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MAPPING PLANT SPECIES RANGES IN THE HAWAIIAN ISLANDS: DEVELOPING A METHODOLOGY AND ASSOCIATED GIS LAYERS

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ABSTRACT

This report documents components of a methodology for projecting the geographic ranges of plant species in the Hawaiian Islands. This consists primarily of the creation of several GIS data layers depicting attributes related to the geographic ranges of plant species. The most important data layer generated here is an objectively-defined classification of climate as it pertains to the distribution of plant species. By examining previous zonal vegetation classifications in light of spatially detailed climate data, we explicitly define broad zones of climate relevant to contemporary concepts of vegetation in the Hawaiian Islands. A second spatial data layer presented here considers substrate age, since large areas of the island of Hawai'i in particular are covered by very young lava flows, which are inimical to the growth of many plant species. The third data layer presented here divides larger islands, which are composites of multiple volcanoes, into definable biogeographic regions, since many species are restricted to a given topographically isolated mountain or a specified group of these. A final spatial data layer depicts human impact, which reduces the range of many species relative to where they formerly occurred. Several other factors that influence the geographic ranges of species, including topography, soils, and disturbance, are discussed here but not developed further due to limitations in rendering them spatially. We describe a method for analyzing these base layers in a geographic information system (GIS), in conjunction with a database of species distributions, to project the ranges of plant species, including the potential range prior to human disturbance and the projected present range. Examples of range maps for several species are given as case studies that demonstrate different spatial characteristics of range. We discuss several potential applications of species range maps including facilitation of field surveys, informing restoration efforts, studies of range size and rarity, studies of biodiversity, conservation planning, and invasive species management.

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Introduction

Hawai`i is home to nearly 1,200 native species of vascular plants, a large proportion of which are listed endangered, candidates or are species of concern (U.S. Fish and Wildlife Service 1992), and a majority of which are restricted to a single island or are limited by habitat (Price 2004). However, non-native species now outnumber native species (Wagner et al. 1990, Wagner and Herbst 1999), with many of the former being invasive threats to native ecosystems (Cuddihy and Stone 1990, Staples and Cowie 2001). The ranges of many native species have been summarized in their taxonomic descriptions (especially those by Wagner et al.(1990)). Species that are important components of forest canopies have been mapped using combinations of fieldwork and aerial photography (Jacobi 1989). Still other species, especially rare species, have had specific locations mapped, most notably by the Hawai`i Natural Heritage Program (now the Hawai`i Biodiversity and Mapping Program) and the U.S. Fish and Wildlife Service. However, as yet there is no single scheme for estimating geographic ranges that can be applied to all vascular plant species.

The most obvious approach to determining the geographic range of a given species would be to simply map its known locations. However, any mapping effort limited to documenting where species have been reliably recorded may prove problematic in several ways. First, widespread species occur at far too many locations to record all of them, and thus only a subset of locations can be recorded with a reasonable effort. On the other hand, many rare species are known only from very scattered locations, and thus it would be difficult to assess their distributions in poorly explored areas. Finally, historically known locations may not fully represent where a species occurred prior to widespread human disturbance. If one could assess the full natural range of a given species, it might offer important clues as to the ecological context in which it evolved, as well as provide a credible basis for its potential restoration at a site. Therefore, an approach applicable to all species would use reasonable amounts of data for each species in order to extrapolate its geographic range in the broadest sense possible. This report describes components of a methodology for projecting the geographic ranges of plant species in the Hawaiian Islands. This consists primarily of the creation of several GIS data layers depicting attributes related to the geographic ranges of plant species. These layers include: 1) climate zones, 2) young lava substrate areas, 3) biogeographic regions, and 4) degree of human impact. A specially constructed database then relates species locations to these GIS layers leading to estimations of their potential geographic range.

The most important data layer described here is an objectively-defined classification of climate as it pertains to the distribution of plant species. By examining previous zonal vegetation classifications in light of spatially detailed climate data, we explicitly define broad zones of climate relevant to contemporary concepts of vegetation in the Hawaiian Islands. A second spatial data layer defines substrate age, since large areas of the island of Hawai'i in particular are covered by very young lava flows, which are inimical to the growth of many plant species. The third data layer divides larger islands, which are composites of multiple volcanoes, into definable biogeographic regions, since many species are restricted to a given topographically isolated mountain or a specified group of these. A final spatial data layer depicts human impact, which reduces the range of many species relative to where they formerly occurred. Several other factors that influence the geographic ranges of species, including topography, soils, and disturbance, are discussed here but not developed further due to limitations in rendering them spatially.

Climate Zone Classification

Climate in the Hawaiian Islands is extremely variable, with precipitation ranging from 250 mm to over 10,000 mm and with temperature regimes ranging from tropical to alpine (Giambelluca and Schroeder 1998). Hawaiian vegetation has been described in terms of climate since the first botanical explorations after European contact. Hillebrand (1888) divided vegetation into four elevation zones, but describes the variation of their breadth as depending on whether they are on windward (wet) or leeward (dry) slopes. A more detailed vegetation description by Rock (1913) similarly defines vegetation according to elevation and windward (wet) vs. leeward (dry) aspects, as well as including descriptions of major component species. The first of these vegetation classifications to include potential vegetation maps, Ripperton and Hosaka (1942) used the dominance of characteristic native and non-native species to define several major vegetation zones. The most recent comprehensive vegetation classification by Gagné and Cuddihy (1990) not only considered different moisture and elevation zones, but defines them somewhat explicitly. While this did not include a vegetation map, the exhaustive descriptions of different sites throughout the state permit many areas to be attributed to a give vegetation type. A series of vegetation maps by Jacobi (1989) served as a basis for the Gagné and Cuddihy classification. Using a combination of extensive fieldwork from the Hawaiian Forest Bird Survey (HFBS) and aerial photographs, these maps attribute finely-resolved areas to detailed vegetation types according to moisture zone, dominant cover, stature, and understory composition. They primarily cover upland areas, however, and particularly areas that include forest bird habitat, since these were the areas surveyed extensively by the HFBS. In addition, they only cover the islands of Lāna'i, Moloka'i, Maui, and Hawai'i. A map by Gon et al. (1998) depicts potential vegetation, but attempts to incorporate influences in addition to climate such as substrate, topography and hydrography for a generalized vegetation map for all islands. We utilize and build upon these latter three vegetation classifications here.

The first step in generating a comprehensive map of climate zones is rectifying the functional definition of each zone with the perception of these on the ground. To do this we first started with a median annual precipitation (MAP) map by Giambelluca et al. (1986), consisting of isohyet lines, which was available in digital form from the State of Hawai'i. We interpolated this map into a continuous surface (with values for each 30 m square cell in a grid) using ArcInfo's TopoGrid command (ESRI 2005), which accommodates line data inputs, unlike other interpolation functions which require point data inputs. Using this new MAP surface, we conducted a preliminary assessment of the agreement between Gagné and Cuddihy (1990) moisture classes with maps created by Gon et al. (1998) and Jacobi (1989). Initially Gagné and Cuddihy define the Dry zone as being less than 1,200 mm annual rainfall, the Mesic zone as being between 1,200 and 2,500 mm annual rainfall, and the Wet zone as being greater than 2,500 mm annual rainfall, although they add itemized exceptions to these as a function of substrate or other influences in sections on individual types. We depicted the precipitation surface with the primary break points (1,200 mm for the Dry-Mesic boundary, 2,500 mm for the Mesic-Wet boundary), producing a map of the three moisture zones according to precipitation. When comparing this precipitation-based moisture zone map to other vegetation maps, a number of disparities were evident. Most notable was the fact that many areas considered Mesic by vegetation maps (Jacobi 1989, Gon et al. 1998), such as the south slope of Haleakala on Maui and the Koke'e region on Kaua'i, receive somewhat less than 1200 mm of precipitation annually.

Moisture Availability Index

A more detailed approach to the nature of moisture availability in different climates (Thornthwaite 1948) assesses moisture availability as a function of annual precipitation and potential evapotranspiration (PET), which represents the moisture demand of the atmosphere as a function of temperature and humidity and is strongly driven by the amount of incoming solar radiation. Bean et al. (1994) found that middle elevations in Hawai'i exhibited lower PET because this lies within the cloud belt and is high enough in elevation to have lower temperatures than sea level, but not so high in elevation as to exceed the trade-wind inversion, above which clouds generally do not form and insolation is comparatively high (Giambelluca and Schroeder 1998). It is highly likely that there is also strong variation in PET depending on aspect to prevailing trade winds and local topographic effects that influence cloud cover, however at present there is insufficient data on PET to map this variation in any detail.

Juvik et al. (1978) considered a function of moisture inputs (through precipitation) and moisture demands (through evapotranspiration) in order to determine the major components of water balance. They thus subtracted PET from MAP to determine areas of potential moisture surplus and deficit on the island of Hawai'i. Another study by Juvik and Tango (2003) establishes a more detailed profile of precipitation, including fog drip inputs, and PET to consider moisture availability on the leeward side of Hawai'i. Following a similar methodology, we considered the difference between MAP and PET (calculated as MAP minus PET). The resulting Moisture Availability Index (MAI) better reflects variation in available moisture than precipitation alone and was used as a primary framework to compare with vegetation maps. We chose breakpoints in the MAI that best fit the concepts of the Dry, Mesic, and Wet vegetation zones in Jacobi's (1989) maps. We chose a breakpoint between Dry and Mesic that corresponds to the often-cited classification by Holdridge (1967), where tropical dry forest climate is defined by those areas where annual PET exceeds MAP (where MAI < 0). We chose a breakpoint between Mesic and Wet that approximates that given by Gagné and Cuddihy (1990); while they define this breakpoint at 2,500 mm MAP, we set the breakpoint in the MAI at the value where 2,500 mm of rainfall is received at 1,000 m elevation (where MAI = 1,661 mm). Table 1 gives the moisture balance values as well as the precipitation cutoffs at different elevations.

We used maps of estimated MAP and PET in order to estimate values of MAI statewide. To characterize PET in different areas, we first derived a generalized profile using data from Bean et al. (1994) which reflects the somewhat lower PET at middle elevations (Figure 1). We then used a statewide Digital Elevation Model (DEM) (standardized to a 30 m cell size and a 1 m vertical resolution) to attribute PET values to areas with different elevations. The resulting surface represents an estimate of PET across all islands. In reality, it is certain that PET varies by island, aspect with respect to trade winds, and other factors, however there are presently not enough measurements of PET in different areas to be able to map this spatial variability in detail. Nonetheless, the projected PET surface represents a rough approximation of spatial variation (with respect to elevation) and can be combined with precipitation values to better represent available moisture. By subtracting the estimated PET value from the estimated MAP value for each grid cell, we generated a surface which estimates MAI statewide. Using the MAI breakpoints defined above, we partitioned the estimated MAI surface (representing MAP minus PET) into the three primary moisture zones (Dry, Mesic, and Wet).

We chose to assess the partitioned MAI surface using Jacobi's (1989) map, since this represents a vegetation classification derived from field observations of vegetation characteristics, and is largely independent of climate. We converted Jacobi's map into a 30 m grid coverage of Dry, Mesic, and Wet zones and compared this to the zones depicted in the estimated MAI surface. The MAI surface agreed with Jacobi's map in 66% of grid cells, was drier than Jacobi's map in 10% of grid cells, and was wetter than Jacobi's map in 23% of grid cells (areas considered unvegetated by Jacobi were not considered, since these represented lava flows across various moisture zones). Figure 2 shows a portion of Moloka'i as an example of how the maps differ.

There are several possible reasons why a given location may be classified differently according to the MAI surface than it is in Jacobi's (1989) map. First, the MAI surface is derived from interpolated precipitation maps that are fairly generalized and in some cases may differ somewhat from actual local climate station data. In other cases, there are comparatively few climate stations, and interpolated precipitation values may not accurately reflect actual MAP. This absence of climate data is particularly acute for remote areas, however many such areas lie within the regions covered by Jacobi's map since these represent large tracts of native vegetation. Thus, where climate data is clearly lacking, Jacobi's vegetation map may more accurately represent available moisture than the estimated MAI surface.

In other areas, however, Jacobi's map differs markedly from the estimated MAI surface in areas with good climate data. Such discrepancies typically are due to at least one of two situations. The first situation includes areas of relatively young lava substrates. Because one of the criteria indicating "Wet" vegetation was the relative cover of tree ferns, even in areas with ample precipitation, relatively young lava substrates largely preclude their growth and the area is classified as "Mesic" in Jacobi's map. Similarly, a more open canopy or shrub cover was an indicator of "Dry" vegetation in many areas of Jacobi's map, even though these areas receive sufficient rainfall to classify as "Mesic"; again however, this occurs typically in areas of young lava substrates. Because of this, young substrate areas are treated in a separate section for this study. The second situation where Jacobi's map classifies areas as drier than the estimated MAI surface are areas of habitat degradation, particularly by introduced ungulates. For example, areas that are Wet according to the estimated MAI surface but where cattle grazing has disturbed the understory and reduced the cover of tree ferns, are classified as Mesic in Jacobi's map. Similarly, areas with open or even no tree canopy and considerable cover by pasture grass are considered Dry in Jacobi's classification, despite reliable climate data placing them in the Mesic or even Wet climate zone. In order to rectify differences between Jacobi's map and the estimated MAI surface, major areas where the two differ were assessed along with local climate data, when available. In areas outside those covered by Jacobi's maps, designations from the map by Gon et al. (1998), descriptions in Gagné and Cuddihy (1990), or another source were used. In many instances, data from individual climate stations provides a more reliable local estimate of MAI than that from the estimated MAI surface, which can be inaccurate due to the generalized nature of the MAP and PET maps. All differences are rectified on a case by case basis in Table 2.

Moisture Zone Map

After resolving differences between the estimated MAI surface and other sources, a new moisture zone map was created. Each of the three primary moisture zones was then further subdivided. The Wet zone was divided into two zones: areas with a MAI value greater than 3,161 (1,500mm above the Wet-Mesic boundary) constitute the "Very Wet" zone, and areas with a MAI value less than 3,161 constitute the "Moderately Wet" Zone. The Mesic zone was divided into two zones: areas with a MAI value greater than 861 constitute the "Moist Mesic" zone, and areas with a MAI value less than 861 constitute the "Seasonal Mesic" Zone. The Dry Zone, because it includes far more area than the Wet or Mesic zones, was subdivided into three new zones: areas with a MAI value between 0 and -389 constitute the "Moderately Dry" zone, areas with a MAI value between -389 and -689 constitute the "Very Dry" zone, and areas with a MAI value less than -689 constitute the "Arid" Zone. The new zones are numbered one to seven from driest to wettest. The combinations of MAP and elevation estimated to place a site within a given zone are depicted graphically in Figure 3.

