Wetlands (2014) 34:335–350
DOI 10.1007/s13157-013-0501-2

ARTICLE

Wetland Loss in Hawai'i Since Human Settlement

Charles B. Van Rees · J. Michael Reed

Received: 23 July 2013 / Accepted: 20 November 2013 / Published online: 6 December 2013

Abstract Wetland inventories are essential to understanding human effects on wetland distributions, estimating rates of wetland loss and setting recovery goals for endangered species. Wetlands in the Hawaiian archipelago (U.S.A.) support human water demands for agriculture, a rapidly expanding urban population, and 222 federally listed threatened or endangered plants and animals. The only published assessment of wetland loss for Hawai'i was done in 1990, before significant advances in Geographic Information Systems (GIS) and computing technology. We estimated wetland loss on the 5 main Hawaiian Islands since human settlement using the National Wetlands Inventory, hydric soil maps, rainfall, and topographic data. We used the Topographic Wetness Index (TWI) to estimate pre-settlement wetlands in sites where hydric soil evidence was unavailable or unreliable. We found that TWI makes a useful complement to hydric soil evidence in estimating wetland loss in highly developed areas. We estimate statewide wetland loss at 15 %, compared to 12 % from the 1990 estimate, ranging from 6 to 8 % loss on Maui, Moloka`i, Hawai'i, and Kaua`i to 65 % loss on Oahu, the most developed of the islands. The majority of wetland losses occurred in coastal areas where 44 % of wetlands have been lost, while only 3 % were lost at higher elevations.

Keywords Wetland loss · Wetland inventory · Hawaiian Islands · Waterbirds · Topographic wetness index · Hydric soils

Electronic supplementary material The online version of this article (doi:10.1007/s13157-013-0501-2) contains supplementary material, which is available to authorized users.

C. B. Van Rees (✉) · J. M. Reed
Department of Biology, Tufts University, 163 Packard Ave., Medford, MA 02155, USA
e-mail: charles.van_rees@tufts.edu

Introduction

The first widely publicized assessment of the ecological services that wetlands provide placed their global value at approximately US$4.8 trillion per year (Costanza et al. 1997). Although the exact value of wetlands is uncertain and context dependent (Turner et al. 2000; Woodward and Wui 2001), it is well established that wetlands provide a wide variety of valuable ecological services (Barbier et al. 1997; Zedler and Kercher 2005; Ghermandi et al. 2010; Blackwell and Pilgrim 2011; de la Hera et al. 2011; Horowitz and Finlayson 2011). This makes wetland losses particularly significant. It is estimated that during the 20th century, more than 50 % of wetlands in parts of North America, Europe, and Australia were lost to anthropogenic landscape change (OECD/IUCN 1996; Millennium Ecosystem Assessment 2005). Information regarding the extent and rate of loss of wetlands is lacking throughout much of the world and warrants further efforts (Scott 1993; Finlayson et al. 1999, Finlayson and Davidson, 1999). Wetland inventories are important in landscape and water planning, and they can play an important role in documenting and anticipating conflicts over water resources (Ellison 2009; Griffin 2012), as well as the losses of wetland-dependent ecosystems and their associated species and ecological services (Jones and Hughes 1993).

Consequently, our goal was to estimate wetland loss from the main islands of the Hawaiian archipelago, a biodiversity hotspot with high rates of extinction due to human activities, introduced diseases, and non-native invasive species (e.g., Ziegler 2002; Reed et al. 2012). The Hawaiian Islands are a volcanic archipelago in the central Pacific Ocean, distributed across 2,450 km. The Hawaiian Islands are the most isolated land mass on the planet, situated 3,800 km from North America and nearly twice that distance from East Asia and Australia. The islands have a wide variety of wetlands, ranging from small, anchialine pools along the coast to large, high-elevation bogs (Stone 1989a). The most extensive types of wetlands on the main Hawaiian Islands (Kaua'i, O'ahu, Moloka'i, Maui, Hawai'i) are freshwater lowland marshes and montane wet forests and bogs (U.S. Fish and Wildlife Service, National Wetlands Inventory data 2010; U.S. Army Corps of Engineers 2012). Despite abundant orographic rainfall, precipitation is unevenly distributed between the windward and leeward sides of the younger, higher elevation islands. Average rainfall on the windward sides of these islands ranges from 2.5 to 7.6 m annually, while the leeward sides of Hawai'i and Maui average only 0.25 m (Meier et al. 1993). This uneven distribution, coupled with intense population growth and water supply uncertainty over the last century, has given rise to competition and conflict over water resources (Gopalakrishnan et al. 1996, 2007; Ridgley and Lumpkin 2000; Miike 2004; Liu 2007; Sheild et al. 2009; Lasky 2010). Contemporary water conflicts on Hawai'i are the product of not only climatic factors but also the area's historical context.

Prior to European arrival, Polynesian colonists managed water extensively through stream diversions and wetland alteration for traditional taro (*Colocasia esculenta*) agriculture (Kirch 2000; Müller et al. 2010). Water diversion and groundwater use increased exponentially with the arrival of Europeans and the advent of plantation agriculture in the 18th and 19th centuries and much of the landscape was converted to sugar cane, pineapple, and rice agriculture (Coulter 1933; Handy et al. 1972; Meier et al. 1993; Wilcox 1996). The decline in the relative economic importance of plantation agriculture after World War II coincided with rapid human population growth and urban development, which had the cumulative effect of extensive wetland loss in Hawai'i, especially on O'ahu (Giambelluca 1986; Meier et al. 1993). For example, the largest wetland in Hawai'i was in the Mana region (central west coast) of Kaua'i, and it was lost to water diversions for sugar cane (Swedberg 1967; Shallenberger 1977).

Currently, basal aquifers are the primary source of freshwater in Hawai'i (Liu 2007), and continued human population growth increases ground-water withdrawals (e.g., Ridgley and Giambelluca 1991; Oceanit et al., 2007) while changes in land use patterns are reducing groundwater recharge (Giambelluca 1986). The uncertainty of Hawaii's water security may give rise to conflicts between societal and ecological needs for fresh water, further threatening Hawaii's remaining wetlands. Water security might be further compromised by global climate change; Hawaiian wetlands and groundwater resources will be affected by shifts in precipitation and temperature regimes, and by sea level rise (Nicholls et al. 1999; Chu et al. 2010; Keener et al. 2012). In contrast, the collapse of the sugarcane and pineapple industries on the Hawaiian Islands in the 1990s has created an unprecedented opportunity for reallocating water and land resources, addressing water scarcity, and for wetland restoration (Ridgley et al. 1997; Ridgley and Lumpkin 2000; Derrickson et al. 2002; Sheild et al. 2009). Accurate information on wetland distributions before human settlement would help inform allocation decision-making and resolution of water conflicts.

The only published estimate of wetland loss in Hawai'i is found in Dahl (1990), which cited an assessment by the United States Fish and Wildlife Service (by A. Yuen, unpubl. data) estimating that Hawai'i had lost 12 % of its wetlands since 1780. Although the analysis by Yuen no longer exists (A. Yuen, and numerous others, pers. comm.), the results were summarized by Kosaka (1990 *in litt*.; available from the authors). This summary notes that all of the estimated wetland loss was from coastal and low-elevation areas (<~300 m), where 31 % of the wetlands were lost; no wetland losses were reported from higher elevations. The summary results from the 1990 study do not provide information specific to particular Hawaiian Islands, nor is information provided on data sources or methods used to analyze data. Island-specific data would be an important addition to any estimate of wetland loss for the Hawaiian Islands, because it is likely that loss varies greatly between islands due to differences in human population size and levels of urbanization. The 1990 study was completed before significant advances in computing and geographic information systems (GIS) technology, which have significantly improved the accuracy and rigor of studies of landscape change. In this paper we present an estimate of anthropogenic wetland loss for the five largest islands of the state of Hawai'i using newly available data and spatial analysis software to improve upon the estimates currently used for wetland management in Hawai'i. We used surveys by government agencies, remotely sensed images, a simple hydrological model, and GIS to estimate the extent of wetlands in Hawai'i in the absence of human activities, and compared this to a current estimate of wetland area to estimate wetland losses since human colonization.

