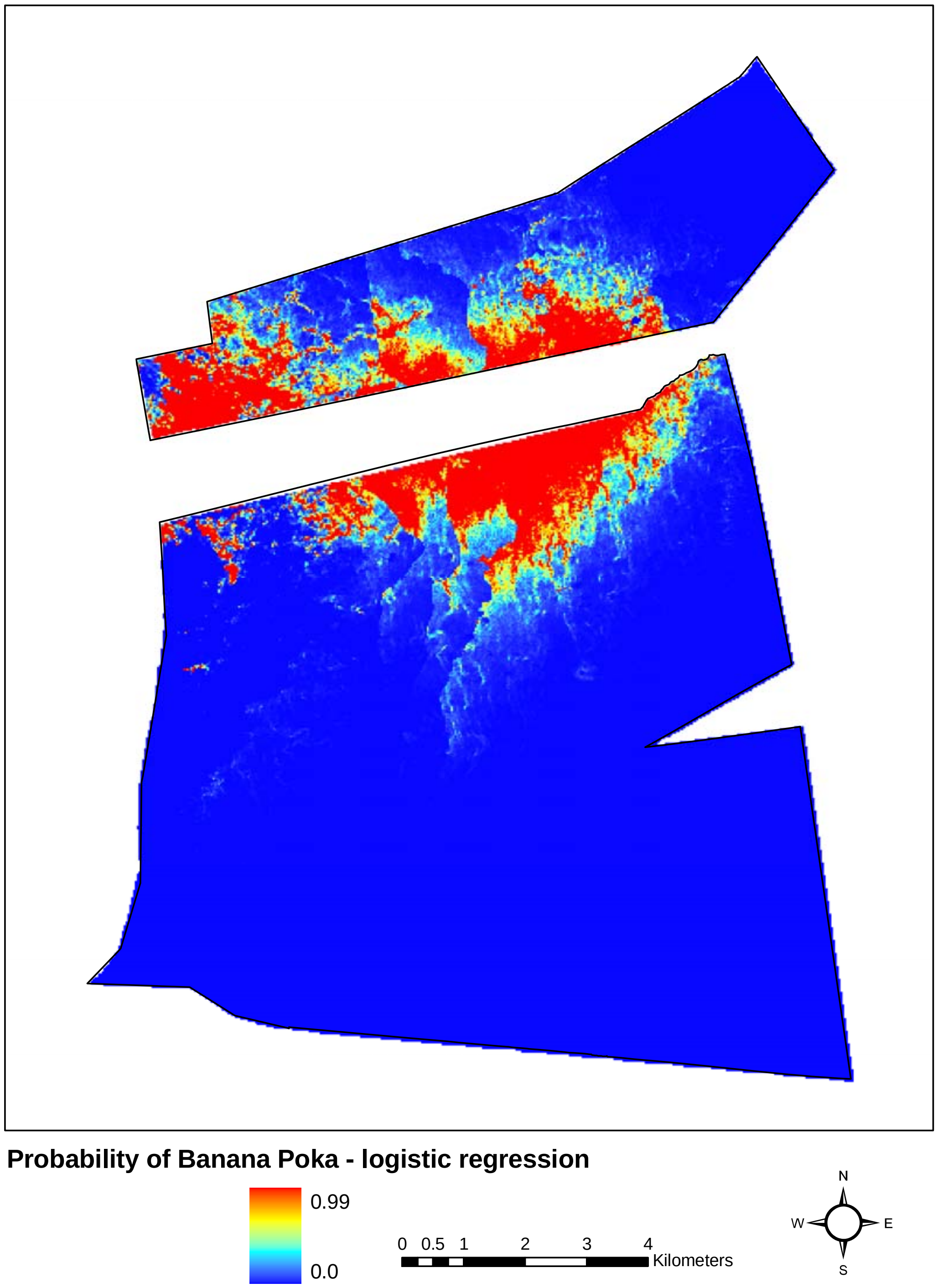
	hairy catsear	pig like taproot	
ilaq80	*Ilex aquifolium*, english holly	forest edge	seed, birds
Juef[1]	*Juncus effusus*, common rush	wet edges	seed
Jute[1]	*Juncus tenuis*, poverty rush	wet disturbed, pastures	seed
loja	*Lonicera japonica*, japanese honeysuckle	mesic to wet, disturbed	seed, bird, stem
loul	*Lotus uliginosus*, big trefoil	forest, pastures	seed
mepo3	*Medicago polymorpha*, burclover	open, dry to mesic, disturbed, pastures	seed
mist[1]	*Microlaena stipoides*, weeping grass	openings in wet forest, shaded sites	seed
nami2	*Nasturtium microphyllum*, onerow yellowcress	wet	seed, vegetatively
oxco	*Oxalis corniculata*, creeping woodsorrel	pastures to shade, disturbed sites	seed, node rooting, birds
padi3	*Paspalum dilatatum*, dallisgrass	open areas	seed
pamo5[1]	*Passiflora mollissima*, banana passionflower		
pecl2	*Pennisetum clandestinum*, kikuyugrass	pastures, forest when disturbed, withstand shade	seed, rhizomes
phda5	*Photinia davidiana*, chinese photinia	mesic forest	seed
popu5[1]	*Polygonum punctatum*, dotted smartweed		
prvu	*Prunella vulgaris*, common selfheal		
rare3[1]	*Ranunculus repens*, creeping buttercup	fields, pastures, disturbed wet forest	seed
rola	*Rosa laevigata*, cherokee rose	mesic forest	seed
ruar2[1]	*Rubus argutus*, sawtooth blackberry	disturbed, pasture, mesic to wet forest	seed, birds, animals
ruac3	*Rumex acetosella*, common sheep sorrel	disturbed mesic forest, pastures	seed
rucr	*Rumex crispus*, curly dock	pastures, early to disturbed areas	seed, animals fur and digestive
sema15	*Senecio madagascariensis*,	mesic forest	seeds, birds, animals

	madagascar ragwort			
trre3	*Trifolium repens*, white clover			
uleu	*Ulex europaeus*, common gorse	pasture, forests, disturbed, under trees	seed, ditches	
vepl2	*Veronica plebia*, island speedwell			
vese[1]	*Veronica serpyllifolia*, thymeleaf speedwell			
zaae	*Zantedeschia aethiopica*, calla lily		rhizomes, seed, birds	