To produce the new moisture zone map, lines were digitized according to whichever data source was considered the most reliable for a given region. In areas where the estimated MAI surface is considered reliable (i.e. where climate data are reliable) boundaries between moisture zones were placed according to appropriate breakpoints in the MAI. In areas where the estimated MAI surface was not reliable, other sources (such as Jacobi (1989) or Gon et al. (1998)) were used to demarcate zonal boundaries. Lines were drawn so as to be smooth and general (rather than depict a false sense of precision by following sinuous boundaries demarcated by a given source) at a scale of 1:70,000. The result is a map of seven moisture zones, each representing a discrete zone of moisture availability for the main Hawaiian Islands (Figures 4 and 5).

Adaptation of the Moisture Zone Map to Species Distributions

The moisture zone map was adapted to reflect patterns in species distributions. First, many species are known from several moisture zones, but are restricted to the areas near the coast; this is separate from being restricted to low elevations, since such species are frequently known from over 100 m elevation on sea cliffs but are not found at comparable elevations inland. Other species have more extensive distributions along the coast than they do inland. For example, *Erythrina sandwicensis* has been recorded in zones 1 through 5 near the coast, but is limited to zones 1 through 4 inland. To depict this coastal zone on the habitat maps, a buffer zone of 500 m was generated from the coastline and those areas falling within it are classified as Coastal and divided among the seven climate zones. This distance was chosen because, while the coastal zone certainly varies in width, the influences of salt spray, wind, and floating water table (the Ghyben-Herzberg effect), the area within 500 m likely contains the vast majority of sites with these conditions.

Another adaptation of the moisture zone classification is a special consideration of the three driest zones (one through three) at higher elevations. These zones are restricted to elevations below 1000 m on all islands except on East Maui and Hawai'i, where extensive areas with drier climates are present at high elevations. These upland Dry regions are largely separate from lowland Dry regions: they are entirely disjunct on Maui, and a comparatively small amount of area at middle elevations connects upland and lowland Dry regions on the island of Hawai'i. In many cases species that are otherwise restricted to the Mesic and Wet zones inhabit one of the three Dry zones at higher elevations on Maui and Hawai'i. This may reflect the fact that these higher elevation areas experience lower daytime high temperatures and therefore lower heat stress than lowland Dry regions. Such occurrences may also be due to moisture input from fog at higher elevations, which may add critical moisture during otherwise dry summer months (Juvik and Ekern 1978, Juvik and Tango 2003). However, these regions also have very poor precipitation records, with generally large distances between climate stations. For example, the central plateau of Hawai'i has only a few rain gages scattered along its margin, with none in its center. Therefore, while these dry upland regions can be considered climatically distinct from lower elevation dry regions, there is little confidence that boundaries among zones 1, 2, and 3 are well defined. Native plant species records are also somewhat limited in these areas, adding further difficulty to confidently placing species within a given moisture zone. For purposes of defining species ranges, we therefore combined these three zones for areas above 1,250 m. This new Upland Dry zone is considered distinct from zones 1 through 3 at lower elevations. The final set of zones used in the species database is presented in Table 3.

Young Substrate Areas

Young lava substrates impose several well known influences on vegetation. The unweathered nature of most volcanic substrates permits little soil formation and results in high degree of drainage which retains less moisture than weathered substrates (Kitayama et al. 1995). In addition, younger soils are deficient in nutrients, particularly nitrogen (Crews et al. 1995). According to a study of several lava flows of varying age within the moderately wet climate zone (Kitayama et al. 1995), lava flows younger than 200 years of age restrict many species and support only very sparse vegetation. However, in drier climate regions vegetation remains stunted on even moderately aged lava flows (Aplet and Vitousek 1994). The pioneer vegetation associated with young lava substrates is likely inimical to the growth of many plant species that cannot tolerate such conditions; on the other hand some species such as *Rumex skottsbergii* and *Scaevola kīlaueae* appear to prefer this type of vegetation (Wagner et al. 1990).

While many studies chronicle the development of vegetation on lava flows within wet climates, comparatively little has been done in areas with drier climate. Stemmerman and Ihsle (1993) demonstrate that in Very Dry, Moderately Dry, and Seasonal Mesic areas (within moisture zones 2 through 4 described here), vegetation exhibits marked changes in composition and dominance with increasing age. Most substrates 3,000 years or older supported well-developed vegetation, as opposed to the pioneer vegetation on younger flows dominated by either sparse or small ʻŌhiʻa (*Metrosideros polymorpha*). A study of litter production across sites receiving different amounts of rainfall (Austin 2002) indicates that a site at Kanikū, within the Moderately Dry zone (zone 3) and with a substrate age of 2,800 years, exhibited characteristics of a pioneer community compared to moister sites with similar substrate age. These characteristics include fewer species, low rates of litter production, low foliar nitrogen concentration, and a dominance by ʻŌhiʻa (which does not dominate on older substrates in drier climate zones).

In summary, it appears that in the wettest areas, young lava substrates support well-developed vegetation within perhaps as little as a few hundred years, whereas in drier areas the process may take up to 3,000 years or more. One exception to this general pattern is comparatively young deep volcanic ash substrates, which exhibit species composition and soil characteristics comparable to very well-developed substrates (Balakrishnan and Mueller-Dombois 1983, Vitousek et al. 1983). To better resolve the general pattern, we assessed substrate characteristics using both geological and climatic GIS maps.

Geologic maps depicting lava flow age are available for the Island of Hawaiʻi (Wolfe and Morris 1996) and Maui (Sherrod et al. 2006). These classify lava age into the following categories: >200 years, 200-750, 750-1,500, 1,500-3,000, 3,000-5,000, 5,000-10,000, >10,000. Some substrates, notably alluvium, were not given an age designation, although in some cases this represents landslide deposits attributable to lava flows of known age. These areas were therefore classified according to the most likely source of parent material. Regardless of their actual age, areas with deep ash substrate were reclassified into the oldest age class (>10,000 years) due to the unique characteristics of this substrate type. The geologic maps were converted to 30 m grids with values representing the seven age classes. We then combined this age class grid with a 30 m grid of climatic moisture zones (defined earlier in this study) to determine the combination of age class and moisture zone at each given location.

In order to determine which age classes should be designated as young lava for each given moisture zone, we examined moisture and substrate age in the context of a land cover classification. This grid, produced by the Hawaiʻi Gap Analysis Program (HIGAP), is based on LandSat TM satellite imagery, and represents major structural vegetation types (Gon 2006). We grouped cover classes according to those that were considered unvegetated or vegetated with what we considered to be pioneer vegetation (including cover classes "Very Sparse Vegetation to Unvegetated" and "Sparse ʻŌhiʻa/Native Shrub"). For each moisture zone by substrate age combination, we examined the proportion of the area covered by sparse vegetation. We excluded areas in the arid zone associated with alpine habitats (above 3,000 m elevation), since these consist almost entirely of sparse vegetation regardless of substrate age. Results are summarized in Table 4.

A clear trend exists where sparse vegetation makes up large proportions of areas with young substrate age. In the wettest areas (zones 6 and 7) no age class had a majority of its area covered by sparse vegetation; instead, areas within the two wettest zones that were on the youngest substrates (< 200 years) tended to be covered in open ʻŌhiʻa with Uluhe (*Dicranopteris linearis*), a mat-forming fern. Nonetheless, studies from areas with this moisture/substrate combination (Kitayama et al. 1995; Aplet and Vitousek 1994) indicate that species composition is limited. Starting with the Moist Mesic zone (zone 5), progressively older substrate age classes are covered primarily (at least 75%) by sparse vegetation. At the Arid end of the spectrum (zone 1), all age classes younger than 3,000 years were covered at least 75% in sparse vegetation. The 3,000 to 5,000 year age class within the Arid zone included nearly as high a proportion of its vegetation covered in sparse vegetation (73%), however much of this area is human modified (the area includes the city of Kailua, Kona and the resort areas to the north), and thus might have had a higher proportion of sparse vegetation originally. This pattern is generally in agreement with that of studies of individual sites, where substrate development takes longer at drier sites.

We decided to consider substrates to be "young lava" as follows: in Moist Mesic through Wet moisture zones (zones 5 to 7), < 200 years; in the Seasonal Mesic zone (zone 4), < 750 years; in the Moderately Dry zone (zone 3) < 1,500 years; in the Very Dry zone (zone 2), < 3,000 years; in the Arid zone (zone 1), < 5,000 years. These areas represent a large portion of the island of Hawaiʻi and a limited portion of the island of Maui and are not found on other islands (Figure 6). While substrate age and climatic moisture are primary drivers of rates of succession, the designation given here should be considered a general estimate of soil and vegetation development. Additional factors, such as elevation or whether the substrate is \`a\`ā or pāhoehoe lava may be of comparable importance in determining the ability of species to colonize lava flows, and require further research.

Biogeographic Regions

By subdividing islands into distinct geographic regions, a species potential habitat can be bracketed by those islands and portions of islands on which the species has been recorded. Isolation of populations on different islands facilitates the evolution of distinct species restricted in their distribution (Carlquist 1980, Wagner and Funk 1995). Furthermore, some islands consist of more than one topographically distinct volcanic mountain, promoting further possibilities for geographic restriction. Consequently, over 40% of native Hawaiian flowering plant species are restricted to a single volcanic mountain (Price 2004). Following Price (2004), the islands of O'ahu, Moloka'i, and Maui were divided into two geographic regions each corresponding to separate volcanic masses. The island of Hawai'i was divided among its five constituent volcanic mountains (Kohala, Mauna Kea, Hualalai, Mauna Loa, and Kīlauea); in addition, Mauna Loa Volcano was subdivided into four sub regions both because it covers far more area than any other volcanic mountain and because its slopes include disjunct areas of certain climate zones. The sub regions of Mauna Loa include: Northwest, positioned between Hualalai and Mauna Kea; Northeast, stretching from Mauna Kea south and including the Mauna Loa Strip of Hawai'i Volcanoes National Park; Southeast, stretching from the Hawai'i Volcanoes National Park boundary to the Kau-South Kona District boundary; and SW Mauna Loa, stretching from the Kau-South Kona District to Hualalai. We generated a GIS coverage (Figures 7 and 8) to explicitly define each of these regions from a composite geological coverage for the island of Hawai'i (Wolfe and Morris 1996), as well as a statewide digital elevation model (USGS open source data) and a land parcel boundary coverage (State of Hawai`i 2006).

Human Impact

Many habitats in Hawai'i are severely altered by human activity. Areas that have been converted for urban or intensive agriculture are likely inimical to the vast majority of native species. In addition to these areas, many ecosystems in Hawai'i are dominated by non-native species (Cuddihy and Stone 1990, Gagne and Cuddihy 1990), which probably also limits many native species. On the other hand, certain native species, even some rare and endangered species, may persist in habitats dominated by non-native species. A map by Gon et al. (1998) categorizes areas as being generally native or non-native dominated. To more precisely identify areas where native species may presently be found, we generated a map that considers three categories of habitat quality: "high" (native dominated vegetation), "medium" (non-native dominated vegetation), and "low" (highly modified landscapes). The primary source for mapping these three categories is the HIGAP land cover classification (Gon 2006). The "high" category includes all HIGAP land cover classes that are considered native dominated or mixed native and alien in order to represent those areas with substantial native species composition. The "medium" category includes areas that are dominated by non-native species but are not otherwise intensively developed. This incorporates all non-native dominated HIGAP land cover classes. The "low" category includes all land cover classes pertaining to urban land, other developed lands, and active cropland. In addition, many areas of former or fallow cropland were mapped as grassland or alien forest in the HIGAP land cover map. These are best included in the "low" category, since they include areas where all native vegetation was removed at one time. These areas are different from other non-native dominated areas where native species may be more likely to have persisted. We converted a GIS layer of the agricultural land use map (ALUM) developed by the State of Hawai'i Department of Agriculture (1980) into a 30 m grid, and then re-classified all cells identified with cropland and other intensive agricultural uses into "low" quality category. Also, areas classified as "Very Sparse Vegetation to Unvegetated" in the HIGAP land cover map cannot be directly attributed to a given habitat quality, because they may represent native pioneer vegetation on lava or barren sites within a non-native dominated area. We therefore assigned to each unvegetated cell the average habitat quality value for all cells within a 3 km radius. Due to limitations in the accuracy of the HIGAP land cover map, the resulting map is still somewhat general but otherwise represents a good approximation of habitat quality (Figures 9 and 10).

To test whether native species tend to occur in areas considered native dominated by our three-level habitat quality map, we utilized a set of point locations, compiled by the US Fish and Wildlife Service, where rare native plant species are known to occur. We selected the points with the highest precision, excluding those where the location was overly general (e.g. "Ko'olau Mountains"). These consist of 5,575 locations and represent over 600 species. We then converted these points to a grid-coverage and determined the number of locations associated with each of the three habitat quality categories. High habitat quality areas make up 46% of all land area, but include 75% of rare plant locations. Medium habitat quality areas make up 41% of all land area, but include just 23% of rare plant locations. Low habitat quality areas make up 13% of all land area, but include less than 2% of rare plant locations. In fact, nearly all of the rare plant locations associated with low habitat quality represented *Abutilon menziesii*, a peculiar endangered species that persists in former sugar cane fields. The habitat quality designations therefore reflect the tendency of native species to be strongly associated with high habitat quality, nominally associated with medium habitat quality, and minimally associated with low habitat quality.

Additional Factors Influencing Species Ranges

There are several other influences on species distributions that deserve mention, although as yet it is not feasible to map them. Different types of topography, including gulches, ridges, and various aspects with respect to the sun, wind and moisture certainly favor some species while restricting others. Unfortunately, while it is feasible to firmly establish a species within a given climate zone, available records often do not consistently contain detailed site information from which a trend might be discerned. While collecting such data for a few species may be possible, this would likely prove extremely difficult for the entire vascular flora. In addition, presently available digital elevation models, while depicting large scale variation in topography, may not include small scale topography. For example, many species either prefer or are now restricted to very steep slopes and cliff faces; such habitats may occur in fairly small pit craters or cracks that are unlikely to be represented at the presently available resolution of digital elevation models. Another potential influence that could be mapped is soils. At present only very coarse and outdated soil maps exist, however the Natural Resources Conservation Service is presently developing a new soils map for the island of Hawai'i. Hydrography is another influence that can be very important in determining suitable habitat, but is at present difficult to map. Large wetland areas can be mapped for example, but attributing species only to those areas potentially omits many smaller wetlands and stream banks far from larger wetland bodies, which would lead to an underestimate of the range. In the future these might be incorporated into more sophisticated species distributional models. It may also be feasible to build mathematically complex statistical models based on trends from several parameters drawn from detailed point data.

