Using Survey Data to Estimate Occupancy and to Model Suitable Habitat throughout the Geographic Range of the Endangered Point Arena Mountain Beaver

William J. Zielinski[a], Fredrick V. Schlexer[a], Jeffrey R. Dunk[b], Matthew J. Lau[c], and James J. Graham[b]

[a] USDA Forest Service, Pacific Southwest Research Station, Redwood Sciences Laboratory
Arcata, California 95521
[b] Department of Environmental Science and Management, Humboldt State University, Arcata
California 95521
[c] Department of Wildlife, Humboldt State University, Arcata, California, 95521

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SUMMARY

We randomly sampled the occurrence of Point Arena mountain beavers (PAMB) from the portion of their geographic range that was accessible (public lands plus private lands where permission was granted). We surveyed 127 25-ha sample units (55.4% of accessible sample units) for PAMB burrows and estimated our probability of detecting burrows, if they were present, at > 90% per visit. Using this information, we estimated occupancy across the accessible portion of the range to be 26.2%. This estimate can serve as a baseline for monitoring occupancy status. Monitoring occupancy across the geographic range, combined with strategically selected locations where abundance and survival can be estimated non-invasively, may comprise a realistic and meaningful monitoring program for this taxon. We also used the detection and non-detection locations to develop a habitat suitability model by relating both sets of locations to remotely sensed predictors. We evaluated 53 *a priori* candidate habitat suitability models and the best-fitting model included: slope (-), terrain roughness index (-), and the density of rivers and streams (+). This model predicted, for every sample unit within the PAMB's geographic range, a value of probability of occurrence from zero to one. We selected the probability value that best separated the sample units into suitable and non-suitable habitat, resulting in an estimate of 70.5 km^2 of suitable habit, or approximately 40.4% of the original

geographic range. Suitable habitat was most common in the middle (along the north-south axis) of the range. A substantial number of suitable areas were predicted along the eastern margin of the range, suggesting that PAMBs may be discovered even farther east than we sampled. New detections in the eastern portions of the range expanded the known geographic range to ~134 km^2 (~235 km^2 if a 3-km buffer is added), moderating concerns about habitat loss, including that predicted by climate change. The identification of high suitability areas allows management agencies to prioritize areas for PAMB conservation planning and to evaluate human impacts on habitat.

INTRODUCTION

The Point Arena mountain beaver (*Aplodontia rufa nigra*) (PAMB) is a burrow-dwelling rodent that is a federally endangered species occurring in a small geographic range in Mendocino County, California (Steele and Litman 1998, USFWS 2009) (Fig. 1). Recovery goals specify minimum standards for the number and size of populations and for monitoring trends in populations and geographic range (Steele and Litman 1998, USFWS 2009), yet quantitative information about population status is limited to abundance estimates within or immediately adjacent to one of the few protected areas within the subspecies' range: Manchester State Park (Northen and Fitts 1998, Zielinski et al. 2013a). Mark-recapture methods were used to estimate population size for two locations within the park, and both had low but stable numbers from 2006 – 2009 (Zielinski et al. 2013a). At other historic locations throughout the subspecies' range, recent searches found no evidence of their burrows (W. Zielinski unpubl. obs.). However, whether new sites had been colonized over the same time period is unknown. An objective and quantitative assessment of the population status of the PAMB throughout its range does not exist despite it being a recovery criterion (USFWS 2009). A comprehensive program is needed to assess the distribution of PAMBs, which would also serve as a baseline for monitoring.

Monitoring an adequate number of locations as intensively as has been done in Manchester State Park to estimate population status is infeasible. An alternative, used extensively in recent wildlife research, is occupancy estimation (MacKenzie et al. 2006). This approach samples the presence (yes [“1”] versus absence [“0”]) of a species within sample units distributed randomly across the landscape and assumes that the frequency of occurrence is an index of population status. The assumption that measures of occurrence collected across the range (distribution) reflect changes in abundance has received considerable support (Brown 1984, Gaston 1996, Stanley and Royle 2005, Noon et al. 2012). Under some circumstances such as when budget is limited or when a species uncommonly detected, presence-absence surveys are more effective than measures of abundance at determining population status (Joseph et al. 2006). Occupancy estimation is a well-established approach for species that are very expensive or difficult to count. The PAMB fits these characteristics and our primary objective was to use occupancy estimation to quantitatively measure the status of the PAMB population throughout its range. Repeated sampling using the same approach can then serve as a population monitoring program, as demonstrated for other species (e.g., Karanth et al. 2011, Gould et al. 2012, Zielinski et al. 2013b).

Relating the detections and non-detections from occupancy surveys to associated environmental variables can also produce a habitat model that predicts a species’ occurrence and distribution (Elith and Leathwick 2009). One of the values of species distribution modeling is that it can produce a map that identifies the location, extent, and configuration of areas where the species is likely to occur. To date, the only habitat modeling for the PAMB has been based on expert opinion (Fitts et al. 2002) or has focused on the habitat at den site locations (Zielinski et al. 2010). Both of these studies examined only a small proportion of the range, within Manchester State Park. Therefore, our second objective was to develop a range-wide map of predicted habitat suitability. This will allow managers to identify likely core areas and potential corridors that can be managed to prevent their degradation. It also complements previous work that explored genetic substructure across the geographic range (Zielinski et al. 2012).

METHODS

Study Area

We defined the PAMB geographic range as the potential range map in the species' five-year status review (USFWS 2009). The USFWS created it by adding a 3.2 km buffer around the perimeter of known locations (except the western boundary, which is the Pacific Ocean). Considering only the outermost points of the detection locations, the geographic range was ~85 km^2; adding the buffer expanded the range to ~174 km^2 (Fig. 1) and this larger area served as the basis of our sampling frame. This area includes a wide array of ecosystems, including coastal dunes and scrub, hardwood riparian forest, and coniferous forest. The western portion of the range is coastal terrace with grassland, coastal scrub, and agricultural (mostly grazing) lands dissected by largely east-west flowing streams with shrub, forb, and hardwood tree riparian areas. To the east, the coastal terrace transitions into foothills and mountains with nearly continuous forests comprised of Sitka spruce (*Picea sitchensis*), redwood (*Sequoia sempervirens*), tan oak (*Notholithocarpus densiflorus*) and Douglas-fir (*Psuedotsuga menziesii*). These forests are divided by high-gradient streams bordered with conifer as well as hardwood (typically red alder [*Alnus rubra*]) cover. The PAMB range, therefore, is characterized by low plains and hills generally lacking forest cover in the west, and mountainous and often steep forested terrain in the eastern portion (Fig. 1). The climate is Mediterranean maritime with relatively cool summers and winters that are wet with only occasional freezing temperatures. Mean annual precipitation exceeds 1,000 mm, with most falling as rain from October to April.

Occupancy Surveys

Using a geographic information system (GIS), we overlaid a rectilinear grid of 25-ha cells on the entire 174 km^2 geographic range that yielded a total of 780 complete, 25-ha cells. Twenty-five hectares was chosen because it was viewed as being small enough to survey by 2 people in one-half day and large enough for us to sample a sufficient number during our study to have a meaningful sample. Our objective was to randomly sample from this population of cells to search for sign of mountain beavers, but not all portions of the range were available for sampling. We had immediate access to 4.6 % of the range because it was in state or federal public ownership; the remainder of the range was on private land and thus required seeking permission. To do so, we took advantage of a previous outreach effort conducted by the Redwood Coast Land Conservancy to locate private landowners willing to allow surveys for either PAMB or a species of federally listed butterfly. In the spring of 2013, we recontacted landowners who had responded positively. This process resulted in permission to survey on approximately 60 km^2 of private land, or roughly 36.2% of the private land in the geographic range. We refer to this combination of public and private parcels as the accessible land base and it comprised 39.1% of the geographic range. The largest area of private land for which we received access was 2,984 ha owned by the Mendocino Redwood Company. The balance of the accessible private land was 3,023 ha owned by multiple individuals and corporations.

To evaluate whether the accessible portion of the range represented a biased subset of the entire range (i.e., sample selection bias, *sensu* Phillips et al. [2009]) we compared the vegetation cover features of accessible and inaccessible areas. To determine if our habitat model could be extrapolated from the accessible lands to the proportion of the land base that was inaccessible, we compared the vegetation cover features of both areas. Using a dominant vegetation type coverage (CalVeg; http://www.fs.fed.us/r5/rsl/projects/classification/system.shtml), we determined that the proportions of the accessible and inaccessible land bases that were in each of 4 vegetation types were roughly equivalent (Table 1). Thus, based on vegetation types at this scale of vegetation typing, we believe the accessible lands are representative of the inaccessible lands and that our habitat model could be applied to the entire geographic range. As further confirmation, we also compared the range of values of the variables in our final habitat model (see Results), for the accessible and inaccessible portions of the range, to determine whether they were similar. If so, it would suggest that the variables useful at predicting PAMB occurrence were not substantially different between the available and unavailable cells.