Materials and Methods

Study Area

We estimated wetland losses for the islands of Hawai'i, O'ahu, Maui, Kaua'i, and Moloka'i; these are the main islands of Hawai'i, comprising 95.6 % of the land area and 97.5 % of the population of the state. The smaller islands of Lana'i and Ni'ihau were excluded because of insufficient or low-quality data. We estimated wetland cover before Polynesian colonization using inventories of existing wetlands, soil survey data, and hydrological models to simulate the distribution of wetlands prior to anthropogenic disturbance. We followed the wetland definition used by the U.S. National Wetlands

Inventory (Federal Interagency Committee on Wetland Delineation 1989), but excluded deepwater marine habitats included in National Wetlands Inventory maps. This definition includes wetlands that are typical for volcanic Pacific islands, including depressional wetlands, sloped marshlands, hanging bogs, high elevation montane bogs, forested wetlands, riverine wetlands, and salt- and mud-flats (U.S. Army Corps of Engineers 2012). To simplify analysis, we excluded small offshore islands, whose contribution to wetland extent was considered negligible, and where human alterations that would affect hydrology have been minimal.

Data Sources

We downloaded National Wetlands Inventory (NWI) data (U.S. Fish and Wildlife Service 2010) using the U.S. Fish and Wildlife Service's wetland mapper tool (http://www.fws.gov/wetlands/Data/Mapper.html) for all of Hawaii's main islands. NWI maps were used as the primary data source in estimating current wetland extent, and as a reference for estimating the distribution of pre-settlement wetlands. We acquired data layers on hydric soils for O'ahu, Maui, Kaua'i, and Moloka'i from the Natural Resources Conservation Service (NRCS) Soil Data Mart (http://soildatamart.nrcs.usda.gov/), which included tabular data updated in 2012 and survey data collected in the early 1970s. The original data for the island of Hawai'i (The Big Island) was incorrect at the time of first analysis, and so new hydric soil data were downloaded in 2013 through the NRCS Web Soil Survey (http://websoilsurvey.sc.egov.usda.gov/App/HomePage.htm) and used for all subsequent analyses We used hydric soils as evidence of pre-settlement wetlands, as in Tiner (2005) (see also Dahl 1990; Moorhead and Cook 1992; Tiner and Bergquist 2003). Hydric soils, soil types that show physical and chemical signs of periods of anoxia and inundation with water, can persist in the environment after alteration of the landscape and hydrological regime, and hence are often used as indicators of lost wetlands (Moorhead 1991). We also used hydric soil data to detect portions of current wetlands not mapped in NWI surveys.

In certain cases, (for example in heavily developed, altered landscapes, or in areas with impervious cover), hydric soil data can be missing (e.g., landcover impedes sampling, as with parking lots) or misleading (e.g., where soil has been altered, removed, or replaced). These instances are most common in urban areas, in which case, hydric soils may not accurately indicate the presence of pre-settlement wetlands (Moorhead and Cook 1992). To account for this uncertainty, we applied the Topographic Wetness Index (TWI, Beven and Kirkby 1979), a hydrological model that uses elevation maps to predict where water would accumulate on a landscape, to gauge whether intensely developed areas were likely to have supported wetlands prior to development. TWI values are calculated using an area's elevation in relation to the surrounding landscape, its slope, and its catchment size. Because the relative (rather than absolute) elevation of an area with respect to its catchment and neighboring pixels is of primary importance to its TWI value, small changes in elevation due to development are not expected to significantly affect TWI values in developed areas. More specifically, wetland filling and development along the flat, coastal plains of Hawaiian Islands likely does not affect the movement of surface water downslope from the steep, nearby mountains. TWI has been shown to accurately predict hydrogeological processes affecting soil morphology (Gessler et al. 1995), and more recently to predict wetland bird assemblages in floodplains (Besnard et al. 2013). We calculated TWI using 10 m digital elevation models created in 2007 (Department of Commerce et al. 2007).

We used three additional data sources for visual analysis of land cover and truthing of wetland estimates. These included Landsat 7 ETM+ images (U.S. Geological Survey 2002), false-color Digital Orthophoto Quarter Quadrangle (DOQQ) images (U. S. Geological Survey, provided by the Hawai'i Geospatial Consortium and the State of Hawai'i GIS Program), and land-cover maps from NOAA's coastal change analysis program (NOAA Coastal Services Center 2000).

Pre-Settlement Wetland Cover Estimation

We processed hydric soil data using Soil Data Viewer 6.0 (Natural Resources Conservation Service 2011) and 6.1 (Natural Resources Conservation Service 2013) in ArcGIS 10.1 (ESRI 2012). Map units were classified as "All Hydric" (all soils in the map unit received a hydric rating), "Partial Hydric" (one or more components of the map unit received a hydric rating), "Unknown Hydric" (at least one component in the map unit received no rating, and at least one received a hydric rating) or "Not Hydric" (no components of a map unit received a hydric rating). In Soil Data Viewer 6.1, map units were classified as "All Hydric" (90–100 % of soil unit rated as hydric), "Mostly Hydric" (50–90 %), "Partially Hydric" (10–50 %) or "Not Hydric" (0–10 %).

All map units classified as "All Hydric" were classified as pre-settlement wetlands. All map units classified as "Mostly Hydric", "Partial Hydric", or "Unknown Hydric" were assumed not to be wetlands unless visual analysis, landcover datasets, or NWI maps showed evidence of a past wetland or that a wetland had been altered (e.g. water diversion channels, drainage canals, etc.). Hydric map units located on currently developed land were considered pre-settlement wetlands lost to development. Hydric map units associated with artificial wetlands (e.g. golf course water hazards, irrigation ponds) were included only if the surrounding landscape indicated historic wetland conditions and if the current hydric conditions were not due to artificial introduction of water (e.g. irrigation, diversion channels, etc.). Included hydric soil units were normally near existing wetlands and their extant hydric soils, or in an area with a high precipitation or TWI value. In all ambiguous cases map units were assumed to not represent pre-settlement wetlands.

We used NWI data to detect extant wetlands that were not recognized by hydric soil surveys. Wetland map features representing artificial wetlands were excluded from pre-settlement estimates. Artificial wetlands were identified by context (surrounding structures), shape, or local map information (e.g. area labeled as "sewage treatment plant"). Map features in undeveloped areas, or with no sign of human alteration to local hydrology, were included as pre-settlement wetlands under the assumption that natural wetlands existing in 2010 existed before human colonization and development.

TWI was calculated using 10 m Digital elevation models and the Geomorphology and Topology toolbox (Evans and Oakleaf 2011) in ArcGIS 10.1. To avoid overestimation of pre-settlement wetlands, TWI was run only on regions identified to have undergone high-intensity development that would preclude soil sampling or would give misleading soil results. Developed areas were identified using Landsat 7 ETM+ and DOQQ images in conjunction with NOAA landcover analyses, and were chosen based on criteria of housing density, amount of impervious cover, and evidence of water management, such as ditches and canals. These areas accounted for 5 % or less of the total land area of the islands analyzed, with the exception of O'ahu, where 18 % was considered highly developed. TWI values, which are unitless and can run from 0 (no water accumulation potential) to higher values with increasing accumulation potential, were calculated for 10 m×10 m pixels within each developed zone. There is no set TWI value associated with the presence of a wetland, so a cutoff value had to be determined for our study area. We did this by running TWI for each of our study islands to determine what values were associated with extant wetlands. We found that pixel values within an island were generally bimodally distributed, with one large peak in the lower end of the range (3–9), and a smaller, right-tailed peak at around 10–12. Pixels falling within the range of the second peak tended to fall within existing wetlands or areas with hydric soils. We therefore set threshold TWI values for the developed portions of each island at the peak of the higher mode of that island's TWI distribution, classifying all pixels with TWI beyond the thresholds as pre-settlement wetlands. The island of Hawai'i was an exception, in that the distribution of TWI values did not create a clear bimodal distribution, but rather a positively skewed unimodal distribution with a tail toward higher TWI values. For this island we chose a threshold value representing the 75th percentile of TWI values on the island, which contained values found in known runoff-fed wetlands. Because of the small proportion of developed land on the island of Hawai'i, our results were fairly insensitive to this threshold value.

Pre-settlement wetland coverage maps were then created by converting modified hydric soil and NWI maps to 10 m×10 m raster images, and combining these with TWI data using the raster calculator in ArcGIS. These maps were then reclassified so that all pixels indicated to be pre-settlement wetland by any of the three datasets were given a value of "1" and all other pixels given a value of "0". Calculations were done independently for each island.