Species Range Mapping

At present the most effective way to map plant species ranges in Hawai'i is by demarcating a general bioclimatic envelope within biogeographic regions the species is known to have been found. To do this we have built upon a database of native Hawaiian plant species that includes data on the distribution of species by geographic region, major habitat type, and elevation range (Price 2004). These data come from published sources, herbarium specimens, unpublished reports and field notes, and targeted field work. The database has been expanded in several ways to accommodate a comprehensive species range mapping program. First, the database now includes data for Hawaiian Pteridophytes based largely on the recently published flora by Palmer (2002) and specimens from the Bishop Museum. It has also been modified to explicitly document species in the climate zones developed here. Where possible, voucher specimens from specific locations document the presence of a species in each applicable climate zone on the zonal map, establish whether it occurs on young lava substrates as defined here, and documents the elevation limits. The full database, derived from that used by Price (2004), contains these data for all native species and includes referenced sources for each data cell.

To generate a map of the estimated range of a given species, the database is used to generate a script in Arc Macro Language (AML). This script can then be read by a terminal-based Grid Module of ArcInfo (ESRI 2005). This method was favored because a single AML script can be used to run a batch process and generate estimated range maps for many species with a single command, and because problems can be intercepted and amended easily. All base layers are converted to a 30-meter grid of values. First, using base layers for climate zones, biogeographic regions, and young lava, as well as a DEM for elevation range, the AML script simply selects out those areas with values appropriate to that species. This represents the estimated natural range of the species prior to human modification of habitat. In some cases a species has been recorded in one biogeographic region on a given island but not in the other. The species range can also be calculated for where it might have occurred in regions in which it has not been recorded. To examine the status of habitat quality within the estimated natural range of a given species, the range can be parsed into areas corresponding to low, medium and high quality habitat. Thus a given species range can be considered in several different ways on a given island on which it is known.

To demonstrate how different ways of viewing a range might be practically applied to different species, we selected four species to use as case studies, including two widespread species (*Sadleria cyatheoides* and *Erythrina sandwicensis*) and two rare species (*Cyanea tritomatha* and *Chamaesyce kuwaleana*). Sample data matrices show presence in biogeographic regions (Table 5) and habitat parameters (Table 6) for the four case study species. Sample range maps for these case studies, along with a description of important patterns, are given in Figures 11 through 16.

Applications of Estimated Range Maps

The estimated ranges generated using these methods can be applied to both natural history questions and conservation management. They can be used either individually for single species applications or collectively for questions pertaining to species assemblages. Following are several proposed applications, several of which are presently being developed.

<u>Facilitating Field Surveys</u>

Field biologists often require tools to focus search efforts on species likely to be in a given area. Using species range parameters and associated GIS maps, it is feasible to produce a list of species potentially within a given area. Often many members of a given genus occur on an island but exist in different geographic regions or different habitats. Field biologists can thus employ the tools developed here to help identify species in their survey area. In other cases, surveys for rare species can be guided by focusing on those areas where the species is most likely to occur. For example, in the case study for *Cyanea tritomatha* (Figure 16) areas of high habitat quality within the estimated range would be targeted to search for the species.

Restoration Efforts

Large areas in the Hawaiian Islands are now dominated by non-native species (Figures 9 and 10). Even in areas dominated by native species, significant disturbance from non-native plants and animals (Cuddihy and Stone 1990) means that many species are likely to have been extirpated from areas in which they formerly occurred. At many sites in the state, rare plants have been outplanted in areas where they formerly grew to expand wild populations, for example the silversword (*Argyroxiphium sandwicense*) on Mauna Kea (Walker and Powell 1999) and several rare dry forest species at Kaupulehu Preserve on Hawai'i (Cabin et al. 2002). In other cases, sites where a given rare species formerly occurred are now highly degraded or may be on lands not presently designated for conservation management. In such cases, outplanting may occur at sites designated for conservation and presumed to constitute appropriate habitat. The method employed here presents a reasonable estimate of suitable habitat for each given species, although other site characteristics, such as substrate or soil type, degree of canopy closure, and associated species must also be taken into consideration. For example, the case study of *Chamaesyce kuwaleana* (Figure 15) suggests that despite severe alteration of its habitat, their may be suitable restoration sites available within its estimated natural range. Producing a list of all species appropriate for a given area will facilitate diverse community-level ecological restoration.

Studies of Range Size and Rarity

A growing body of work seeks to understand the causes of variation in the size of species geographic ranges. Many geographically restricted species are threatened with extinction, and therefore information about the nature of their rarity may be useful to their conservation (Gaston 2002). Nearly half of Hawaiian plant species are naturally restricted to a single island (Price 2004), and this rarity is correlated with restriction to few habitats and a narrow elevational range (Price and Wagner 2004). The method presented here produces comparatively precise estimates of both the natural range size and the probable present range size (by taking into account human-induced range reduction). These two estimates vary independently among species, and therefore a species that is presently rare may have been quite common in the past. For example, in the case study for *Eythrina sandwicensis* (Figures 13 and 14), a species that was probably extremely widespread prior to human landscape modification, has undergone range reduction to the point that it is now somewhat rare. By comparison, the case study for *Cyanea tritomantha* (Figure 16) suggests that this species was already somewhat rare prior to human landscape modification. This distinction between human-induced rarity and natural rarity may have important management implications, since naturally rare species may be better adapted to maintaining small populations than species that have lost much of their original population structure (Gaston 1994).

Studies of Biodiversity

Examinations of patterns in biodiversity frequently use species richness maps produced by overlaying the ranges of all species of interest within a region (Flather et al. 1997, Hortal et al. 2001, Lennon et al. 2004). Using the methodology presented here, species range estimates and derivative richness maps are highly resolved compared to country- or continent-scale maps used in most studies. With high resolution richness maps, more detailed analyses of the factors contributing to biodiversity are feasible. While factors such as habitat, elevation, and island age have been examined in the Hawaiian Islands (Price 2004), more spatially explicit analyses may elucidate complex interactions among factors not apparent through other analyses.

Conservation Planning

Species range maps may be employed in Gap Analysis Programs (GAP), where they are compared to the spatial placement of conservation areas in order to identify gaps in conservation effort (Scott et al. 1993). The national GAP program seeks to incorporate this type of analysis for all U.S. States to produce a comprehensive evaluation of biodiversity conservation (Scott and Csuti 1992). The Hawai'i GAP program is unique among these in incorporating endangered plant species ranges, rather than vertebrates only as in other state GAP programs (Gon 2006). Nonetheless, there is debate as to whether GAP appropriately incorporates critical aspects of species conservation (Burley 1988, Flather et al. 1997). While the Hawai'i GAP program considered federally endangered plant species only, examination of all plant species may produce different results. Moreover, there may be alternative measures of conservation value independent of federal listing or total richness. Potential measures include richness of species exhibiting natural geographical rarity or richness of species exhibiting human-induced rarity (i.e. have small range size after human impact). The comprehensive nature of these measures of conservation value, coupled with their comparative detail, may promote landscape-scale tools for conservation planning not possible in other regions.

Invasive Species Management

Invasive plant species pose a serious threat to Hawaiian ecosystems by displacing and competing with native plant species and disrupting key ecological processes (Cuddihy and Stone 1990). Conservation agencies and organizations expend considerable resources to control highly invasive plant species such as *Miconia calvescens*. New invasive threats appear each year as incipient populations expand. By using known or projected environmental parameters, the potential range of a given invasive species can be estimated. Using such an estimated range can help assess the degree of threat posed by a given invasive species and may inform management efforts to strategically search for and control incipient populations before the species becomes a widespread problem. For example, a study of several non-native species on Maui by Price and Jacobi (2006) used similar methodology to assess the potential for range expansion relative to presently known distributions. The resulting analysis may inform strategic plans for control of species considered most likely to expand their ranges and negatively impact native ecosystems or rangeland resources.

Summary and Future Modeling Efforts

The tools and methods presented here provide a simple but comprehensive way to generate maps of the estimated natural ranges and probable present ranges of Hawaiian plant species. Nonetheless these estimates will need to be reassessed or refined periodically. The prospect of new location data based on continued fieldwork may result in new parameters and necessitate reassessing the range estimate for a given species. For example, species continue to be discovered on islands or in habitats where they were previously unknown. The development of new GIS layers (including soils, geomorphology, highly-refined canopy cover) coupled with point-quality location data for all known locations of a given plant species will promote more sophisticated modeling methodologies based on probability and including error estimates, and capable of being subjected to rigorous model testing. At present however, the methodology documented here presents a useful first approximation of the ranges of Hawaiian plant species not previously available.

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Table 1. Moisture Availability Index values and approximate precipitation cutoff zones at different elevation boundaries of primary moisture zones.

Note that the Dry-Mesic boundary occurs where MAP is equal to PET (MAI equals zero). Precipitation cutoffs are given for several elevations. For any given moisture zone boundary, the lowest precipitation cutoff value is at 1000 m where PET is lowest. At lower or higher elevations, more precipitation is needed to balance out the higher PET values there. Cutoff values for Dry-Mesic and Mesic-Wet Boundary are not given above 2500 m elevation because all areas high than that are within the Dry zone.

Boundary	**MAI value (mm)**	**MAP (mm) at 0 m**	**MAP (mm) at 500 m**	**MAP (mm) at 1000 m**	**MAP (mm) at 1500 m**	**MAP (mm) at 2000 m**	**MAP (mm) at 2500 m**
Dry-Mesic	0	1300	1000	800	900	1050	1500
Mesic-Wet	1661	3000	2700	2500	2600	2750	3200

Table 2. Itemized rectification of Moisture Availability Index with other sources.

All major areas where the estimated MAI surface differs in classification from another data source are listed. In some cases, the estimated MAI surface was upheld despite another source suggesting a different zone. In other cases, especially where climate stations are lacking, another data source is used to classify the area. When another source is used, the amount of area differing from the estimated MAI surface is given. Frequently used sources are given as follows; J = Jacobi (1989); G = Gon et al (1998); GC = Gagné and Cuddihy (1990); S = Climate station data from Giambelluca et al. (1986). Individual climate stations are indicated by State Key Number ("S-[number]"); adjusted median annual precipitation values and elevations are given for each along with zone designation according to Table 1.

2A. Ni`ihau

Description of area	**Zone from MAI surface**	**Zone indicated by other data sources**	**Zone used**	**Area (km^2) differing from MAI surface**
Summit Area	-	Mesic (G); no climate data	Mesic	-
Remainder of Upland	-	Dry (G); no climate data	Dry	-

2B. Kaua'i

Description of area	Zone from MAI surface	Zone indicated by other data sources	Zone used	Area (km^2) differing from MAI surface
Lower elevations of Waimea Canyon	Mesic	Dry (GC); no stations in upper Canyon; stations on either side clearly Mesic, so area probably interpolated to Mesic; however slightly lower precipitation associated with large area of lower elevation would make the Dry.	Dry below 500 m, except for eastern arms of major canyons	20
Bottom of Kalalau Valley	Wet	Mesic (G, GC)	Mesic below rim	3
Mohihi/upper Koaie Canyon	Wet	Mesic (S); S-1083 (Mohihi Upper Xing) is 2185 mm at 1100 m (Mesic); S-1085 (Mohihi Koaie Div) is 2113 mm at 1000 m, (Mesic); S-1080 (Paukahana) is 2290 mm at 1100 m (Mesic)	Shifted Wet/Mesic boundary East	11

2C. O'ahu

Description of area	**Zone from MAI surface**	**Zone indicated by other data sources**	**Zone used**	**Area (km^2) differing from MAI surface**
Waianae Mountains	Mesic	Wet (G); indicates 5 wet summits: Kaala, 4 small summits in Southern Waianae's; little station data	Etimated wet above 800 m on Kaala only	8
Windward Koolau Mts. below Pali	Mesic	Wet (G); few stations (S): S-786 (Nuuanu Pali) is 2434 mm at 300 m (Mesic); S-788.1 is 2175 mm at 200 m (Mesic); S-787 is 1908 mm at 100 m (Mesic)	Mesic	-
Kuliouou Summit, Eastern Koolau Mts.	Mesic	Wet (G); no stations	Wt around 500 m	3
Leeward Southern Koolau Mts.	Mesic	Dry (G); station (S): S-773 is 1402 mm at 200 m (Mesic)	Mesic	-
Mānoa cliffs trail area	Wet	Mesic (S); S-784 (Pauoa Flats) is 4134 mm at 500 m (Wet); S-780 (Tantalus Peak) is 3119 mm at 500 m (Wet, near Mesic boundary); other stations to southwest are Mesic	At Mesic-Wet boundary	2

2D. Molokaʽi

Description of area	Zone from MAI surface	Zone indicated by other data sources	Zone used	Area (km^{2}) differing from MAI surface
Upper Waialeia to upper Waikolu	Mesic	Wet (J); no stations	Wet	5
Puu Alii	Mesic	Wet (J); no stations	Wet	4
Pelekunu Valley	Wet	Mesic (J); stations (S): S-543 (Pelekunu Ridge) is 2604 mm at 200 m (Mesic)	Mesic	4
Upper Wailau Valley	Wet	Mesic (J); station (S): S-544 (Puu Lua) is 3908 mm at 600 m (Wet)	Wet	5
Olokui, northern slopes	Mesic	Wet (J); no stations	Wet down to SL, not including Waiehu	5
Upland including upper Papalaua and Halawa drainages	Mesic	Wet (J); no stations	Wet	10
Upper Mapulehu, Pukoo, Honumuni	Wet	Mesic (J); area possibly degraded; boundary midway in between MAI surface and Jacobi (G)	Wet/Mesic	8
Upper Kawela region	Mesic	Dry (J); no stations; area possibly degraded; Mesic (G)	Mesic	12
Lower Kawela east to Pukoo middle elevation	Mesic	Dry (J) where covered; no stations; Dry (G)	Mesic/Dry	24
Lower Halawa Valley and surrounding ridges	Dry	Mesic (G); rainfall isohyets about 1000mm (S); S-542.1 is 918 mm at 300 m (Dry); rainfall record from S-542.9 (Halawa Valley) from the Hawaiʽi State Climate Office is 49.15” (= 1248 mm) at Sea Level (Dry, near Mesic Boundary)	Mesic/Dry	8

2E. Lānaʻi

Description of Area	**Zone from MAI surface**	**Zone indicated by other data sources**	**Zone Used**	**Area (km^2) differing from MAI surface**
Summit	Mesic	Wet (J); station (S): Lānaʻihale (Mesic)	Wet	4
Mid elevation	Dry	Mesic (J); interpolation appears too general, climate stations suggest Mesic; stations (S): S-685 (Waiakaeakua) is 708 mm at 600 m (Dry, near Mesic boundary); S-672 (Lānaʻi City) is 875 mm at 500 m (Dry, near Mesic boundary); S-697 (R-13) is 646 mm at 500 m (Dry)	Dry up to about 600 m, perhaps lower to N	17