Not all 25-ha cells in the accessible land base were 100% accessible; those that had >80% of their area accessible were eligible for inclusion in our sample, resulting in a total of 193 potential 25-ha sample units. Initially we randomly selected 100 of these for inclusion in our sample. After this selection we learned of additional private lands (36, 25-ha units) that were accessible and from these we randomly selected 27 more units for a total of 127 sample units (Fig. 2). Each of these sample units was surveyed for the presence of at least one PAMB burrow. If this occurred, the survey for the unit was concluded. When one burrow is found typically others are also present (WJZ and FVS, pers. obs.), but we did not enumerate them for this study. PAMB burrows are distinctive; they are much wider (~20 cm) than the burrows of the most common other burrowing mammal, the pocket gopher (*Thomomys* sp.). Species of other burrowing mammals are either very rare (e.g., badger [*Taxidea taxus*]) or produce very different burrow openings (e.g., California ground squirrel [*Otospermophilus beecheyi*], striped skunk [*Mephitis mephitis*]). Four field technicians were trained by an experienced researcher (FVS) to search for and verify the identity of PAMB burrows. The technicians' skill at burrow identification was periodically validated by their supervisor (FVS). Each survey visit consisted of a team of 2 technicians thoroughly searching up to 10 ha of each 25-ha unit in habitat conditions most likely to be inhabited by PAMB. This strategy allowed us to maximize the number of sample units we could search and is similar to that used for occupancy surveys for other species (e.g., Karanth et al. 2011). Previous work (e.g., Zielinski et al. 2012) suggested that we were most likely to discover PAMB burrows in areas where there was a mix of overhead cover and canopy openings, near streams or drainages, or where there were changes in topographic relief. Thus, as the technicians planned their surveys each day, these areas were prioritized for searches when they occurred within a sample unit. Using these constraints, the 2 technicians typically searched parallel paths 50-100 m apart in the sample unit. Searching 10 ha took from 1-4 h, depending on the terrain and access. The surveyors verified that they were searching within the specified sample unit by recording the search path on a Geographic Positioning System of one of the 2 technicians. Cells were sampled from May – August 2013.

The team of surveyors visited sample units only once if during the first visit they discovered a PAMB burrow (i.e., confirmed occupancy). If, however, they did not detect any burrows, a second pair of technicians searched the unit on a subsequent day (usually within the same week). Thus, each sample unit had a "detection history" that was either: detection on the first occasion (notation "1"), detection on the second of 2 sample occasions (notation "01"), or no detection on either occasion (notation "00"). These search replicates allowed us to estimate the probability of detection if present (MacKenzie et al. 2006), which is the proportion of sample occasions when the first survey resulted in no detection and the second survey resulted in a detection ("01"). The information from these sample units provides an estimate of the number of occasions when surveys overlooked a burrow, and is used to adjust the naïve estimates of occupancy to account for uncertainty in detection. Thus, our estimate of occupancy will be the proportion of sample units where a PAMB burrow was actually detected (the naïve occupancy estimate) *plus* the proportion of sample units where we estimated a burrow was overlooked (the adjusted occupancy estimate).

Occupancy and probability of detection was modeled using the software PRESENCE (Ver. 6.2; Hines 2006). We tested the fit of the data to 3 models. The first assumed that sites were homogenous in respect to occupancy (i.e., "1 group") and had a constant probability of detection for both the first and the second visit ("Constant *p*"). The second assumed 1 group but that probability of detection differed between visits ("Survey-specific *p*"). The third assumed that the sample units were heterogeneous, belonging to 2 or more groups in respect to occupancy and had a constant probability of detection. The best model was determined by evaluating the relative model fit using Akaike's Information Criteria (AIC) and AIC weights (Burnham and Anderson 2002).

Habitat Modeling

We suspected that informative landscape-scale variables would come from one or more of the following categories: anthropogenic (e.g., roads), topographic, hydrologic, and biotic (classified remotely sensed vegetation-related variables) and edaphic. Various pre-existing sources for variables within each category were investigated to find those that: (a) had a link to the ecology of mountain beavers, (b) were available for the entire geographic range, and (c) were variable enough across the range to be useful at distinguishing detection from non-detection locations. The list of variables that remained after this filtering was reduced further by eliminating one of a pair that were highly correlated ($r > 0.80$). The final set of 10 predictor variables (Table 2) were down-sampled to match the 25-ha sample unit and used to create a collection of *a priori* univariate and multivariate models (Appendix I) chosen to represent alternative views of environmental factors that might affect PAMB distribution (Burnham and Anderson 2002).

We used non-parametric logistic regression, a subset of Generalized Additive Models, with loess smoothing functions (Cleveland 1985) to compare models representing the relationship between sample units with a PAMB detection and those without. We evaluated each model's fit to the data using the bias-corrected Akaike's Information Criteria with correction (AIC_c) (Akaike 1973). We calculated relative importance values for individual variables by determining the gain in AIC_c value when each variable was removed from the final model. We evaluated model discrimination by integrating the area under the receiver operating characteristic curve (Area Under the Curve [AUC]; Fielding and Bell 1997). Random predictions result in an AUC value of 0.5, whereas a perfect prediction assumes the maximum value of 1.0. We performed cross validation of the best model to determine how robust it was to perturbations of the data used to develop it. Cross validation was done by removing a random 10% subset of the developmental data, training the model on the remaining 90% of the data, then classifying the with-held 10%. This process was repeated 10 times with replacement. The best-fitting model resulted in a prediction of habitat suitability for each sample unit that ranged from 0 to 1.

To distinguish suitable from unsuitable habitat along the continuous range of habitat suitability values we chose a threshold value that optimized Cohen's Kappa value (Cohen 1960). We evaluated Kappa at 26 alternative cut-off points for classifying detection and non-detection units, at 0.01 increments, starting at predicted values of 0.20 and continuing to 0.45. The optimal cut-off was the point above which the Kappa value did not increase. Sample units with values above this value were classified as suitable, below this value they were classified as unsuitable. We also evaluated the proportion of the range that is suitable, the proportion of each of the primary watersheds (as originally identified in Zielinski et al. 2012), and the proportion of the range that is north and south of the Garcia River, a putative geographic feature that has influenced genetic substructure in the PAMB (Zielinski et al. 2012).

RESULTS

Occupancy Surveys

A total of 127 sample units were surveyed. The detection of mountain beaver burrows at 33 of these resulted in a naïve estimate of occupancy of 0.259 (Fig. 3). Thirty surveys detected evidence of burrows on the first visit, the balance of positive detections (n = 3) were confirmed on the second visit after failing to detect a burrow on the first visit. An average (SD) of 1.0 (0.8) hours was spent searching sample units before a detection occurred and 1.6 (0.9) hours in sample units where no burrow was detected. The "1-group, constant *p*" model best fit the data (AIC wt

= 0.7311; Table 3) resulting in an adjusted estimate of occupancy of 0.262 (SE = 0.039; 95% CI = 0.1927 – 0.3466). The per-visit probability of detection (*p*) was 0.90 (SE = 0.061). When this is compounded by the maximum number of visits possible (n = 2), the total probability of detection for the survey protocol was very high ($1 – [1- 0.90]^2 = 0.99$), suggesting high confidence in detecting evidence of mountain beavers when it was present.

We detected PAMBs in some sample units that were within the 3-km buffer beyond the original distribution of PAMB locations provided by the USFWS (USWFS 2009). The original range was calculated as ~85 km^2 by enclosing the marginal locations in the north, east, and south and extending the range to the coastline in the west. Our new marginal locations, especially in the east and the north, expanded the geographic range from ~85 km^2 to ~134 km^2 (Fig. 3).

Habitat Modeling

Of the 53 *a priori* models evaluated, the top-ranked model [SLOPE + TRI + RIVSTREAM] accounted for a dominant proportion of the Akaike weight (0.85) (Table 4). The next 2 highest ranking models had weights that were far less (0.098 and 0.036, respectively, Table 4) but also included 2 or 3 of the variables included in the top model (Table 4). The variables in the top 3 models included variables from the topographic and hydrologic groups (SLOPE, ASPECT, TRI, and RIVSTREAM). The top model had an AUC value of 0.837, meaning that using this model a randomly selected detection location will have a larger predicted habitat value than a randomly selected absence location 83.7% of the time. RIVSTREAM was the most influential variable in the top model. When it was removed from the top model, the AIC_c value increased by 18.8 points, compared to removing SLOPE and TRI which increased the AIC_c value by 4.3 and 9.0 points, respectively.