Current Wetland Inventories

NWI maps were used as the main data source for current wetland estimates. Deepwater marine habitats were excluded for the analysis, but artificial wetlands were included to recognize where human development contributed to the total extent of current wetlands. For many existing wetlands, the spatial extent of associated hydric soils was beyond the limits of the wetland identified by the National Wetlands Inventory. In such cases, our methods would cause pre-settlement wetlands to appear larger than current wetlands simply because different evidence was used for each estimate. To avoid this potential bias toward wetland loss, we augmented NWI surveys with hydric soil data. All hydric soil map units corresponding to natural wetlands were identified as current wetlands. Natural wetlands were identified by shape, presence on undeveloped landscape, and distance from nearest development, as well as through maps of protected areas. On developed lands, hydric soil map units were counted as current wetlands if (a) they were adjacent to or apparently resultant from an existing wetland feature or (b) visual analysis indicated an extant wetland was possible in the region (water sources evident without diversion canals, houses, impervious cover, etc.). Hydric soil units on completely undeveloped areas without wetlands indicated by NWI data were considered current wetlands to avoid showing wetland loss where no development had occurred. In the few ambiguous cases, hydric soil units were included as current wetlands to maintain a conservative estimate of wetland loss. Ambiguous cases were often very small portions map units or portions of map units, and were found to account for negligible differences in results. NWI and hydric soil layers were converted to raster files and reclassified using the same processing steps as for pre-settlement data, then added to create a complete map of current wetlands.

Performance Evaluation of Thresholded TWI Model

We tested the wetland detection ability of the thresholded TWI model for each island by comparing raster output maps from the model to "truthing" maps of the current hydric soil and wetland areas. Truthing maps were created by rasterizing (10 m×10 m pixels) and combining hydric soil and wetland maps for each island. We then used the raster calculator function in ArcGIS to create a layer which displayed overlap and disparity between the TWI model's wetland estimations and existing wetland features for the entire landscape of each island. We calculated true positive rates as the percentage of actual wetland pixels (based on hydric soil and NWI data) classified as wetlands by the model, and true negative rates as the percentage of non-wetland pixels correctly classified as non-wetlands. We expected that the true-positive rate would be low for two reasons: 1) wetlands lost to human alteration and not detected by hydric soil evidence would be recognized as false positives, when in fact they represented true positives 2) wetlands that are sustained by coastal flooding, rainfall, or artificial means not related to topography (e.g. pumping, river diversion) would be recognized as non-wetlands, raising the false-negative rate and thus reducing true positive rate. A low true positive rate would lead to underestimates of wetland loss, which are in concordance with the conservative nature of this study. We repeated these evaluation methods using only low-elevation (<304 m) areas to eliminate montane and rain-fed wetlands, to test our hypothesis that non-surface-water fed wetlands were being poorly detected by the model.

Wetland Loss

Overall wetland loss statistics were calculated by subtracting pixel counts of current estimates from pre-settlement estimates. Maps of wetland loss distribution were produced by subtracting pre-settlement estimate images from current estimate images in the raster calculator. Inventories were subdivided by elevation category (coastal plains, elevation <304.8 m, vs. mid to high elevations, elevation >304.8 m), and values for loss in each elevation category calculated. These elevation categories were selected to allow direct comparison to the 1990 estimate of wetland loss in Hawai'i (Kosaka, *in litt*.)

Results

TWI Model Performance

TWI pixel values ranged from 0 to ~35 among all islands. Threshold TWI values used in this study for designating a developed area as having supported a pre-settlement wetland were: 9.85 for Hawai'i, 11.2 for O'ahu, Maui 11.0, Kaua'i 12.6, and 11.12 for Moloka'i. True positive and negative rates, as well as overall concordance of the thresholded TWI model are shown in Table 1. True positive rates were generally very low (between 6 and 40 %) for the entire landscape of each island, but doubled or nearly doubled for each island when excluding higher-elevation areas. True negative rates were high (80–85 %) for both whole-landscape and low-elevation analyses. False positive rates for each island (not shown) were low, 0.5–10 %.

Unsurprisingly, the thresholded TWI model was generally unable to predict the presence of wetlands created and sustained by water sources independent of natural surface water flow, such as coastal inundation, irrigation, and extremely high rainfall. This last category was important in high-elevation forested areas on the islands of Hawai'i and Kaua'i, which sustain hydric soil conditions despite steep slopes. The thresholded TWI model successfully identified several developed areas that were known a priori to have supported surface-water wetlands prior to development, e.g. the area in and around Kailua, O'ahu, which was formerly part of the larger wetland now restricted to Kawainui marsh (Fig. 1).

Wetland Loss

We estimated that the state of Hawai'i has lost 192 km^2, or 15 % of its pre-settlement area of wetlands, and that these losses were spread unevenly across the islands and across elevational strata. Our data do not provide the causes of loss directly, but some of these can be inferred from location. The islands of Maui, Moloka'i, and Kaua'i experienced losses on the order of 6–8 % of their estimated pre-settlement total, and each has lost <30 km^2 of wetland (Fig. 2; raster datasets available through a link at http://ase.tufts.edu/biology/labs/reed/publications/supplementary.htm). The island of O'ahu had the highest gross wetland loss, about 106 km^2, or 65 % of the island's estimated pre-settlement wetlands, accounting for 55 % of losses statewide (Fig. 2). The second highest observed loss was on the island of Hawai'i, where 40 km^2 were lost, although this accounts for only 8 % of its pre-settlement total (Fig. 2).

Wetland losses on all islands were greater at lower elevations than at higher elevations (Table 2). Losses in lower elevations accounted for 88 % of total wetland losses statewide. The islands of Moloka'i and Kaua'i show almost no loss of higher elevation wetlands and about 15 % wetland loss in coastal regions. Mid-to-high elevation losses are negligible on Maui, but low elevation losses are estimated at 35 %. Gross wetland losses at mid to high elevation were highest on Hawai'i (~20 km^2), although O'ahu lost the largest fraction of its pre-settlement mid to high elevation wetlands (9 %). This is reversed in low elevation and coastal wetlands, where O'ahu had the greatest gross wetland loss, but Hawai'i lost the largest percentage of its low elevation wetlands. Hawai'i and O'ahu lost 75 % and 71 % of their low elevation wetlands, respectively (Table 2).

Wetland losses on Moloka'i were minimal and sustained mainly in southeastern coastal regions. These losses were likely from coastal development. Based on proximity to NWI-identified current wetlands, most lost wetlands were

Table 1 Overall concordance (%), true positive rates, true negative rates, and sample sizes (number of pixels) classified by the thresholded TWI model (see text for details)

	Overall concordance	True positive rate[a]	True negative rate	Sample size (pixels)
Island-wide				
Hawai'i	79.6	14.0	83.5	104,423,614
O'ahu	83.2	40.7	85.4	15,464,181
Maui	75.6	6.1	90.7	18,877,308
Moloka'i	72.8	20.6	79.1	6,752,914
Kaua'i	45.8	22.0	69.3	3,468,020
Total	78.4	15.0	84.2	148,986,037
Coastal				
Hawai'i	76.8	28.8	77.9	20,025,440
O'ahu	77.7	42.3	80.1	10,943,002
Maui	80.6	16.3	84.3	7,375,926
Moloka'i	66.8	28.3	71.2	4,227,796
Kaua'i	86.2	37.2	92.9	7,893,656
Total	78.2	33.0	81.0	50,465,820

'Coastal' refers to a reduced area of analysis below 304 m, which excludes a large portion of rain-fed wetlands

[a] Low true positive rates were expected due to wetland loss and the presence of wetlands not maintained by topographic surface water flow (e.g. coastal inundation, heavy rainfall, pumping)

likely freshwater emergent and freshwater forested/shrub wetland. The majority of estimated loss was indicated by the threshold TWI model, which suggested likelihood of pre-settlement wetlands on patches of developed land; this assessment was often supported by hydric soil evidence. Extensive areas of cultivated land in the center of the island showed little evidence of developed wetlands. Highly developed areas in this agricultural region that were recorded as lost wetlands were supported only by TWI evidence.