2F. Maui

Description of Area	Zone from MAI surface	Zone indicated by other data sources	Zone Used	Area (km^2) differing from MAI surface
Middle Honokohau region	Wet	Mesic (J); Stations (S): S-480 (Honkohau) is 3556 mm at 300m (Wet); S-477.1 (Honokohau Ridge) is 3368 mm at 700 m (Wet); S-477 (Haelaau) is 3125 mm at 900 m (Wet); S-476 (Honokowai Intake) is 2824 mm at 600 m (Wet/Mesic boundary)	Wet	-
Windward Eastern Slope of West Maui	Mesic	Wet (J); no stations	Wet	4
Iao Valley bottom	Wet	Possibly Mesic: S-387.2 (Iao Needle) is 1828 mm at 300 m (Mesic); Iao Valley is similar in breadth to Pelekunu (3 km), which may be wide enough to depress precipitation relative to surrounding peaks and ridges.	Mesic below around 700 m; lower on N side where precipitation likely higher	7
Central Ukumehame and Olowalu Valleys	Wet	Possibly Mesic, similar to Iao	below 700m considered Mesic	
Puu Kane	Mesic	Probably Wet; larger ridges just N of Puu Kane are Wet at about 800 m (J)	Wet above 800 m	1
Puu Lio, Kapilau Ridge		Probably Wet; Hanaula summit is Wet above 1100 m (J); Puu Kane, Iao Valley asserted Wet at 800 m	Wet above 900 m	2
Hanaula, Lihau, and Helu Summits	Mesic	Wet above 1100 m (J)	Wet	2; >1; 2
Kula region	Dry	Mesic (G); many stations indicate Dry (S); exception is uppermost Kula: S-330 (Gomi) 833 mm at 1100 m (Dry-Mesic Boundary)	Mostly Dry, Mesic above 1100 m	4
Upper Peahi region	Wet	Mesic (J); area degraded; S-435 (Opana Gulch) is 3295 mm at 400 m (Wet); S-488.4 (Kaupakulua) is 2378 mm at 300m (Mesic, near Wet boundary); S-446 (Kailua) is 3115 mm near Sea Level (Wet); S-436 (Kailiili) is 3242 mm at 800 m (Wet)	Wet	-

2F. Maui (continued)

Description of Area	Zone from MAI surface	Zone indicated by other data sources	Zone Used	Area (km^2) differing from MAI surface
Pohaku Palaha to Kaupo Gap	Wet	Mostly Dry (J); Mesic with some Dry (G); S-259.3 (Paliku) is 4890 mm at 2000 m (Wet); this is very likely an error; this value influenced the interpolated precipitation map in the region	Mesic	21
Kaupo Gap to Upper Nuu	Mesic	Mostly Dry with Mesic inclusions (J); area degraded through grazing; S-256.1 (Puu Kao) is 1302 mm at 1100 m (Mesic); S-257.1 (Nakula) is 766 mm at 500 m (Dry, near Mesic boundary); S-257.2 (Keeke) is 1053 mm at 200 m (Dry); S-257.4 (Kaupo Store) is 1405 mm near Sea Level (Mesic, near Dry boundary)	Mesic	-
Upper Nuu to Ulupalakua	Dry	Mesic (G); Mesic-Dry boundary according to station data (S): S-254.1 (Manukahi) is 945 mm at 1000 m (Mesic, near Dry boundary); S-251.1 (Luapelani) is 830 mm at 900 m (Mesic, near Dry boundary); S-250 (Ulupalakua Ranch) is 804 mm at 600 m (Dry, near Mesic boundary)	Shifted Dry-Mesic boundary slightly down in elevation	10
Haleakala Crater	Mesic	Dry (G); Dry/unvegetated (J); S-259.5 (Holua) is 1226 mm at 2100 m (Dry-Mesic boundary)	Mostly Dry; Dry-Mesic boundary as follows: Koolau gap, 2100 m; Kaupo Gap 2000 m around	16
Haleakala outer slopes	Dry/Mesic	South slope with Mesic patches up to 2200 m (J); S-267.2 (Polipoli Spring) is 1269 mm at 2000 m (Mesic); S-338 (Haleakala Ranger Station) is 1328 mm at 2200 m (Dry-Mesic Boundary); Additional mean annual rainfall data stations from Thomas Giambelluca, University of Hawai`i (accessed from http://webdata.soc.Hawai`i.edu/climate/HaleNet/): Horseshoe Puu (East Rift) over 6000 mm at 1930m (Wet); Treeline (East Rift) is 4756 at 2260m (Wet); Pohaku Palaha is 2477 mm at 2460m (Mesic)	On South and West slopes, Dry-Mesic Boundary is 2200 m; on NE slope, Dry-Mesic boundary is 2500 m	21; 16

2G. Kaho`olawe

Description of Area	Zone from MAI surface	Zone indicated by other data sources	Zone Used	Area (km^2) differing from MAI surface
Summit region	Dry	Very small area of Mesic at summit (G); no climate station data; about 625mm MAP at 300m estimated from Giambelluca and Schroeder (1998) (Dry)	Dry	-

2H. Hawai`i

Description of Area	Zone from MAI surface	Zone indicated by other data sources	Zone Used	Area (km^2) differing from MAI surface
Southwest of Kohala Summit	Mesic	Wet (J, G); S-183.5 (Kohala Summit) is 2685 mm at 1500 m (Wet); S-195 (Koiawe Upper) is 3127 mm at 1000 m (Wet)	Wet	23
West of Pololu Valley	Wet	Mesic (J); area degraded; S-181 (Makapala Nursery) is 2831 mm at 500m (Mesic, near Wet boundary)	Wet	-
East of Waipio	Wet	Mesic according to stations (S); S-200 (Puu Alala) is 1986 mm at 900 m (Mesic); S-192.6 (Waimea Reservoir) is 1514 mm at 900 m (Mesic)	Mesic	4
Region above Hakalau National Wildlife Refuge	Mesic	Dry (J); area degraded; S-82 (Puu Oo) is 2197 mm at 1900 m (Mesic); S-125.1 (Puakala) is 2362 mm at 1900 m (Mesic, near Wet boundary); S-117 (Halepiula) is 1125 mm at 1700 m (Mesic, near Dry boundary)	Mesic	-
Hakalau National Wildlife Refuge	Wet	Mesic (J); somewhat degraded; S-128 (Nauhi Gulch) is 3247 mm at 1600m (Wet)	Mesic-Wet boundary adjusted downward closer to Jacobi map	34
Windward Humuula Saddle Area	Dry	Mesic at Puu Huluhulu (J); S-80 (Kalaieha) is 910 mm at 2000 m (Dry, near Mesic boundary)	Mesic up to Puu Huluhulu	37
Kīlauea Forest Reserve/Kulani	Mesic	Wet (J); stations suggest near boundary (S), but well-studied area in terms of vegetation	Wet	42
Kīlauea East Rift	Mesic	Wet (J); no stations	Adjusted Wet-Mesic boundary to follow Jacobi	90
Kau Desert Area	Mesic	Dry (J); Mostly young lava; lack of stations; older precipitation map (State of Hawai'i 1975) shows area as drier: Kipuka Nene area is about 900 mm at 900 m (Dry-Mesic boundary)	Mostly Mesic; extended dry to Kipuka Nene area	38

2H. Hawai'i (continued)

Description of Area	Zone from MAI surface	Zone indicated by other data sources	Zone Used	Area (km^2) differing from MAI surface
Kapapala Region	Mesic	Dry (J); in much of area lava is younger than 750 years; other areas degraded; S-43.2 (Pahua Mimi) is 1596 mm at 1600 m (Mesic); S-43.1 (Mauna Iu) is 1244 mm at 1400 m (Mesic); S-37 (Pakao) is 1689 mm at 1500 m (Mesic); S- 38.1 (Mauna Loa 6700) is 1499 mm at 2000 m (Mesic)	Mesic; extended up above Kau Wet region	-
Kau Wet Region	Mesic	Wet (J); wet area restricted in MAI map, but few stations	Wet following Jacobi	>200
Kau Upper Mesic	Dry	Possibly Mesic; Wet region extends higher than shown by climate data, therefore interpolation of higher elevations probably also lower than actual MAP; directly above other windward Wet regions, Mesic extends to 2400m	Mesic to 2400m in Ainapo region above Kau Wet Region	35
Kahuku just below highway	Mesic	Dry (G); S-7 (Kiolakaa) 1380 mm at 300m (Mesic); S-5 (Kamaoa) 946 mm at 400 m (Dry, near Mesic boundary)	Mesic down to about 450m	-
Kona Wet Region	Mesic	Wet (J); about 10 stations, probably variable time coverage	Wet following Gon et al. (2003), Jacobi	200
Upper Papaloa-Puu Lehua Region	Dry	Patchily Mesic (J); S-73 (Puu Lehua) is 722 mm at 1500 m (Dry, near Mesic boundary); S-74 (Kanahaha) is 684 mm at 1600m (Dry); S-77 (Papaloa) is 622 mm at 1600 m (Dry); S-75 (Ahu a Umi) is 625 mm at 1600 m (Dry)	Mesic area incorporates areas defined as such by Jacobi; although stations suggest Dry, unique summer cloud cover probably moderates moisture and adds fog input	160

2H. Hawai‘i (continued)

Description of Area	Zone from MAI surface	Zone indicated by other data sources	Zone Used	Area (km^2) differing from MAI surface
Hualalai, upper	Dry	Patchily Mesic (J); S-70.14 (Reservoir Palani Ranch) is 808 mm at 1500 m (Dry, near Mesic boundary); S-71 (Honuaula) is 940 mm at 1900 m (Dry, near Mesic boundary)	Mesic slightly higher at 1900 m	13
Puu Waa Waa cone, & area down to 900m	Dry	Patchily Mesic (J); area degraded; also somewhat young lava; S-94.1 (Puu WaaWaa Ranch) is 720 mm at 1000 m (Dry-Mesic boundary); S-94.3 (Mamane Paddock) is 620 mm at 1000m (Dry); S-71.1 (Waihou 1) is 730 mm at 1000 m (Dry-Mesic boundary)	Mesic above 900 m, from base of cone extending West	20

Table 3. Climate Zones adapted in plant species database, by island.

Climate Zone	Moisture Zones	Islands
Coastal - Arid	1	All islands
Coastal - Very Dry	2	All islands except Lānaʽi
Coastal - Moderately Dry	3	All islands except Lānaʽi and Kahoʽolawe
Coastal - Seasonal Mesic	4	All islands except Lānaʽi and Kahoʽolawe
Coastal - Moist Mesic	5	Kauaʽi, Molokaʽi, Maui, and Hawaiʽi
Coastal – Moderately Wet	6	Molokaʽi, Maui, and Hawaiʽi
Coastal - Very Wet	7	Maui only
Arid	1	All islands
Very Dry	2	All islands
Moderately Dry	3	All islands except Kahoʽolawe
Seasonal Mesic	4	All islands except Kahoʽolawe
Moist Mesic	5	All islands except Ni`ihau and Kahoʽolawe
Moderately Wet	6	All islands except Ni`ihau and Kahoʽolawe
Very Wet	7	Kauaʽi, Oʽahu, Molokaʽi, Maui, and Hawaiʽi
Upland Dry	1,2,3	Maui and Hawaiʽi only

Table 4. Percent "sparse" or "very sparse" vegetation cover according to HIGAP land cover map within each substrate age by moisture class combination.

Age by moisture combinations with more than 75% of their area being sparsely vegetated are designated as young substrates and are shown in bold. Areas within zone 6 and 7 (Moderately Wet and Very Wet) and in the youngest substrate age class (<200 years) are also considered young substrate areas since their vegetation is limited in species composition. In addition, areas within moisture zone 1 (arid) and in the 3,000 to 5,000 year old substrate age class, while being only 73% covered in sparse vegetation, are also nominally included.

Age (in years)	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	Zone 6	Zone 7
< 200	**94**	**99**	**98**	**95**	**76**	**58**	**7**
200-750	**92**	**99**	**84**	**82**	39	9	5
750-1,500	**63**	**96**	**75**	58	17	3	0
1,500-3,000	**79**	**91**	58	38	10	2	0
3,000-5,000	**73**	67	29	20	4	1	0
5,000-10,000	29	54	22	11	2	3	1
> 10,000	6	15	6	6	2	2	2

Table 5. Biogeographic Regions for case study species.

For each species, “X” indicates that there is a record for that species from the given biogeographic region.

	Niiahu	Kauaʻi	Oʻahu - Waianae	Oʻahu - Koolau	Molokaʻi - West	Molokaʻi - East	Lānaʻi	Maui - West	Maui -East	Kahoolawe	Hawaiʻi - Kohala	Hawaiʻi – Mauna Kea	Hawaiʻi - Hualalai	Hawaiʻi - Kīlauea	Hawaiʻi – NW Mauna Loa	Hawaiʻi – NE Mauna Loa	Hawaiʻi – SE Mauna Loa	Hawaiʻi – SW Mauna Loa
Sadleria cyatheoides		X	X	X		X	X	X	X		X	X	X	X	X	X	X	X
Erythrina sandwicensis	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Cyanea tritomatha											X	X				X	X	
Chamaesyce kuwaleana			X	X														

Table 6. Habitat parameters for case study species.