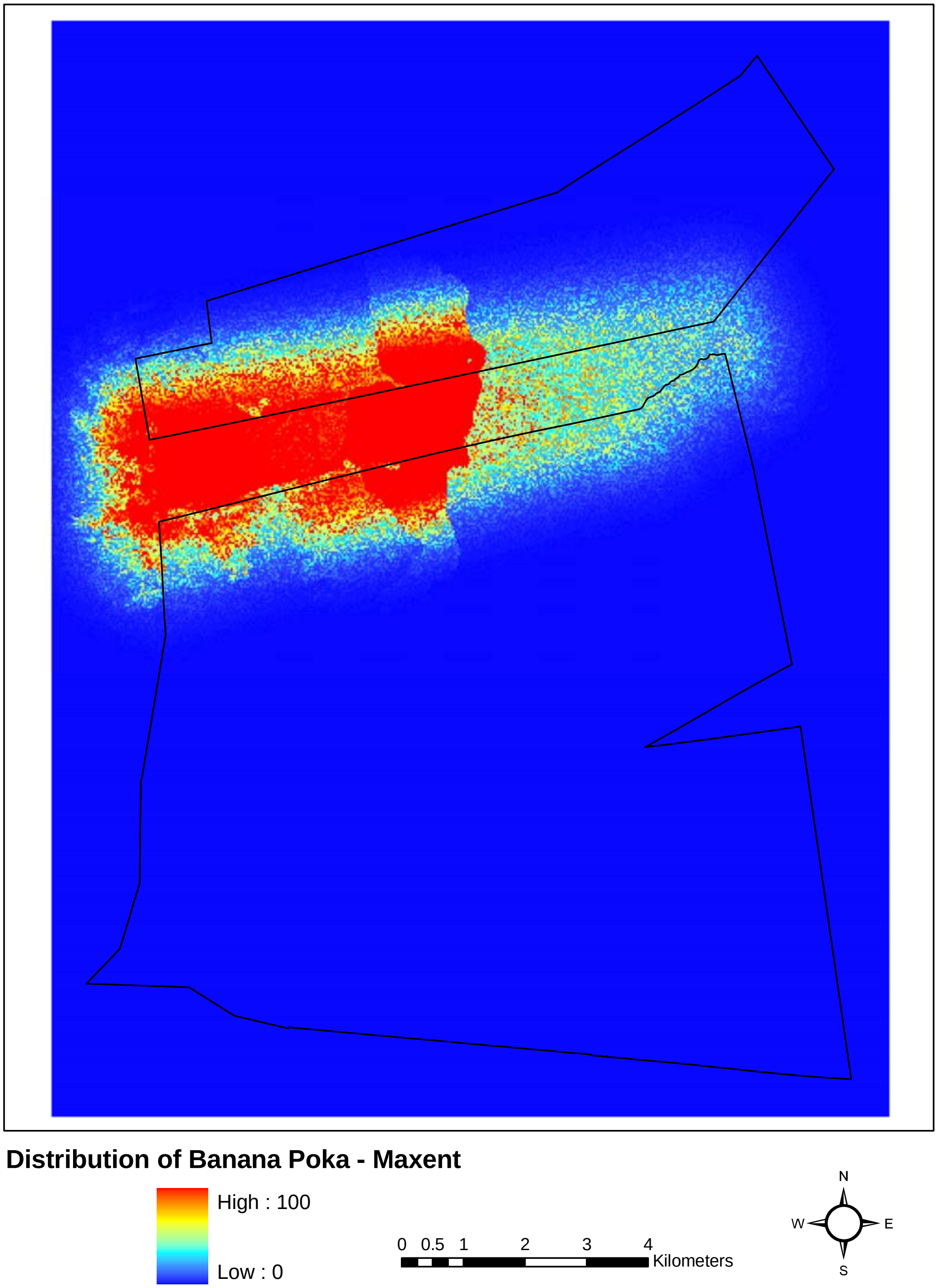
Appendix 3. Non-native plant species distribution and models.



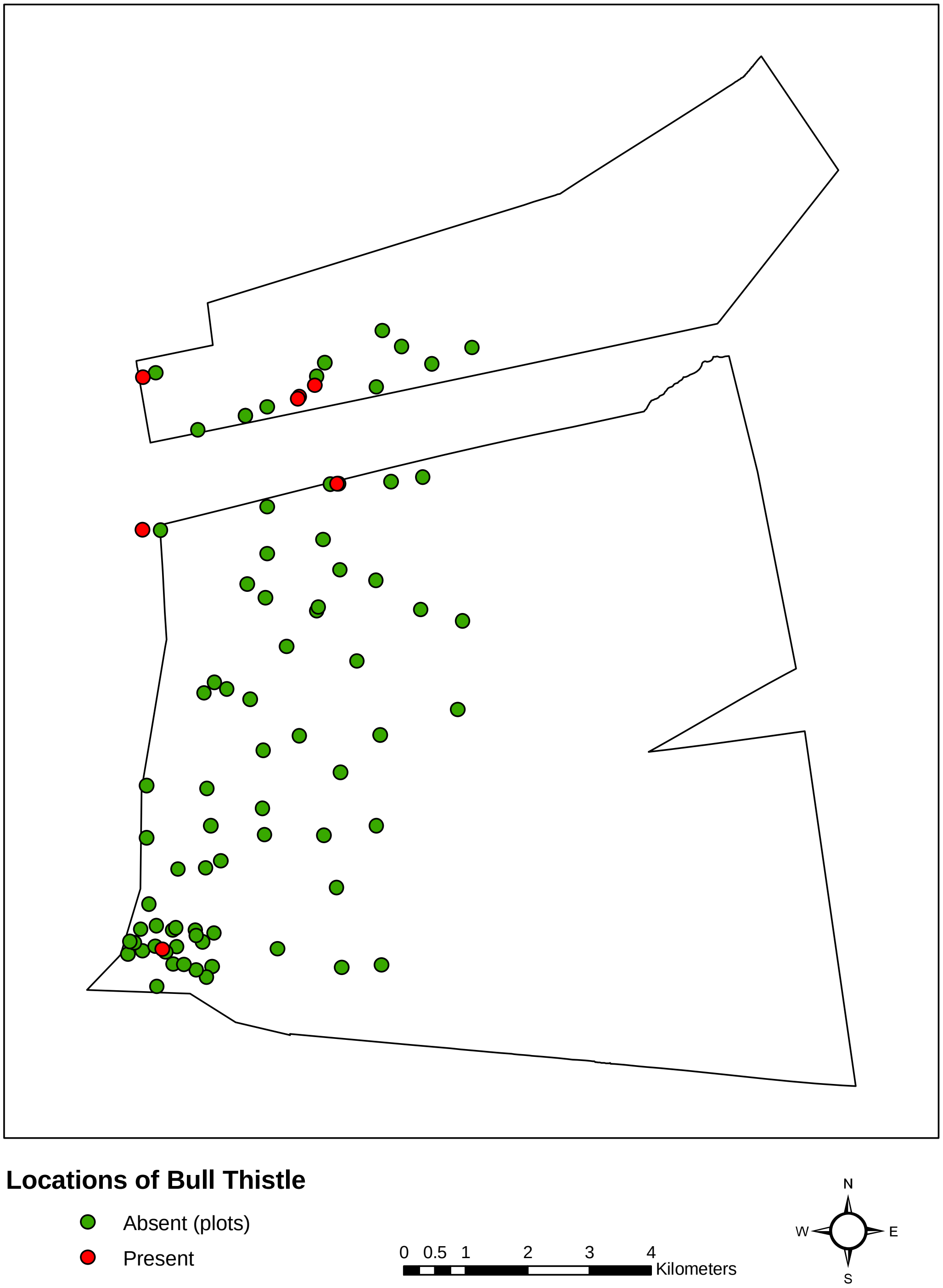
Appendix 3a. Locations where banana poka was found by plots and incidental mapping.