Based on our analyses, Kaua'i retains 100 % of its extensive mid-to-high elevation wetlands, and has sustained only small losses in coastal areas. The majority of loss was in low-density development and agricultural areas, and was therefore not assessed using TWI, but rather was supported by hydric soil evidence. Wetland loss on this island is presumably more from filling or alteration of local hydrology for drainage and irrigation than from direct development. Hydric soil and some TWI evidence indicate that river-fed freshwater emergent wetlands were lost around suburban developments along the southwest and east coasts, including Kekaha, Waimea, Hanapepe, 'Ele'ele, Lihu'e, and Kapa'a (locations of sites named in the results are shown in Fig. 2c, wetland loss maps). Substantial conversions of riparian wetlands to irrigated agriculture are notable along the island's north side, near Princeville, but account for minimal losses because abundant artificial wetlands were created in the region. Similar changes are evident in the Mana plain on the island's west side, where evidence suggests the presence of a large pre-settlement wetland now replaced with artificial wetlands, a reservoir sewage treatment plant, and agricultural fields. If these artificial wetlands were not included in our assessment of Kaua'i's wetland losses, the island's low elevation losses would be considerably higher.

Wetland loss on Maui (24 km^2) was only slightly higher than on Kaua'i, but accounted for a larger fraction of the

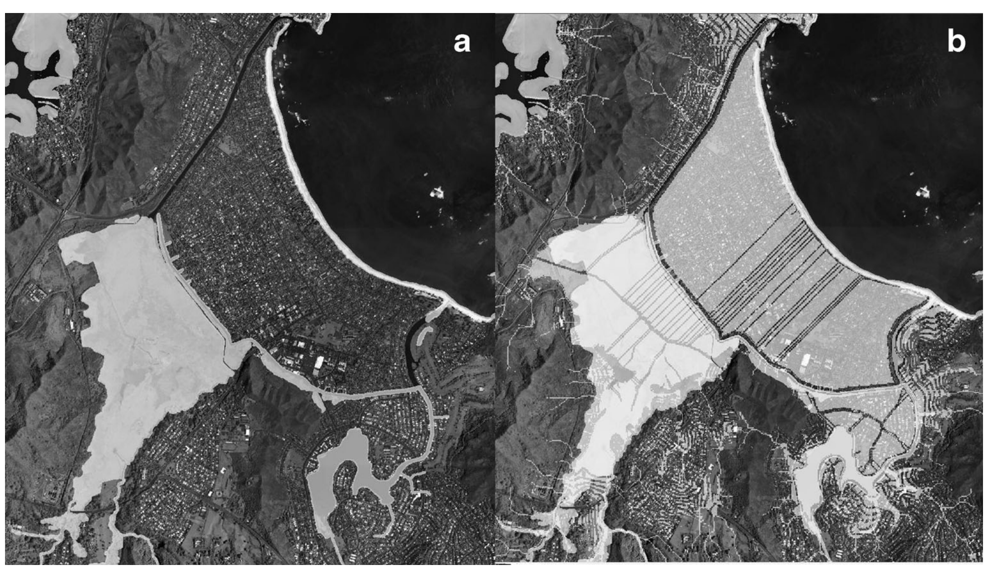

Fig. 1 False-color Digital Orthophoto Quarter Quadrangle (DOQQ) image of the Kailua town area of eastern O'ahu (see Fig. 2 for location) showing National Wetlands Inventory (NWI) surveyed wetlands (*light gray*, *left image*) and NWI wetlands overlaid by the Topographic Wetness Index (TWI) threshold model (*light gray*, *right image*). The Kawainui marsh is the large wetland feature on the left side of both images. (For full color versions of these images, see Fig. 1S, Electronic Supplementary Material 2)

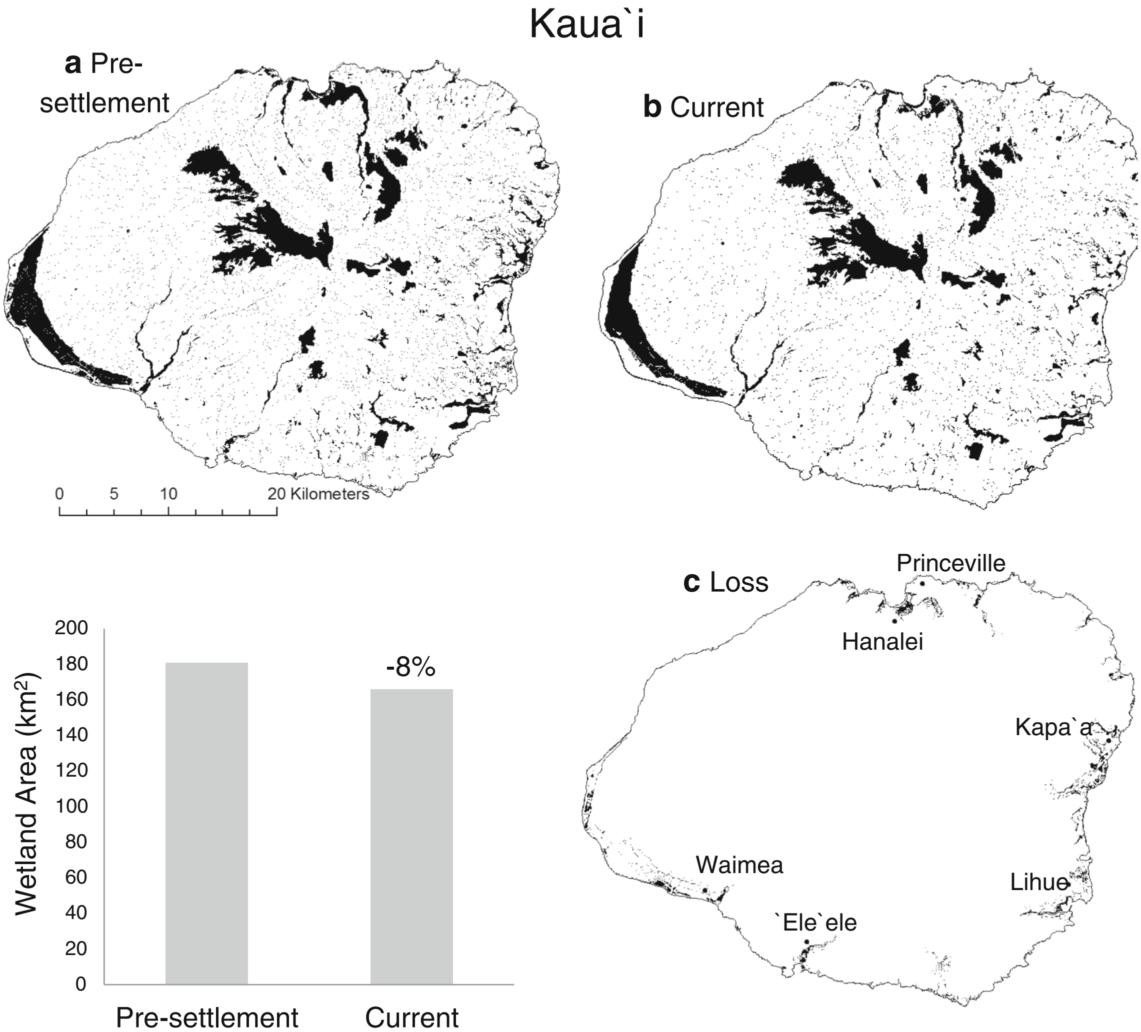

Fig. 2 Maps of **a** pre-settlement wetland cover, **b** current wetland cover, and **c** wetland loss on the five largest islands of Hawai'i; these islands represent just over 95 % of the state's land cover. For each island we also include a bar graph showing original vs. current wetland cover. Sites mentioned in the results are labeled by name on the loss (**c**) maps; cities and towns are indicated with a *black dot* where possible without distracting from results. (For color versions of these images, see Fig. 2S, Electronic Supplementary Material 3)

island's wetlands. The vast majority of losses were sustained around urban and suburban coastal developments like Kihei on the south side of the island, Kahului in the north, and Lahaina in the west. The evidence for most of these losses was generated by the thresholded TWI model, although on the west side of the island it was also supported by the presence of hydric soils in the Mana plain. Given the location of losses in more developed areas, it is more likely that they were caused by direct development and filling of wetlands.

The island of Hawai'i suffered the second-largest loss of wetlands overall, and these losses were distributed almost evenly between higher and lower elevations. Loss on Hawai'i is indicated almost equally by hydric soil and TWI indicators. High TWI values were evident in developed areas around Hilo (Coastal, East), Hawaiian Beaches (Southeast of Hilo) and Waimea (North), the last where it abuts the Pu'u O'Umi Natural Area Reserve. Several patches of partially hydric soil are reported beneath what is now Mountain View (South of Hilo), and account for the remaining wetland loss on the island. NWI surveys show freshwater forested scrub/shrub wetlands contained within adjacent, undeveloped hydric soils North and West of Hilo, suggesting that the lost wetlands in the vicinity may have been primarily of this type. Wetland loss indicated by TWI near the Pu`u O'Umi Natural Area Reserve would likely be of the same type, which is abundant in the nearby reserve. Lowland wetlands around Waiakea Pond and the Banyan Golf Course in East Hilo were most likely freshwater emergent or coastal, estuarine wetlands.