	Lower Elevation Limit (m)	Upper Elevation Limit (m)	Lower Moisture Limit (zone)	Upper Moisture Limit (zone)	Lower Coastal Moisture Limit (zone)	Upper Coastal Moisture Limit (zone)	Upland Dry Zone	Young Lava Substrates
Sadleria cyatheoides	5	2348	4	7	4	7	X	
Erythrina sandwicensis	0	854	1	4	1	5		X
Cyanea tritomatha	350	1524	6	7	0	0		
Chamaesyce kuwaleana	10	500	2	3	2	3		

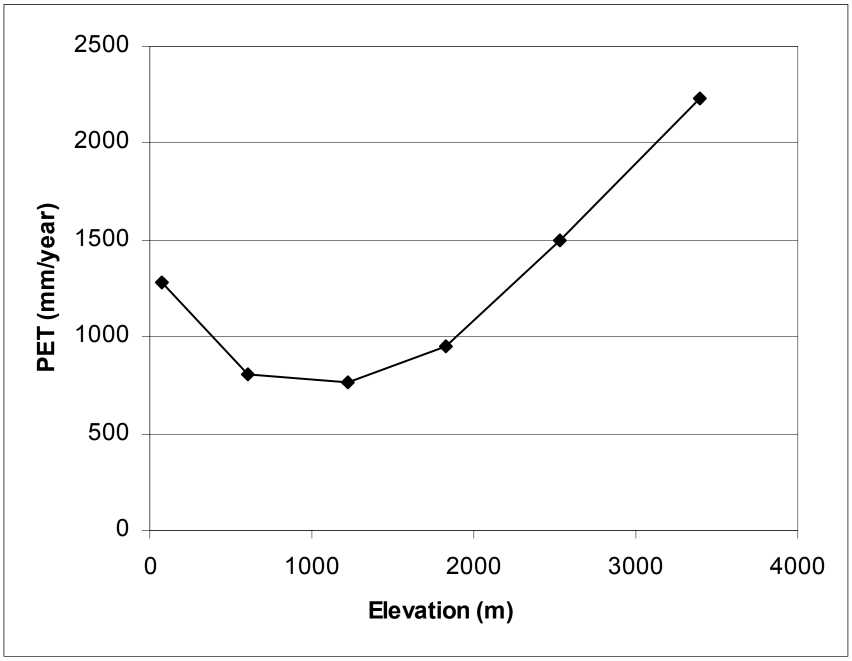

Figure 1. Elevational profile of potential evapotranspiration derived from Bean et al. (1994)

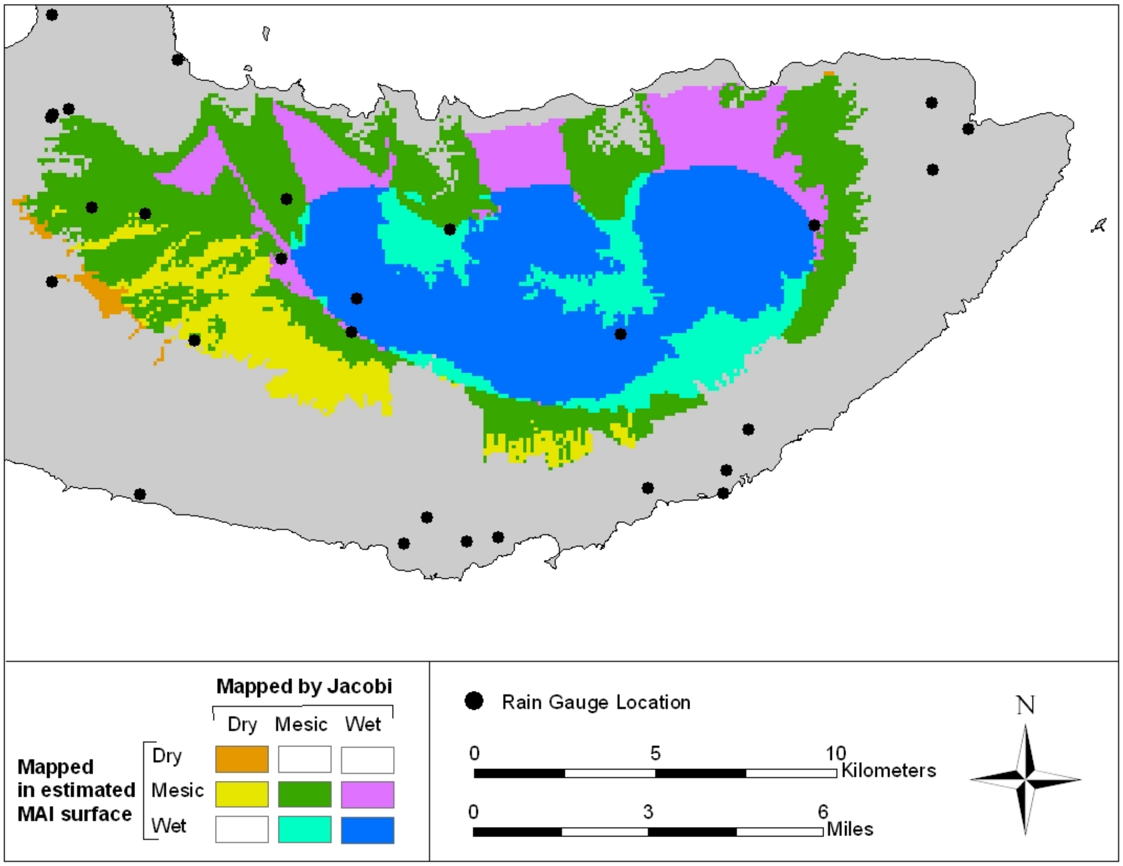

Figure 2. Comparison of estimated Moisture Availability Index surface with Mapped Vegetation from Jacobi (1989).
Areas of agreement between the two are shown in orange (for Dry areas), green (for Mesic areas), and Dark Blue (for Wet areas). Areas of disagreement are colored according to which combination of designations that were given. Areas in gray were not covered by Jacobi's maps. Locations of rain gauges are shown for reference.

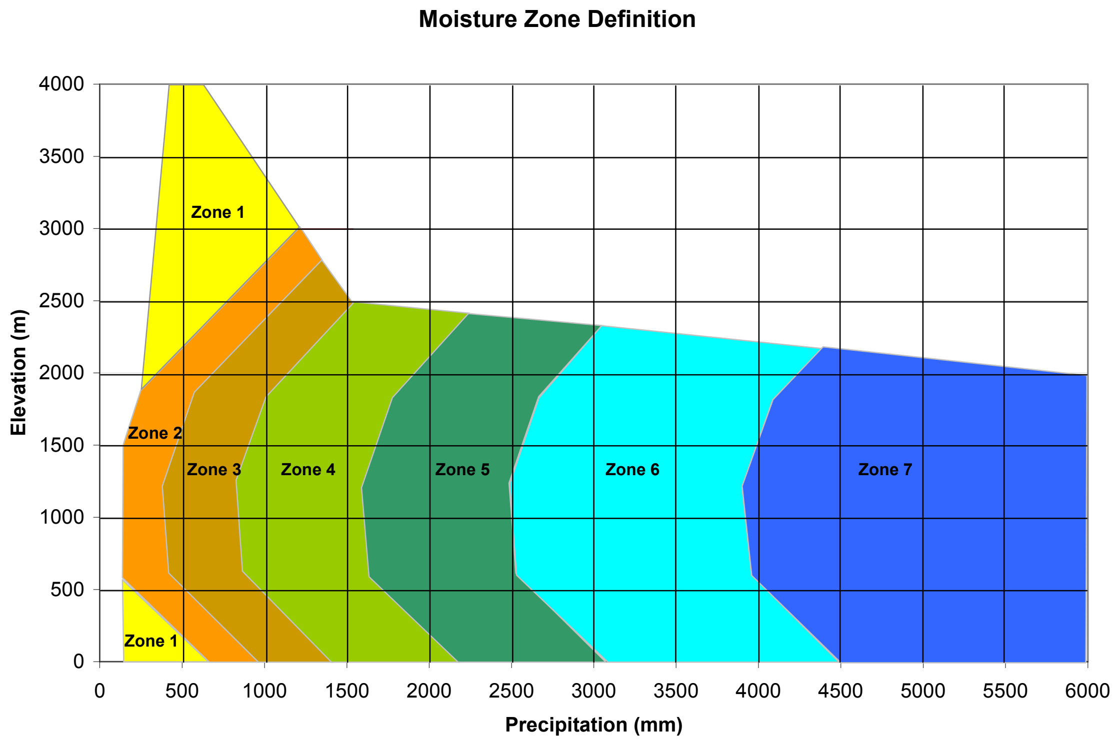

Figure 3. Approximate precipitation and elevation values used to define the seven moisture zones.

Definition of zones is as follows: Zone 1, Arid; Zone 2, Very Dry; Zone 3, Moderately Dry; Zone 4, Seasonal Mesic; Zone 5, Moist Mesic; Zone 6, Moderately Wet; Zone 7, Very Wet. Sites in middle elevations may be in wetter moisture zones than areas with comparable rainfall at higher or lower elevation. This as a function of depressed PET in middle elevations (Figure 1) and results in higher available moisture. Zonal boundaries only extend to precipitation-elevation combinations that exist; for example there is no location above 2300 m that receives more than 3000 mm. Note that the drier zones are more narrowly defined; this is partly because areas receiving little rainfall are spatially extensive and thus more finely subdivided, and partly because these are critical moisture thresholds affecting plant species ranges.

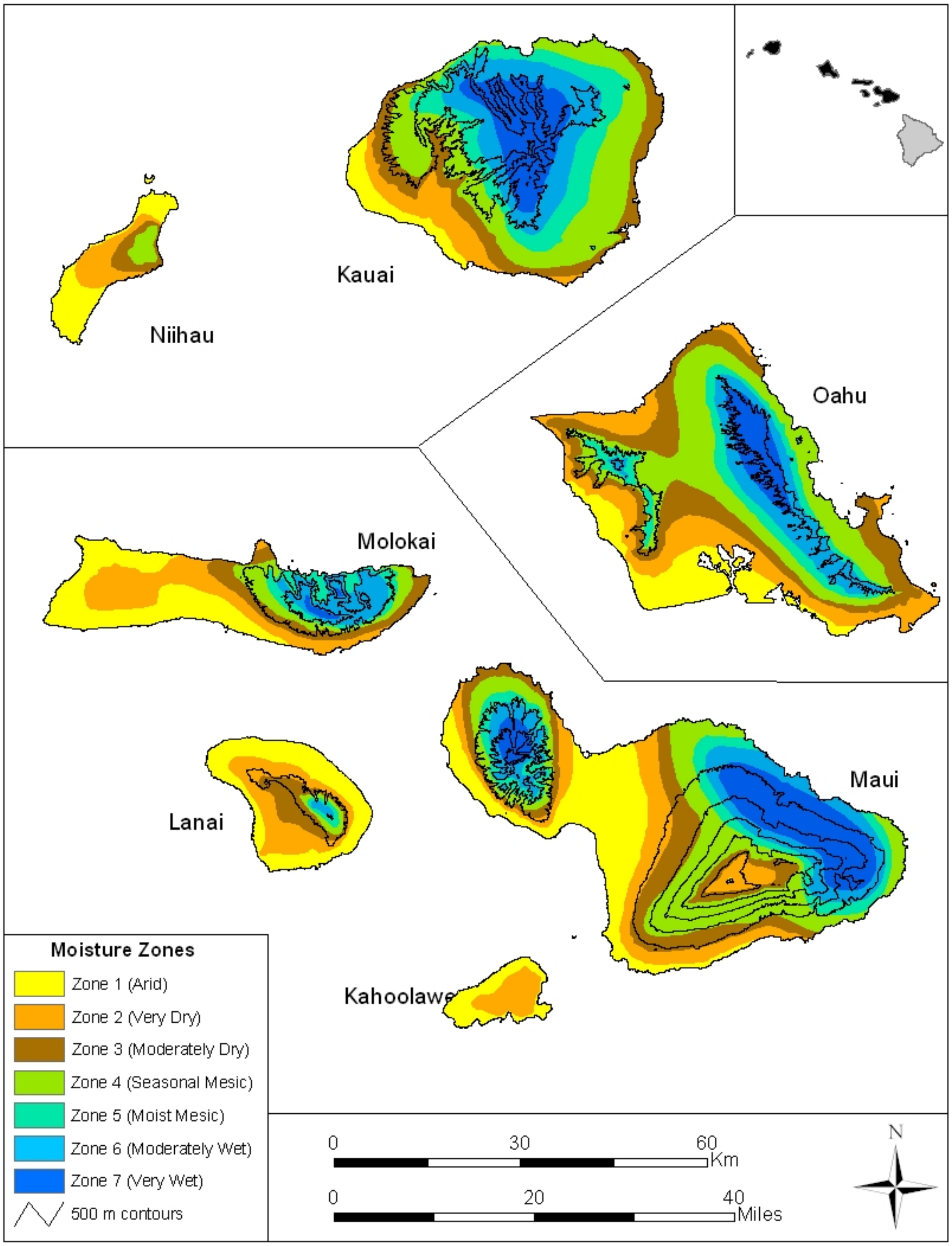

Figure 4. Moisture Zones on Ni`ihau, Kaua`i, O`ahu, Moloka`i, Lāna`i, Maui and Kaho`olawe.

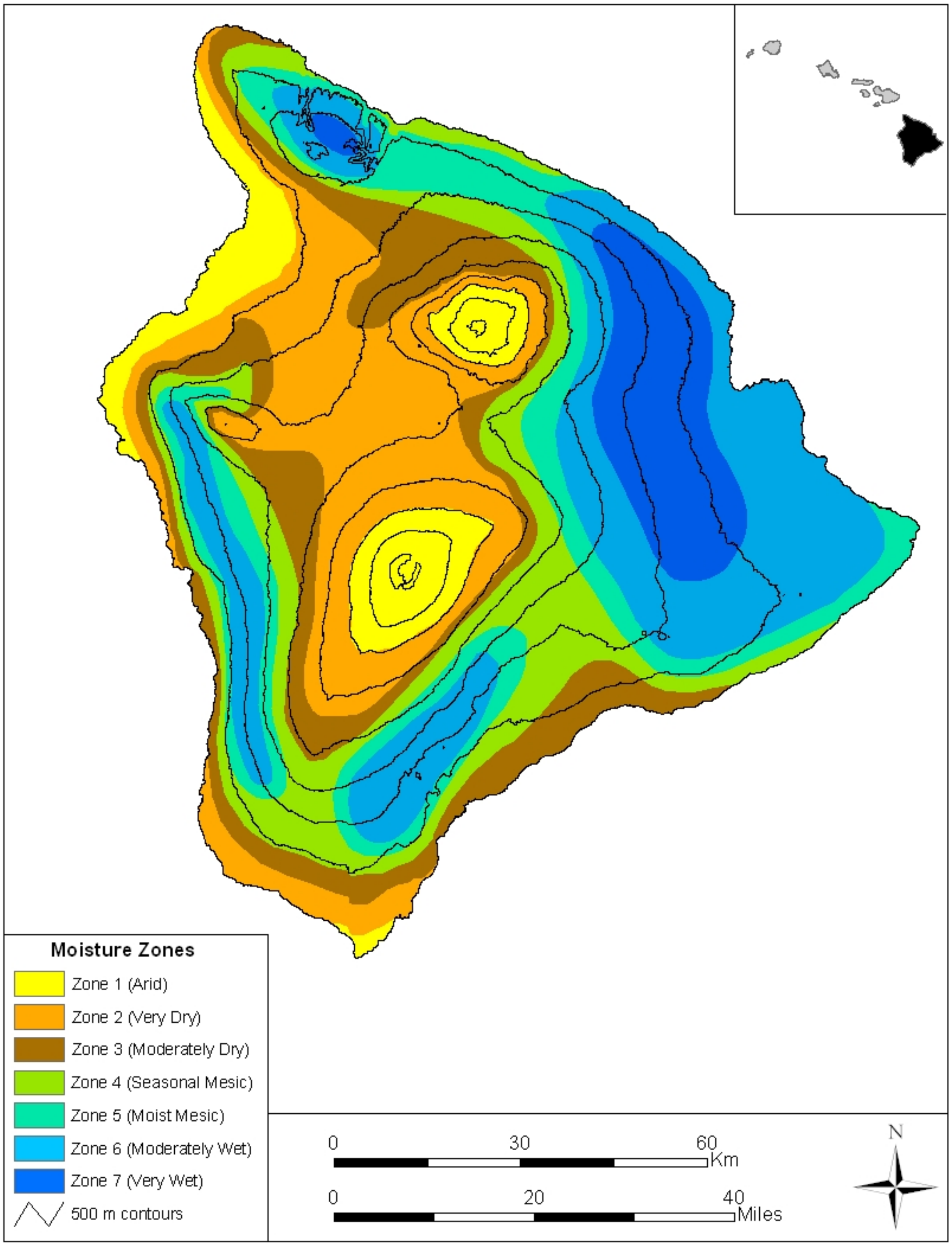

Figure 5. Moisture Zones on the island of Hawai`i.