Detections occurred in sample units that, on average, were on more level slopes, with lower terrain roughness indices, and higher densities of rivers and streams (Fig. 4). This model provided good separation between the predicted values of detections and non-detections (Fig. 5A), with the maximum predicted value of 0.95 for a site with a detection. This model was also very robust to cross validation, producing equally good separation between predicted values of detections and non-detections (Fig. 5B) and an AUC value of 0.85. Cohen's Kappa for the top model achieved its maximum value at a cut-off of 0.34. This resulted in a total of 281 full plus partial sample units that exceeded this value (Fig. 6A, B). Recognizing that sample units predicted to be habitat will contain some small areas that are not suitability habitat for PAMB while those units predicted to not contain habitat could have small areas that are habitat, we can assume that our model averages these and then predict that the total suitable habitat for the PAMB is about 70.5 km^2 or 40.4% of the ~174 km^2 geographic range as originally estimated (USFWS 2009). Using the same approach, all watersheds in the range had at least 25% of their area in suitable habitat; the Moat Creek watershed had the highest at 47% (Table 5). The areas north and south of the Garcia River, which previous research suggested influenced historical gene flow, were 28.9% and 39.3%, respectively (Table 5).

Comparing the range of values for each of the predictors, in the accessible and inaccessible portions of the geographic range, allows us to evaluate our assumption that these 2 areas are equivalent in respect to features associated with PAMB occurrence. The percent of units in the inaccessible areas that had values that exceeded the minimum or maximum for SLOPE, TRI and RIVSTREAM (the 3 variables in the best model) were 0.5%, 0.0% and 0.0%, respectively (unpubl. results). This suggests that the inaccessible portions of the range resembled the accessible portions that were sampled, in respect to the range of values for the key predictors in the model.

DISCUSSION

Point Arena mountain beavers were estimated to occur at 26.2% of the sample units we surveyed. Our survey method had a high probability of detecting evidence of the PAMB when it was present (> 90%), leading to confidence in the precision of our estimates of occupancy. Ours is the first estimate of range-wide occupancy produced for this taxon and represents a potential baseline for quantitatively monitoring the subspecies' distribution (Fig. 7). This would most efficiently be accomplished by repeatedly surveying the same sample units we sampled using multiple-season occupancy models (MacKenzie et al. 2006) to estimate trends in occupancy over time. A similar program has been in place for approximately 10 years to monitor the southern Sierra fisher (*Pekania pennanti*) population (Zielinski et al. 2013b). Because the USFWS is responsible for a status review every 5 years, this is a reasonable resample frequency. Not only would a program of this nature allow responsible agencies to monitor occupancy, but it would also provide opportunities to identify where sample units transition from occupied to non-occupied ("extinction") and vice versa ("colonization") (MacKenzie et al. 2003), providing insights about metapopulation dynamics and turnover rates (e.g., Royle and Kéry 2007).

Ours was a 55.4% sample, when 127 sample units were drawn from 229 units accessible for surveying. The sample included 88.2% private lands and 11.8% public lands, which was fairly representative of the distribution of these ownerships in the original geographic range (95.3% and 4.6%, respectively). We do not, however, suggest that our population occupancy model applies to the entire range, at least for the purpose of monitoring. Although the lands that were accessible included cover types that were representative of the lands that were inaccessible (see Table 1), this extrapolation is not necessary for the purposes of establishing a monitoring program. All that is necessary is to resample the same 127 sample units on each monitoring occasion; this will produce an unbiased estimate of the distribution on the accessible lands. The occupancy estimate, reevaluated every 5 years, would be defined as an “estimate of population status for the accessible portion of the geographic range.”

Currently, recovery and delisting of the PAMB is based on demonstrating the persistence of a specified number of “populations”, each with a specified number of individuals occurring over a minimum area, for a specified period of time (Steele and Litman 1998: iii - iv). Data with this resolution has not been gathered to date and it will continue to be problematic due to the logistical and economic challenges associated with delimiting a population and estimating its size. We encourage lead agencies to consider a new view for recovery; that of evaluating a combination of: (1) occupancy rates across the accessible portion of the range (such as we have proposed here) – provided that there are no substantial changes to accessibility − combined with (2) estimates of abundance and survival at several representative locations throughout the range. The first component would be implemented by repeating the occupancy surveys described here. The second would be implemented by continuing the monitoring of abundance and survival at the 2 sites in Manchester State Park (Zielinski et al. 2013a) and by adding a few additional sites across the range with similar intensive demographic monitoring.

A recovery plan should also consider thresholds at which further management is necessary based on the results of the monitoring program. We are not aware of a threshold that has been proposed for the PAMB. Lack of forethought on this topic has been a source of criticism of species monitoring plans (Lindenmayer et al. 2013). We do not have an answer to this question, but encourage the state and federal authorities to initiate a discussion on this topic. Ideally, this program would specify one or more thresholds and actions to be taken when monitoring results indicate significant increases or decreases in occupancy, demographic performance, or both.

The best-fitting habitat model was comprised entirely of topographic and hydrologic variables: SLOPE, TRI, and RIVSTREAM. In this mountainous and highly dissected landscape, the places where PAMBs were detected had more gentle slopes, reduced terrain roughness, and higher densities of rivers and streams than the places where PAMBs were not detected. These places were influenced by the interactive forces of topography and hydrology that most likely resulted in conditions with wetter soils and well developed, multi-layered vegetation. Predictor variables related to soils or to vegetation (e.g., greenness, bulk density) were not in the best-fitting models. This doesn't mean that they are not important to the biology of PAMBs, which require available water and succulent vegetation to balance water demands (Nungesser and Pfeiffer 1965) and soils with appropriate composition essential for burrow construction (Hacker and Coblentz 1993). The topographic variables in the top model probably performed well because they are good predictors of the plants and soil conditions that are life requisites of PAMBs. Abundant and diverse vegetation occurs on gentle slopes and even terrain in locations where moisture accumulates, producing soils that are presumably soft enough for burrow construction. The association with rivers and streams is likely related to the availability of open water, a necessity for PAMB water balance and a major influence on the distribution of wetland plants and soils used for food and burrow construction, respectively. Interestingly, when values for 2 soil variables - soil bulk density and percent clay - are examined at sample units that are arranged from highest to lowest probability of occurrence, the values for both variables are lowest where the probability of occurrence is highest (W. Zielinski, unpubl. data). This suggests that despite their exclusion from the top model they may be linked to PAMB occurrence and that sample units with soils that have lower bulk densities and percent clay may be more amenable to burrowing. Finally, it is important to note that in modeling exercises of this nature the top-ranking model simply represents the best performing model supported by the data. The variables included in this model do not represent the sum total of factors influencing PAMB. The best model combines predictive ability (reduced deviance) as well as parsimony (i.e., a penalty is incurred for each of the model's estimated parameters). It does provide good predictive ability, but managing only for the variables in the model would be a mistake because the model is an abstraction of habitat factors influencing PAMBs (see Dunk and Hawley 2009).

The habitat model helps us understand features associated with PAMB presence, but it also can serve as a tool for monitoring and managing habitat. Typically, a model of this nature could be used for monitoring habitat suitability by updating the predictor values in the top model every few years and generating a new map of predicted suitability (e.g., Tuanmu et al. 2011). However, the best model includes only topographic and hydrologic variables, which are unlikely to change except over long time periods. Although areas with high predicted suitability may not change their topographic features or hydrologic characteristics, they will be places where suitable vegetation and soils are likely to occur and where land disturbing activities will likely have more effects on the PAMB population than places when the model predicts lower suitability.

The map of predicted probabilities also can serve strategic conservation planning needs by identifying areas that were not surveyed, but where predicted suitability was high and PAMBs are likely (Fig. 6). These locations identify where conservation interests could achieve strategic conservation goals by seeking to protect them from degradation or develop conservation agreements. Particularly promising areas for this purpose are in the central portion of the range (on the north-south axis), the southern half of the range, and the coastal portions of the northern half of the range (Fig. 6).

Our work is an example of how surveys conducted on one portion of the geographic range – the accessible areas – can result in predictions that can benefit the conservation of a taxon on the unsurveyed portions of the range. Endangered species often inhabit private lands where access is prohibited. Remotely sensed variables are available across all ownerships permitting the development of GIS-based models that can predict species occurrences even where surveys are not allowed. Our research illustrates the conservation benefits of using remotely sensed variables for developing models for endangered species across mixed ownership landscapes (e.g., Wilson et al. 2013).