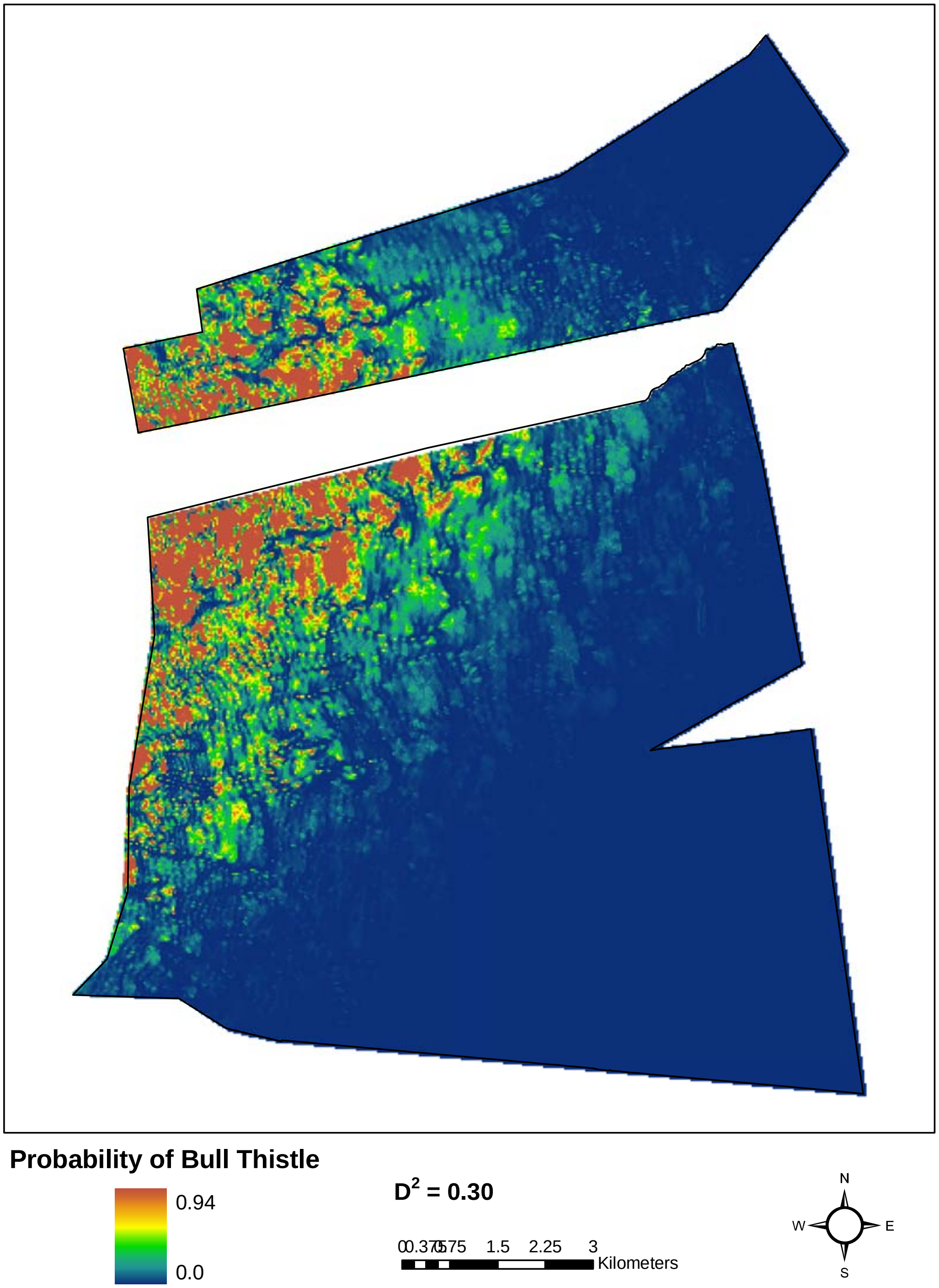
Appendix 3b. Probability of banana poka as modeled using logistic regression.



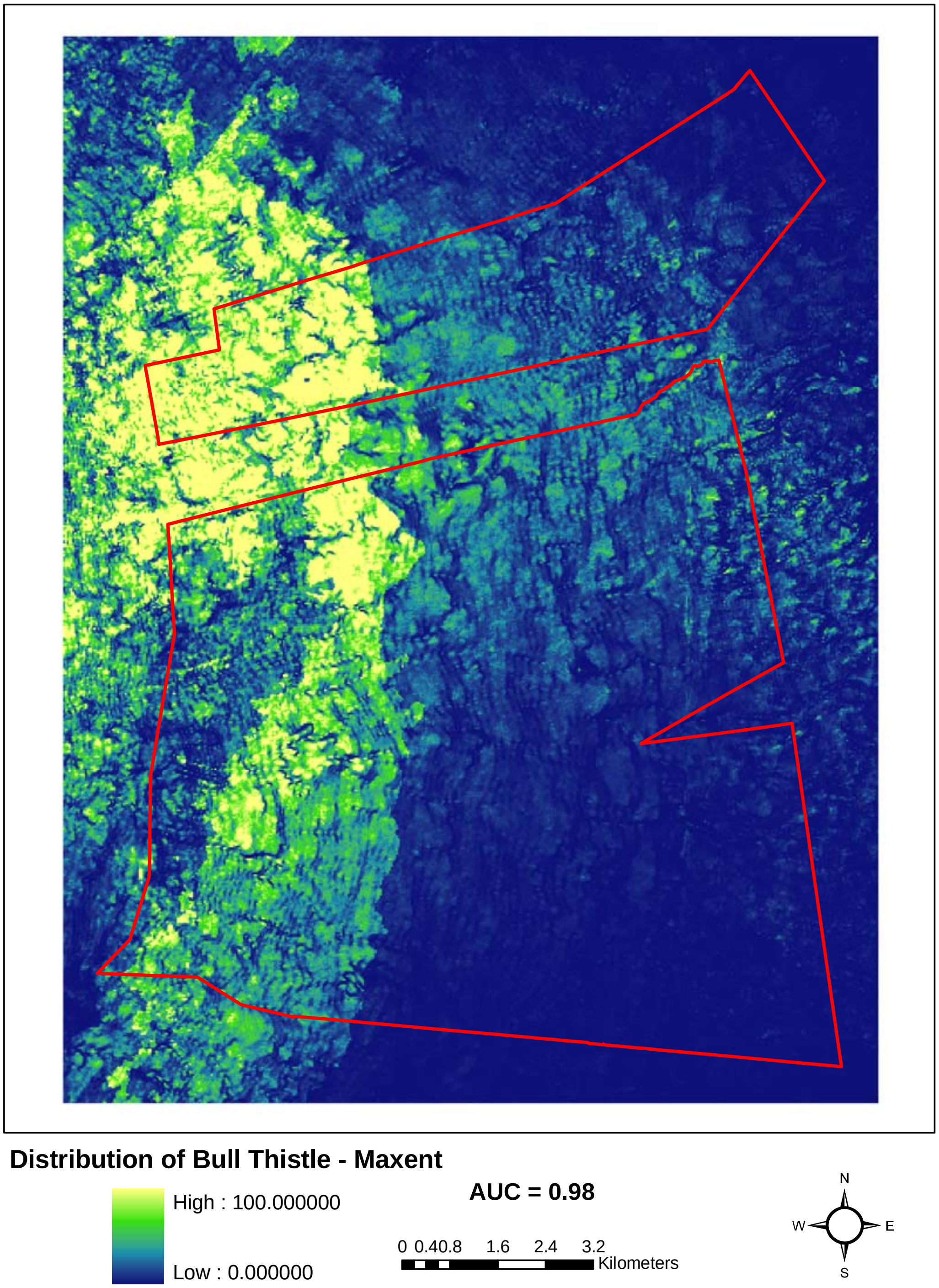
Appendix 3c. The potential distribution of banana poka as modeled by Maxent.