Coastal wetland losses on O'ahu are extensive and generally supported by multiple sources of evidence. Based on our analyses, Hono'lulu, Pearl Harbor, and Kapolei regions formerly supported large tracts of estuarine and marine wetland along the coast, with areas of freshwater emergent and freshwater scrub wetlands farther inland along streams. Wetland

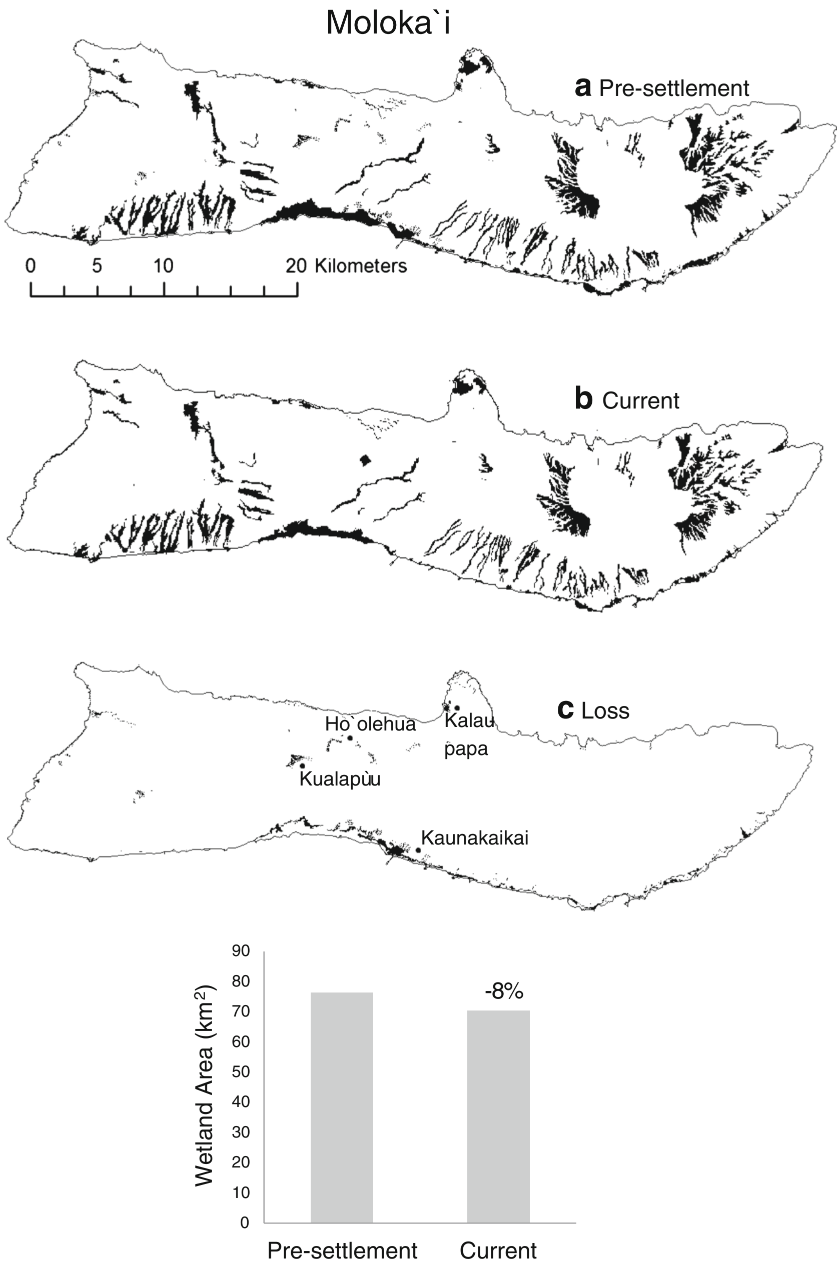

Fig. 2 (continued)

losses in the less developed part of the region are indicated by hydric soil evidence, while in the most heavily developed parts, the thresholded TWI model shows dense areas with a high likelihood of having supported wetlands. Large losses of freshwater emergent wetland are also evident in Kailua and Kane'ohe, the former indicated by TWI model evidence and the latter by hydric soils. On the northern side of the island, hydric soil evidence suggests extensive wetland losses from Waialua Bay to Mokuleia. Wetland losses on the Windward side of O'ahu, especially around Kane'ohe, may have originally been due to redistribution of water from the windward to the leeward side of the island for irrigation purposes, although most wetland loss in the last 50 years or so in all parts of the island is most likely from urban and suburban development.

Discussion

Use of TWI in Pre-Settlement Wetland Assessment

As a simple steady-state wetness index, the topographic wetness index (TWI, also referred to as the Compound Topographic Index) determines where water is likely to

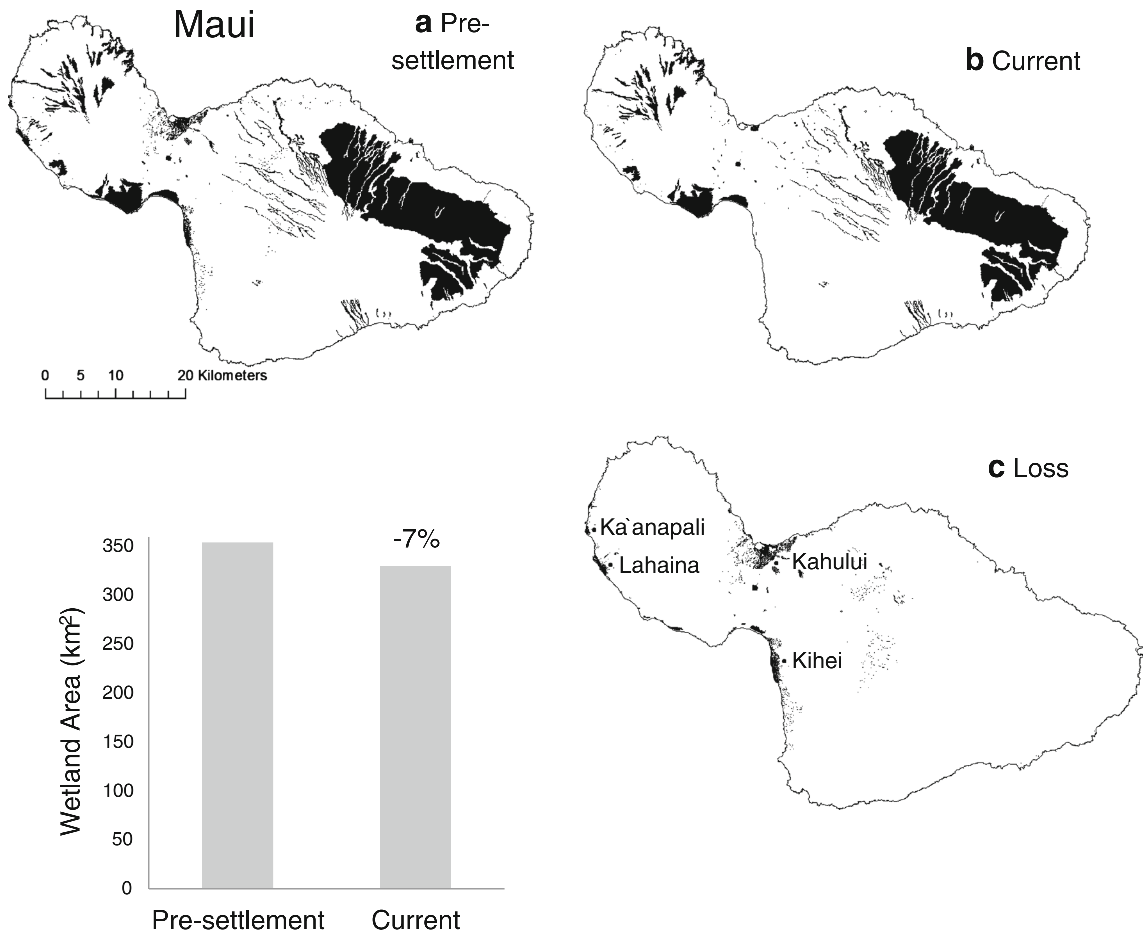

Fig. 2 (continued)

accumulate on a landscape given hypothetical conditions of uniform rainfall (Beven and Kirkby 1979; Besnard et al. 2013). As we predicted, the TWI model performed well when identifying wetlands created by conditions of surface water flow, but poorly when identifying wetland areas where other mechanisms were responsible for wetland or hydric soil conditions. When a portion of such non-surface-water wetlands were removed from the study area (by analyzing only low-elevation areas) the true positive rate more than doubled overall, implying that lower true-positive rates in our study were due to the presence of wetlands that do not depend on surface flow. It is important to recognize that in our study the true positive rates for wetlands sustained by surface water flow were underestimated by even the low-elevation evaluation, due to wetland loss and the predominance of wetlands sustained by artificial means and coastal flooding at lower elevations. Extremely low false positive rates and generally high true negative rates show that the TWI model is much more likely to underestimate wetland loss than overestimate it, which is consistent with our goal in this study that if we erred in estimating wetland loss that we erred conservatively.