When the PAMB was listed as endangered, the primary threat to the subspecies was habitat loss. The most recent status review (USFWS 2009) notes that “the loss and modification of suitable habitat continues to be the primary threat to Point Arena mountain beavers, especially on private lands." Our habitat model cannot be used to monitor habitat loss related to changes in vegetative conditions. The classification schemes of available GIS vegetation layers were typically too coarse to be useful. For example, some considered all the cover types in the eastern portion of the range as "forest", other layers only classified the forested lands with high resolution leaving the mixed use lands in the western portion unclassified. Most layers were incapable of identifying small patches of riparian vegetation which may be particularly important to PAMB. Key to improving habitat mapping in the future will be the improvement in remotely sensed vegetation information, which may require creating new habitat suitability models. Soils maps were also not particularly helpful. Although recently updated for Mendocino County (USDA Natural Resources Conservation Service, 2012), soils maps had large unclassified areas. Promising variables that may be related to the ease of burrowing (e.g., "soil preparation – surface") did not have sufficient variation across the range to be useful in discriminating detection from non-detection locations. If development and disturbance on private land continues to be a primary threat, the monitoring of habitat loss - on a parcel-by-parcel basis - will be necessary, as is currently done as part of the environmental review process conducted by the USFWS (USFWS 2009:17).

Suitable and unsuitable habitat was distinguished based on a threshold predicted value. Above that value, sample units were designated as habitat, while below that value they were designated non-habitat. Applying this threshold resulted in 281 full or partial sample units (or approximately 70.5 km^2) designated as "suitable". This represents 40.4% of the range, substantially higher than a recent estimate of 10.1% (K. Wear, USFWS, cited in USFWS 2009). The difference is probably due primarily to the latter estimate being based on expert opinion about suitable vegetation types while ours was based on predicted suitability derived from an empirical statistical model. Additionally, our estimate was based on the optimal choice of a cut-point of predicted probability (i.e., 0.34); a choice above or below this value would lead to different values for the proportion of the range comprised of suitable habitat. Finally, all habitat classification systems assume assessment areas – pixels, polygons or sample units – are categorized as either suitable or unsuitable *in their entirety*. As this is unlikely to be the case, our 25-ha sample units may result in higher estimates of suitability than if smaller units were considered.

Resampling the remotely-sensed predictor layers can potentially influence the habitat model results. The predictor variables used for this study were those available from remotely sensed data (see Table 2). The data vary in their ability to represent phenomenon on the earth based on their resolution and the complexity of the area within each cell or pixel (Cracknell, 1998). We "down sampled" existing GIS layers to match the 25-ha sample unit size by taking the mean value of all the cells within each sample unit. Increasing the size of the cells for the predictors has reduced model accuracy in previous studies (Gottschalk et al. 2011). Because there are inherent inaccuracies in all spatial data, increasing the cell size has actually increased model performance in other studies because the inaccuracies have been averaged out (Guisan 2007). Our study was specifically designed for long-term monitoring of PAMB with limited time and resources for field sampling. With additional resources, data could be collected that would allow a higher resolution model of PAMB habitat to be created.

Our work, based on burrow evidence, resulted in an expansion of the known range of the PAMB. Our survey area included the portion of the range added by the USFWS where previous locations had not been reported. Our sampling in this area resulted in the detection of 8 new locations (Fig. 3) that increases the range with documented presence to ~134 km^2. We suggest this become the basis for an updated geographic range map. If the USFWS adds a 3-km buffer to this new area, the area of the species range increases from the current ~174 km^2 to ~235 $km^{2.}$ We do not know if the range has actually expanded since the original listing or is the result of expanded survey effort. Suitable areas predicted by our habitat map along the eastern margin of the current range (Fig. 6A, B) suggests that the actual range may extend even further east, northeast and southeast of the expanded range.

Shotwell (1958) and the USFWS (2009) suggest the present range size reflects contractions that resulted from drying due to regional climate as well as vegetation and topographic changes since the Eocene. The increase in range size revealed by our sampling provides some reassurance that this pattern of contraction has not progressed significantly, at least in the past few decades. However, we are aware that recent changes may be of a different order of magnitude than the more significant changes in range that are influenced by changes in climate that occur at much longer time frames. A larger known range, compared to when the taxon was listed, may ameliorate some of the concern about the impacts of anthropogenic habitat loss. Likewise, the larger known range and burrow system numbers may ease concerns regarding the potential effects of climate change such as increased drought, more variable precipitation, and sea level rise along the coast (USFWS 2009).

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Table 1. The proportion of 4 cover types, classified using the CalVeg vegetation classification system (http://www.fs.fed.us/r5/rsl/projects/classification/system.shtml) and identified by accessibility within the PAMB geographic range.

Vegetation Type	Accessible land area (4,908 ha)	Inaccessible land area (12,110 ha)
Forest	0.60	0.60
Grassforbshrub	0.30	0.27
Non-habitat	0.05	0.09
Riparian	0.05	0.04

Table 2. Final set of predictor variables used to model range-wide PAMB habitat. Definitions apply to the assessment of the variable averaged for each 25-ha sample unit.

Variable	Abbreviation	Definition
Greenness Index	GREENNESS	Calculated using a tasseled-cap transformation and 7 bands from Landsat 7 ETM+ (Huang et al. 2002). The greenness index produces cell values where higher numbers indicate an increased presence of chlorophyll and healthy vegetation. Values for each sample unit were extracted from the greenness raster using BlueSpray (BlueSpray Ver. A0.0, 2014.) and represent the mean value of all the pixels within each sample unit.
Wetness Index	WETNESS	Calculated using a tasseled-cap transformation and 7 bands from Landsat 7 ETM+ (Huang et al. 2002). The wetness index portrays vegetation moisture. This index is sensitive to soil and plant moisture and vegetation structure. Values for each sample unit were extracted from the wetness raster using BlueSpray (BlueSpray Ver. A0.0, 2014) and represent the mean value of all the pixels within each sample unit.
Aspect	ASPECT	Calculated using the Aspect tool (Spatial Analyst license) in ArcGIS v.10.1 with a 1-arc second DEM downloaded from the USGS National Elevation Dataset (NED, http://ned.usgs.gov/downloads.asp, downloaded 16 November 2013), then cosine transformed to represent “northness”. Values for each sample unit were extracted from the aspect raster using BlueSpray (BlueSpray Ver. A0.0, 2014) and represent the mean “northness” value of all the pixels within each sample unit.

Slope	SLOPE	Calculated using the Slope tool (Spatial Analyst license) in ArcGIS v.10.1 with a 1-arc second DEM downloaded from the USGS National Elevation Dataset (NED) on 13 November 2013. Values represent degree of slope. Values for each sample unit were extracted from the slope raster using BlueSpray (BlueSpray Ver. A0.0, 2014) and represent the mean value of all the pixels within each sample unit.
Terrain Roughness Index	TRI	Calculated with the NED DEM by looking at an 8-cell neighborhood for each 30m- pixel. Specifically, it calculates the difference of the cell value and the mean of the 8-cell neighborhood. The resulting raster layer can be reclassified based on the TRI categories defined by Riley et al. (1999), ranging from flat to extremely rugged (values from 0-1). Values for each sample unit were extracted from the TRI raster using BlueSpray (BlueSpray Ver. A0.0, 2014) and represent the mean value of all the pixels within each sample unit.
Relative Position Index	RPI	Calculated with the NED DEM by examining each pixel's relative position with respect to its local neighborhood (Jenness 2004). Values range from 0-1, indicating low to high ruggedness. Values for each sample unit were extracted from the RPI raster using BlueSpray (BlueSpray, Ver. A0.0, 2014) and represent the mean value of all the pixels within each sample unit.
Secondary roads	SROADS	Downloaded from USGS, The National Map Program (http://nationalmap.gov/viewer.html). Includes networks of local neighborhood streets as well as major roadways in the study area. Includes primarily public paved and unpaved roads (http://www.census.gov/geo/maps-data/data/tiger-line.html; downloaded 16 November 2013). Values for each sample unit represent length of secondary roads within each unit. This includes all paved and unpaved public roads. Ground-checking revealed that

		it also includes the majority of unpaved roads on private land.
Rivers and streams	RIVSTREAM	Downloaded from USGS, The National Map Program. Values for each sample unit represent length of rivers and streams within each unit. Includes intermittent streams.
Bulk Density	BD13	Downloaded from the USDA Web Soil Survey (http://websoilsurvey.sc.egov.usda.gov/App/HomePage.htm). Bulk density describes the oven-dry weight of soil material less than 2 mm in size per unit volume of soil at water tension of 13 bars. The ratings are measured in units of grams per cubic centimeter. Values for each sample unit were extracted from the bulk density raster using BlueSpray (BlueSpray, Ver. A0.0, 2014) and represent the mean value of all the pixels within each sample unit.
Percent clay	PERCENT CLAY	Downloaded from the USDA Web Soil Survey. This variable describes the percent of soil content containing clay particles. Values for each sample unit were extracted from the percent clay raster using BlueSpray (BlueSpray, Ver. A0.0, 2014) and represent the mean value of all the pixels within each sample unit.