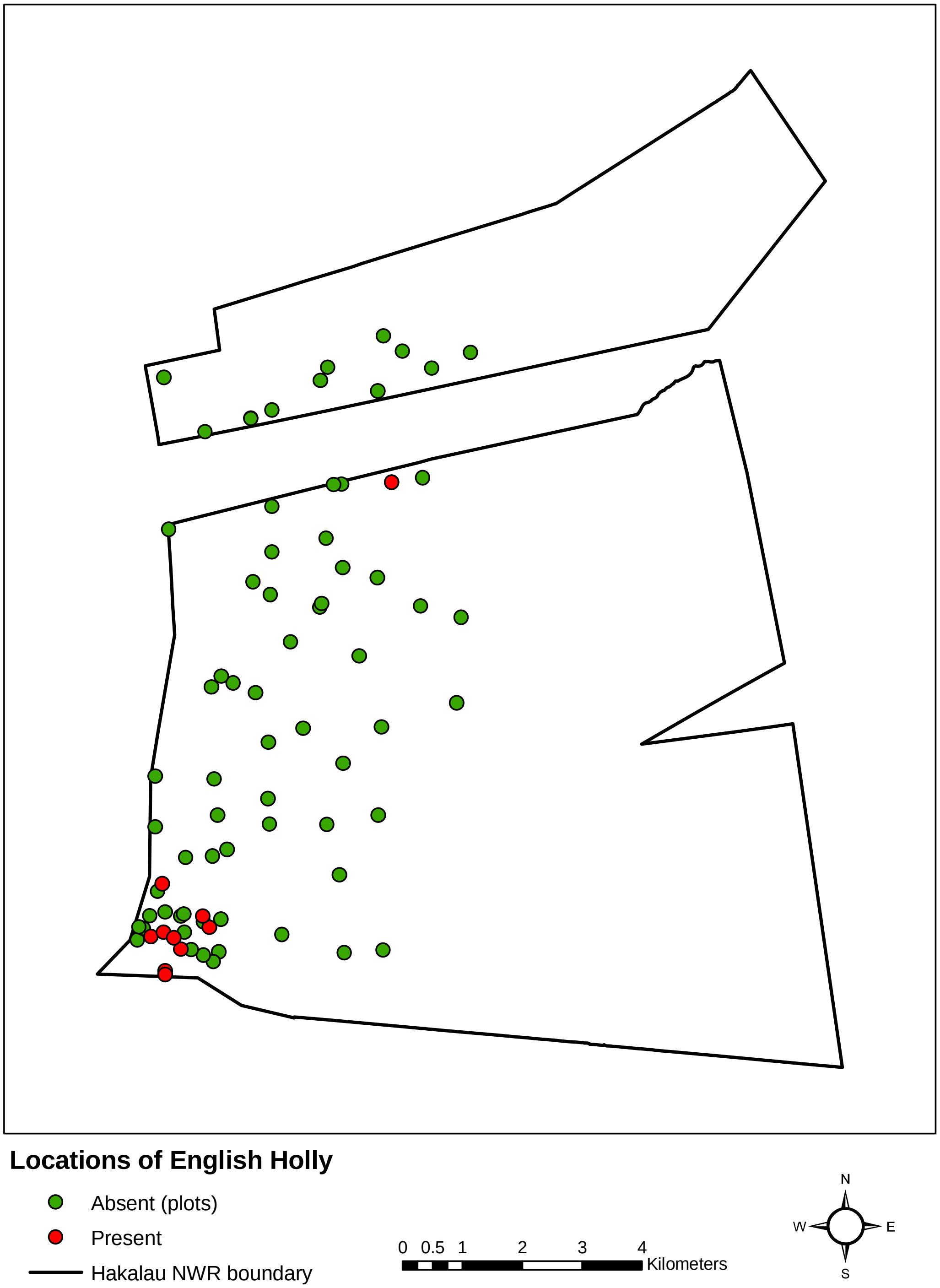
Appendix 3d. Locations where bull thistle was found by plots and incidental mapping.



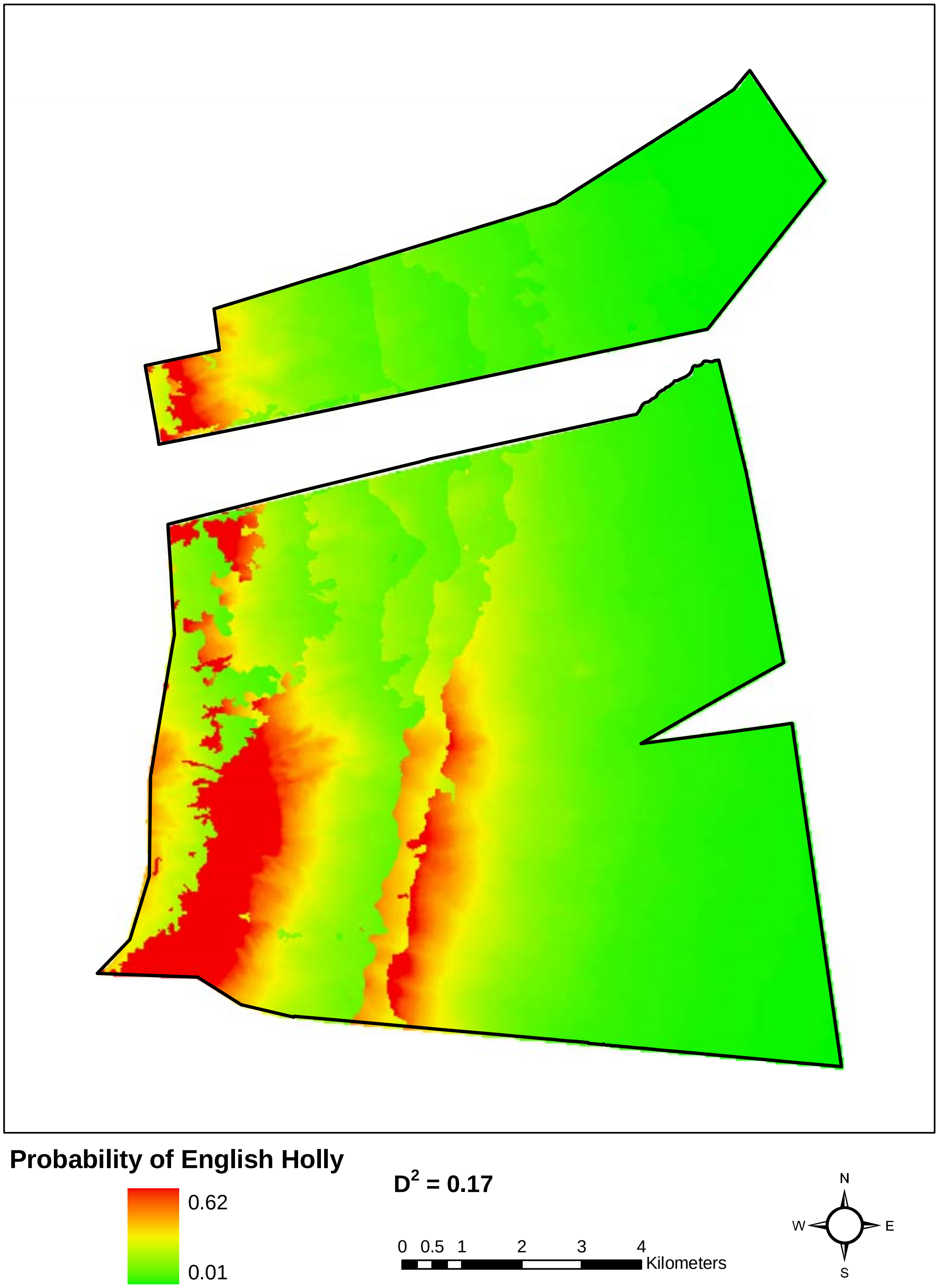
Appendix 3e. Probability of bull thistle as modeled using logistic regression.