Our study indicates that TWI can be very successful at identifying current wetlands sustained by surface runoff or areas where wetlands of that type were supported prior to human settlement. However, the TWI model does not account for precipitation patterns and soil types, which are important factors in determining whether water will actually accumulate in an area, even if local topology indicates it is possible. Even if an area is flat, low, and has a large catchment, if there is no precipitation a wetland will not form. Similarly, if soils do not retain water, it will percolate into the groundwater and not be sustained near the surface. Consequently, relying solely on TWI to identify pre-settlement wetland locations could lead to overestimates of wetland distributions, although our analysis for the Hawaiian Islands shows that this is far less likely than is underestimation.

TWI could underestimate pre-settlement wetland cover where soil and precipitation conditions support wetlands despite topological traits that do not indicate they would accumulate water. The latter is evident in the Kohala Forest Reserve on the Northeastern side of the island of Hawai'i, where steep slopes give relatively low TWI values, but

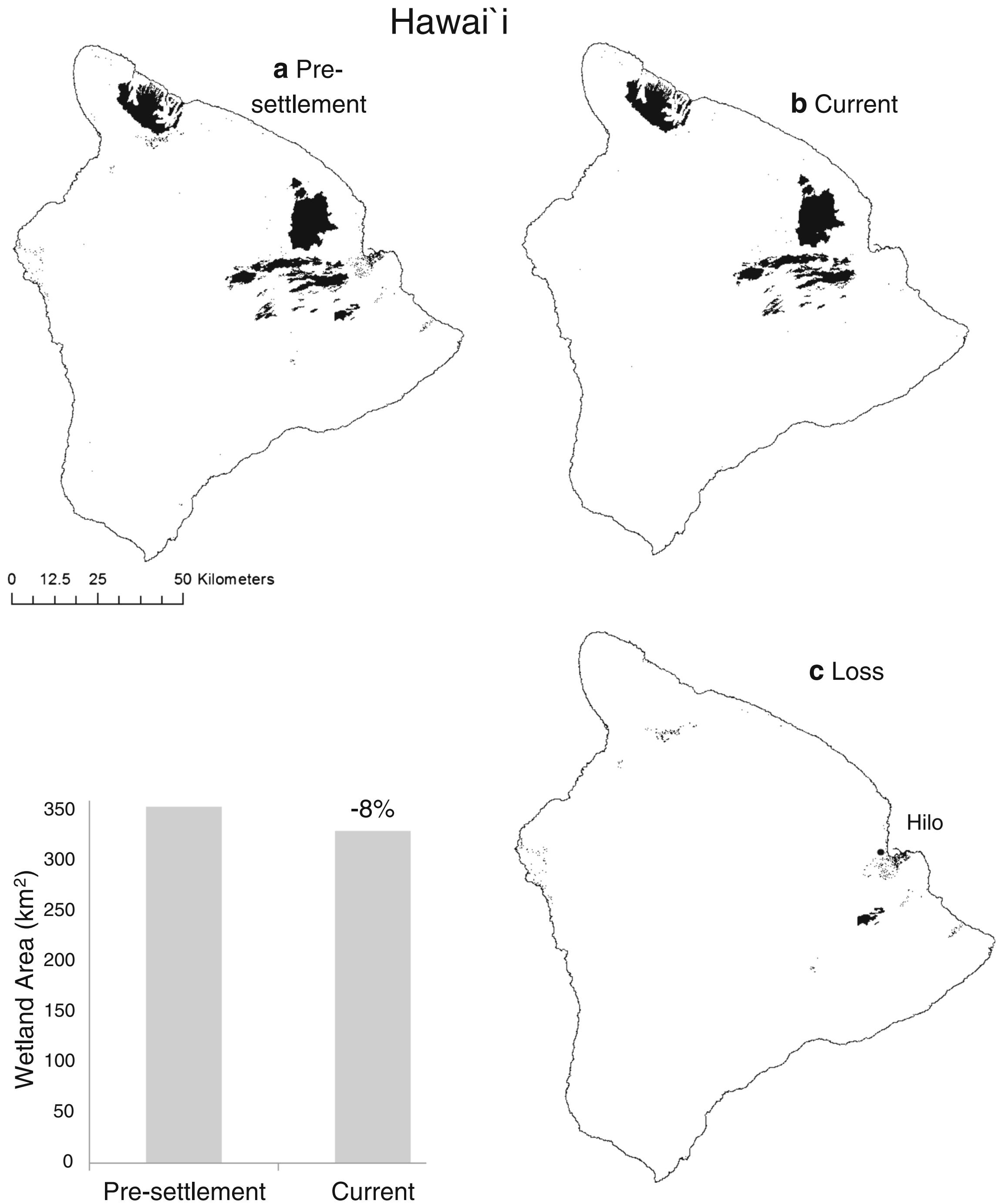

Fig. 2 (continued)

wetlands persist because of annual rainfall in excess of 6 m (Giambelluca et al. 2013). Given the high rainfall rates on even the dry sides of the Hawaiian Islands, the potential bias for overestimation is unlikely when applying TWI in that region. We conclude that hydrological models like TWI are practical and convenient tools for assessing the likelihood of an area supporting a pre-settlement wetland. We also suggest that they could be improved by including information such as rainfall and soil type. The thresholded TWI model is best used in areas where wetlands are most likely sustained by surface flow. On oceanic islands, it may be most convenient to use TWI for low-elevation wetland inventories, where wetlands are less likely to be fed by orographic rainfall. In such cases, it is an excellent tool for creating conservative estimates of pre-