Table 3. Top ranked models to estimate occupancy for the PAMB from sampling across their geographic range in Mendocino, County California. The models were derived from data collected from May - August, 2013. Akaike's Information Criterion (AIC), change in AIC (ΔAIC), AIC weight (w,), likelihood, and number of parameters for each model are identified.

Model	AIC_c	ΔAIC	w_i	Model likelihood	Parameters
1-group, constant *p*	169.62	0.0	0.731	1.00	2
1-group, survey-specific *p*	171.62	2.00	0.269	0.37	3
2-group, constant *p*	173.62	4.00	0.090	0.135	4

Table 4. Top-ranked habitat models for the PAMB from sampling across their geographic range in Mendocino, County California derived from data collected from May - August, 2013. Akaike's Information Criterion (AIC_c), AIC weight (w,), cumulative weight, and difference in weight between top-ranked and listed model (wt_i) are presented.

Model	AIC_c	AIC wt (w_i)	Cum. Wt.	$wt_{highest}wt_i$
SLOPE + TRI + RIVSTREAM	92.79	0.848	0.848	1.000
TRI + RIVSTREAM	99.10	0.098	0.946	8.64
ASPECT + SLOPE + TRI + RIVSTREAM	99.12	0.036	0.981	23.70

Table 5. Percent suitable habitat (using the 0.34 predicted suitability cut point), and area of suitable habitat, in the 9 major watersheds identified in Zielinski et al. (2012) and north and south of the Garcia River, a feature associated with major genetic differentiation in PAMB (Zielinski et al. 2012).

Watershed	Percent suitable habitat	Area of suitable habitat (ha)
Mallo Pass Creek	28.9	1597.7
Alder Owl Creek	37.5	68.4
Alder Creek	27.5	554.0
Brush Creek	31.0	898.8
Lagoon Creek	29.2	243.4
Garcia River	41.7	1376.5
Garcia Hathaway Creek	38.4	494.7
Point Arena Creek	39.5	381.9
Moat Creek	47.0	750.6
North of Garcia River	28.9	4075.0
South of Garcia River	39.3	2289.0

Appendix I. Candidate models of environmental factors used to distinguish between sample units with PAMB detections and those without detections (see Table 2 for definitions of variable abbreviations).

	Biological Models				
1	GREENNESS				
2	WETNESS				
3	GREENNESS	WETNESS			
	Topographic Models				
4	TRI				
5	SLOPE				
6	RIVSTREAM				
7	ASPECT	TRI			
8	SLOPE	TRI			
9	ASPECT	RPI			
10	SLOPE	RPI			
11	ASPECT	SLOPE			
12	TRI	RIVSTREAM			
13	SLOPE	RIVSTREAM			
14	ASPECT	SLOPE	TRI		
15	ASPECT	SLOPE	RPI		
16	ASPECT	SLOPE	TRI	RPI	
17	ASPECT	SLOPE	TRI	RPI	RIVSTREAM
18	ASPECT	SLOPE	TRI	RPI	SROADS
19	ASPECT	TRI	RIVSTREAM		
20	SLOPE	TRI	RIVSTREAM		
21	ASPECT	RPI	RIVSTREAM		
22	SLOPE	RPI	RIVSTREAM		

23	ASPECT	SLOPE	RIVSTREAM			
24	ASPECT	SLOPE	TRI	RIVSTREAM		
25	ASPECT	SLOPE	RPI	RIVSTREAM		
26	ASPECT	SLOPE	SROADS			
27	ASPECT	SLOPE	SROADS	RIVSTREAM		
28	ASPECT	TRI	RPI	RIVSTREAM		
29	SLOPE	TRI	RPI	RIVSTREAM		
	Soil Models					
30	CLAY					
31	CLAY	BD13				
32	BD13					
	Multiple Class Models					
33	WETNESS	GREENNESS	TRI			
34	WETNESS	GREENNESS	TRI	RIVSTREAM		
35	WETNESS	GREENNESS	TRI	RIVSTREAM	SROADS	
36	WETNESS	SLOPE	RIVSTREAM			
37	GREENNESS	SLOPE	RIVSTREAM			
38	WETNESS	ASPECT	TRI			
39	WETNESS	ASPECT	TRI	RIVSTREAM		
40	WETNESS	ASPECT	TRI	RIVSTREAM	SROADS	
41	WETNESS	ASPECT	RPI			
42	WETNESS	ASPECT	RPI	RIVSTREAM		
43	WETNESS	GREENNESS	TRI	BD13		
44	WETNESS	GREENNESS	TRI	BD13	RIVSTREAM	
45	WETNESS	GREENNESS	TRI	BD13	RIVSTREAM	SROADS
46	WETNESS	SLOPE	BD13	RIVSTREAM		

47	GREENNESS	SLOPE	BD13	RIVSTREAM		
48	WETNESS	ASPECT	TRI	BD13		
49	WETNESS	ASPECT	TRI	BD13	RIVSTREAM	
50	WETNESS	ASPECT	TRI	BD13	RIVSTREAM	SROADS
51	WETNESS	ASPECT	RPI	BD13		
52	WETNESS	ASPECT	RPI	BD13	RIVSTREAM	
53	WETNESS	ASPECT	RPI	BD13	RIVSTREAM	SROADS

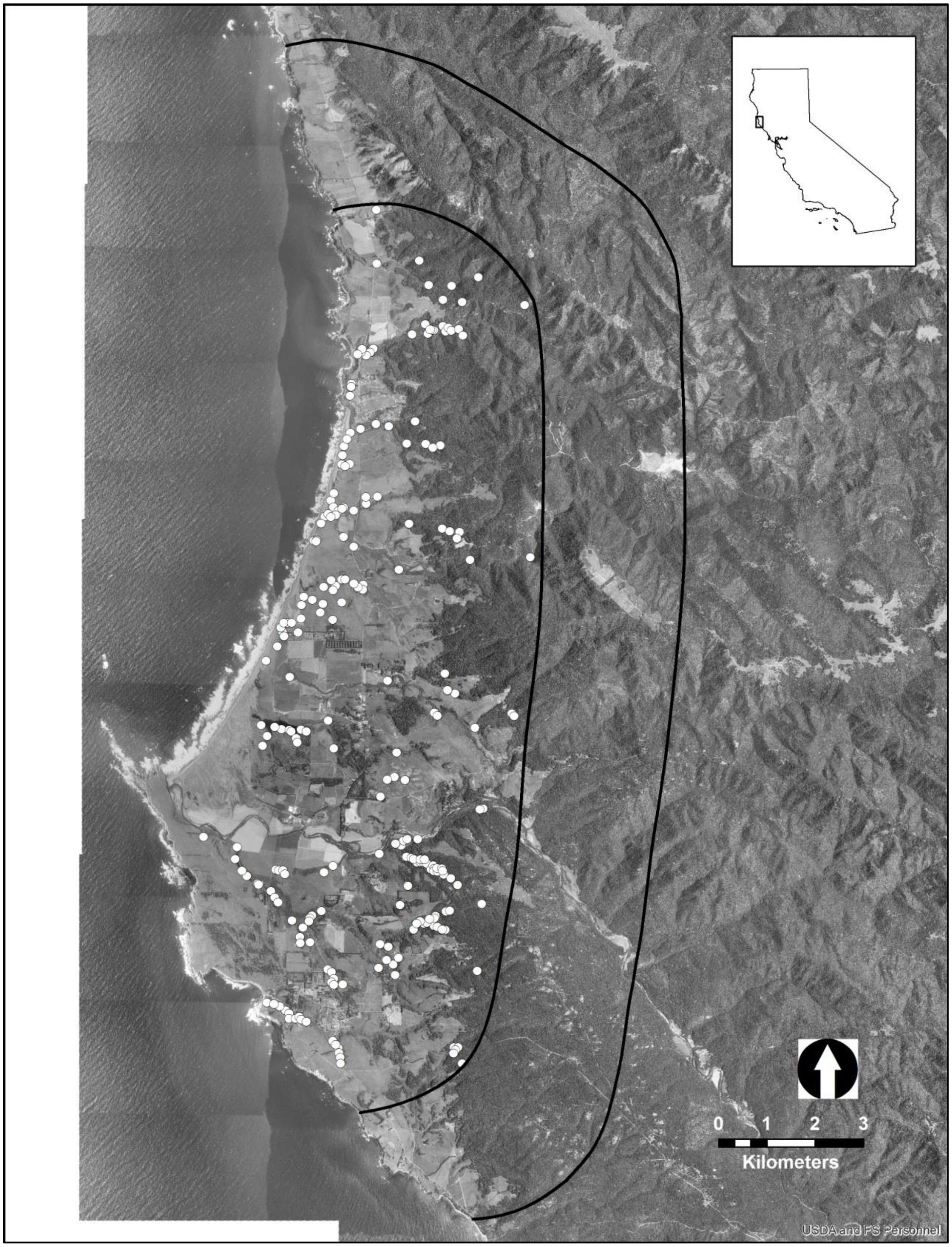


Figure 1. Distribution of the known sites (white dots) identified in the 5-year status review for the PAMB (USFWS 2009). The innermost line encircling the sites smooths the minimum convex polygon of the geographic range based on site records (~ 85 km^2). The outermost line represents a 3-km buffer and encompasses an area (~ 174 km^2) the USFWS (2009) designates as the historic distribution (USFWS 2009). The background is aerial imagery from the USDA National Agriculture Imagery Program (NAIP) illustrating the largely forested eastern portion of the range (darker areas) and the western portion that includes more grassland, agriculture, and pasture (lighter areas).