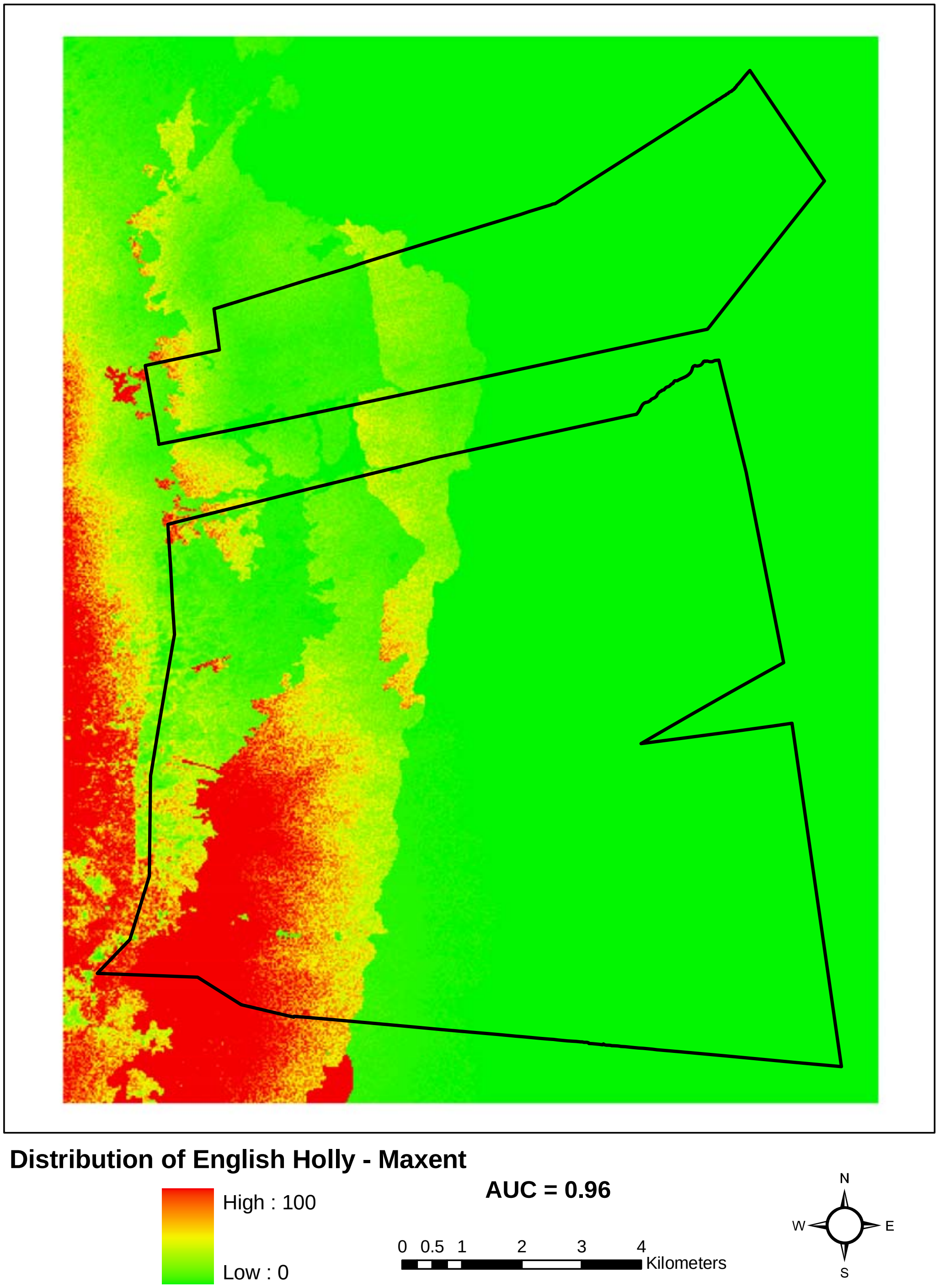
Appendix 3f. The potential distribution of bull thistle as modeled by Maxent.



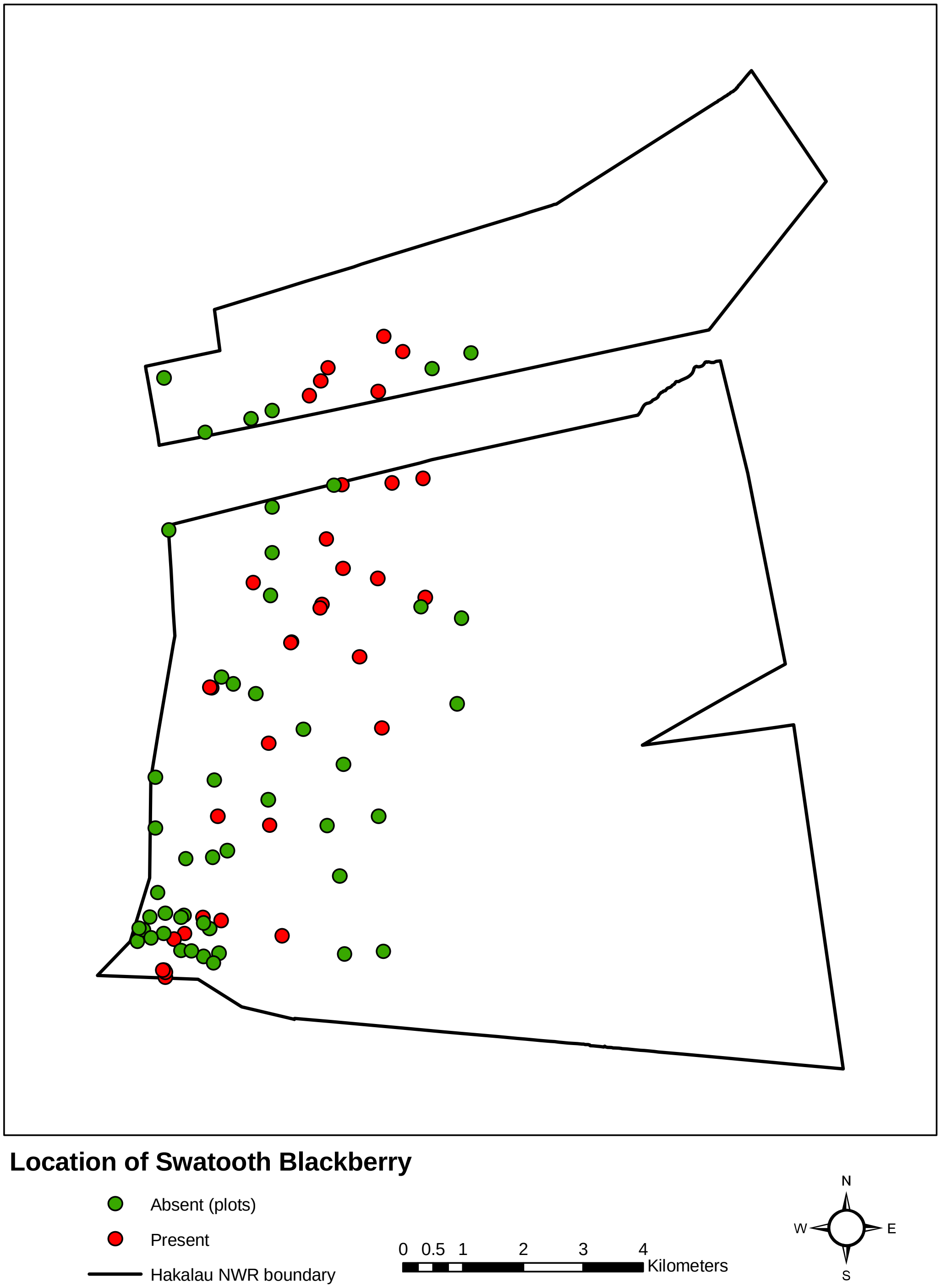
Appendix 3g. Locations where English holly was found by plots and incidental mapping.