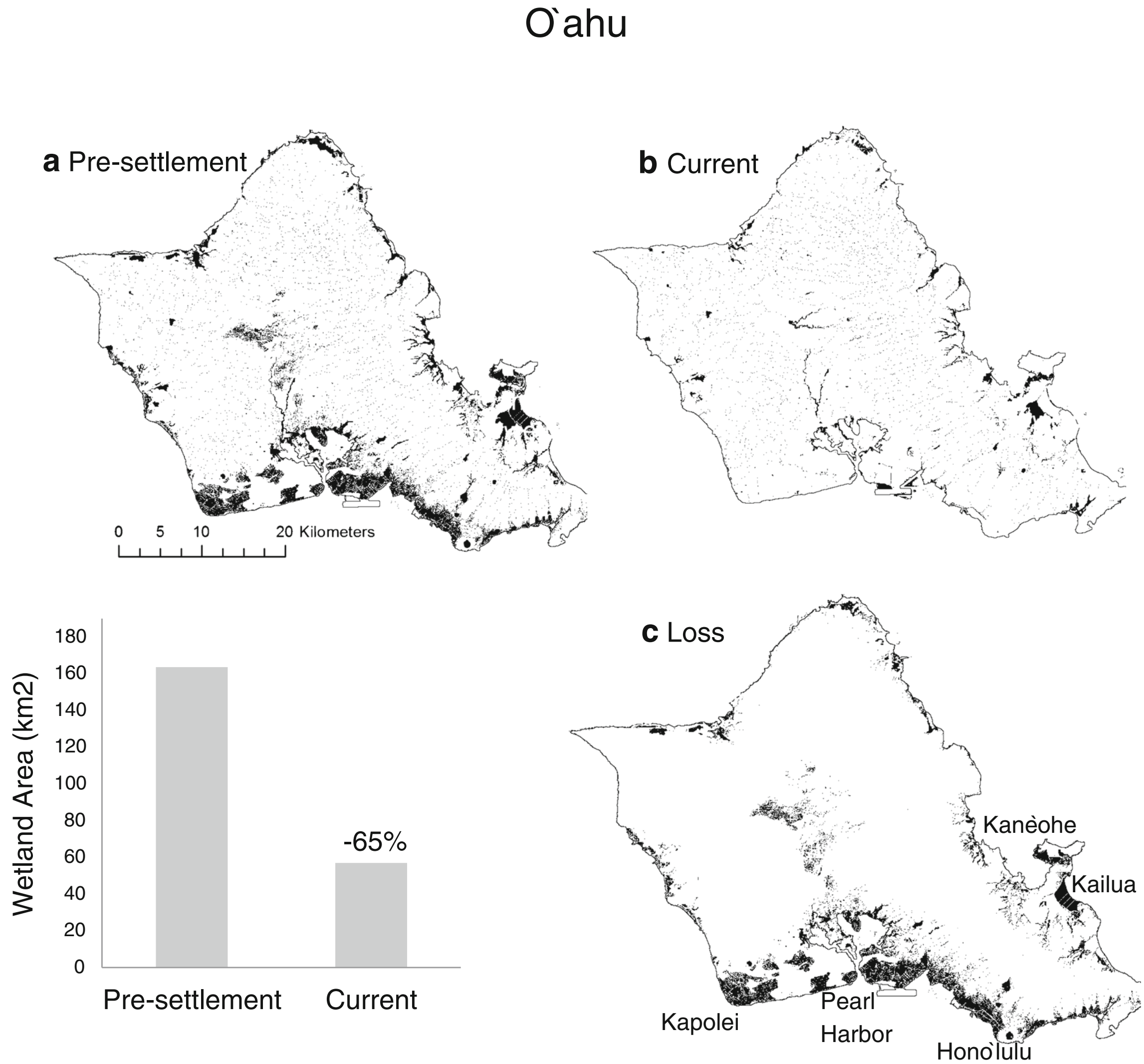

Fig. 2 (continued)

development wetland loss where other, more reliable sources of evidence are unavailable.

Loss of Wetlands in the State of Hawai'i

Our estimate of 15 % wetland loss in Hawai'i since human settlement is 25 % greater than the previous estimate for the state, which was 12 % (Kosaka *in litt*. 1990). More significantly, our estimate of wetlands lost was much higher. There are a number of differences between the studies that might have contributed to this difference, but since the original documentation of the earlier analysis is lost, some of the differences are speculation. The first difference manifests in the observation that our estimates for pre-settlement wetland area, current wetland area, and gross wetland loss for the state were each about an order of magnitude higher than the earlier estimates, indicating that we included or identified substantially more pre-settlement and current wetland area in the state. Specifically, the NWI data used in this study recognized more than three times as much current wetland area for the state than did the Yuen/Kosaka study (652 km^2 vs. 210 km^2, respectively). The definition of wetlands used in our study and by the U.S. Fish and Wildlife Service in 1990, however, should not have differed. We, and the National Wetlands Inventory, used Cowardin et al. (1979) for wetland definitions, which is the standard for the U.S. Fish and Wildlife Service (where the Yuen study was done). Despite this, the earlier assessment might still have used a subset of wetland types.

Another potential difference between the studies is that we estimated wetland loss since first human settlement, which occurred around 500 C.E. (Graves and Addison 1995), while the previous study attempted to estimate wetland loss since 1780 (Kosaka *in litt.* 1990). However, we think that the large differences in results between the two studies are more likely due to our study having available more numerous and accurate data sources (e.g., soil layers) as well as more sophisticated

Table 2 Estimated pre-settlement and current wetland areas, gross wetland losses, and percentage losses for each island subdivided by elevation category: 'coastal' is elevation <304 m

Island	Elevation	Pre-settlement wetland area (km^2)	Current wetland area (km^2)	Gross wetland loss (km^2)	% Wetland area lost
Moloka'i	Mid & High	30	29.8	0.21	0.69 %
	Coastal	45.7	39.9	5.84	13 %
Kaua'i	Mid & High	76.8	76.8	0	0 %
	Coastal	101	86.2	15	15 %
Maui	Mid & High	298	293	4.86	1.6 %
	Coastal	56	36.4	19.6	35 %
Hawai'i	Mid & High	470	451	19	4.2 %
	Coastal	27	6	21	75 %
O'ahu	Mid & High	6.13	5.58	0.55	9 %
	Coastal	152	43.8	108	71 %
Total	Mid & High	881	854	27	3 %
	Coastal	382	213	169	44 %
Total, Kosaka (*in litt*. 1990)	Mid & High	147	147	0	0 %
	Coastal	91	63	28	31 %

Elevation categories chosen to match the 1990 Hawai'i wetland loss assessment (last rows)

analytical tools that were unavailable in the previous study. This resulted in a more comprehensive survey of wetlands and evidence of wetlands in the state of Hawai'i.

Our estimates of wetland loss in Hawai'i since human settlement may be conservative. In particular, by restricting the use of the TWI model to areas of heavily developed land, we did not include potential pre-settlement wetlands in less-developed areas that were not indicated by hydric soil data but were indicated by TWI values (results not shown). Our estimate of wetland loss was also conservative because we included all types of artificial wetlands in our inventories of current wetlands, which biased the results toward lower losses of natural wetlands. The potential for underestimating losses due to artificial wetlands is especially evident on the Mana plain (west side of Kaua'i), where what is known to have been a large pre-settlement wetland near Ka'anapali and Lahaina has been replaced by many artificial wetlands (Swedberg 1967; Engilis and Naughton 2004). If one considers merely water storage as an ecosystem value, this conversion might not be as much of an underestimation, but if one values ecological services and wetland value to native wildlife, artificial wetlands tend to be functionally inferior to natural wetlands (e.g., Elphick 2000; Ma et al. 2004; Bellio et al. 2009). Even natural wetlands within urban landscapes can have reduced function for wetland specialists (e.g., Ehrenfield 2000; Tavernia and Reed 2010). Wetlands in non-urban sites might also have reduced value for native wildlife (including plants) due to the presence of exotic invasive plants and predators (U.S. Fish and Wildlife Service 2011).

The results of our study are especially important for the long-term management of wetlands in the state of Hawai'i because of the large number of wetland-dependent threatened and endemic species and the multitude of threats to wetland habitats on these and other small Pacific islands, particularly for coastal wetlands (SPREP 2011). This will be particularly true for adaptive planning for climate change and its effects (e.g., Hartig et al. 1997; Nicholls 2004). Of concern from an ecological standpoint is that, like Kosaka *in litt*. (1990), we found the vast majority of wetland losses in Hawai'i occurred along the coastal plains. Unfortunately, these low-elevation wetlands are also the most important for wetland species of conservation concern (Griffin et al. 1989; U.S. Fish and Wildlife Service 2011; Reed et al. 2011 Reed et al. 2012). Climate change and sea level rise are likely to pose a significant future threat to coastal wetlands (Nicholls et al. 1999; Nicholls 2004), especially on geologically younger islands such as Hawai'i and Maui, which are still undergoing relatively high rates of subsidence (Moore 1970; Ludwig et al. 1991). Wetland restoration or creation will be especially important in areas like O'ahu where the vast majority of coastal wetlands have been lost.

Our estimates of wetland loss correspond well with the intensity of development on individual islands in the state. For example, the two most populous islands, O'ahu and Hawai'i, have lost the highest proportion of their pre-settlement wetlands. Urban and rural development currently appears to be the largest cause of wetland loss on the Hawaiian Islands, especially in the Hono'lulu and Pearl Harbor areas, where extensive natural and artificial wetlands once existed

(Summers 1964; Shallenberger 1977). This pattern of wetland loss is generally consistent with recent trends elsewhere in the United States, wherein wetland losses were initially from agricultural development, but are more recently brought about by development. (Dahl 1990, 2006). Making general comparisons to other tropical islands, however, is more difficult because of the dearth of inventory data in even current wetlands, let alone pre-settlement wetland cover (Scott 1993). It is recognized, however, that wetland specialist species and ecosystem services from wetlands are at risk in Oceania and that at least some of that risk is due to wetland loss (Millennium Ecosystem Assessment 2005). From the available limited data for other islands in Oceania (e.g. Guam, American Samoa), reviews by Scott (1993) and Ellison (2009) suggest that, as indicated by our study, urbanization is the primary threat to coastal wetlands, and is threatening endemic flora and fauna dependent upon wetland habitats. Wetland losses in the Hawaiian Islands are also similar to loss patterns in Caribbean Islands, which were caused by the expansion of coastal settlements, agriculture, and then (and currently) by development for the tourist industry (reviewed by Bacon 1987).