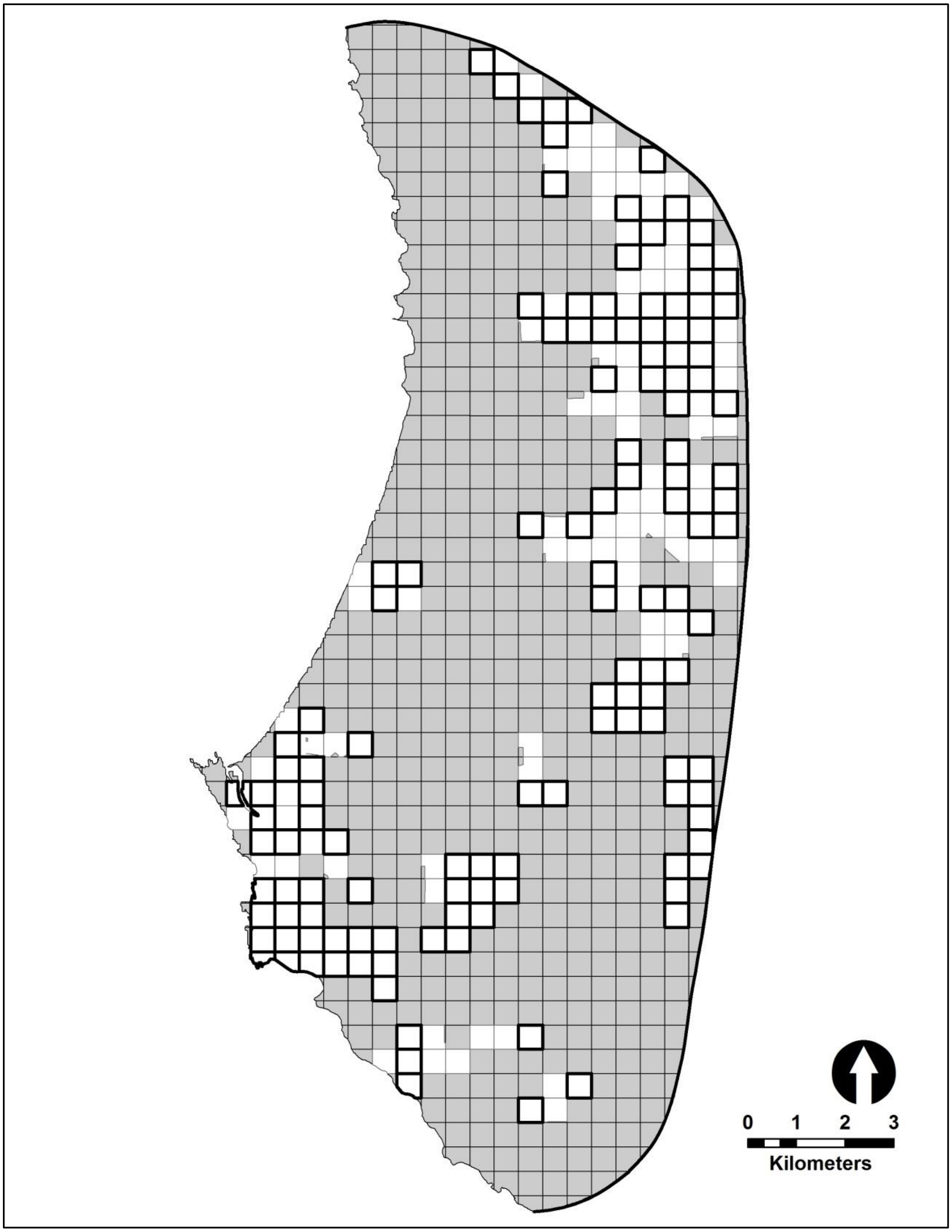


Figure 2. The 193, 25-ha grid cells (white squares) from which 127 sample units (squares with bold perimeters) were randomly selected to survey for PAMBs in the summer of 2013. Parcels accessible for sampling are in white, inaccessible parcels areas in gray.

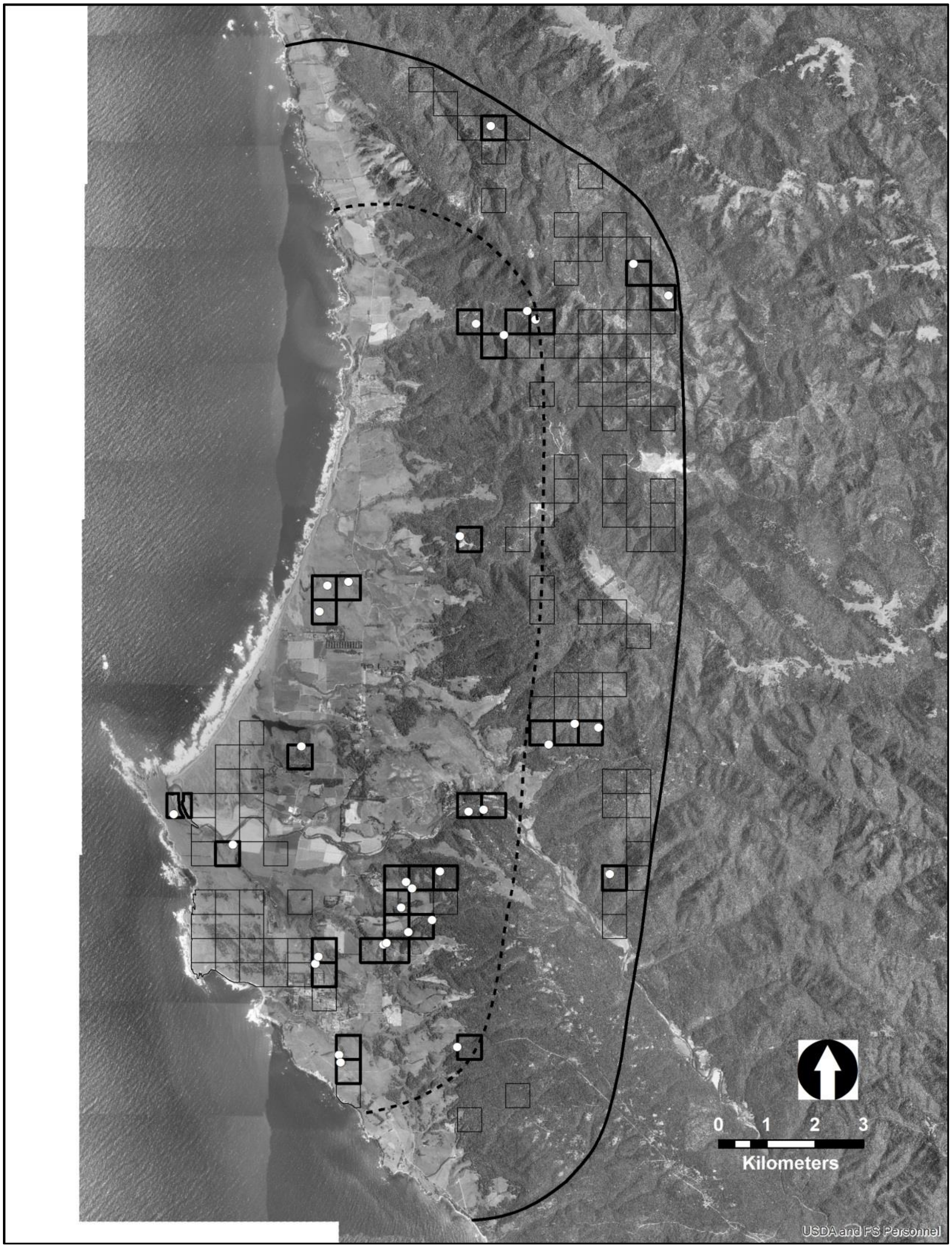


Figure 3. The 127 sample units used to survey for PAMBS during the summer of 2013. The 33 sample units with detections are noted with bold perimeters and a white dot to indicate the location of the detection.