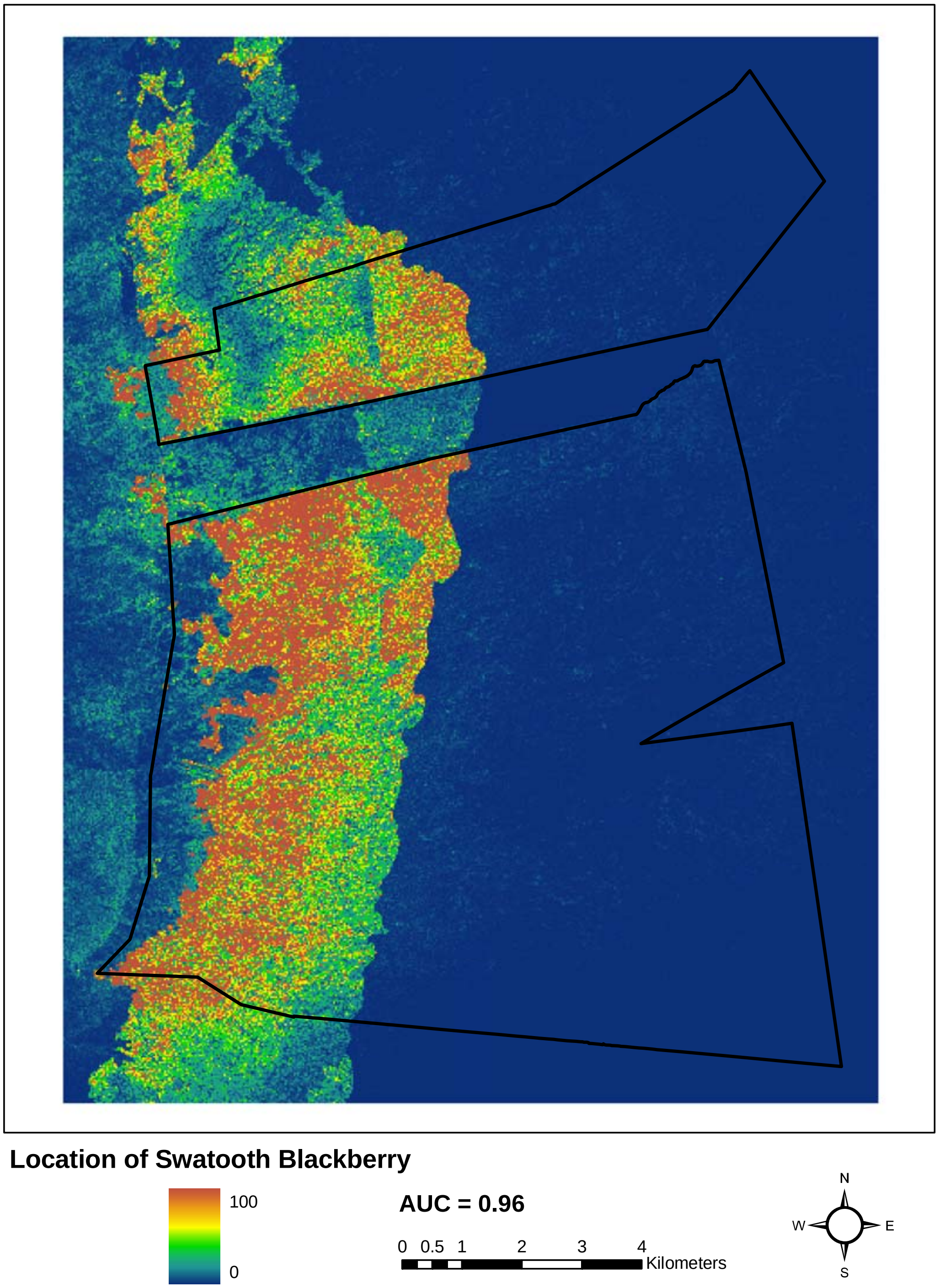
Appendix 3h. Probability of Enghlish holly as modeled using logistic regression.



Appendix 3i. The potential distribution of English holly as modeled by Maxent.