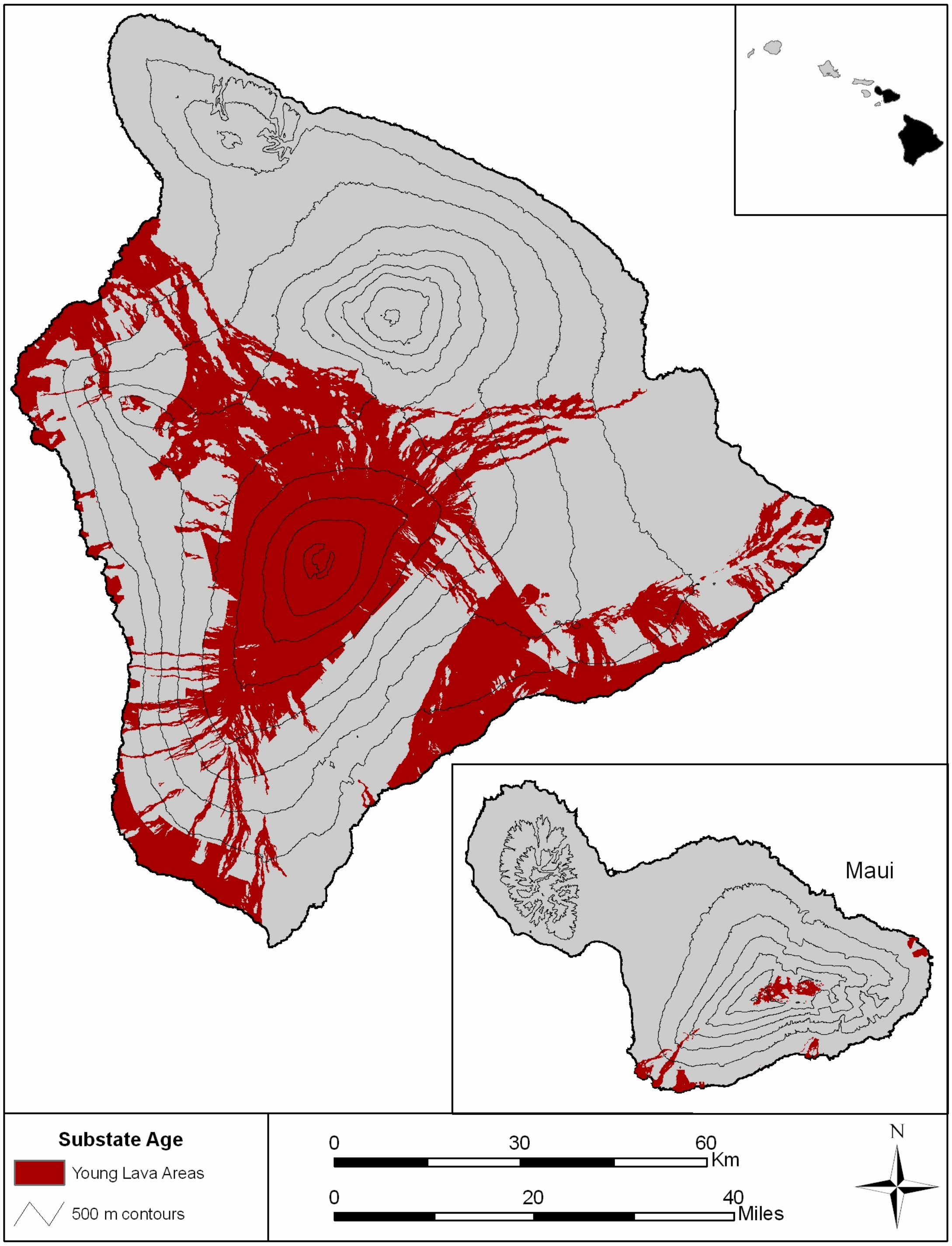

Figure 6. Young lava substrates on the islands of Maui and Hawai`i.

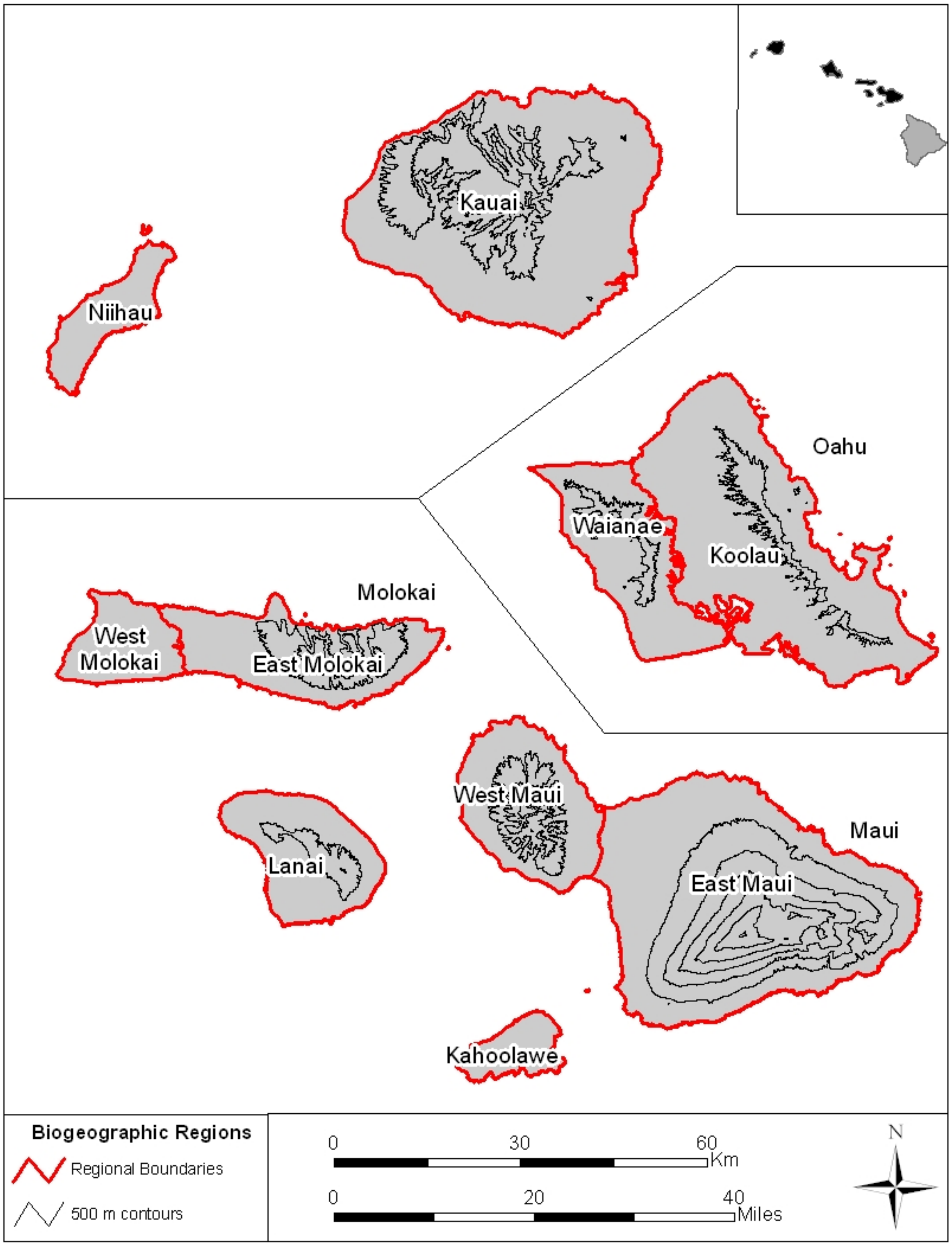

Figure 7. Biogeographic Regions on Ni`ihau, Kaua`i, O`ahu, Moloka`i, Lāna`i, Maui and Kaho`olawe.

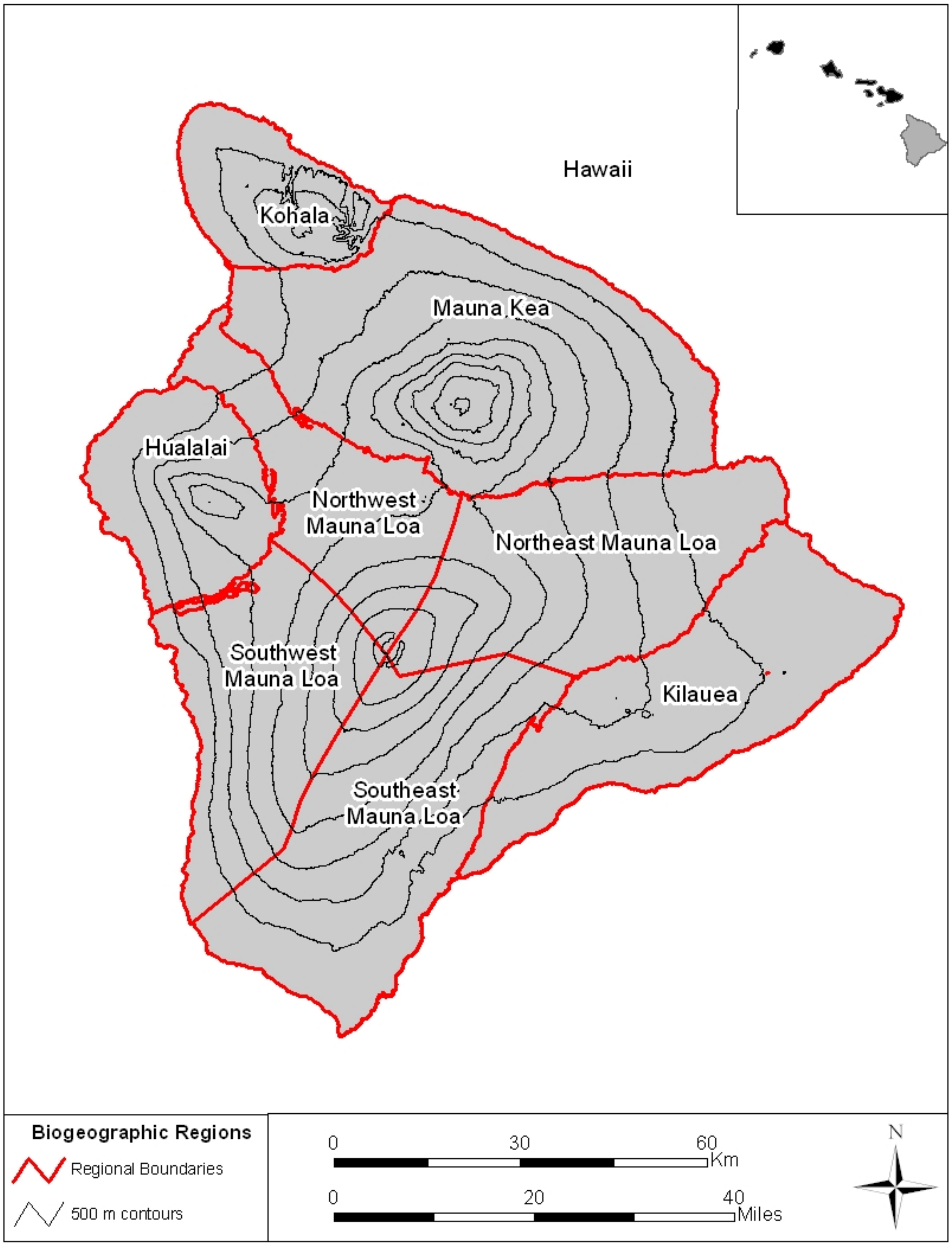

Figure 8. Biogeographic Regions on the island of Hawai`i.

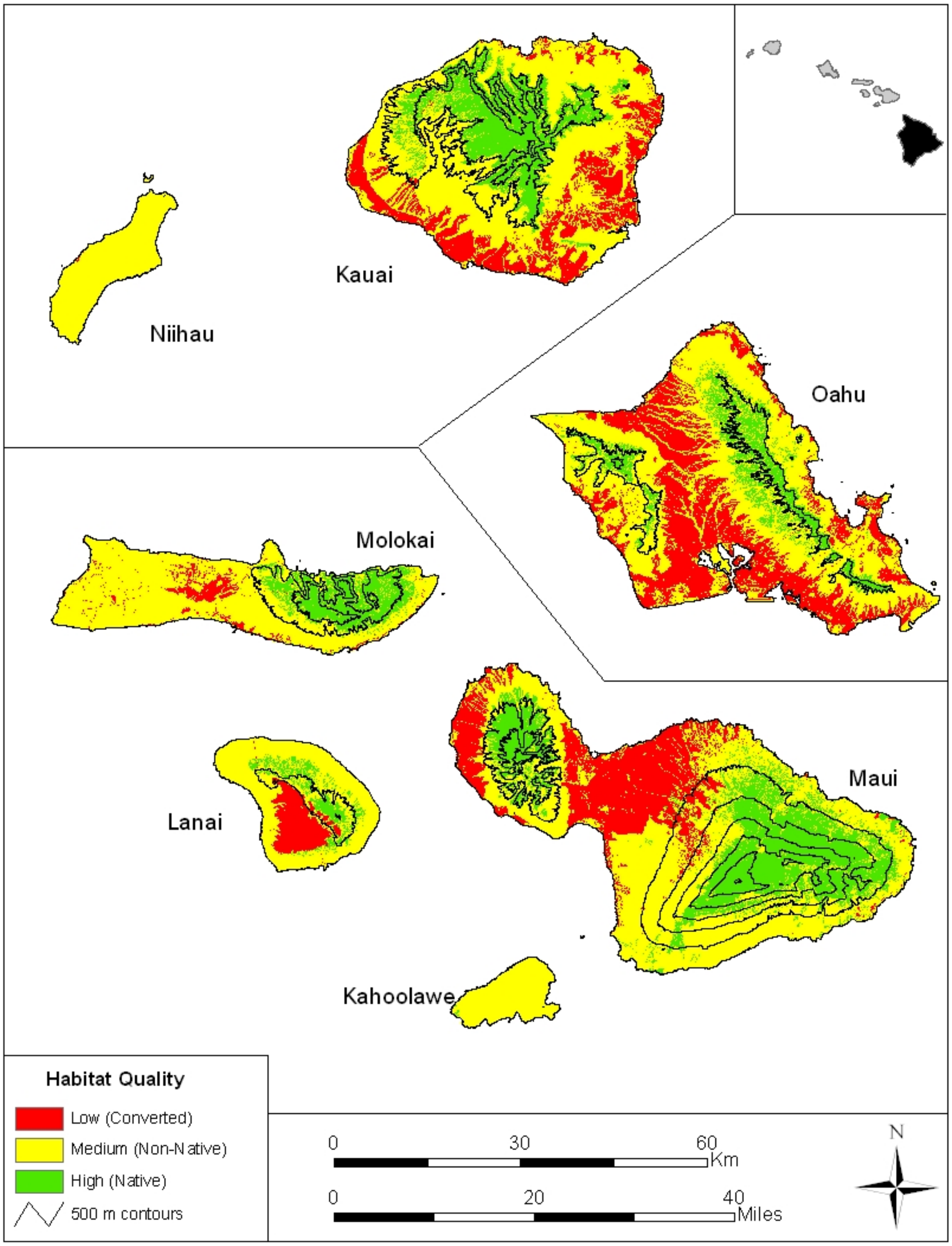

Figure 9. Habitat Quality on Ni`ihau, Kaua`i, O`ahu, Moloka`i, Lāna`i, Maui and Kaho`olawe.