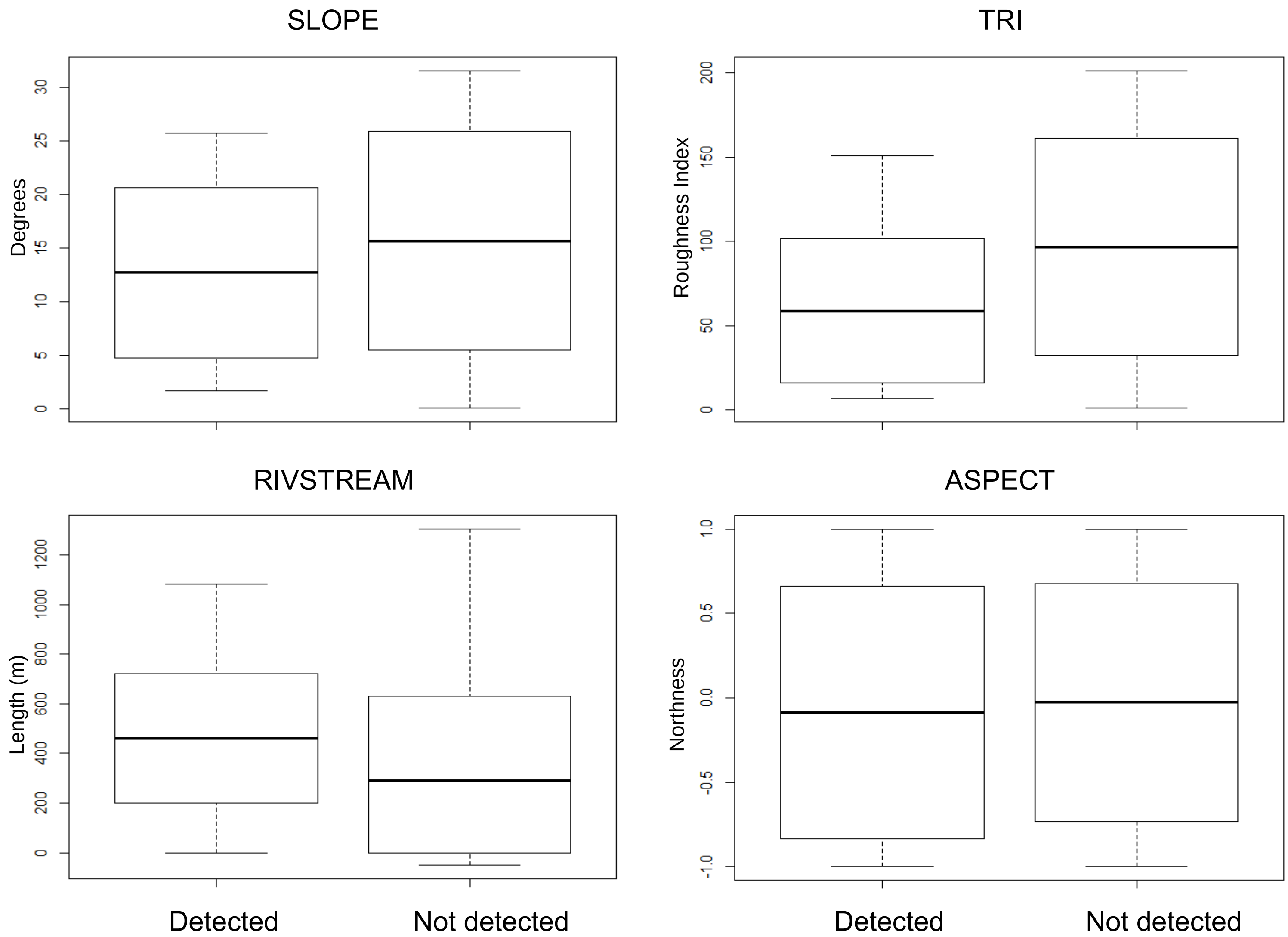
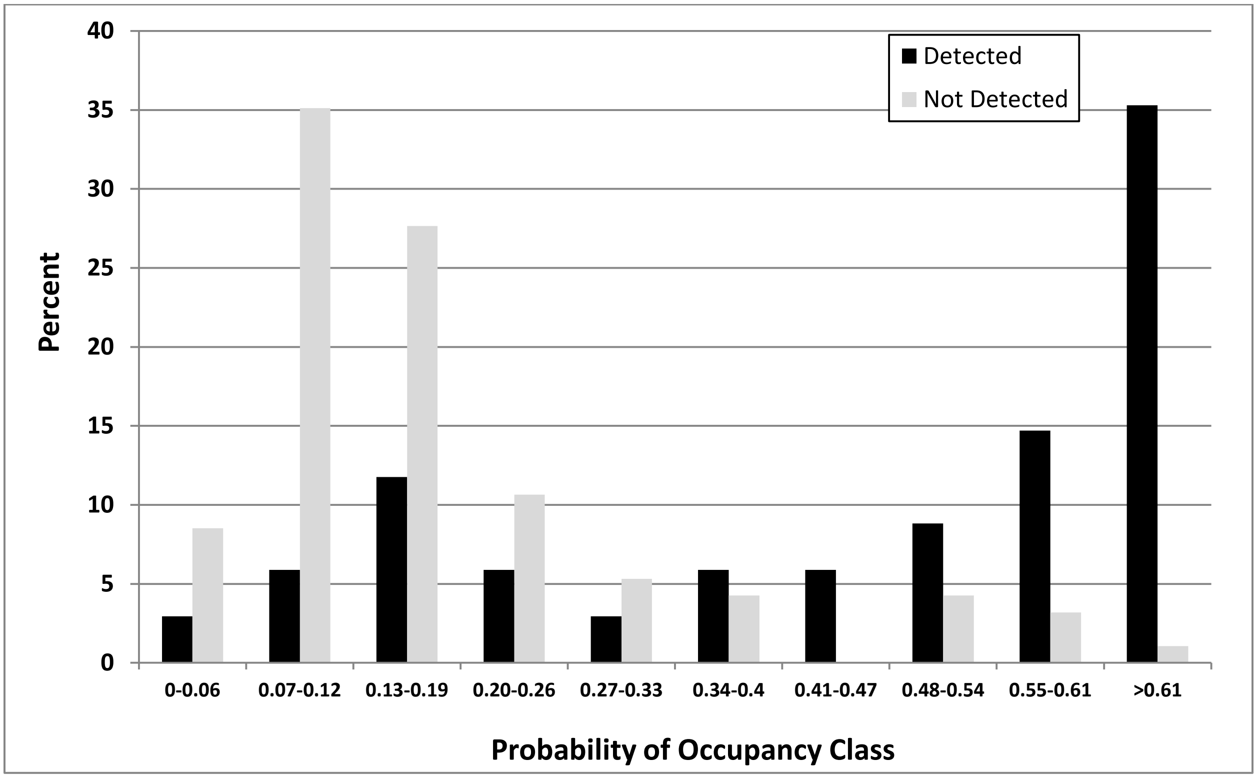


Figure 4. Boxplots for the 4 variables in the top 3 habitat models (SLOPE, TRI, RIVSTREAM, ASPECT). The black bar is the mean value, the box represents the standard deviation, and the bars represent the range in values for the 33 sample units with detections and the 94 sample units with no detections. See Table 2 for definitions for the variables.