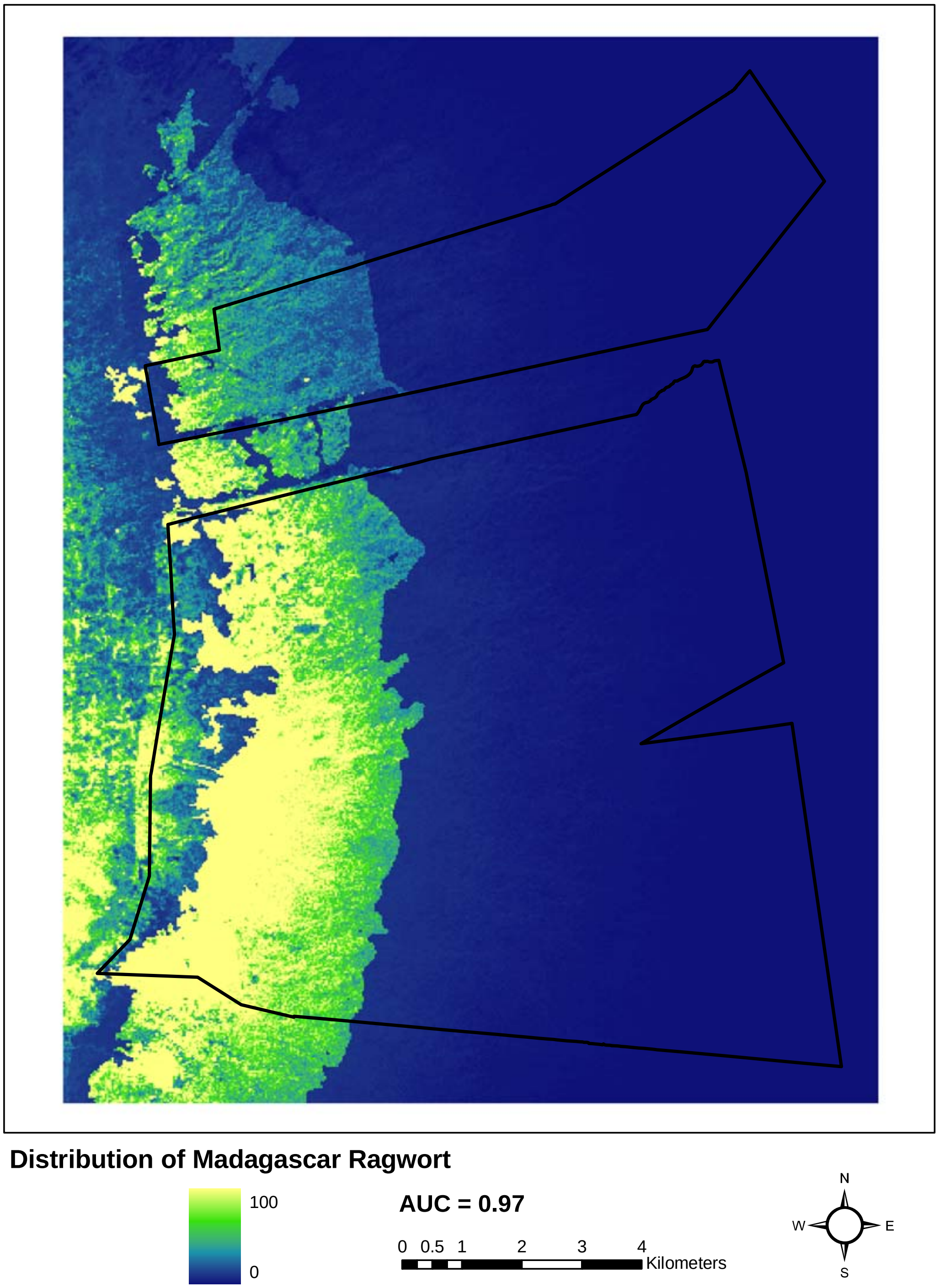


Appendix 3j. Locations where blackberry was found by plots and incidental mapping.

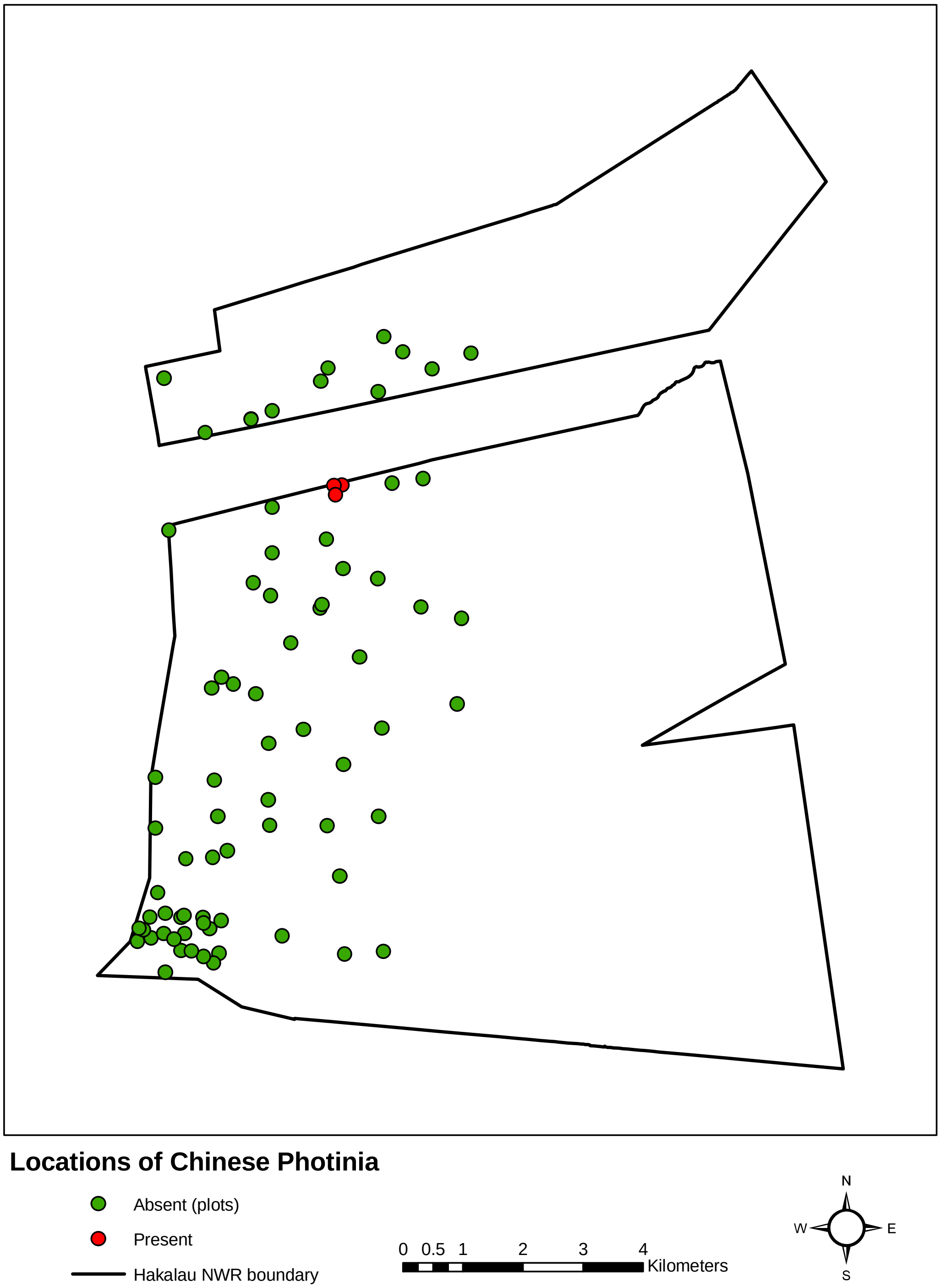


Appendix 3k. The potential distribution of blackberry as modeled by Maxent.