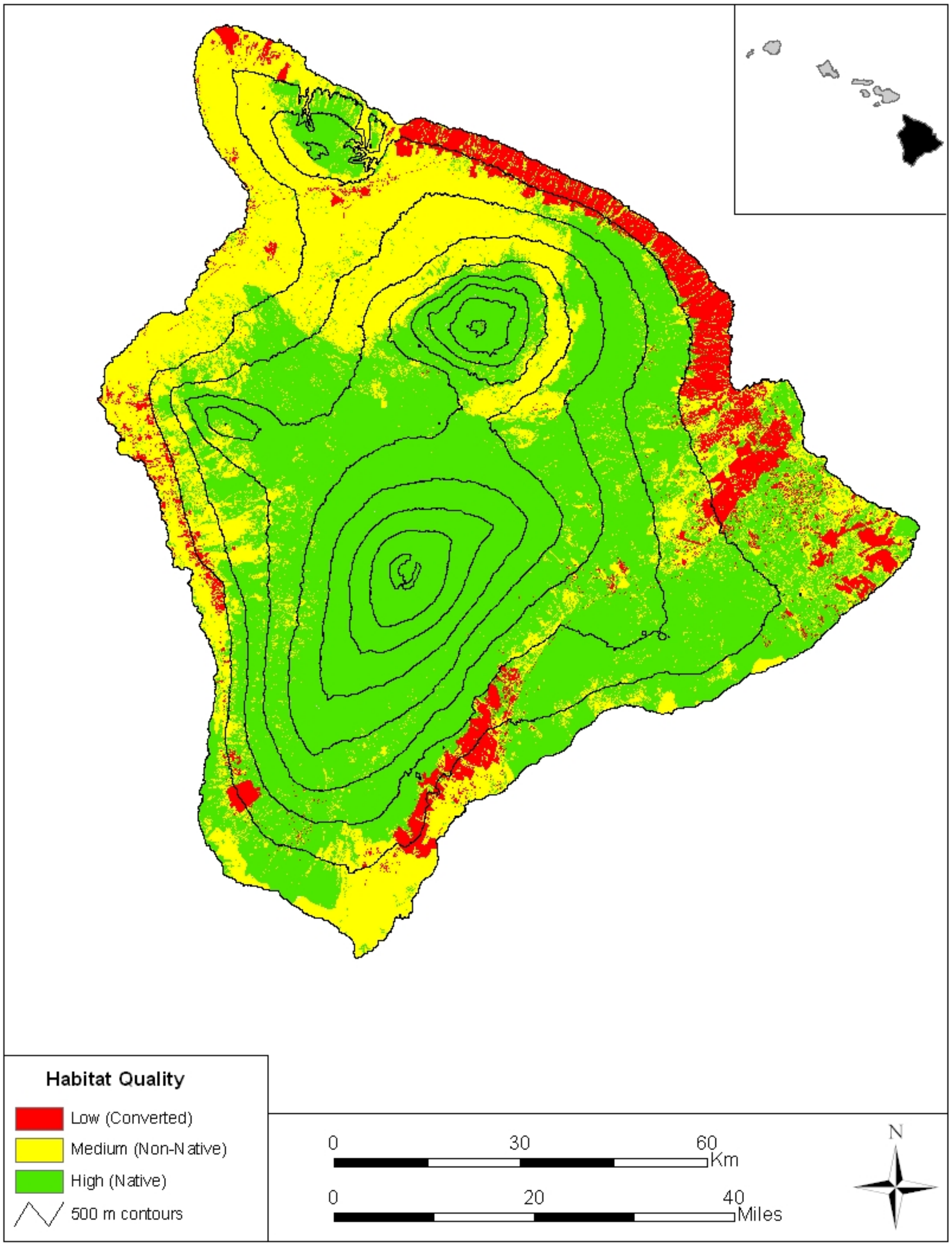

Figure 10. Habitat Quality on the island of Hawai`i

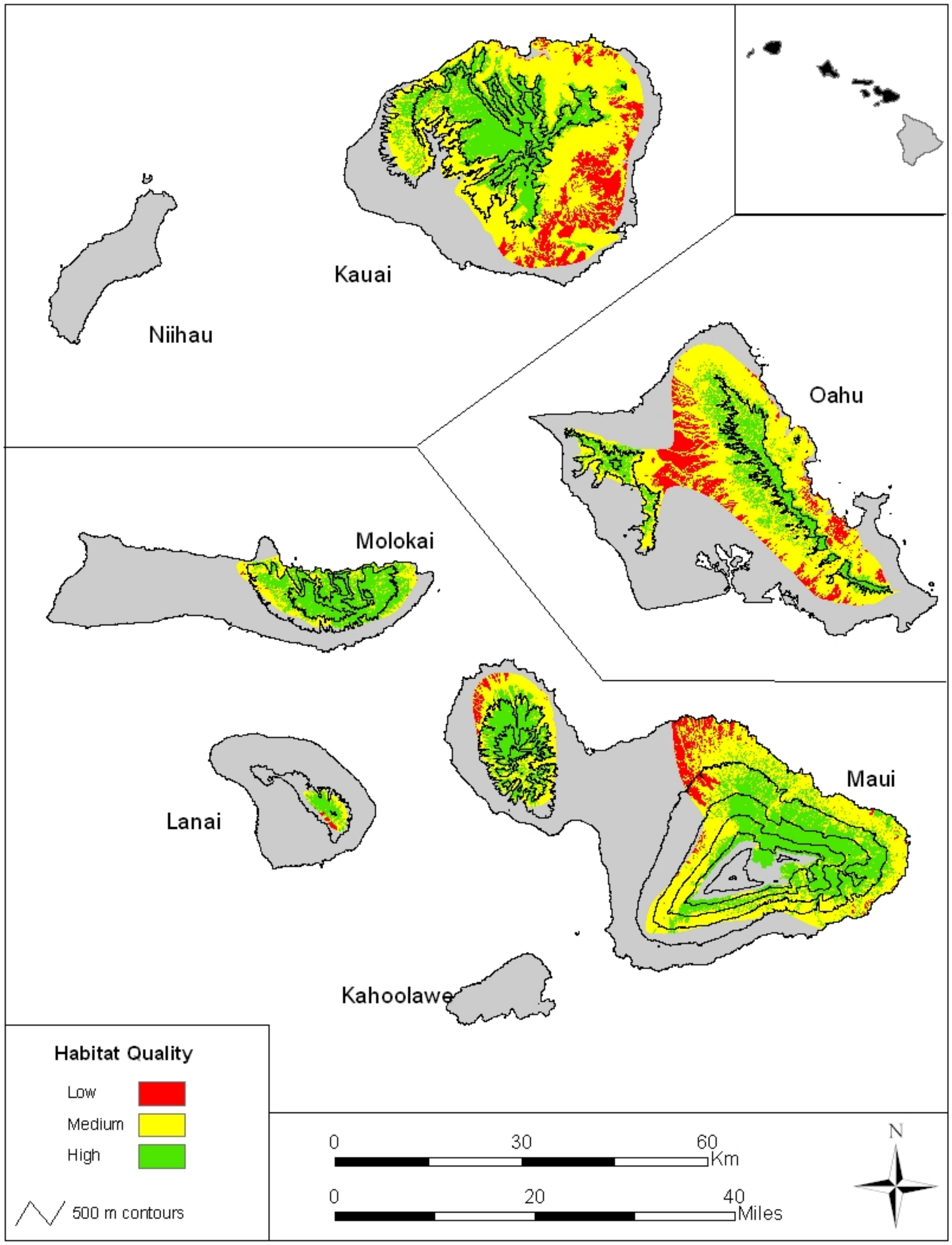

Figure 11. Range of *Sadleria cyatheoides* on the islands of Ni`ihau, Kaua`i, O`ahu, Moloka`i, Lāna`i, Maui and Kaho`olawe.
This species is known from Mesic and Wet habitats (moisture zones 4 through 7) across a wide elevational range on many islands. It also extends into dryer areas in upper elevations on Maui and Hawai'i (the Upland Dry zone), but does not extend into drier habitats at lower elevations. The status of habitat for this species reflects a commonly seen pattern for upland Wet/Mesic species where much of the estimated natural range remains in high or medium quality habitat.

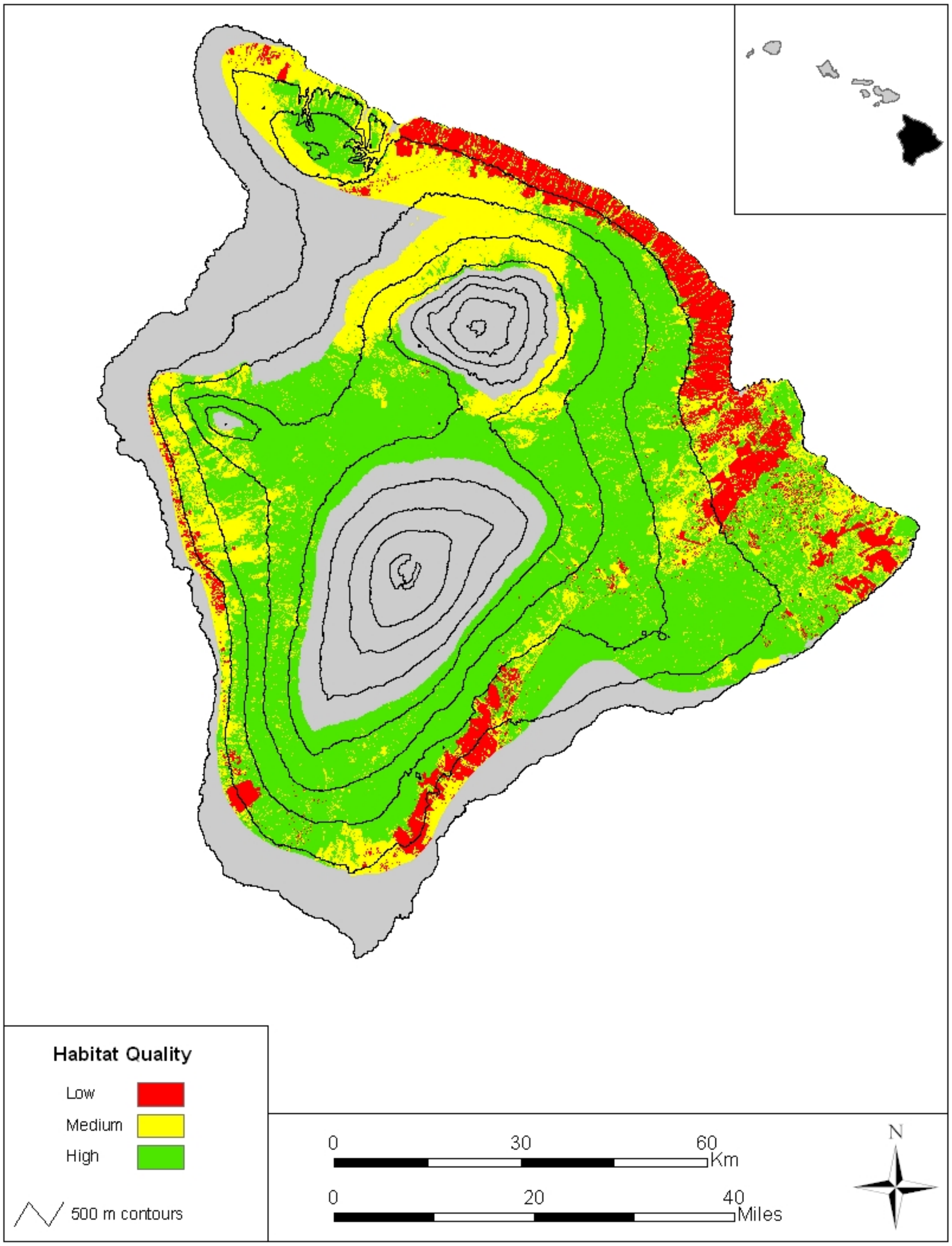

Figure 12. Range of *Sadleria cyatheoides* on the island of Hawai`i.