A



B

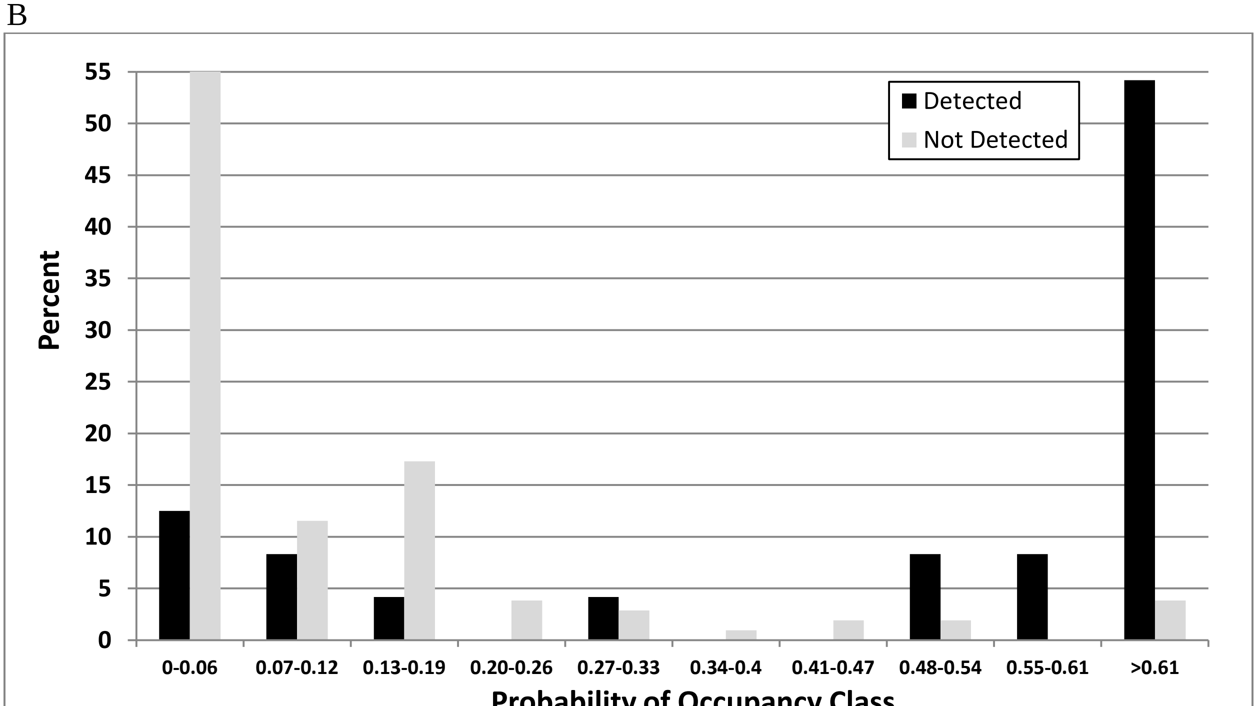


Figure 5. Distribution of PAMB detection and non-detection sites among 10 probability of occupancy "bins" based on the best performing model (SLOPE+TRI+RIVSTREAM): (A) using the full data set from all sample units and (B) the distribution of 10 cross-validated data sets. The final bin, >0.61, was chosen because of the general decline in occurrences in units that exceeded this value.

41

A B

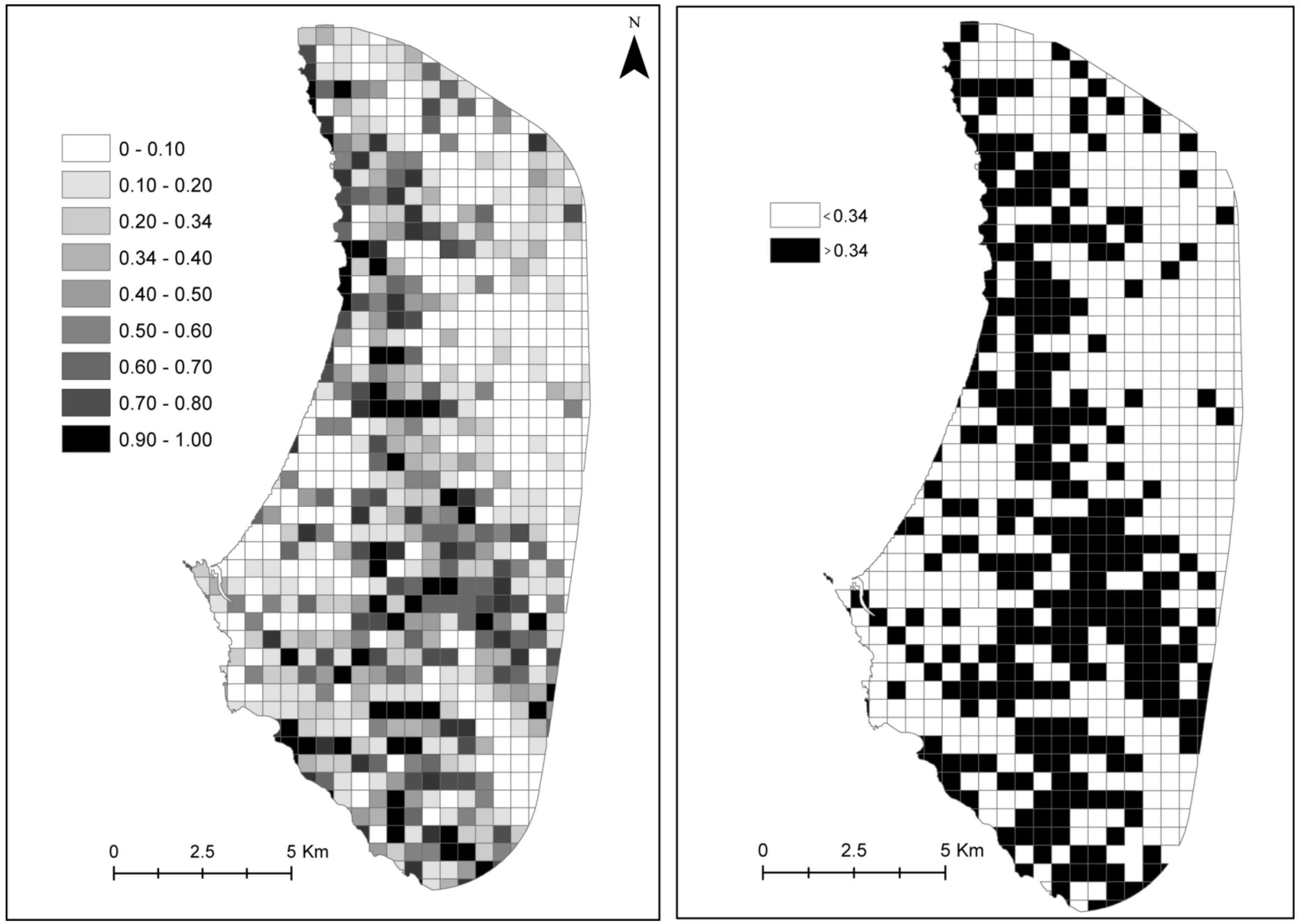


Figure 6. Map of the predicted values of habitat suitability for full and partial 25-ha sample units across the range of the PAMB in Mendocino County, California. (A) Each color shade represents a 0.10-range of predicted values from lightest (0 – 0.10) to darkest gray (0.91 – 1.00). (B) The suitable cells (> 0.34 predicted value) depicted in black and the unsuitable cells (< 0.34 predicted value) in white. Simulation analysis (see text) identified an optimal 'cut off', or threshold, to distinguish suitable from unsuitable predicted habitat values, of 0.34.

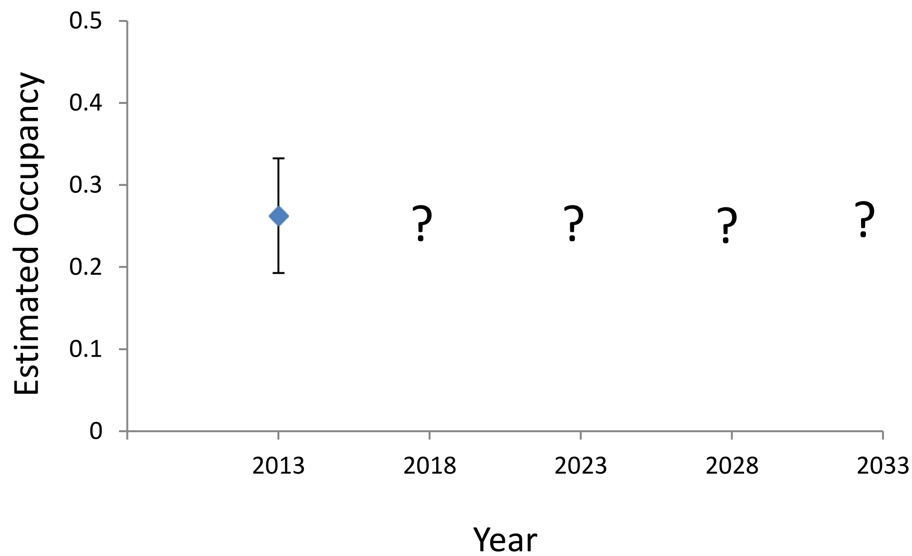


Figure 7. A hypothetical plot of monitoring occupancy for the 127 sample units surveyed across the PAMB geographic range. The current estimate is represented at “2013” followed by place holders for estimates from successive 5-year reassessments of the same 127 sample units.