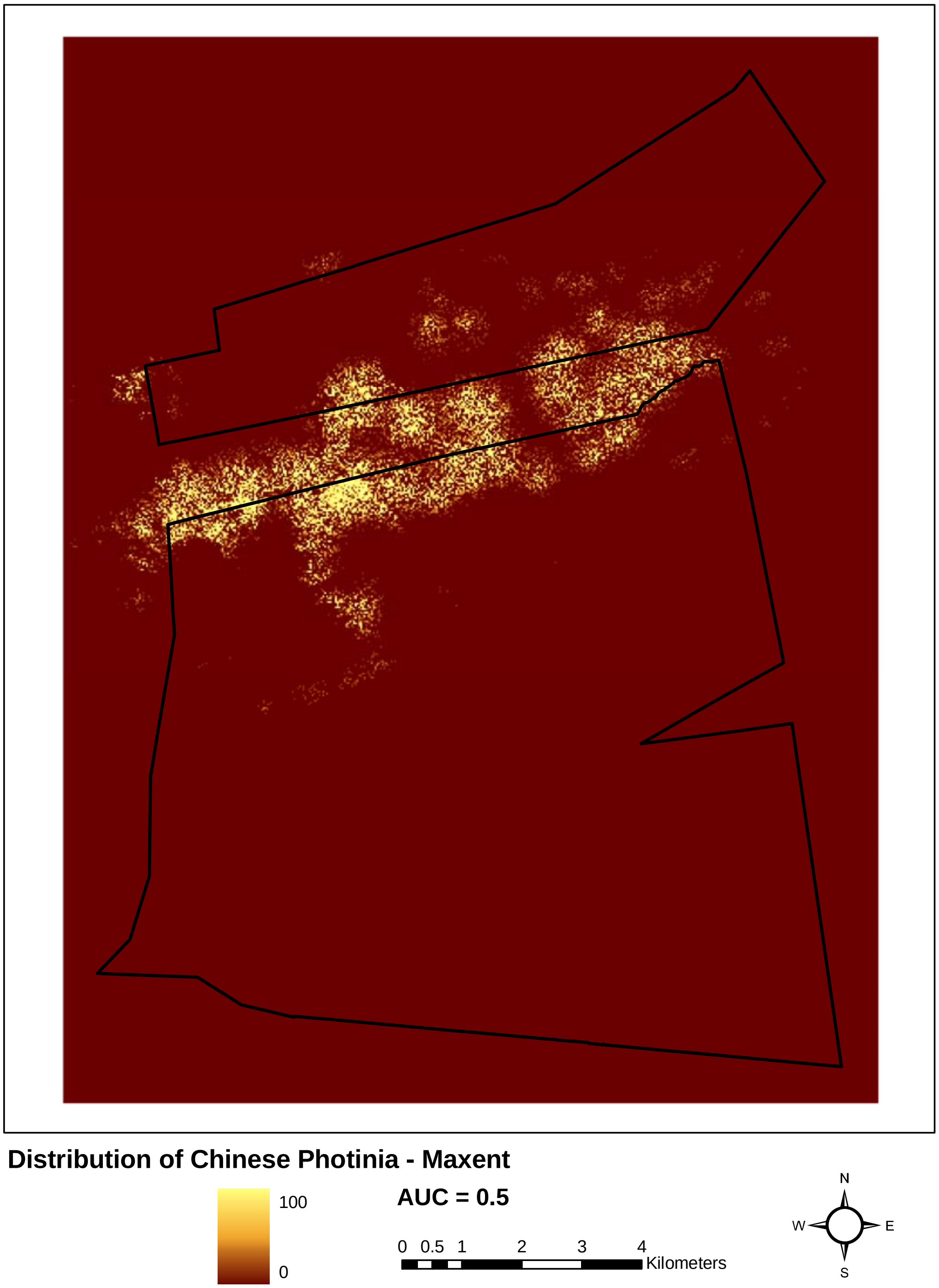
Appendix 31. Locations where Madagascar ragwort was found by plots and incidental mapping.



Appendix 3m. The potential distribution of Madagascar ragwort as modeled by Maxent.



Appendix 3n. Locations where photinia was found by plots and incidental mapping.



Appendix 3o. The potential distribution of photinia as modeled by Maxent.

Appendix 4. Species of concern and model results.

Species	Model	D2/AUC	Coefficients (logistic) or Percent Contribution (Maxent)
Banana poka	Spatial data	D^2 = 0.67	Probability = -44.5+0.22*green-0.08*ndvi+0.01*ele-0.003*pihadist+0.1*slope+3.04*vegmoisture
Banana poka	Plot data	D^2 = 0.26	Probability = -3.1+1.1*poop+0.18*soil
Banana poka	Plot and spatial data	D^2 = 0.69	Probability = -22.26+0.43*soil+0.17*green-0.1*ndvi+0.001*ele-0.004*pihadist+0.17*slope
Banana poka	Maxent	AUC = 0.98	piha = 57.7, vegmoisture = 37.5, east = 3.5, ele = 0.5, north = 0.3, green = 0.3, bright = 0.2
Bull thistle	Spatial model	D^2 = 0.30	Probability=-11.0+0.002*ele-0.001*piha-0.17*slope
Bull thistle	Plot	n/a	
Bull thistle	Plot and spatial data	n/a	
Bull thistle	Maxent	AUC = 0.98	Vegmoisture = 54.4, slope = 18.2, pihadist = 14.2, green = 5.8, ele = 4.3, ndvi = 2.8, aspect north = 0.3, gulch distance = 0.1
English holly	Spatial data	D^2 = 0.17	Probability=-23.9+0.003*ele+0.84*vegetation moisture
English holly	Plot data	D^2 = 0.55	Probability=-13.2+0.23*nativerich+1.1*nonrichness-13.63*bioturb-0.81*poop-0.86*soil+0.05*wood-0.03*moss+0.03*canopycover
English holly	Plot and spatial data	D^2 = 0.77	Probability=-142.24+3.38*non-native rich+0.32*wood-0.12*moss+0.11*canopycover+0.01*ele+3.32*vegetation moisture
English holly	Maxent	AUC = 0.96	veg moisture = 47.8, ele = 44.4, piha dist = 3.5, east = 2.3, green = 1.2, gulch dist = 0.8
Sawtooth blackberry	Spatial data	D^2 = 0.09	Probability=-1.01-0.0002*pihadist+0.39*vegetation moisture
Sawtooth blackberry	Plot and spatial data	D^2 = 0.37	Probability=14.16-0.27*nat rich+0.36*non-native rich-0.02*ndvi-0.003*ele+0.11*slope+0.82*vegetation moisture
Sawtooth blackberry	Plot	D^2 = 0.12	Probability=-1.91+0.21*non-native rich+0.23*animaltracks+0.07*bioturbation-0.06*rock
Sawtooth blackberry	Maxent	AUC = 0.96	Vegmoist = 70.8, pihadist = 7.3, wet = 6, ele = 5.5, north = 4.5, gulch dist = 2, slope = 1.4, east = 1.4, bright = 0.8, green = 0.3
Madagascar ragwort	Spatial data	n/a	

Madagascar ragwort	Plot and spatial data	n/a	
Madagascar ragwort	Plot	$D^2 = 0.41$	Probability=-4.32+0.14*wood-0.12*moss
Madagascar ragwort	Maxent	AUC = 0.97	vegmoisture = 57.9, ele = 37.1, green = 4.4, north = 0.3, gulch dist = 0.3
Chinese photinia	Spatial data	n/a	
Chinese photinia	Plot and spatial data	n/a	
Chinese photinia	Plot	n/a	
Chinese photinia	Maxent	AUC = 1.0	Pihadist = 34.1, gulch dist = 22.9, vegmoist = 19, north = 18.9, bright = 4, east = 0.7, ele = 0.3, green = 0.1

Spatial Variables:
pihadist = distance from state piha section.
vegmoisture = vegetation type moisture, surrogate for precipitation
gulch dist = distance from gulch
north = aspect, degrees from north
east = aspect, degrees from east
ele = elevation
bright = remote sensed information, tasselcap bright
green = remote sensed information, tasselcap green
wet = remote sensed information, tasselcap wet
ndvi = remote sensed information, ndvi

Plot Variables:
canopy cover = canopy cover of entire plot
wood = average % cover of wood in subplot
moss = average % cover of moss in subplot
animaltracks = average % cover of animal tracks in subplot
bioturbation = average % cover of animal disturbance in subplot