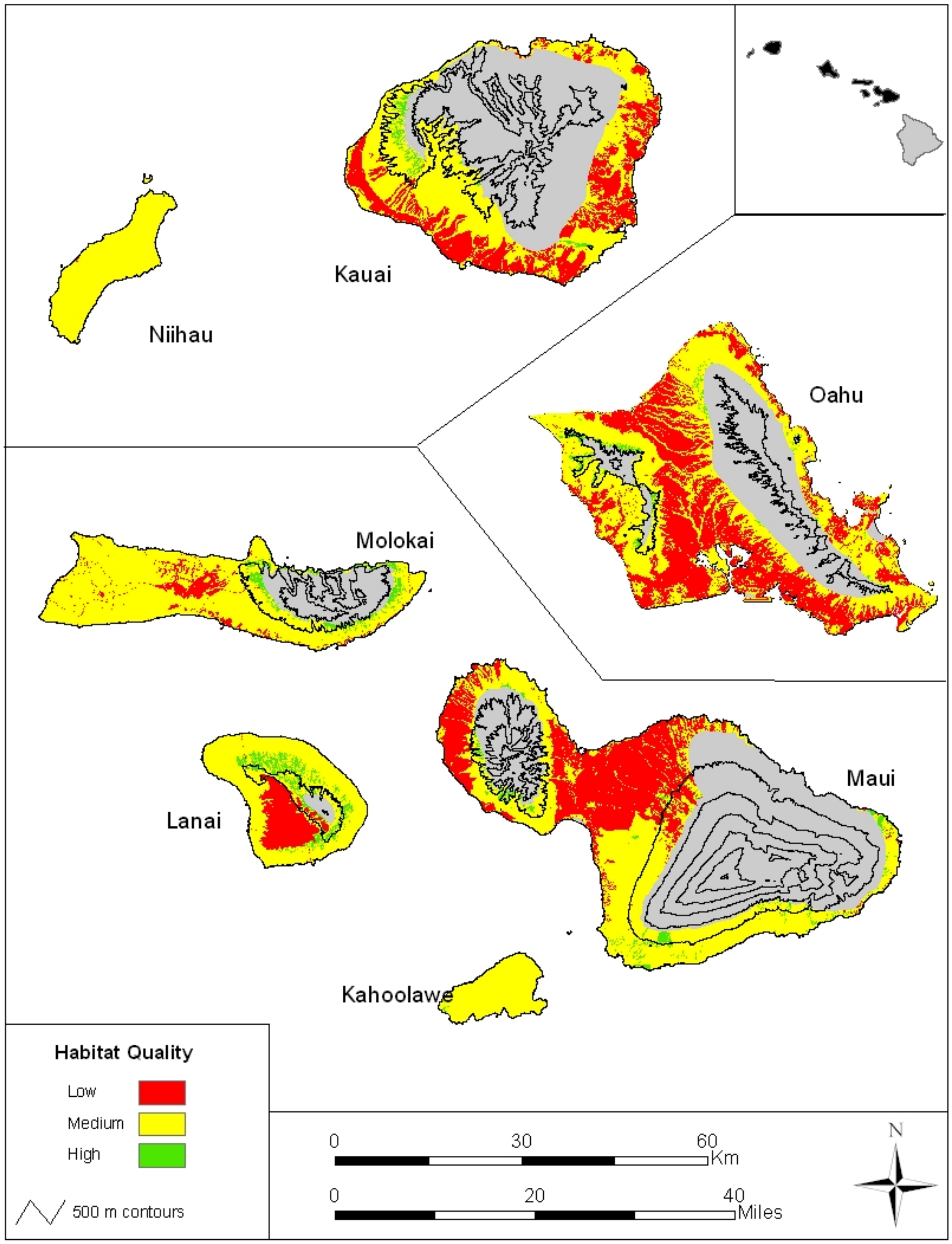

Figure 13. Range of *Erythrina sandwicensis* on Ni`ihau, Kaua`i, O`ahu, Moloka`i, Lāna`i, Maui, and Kaho`olawe.
This species is known from Arid to Seasonal Mesic habitats (moisture zones 1 through 4) at low elevations on many islands. It also extends into Moist Mesic areas (zone 5) along the coast, but not inland. The status of habitat for this species is typical for species restricted to drier lowland areas where much of the estimated natural range is medium or low quality habitat.

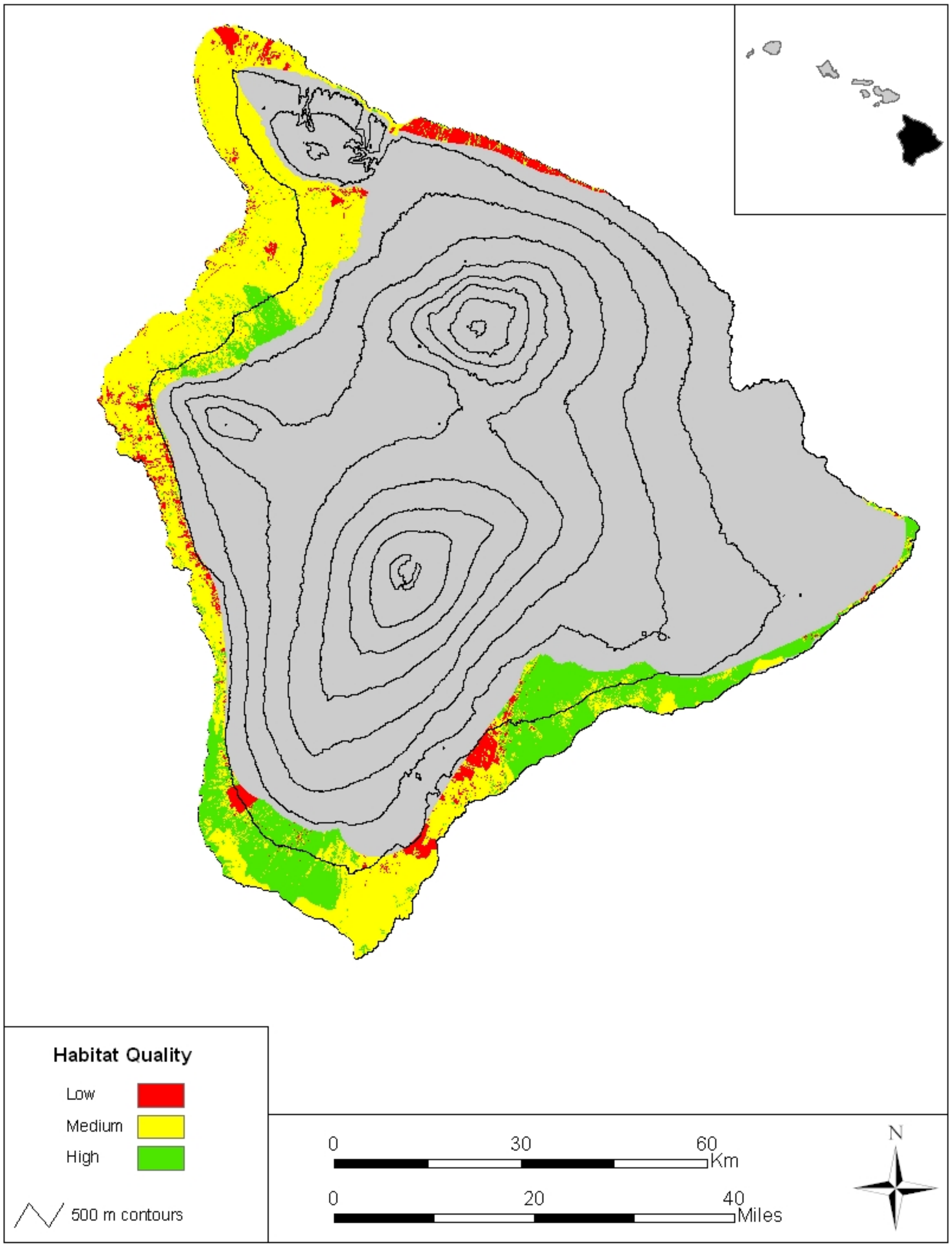

Figure 14. Range of *Erythrina sandwicensis* on the island of Hawai`i.

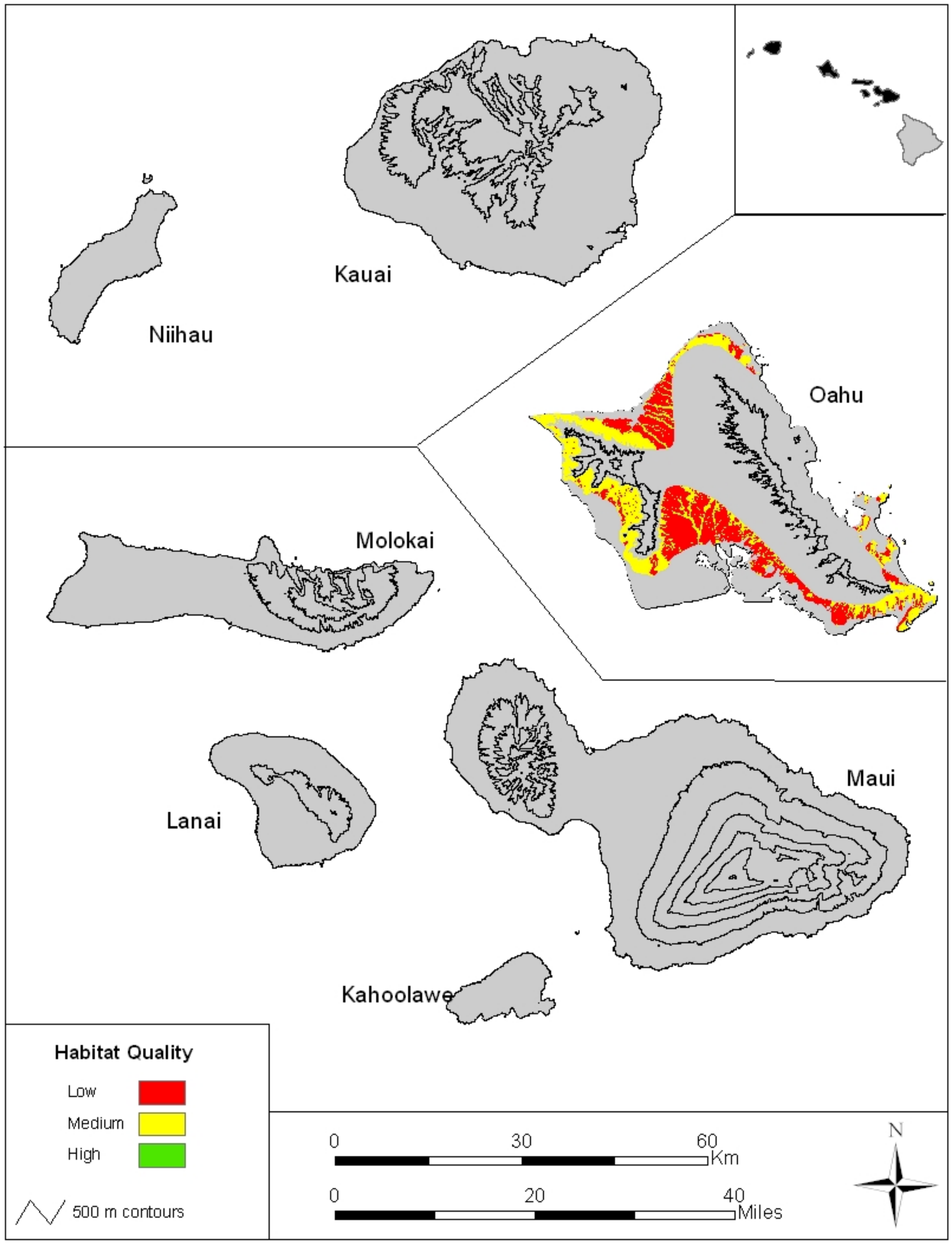

Figure 15. Range of *Chamaesyce kuwaleana.*
Like a majority of native Hawaiian plants, this species is considered rare in being restricted to a single island and has a narrow range of climate zones and elevations. It is additionally rare because the majority of its estimated natural range lies in low quality habitat. This suggests that it has been greatly reduced in extent, but also indicates plausible areas where populations of the species might be restored.

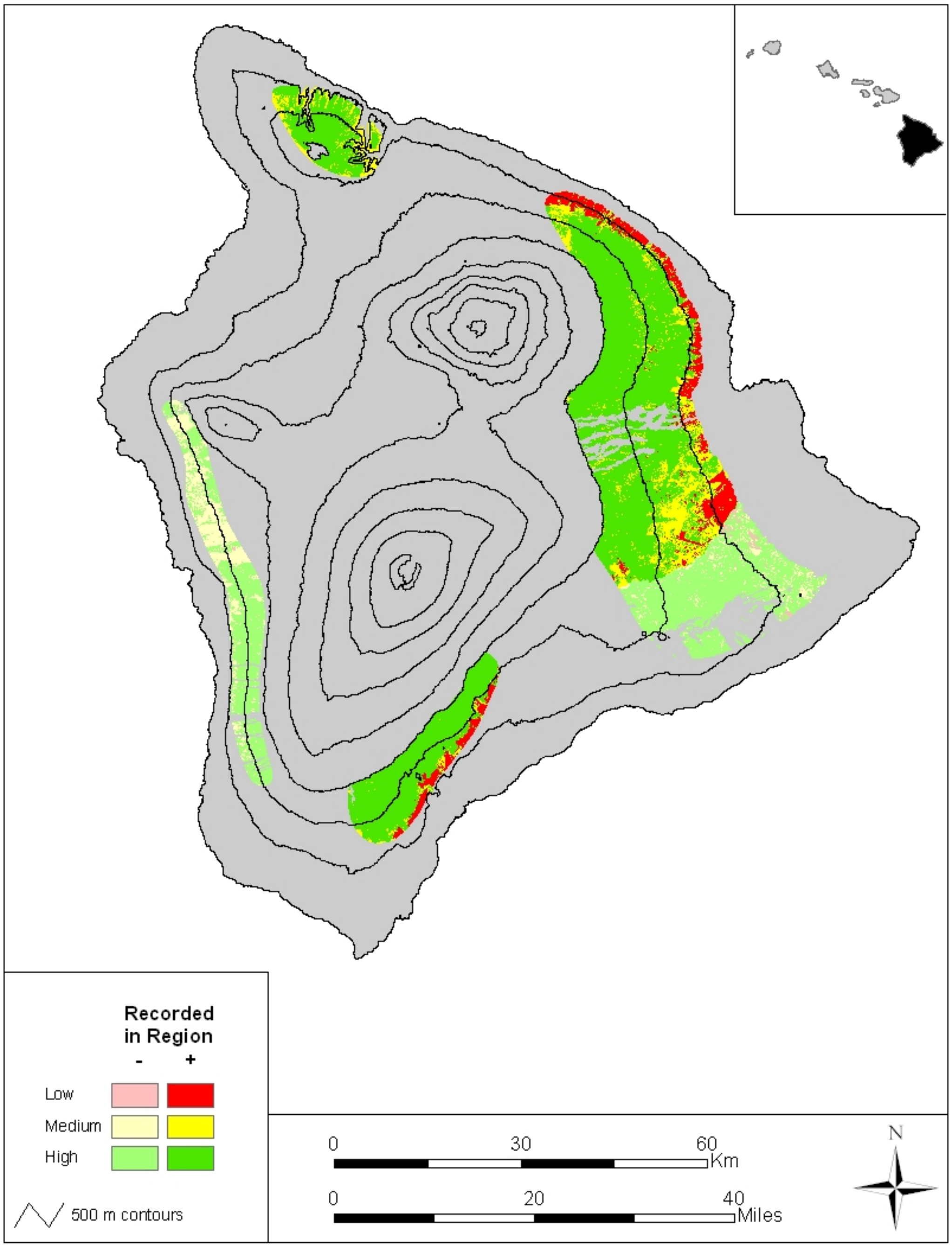

Figure 16. Range of *Cyanea tritomantha*.r species restricted to a single island, this one is also known from only some biogeographic regions on that island. Many species exhibit this pattern where a portion of the island may have appropriate habitat, but the species has never been recorded there (note the lighter color depicting regions of the island where it has not been recorded). In some cases the species is naturally restricted, in other cases there has been insufficient sampling in its potential habitat.