Conclusion

We have identified extensive lowland wetland losses in the state of Hawai'i, particularly on O'ahu. The lower estimated losses on the other islands are deceptive in that significant gains in artificial wetlands in those regions mask more substantial losses of natural wetlands. From an ecosystem services and wildlife perspective, many benefits provided by natural wetlands have still been lost, although the area of what may generally be called wetlands has changed little. Consequently, the loss of wetland ecosystem services would be underestimated by our assessment.

The collapse of the sugar cane and pineapple industries starting in the mid-1990s created a state of transition whereby opportunities for wetland restoration arose (Ridgley et al. 1997). To provide some idea of the amount of water that might be reallocated, in 1996 the sugar industry applied 1.05 million cubic meters per day of water to cane fields; roughly 19 % of water use in the state of Hawai'i (Gopalakrishnan et al. 1996). This was already considerably less than the amount of agricultural water used during the peak of the sugar industry over the previous several decades. In 1985, agricultural fresh water use was 64 % of Hawaii's use, which declined to 55 % in 1990 (Department of Business Economic Development and Tourism (Hawai'i), 1993 and 1994). Agricultural water use has declined to 5 % of total use in recent years (CH2M Hill 2013).

Despite this freeing of agricultural water, water demand is rising in Hawai'i due to urban development and rapid population growth (Gopalakrishnan et al. 2007), leading to increased conflicts over water resources. For example the Waiahole ditch, which formerly transferred water through the Ko'olau mountain range to sugar plantations on the center of the island, has become the center of a fierce dispute over the water resources it transports (Gopalakrishnan et al. 2007). Urban development is greatest on O'ahu, the island with the greatest wetland losses to date (this study), and it is predicted that groundwater use on O'ahu will exceed recharge rates by 2018 (Hawai'i Water Resources Act of 2005, http://www.gpo.gov/fdsys/granule/CREC-2005-09-13/CREC-2005-09-13-pt1-PgH7830/content-detail.html). As human needs for water on the islands grow, they will likely come into conflict with ecological needs and the laws protecting endangered species (e.g., the U.S. Endangered Species Act). Wetlands on Hawai'i support 222 taxa (species, subspecies, varieties, island populations) of plants and animals that are listed under the U.S. Endangered Species Act (ESA), most of which are endemic to the islands (Online Resource 1). To put this number in perspective, ESA-listed taxa native to Hawai'i account for 28.5 % of the 1,476 listed, and of these 53 % occupy wetlands in at least part of their range.

Human activities have affected wetland wildlife since the arrival of Polynesian settlers, who arrived as early as 500 C.E. (Graves and Addison 1995). These early settlers converted and drained wetlands for agriculture, especially the cultivation of taro (Kirch et al. 2004). With the arrival of Europeans, wetlands were lost to the urban development and the reallocation of water for irrigated agriculture (Stone 1989a; Wilcox 1996; Ellison 2009). Subsequent to both Polynesian and European settlement of Hawai'i were impacts to native wildlife from introduced, invasive competitors, predators, and diseases (e.g., Stone 1989b; U. S. Fish and Wildlife Service 2011; Reed et al. 2012). For example, despite containing approximately 280 ha of wetlands, Kawainui Marsh, a wetland on O'ahu that is designated as a Ramsar site, until recently provided less than 8 ha of habitat for native waterbirds because the rest was overgrown with non-native, invasive vegetation (Ramsar Sites Information Service; http://www.wetlands.org/RSDB/default.htm). The U.S. Army Corps of Engineers has begun efforts to change this trend; for example in restoring 16 ha of habitat in the Kawainui marsh which makes available an additional 9.7 ha of wetland habitat. Wetlands like the Kawainui will require regular removal of non-native invasive plants to remain suitable (U.S. Army Corps of Engineers 2008). Climate change will exacerbate threats to wetland specialists (Loope and Giambelluca 1998; Benning et al. 2002; Baker et al. 2006; Atkinson and LaPointe 2009; Reynolds et al. 2012), making wetland protection and mitigation even more important.

The potential to take advantage of alternative or additional uses of freed agricultural water, such as restoring or creating wetlands for endangered species protection or other wetland services, is disappearing rapidly. Fortunately, unlike many natural resources, water is a flexible resource; that is, the same water can be used sequentially for many objectives (e.g., Hawai'i Division of Land and Natural Resources 2005; Islam and Susskind 2013). Consequently, it is important to convene stakeholders and determine common goals in order to protect multiple wetland and water-use values in the state while allowing efficient and equitable use of this valuable resource (Rahaman and Varis 2005; Field et al. 2007; Gopalakrishnan et al. 2007; Sheild et al. 2009).

Acknowledgments This research was supported by the Tufts University Water Diplomacy IGERT (NSF 0966093). This work was significantly improved by the comments of two anonymous reviewers. We thank Carl Zimmerman of Tufts University for technical assistance with ArcGIS and in planning GIS analysis protocols. We also thank Magaly Koch of Boston University for direction in finding land cover reference datasets, and Laurie Base and Jing Zhu of the department of Urban Environmental Policy Planning at Tufts University for providing information and resources on the use of the compound topographic index. We thank Cynthia Stiles and Tony Rolfes of USDA NRCS Hawai'i for providing historic soil maps of soil cover on Oahu, and Steve Peaslee, Steve Speidel and Tammy Cheever of the NRCS National Soil Survey Center for help with soildataviewer and acquisition of NRCS hydric soil surveys. Aaron Nadig and Michael Silbernagle (USFWS) and Andy Engilis (Univ. of California, Davis) provided important input in discussing Hawaii's wetlands. We thank the Hawai'i Geospatial Consortium and the State of Hawaii GIS Program, especially Ron Canarella, for access to the Hawaii DOQQ data. We thank Emily White of the Massachusetts Trustees of Reservations for reviews of the initial drafts of the project and input in discussing wetland loss. Finally, we thank Kelly Carignan of the NOAA National Geophysical Data Center for assistance with metadata on coastal relief maps of the Hawaiian Islands. This paper is dedicated to the memory of Ron Walker, who spent his career working to protect Hawaii's wetlands and their wildlife.

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On-line Supplemental Material from
van Rees, C.B. and Reed, J.M. Wetland loss in Hawai`i since human settlement

Table 1S Taxa (species, subspecies, and varieties) listed as threatened (TH) or endangered (EN) under the U.S. Endangered Species Act (http://www.fws.gov/endangered/species/us-species.html accessed June 2013) that use wetland ecosystems for part or all of their range. Ecosystems considered wetlands included: wet and moist forests, wet shrublands, wet cliffs, and stream and waterfall margins. Species whose entire range is found within wetlands is marked with an "X" under "Entire range in wetlands"; species without an X are those whose ecosystem use also includes non-wetlands. Range is given by island; "All main islands" refers to species found on Hawai`i, Kaua`i, O`ahu, Maui, and Moloka`i. Animals are listed first, followed by plants; in alphabetical order by scientific name. References are listed at the end of the document.

Scientific Name	Status	Range	Entire range in Wetlands	Ecosystem	References
Animals					
Achatinella spp. (~40 species listed together)	EN	O`ahu		Wet montane forest	1
Anas laysanensis	EN	Laysan, Midway	X	Lowland wetland, salt flats	2
A. wylvilliana	EN	Hawai`i, Kaui, Maui, O`ahu	X	Lowland wetland, montane wetland	3
Drosophila differens	EN	Moloka`i	X	Montane wet forest	4
D. heteroneura	EN	Hawai`i		Montane mesic to wet Forest	4
D. mulli	EN	Hawai`i	X	Montane wet forest	4
D. neoclavisetae	EN	Maui	X	Montane wet forest	4
D. ochrobasis	EN	Hawai`i		Montane mesic to wet forest	4
D. sharpi	EN	Kaua`i, Niihau	X	Montane wet forest	5
D. substenoptera	EN	O`ahu	X	Montane wet forest	4
Erinna newcombi	TH	Kaua`i	X	Freshwater streams	6
Fulica alai	EN	All main islands	X	Lowland wetland	3
Gallinula chloropus sandvicenis	EN	Kaua`i, O`ahu	X	Lowland wetland	3
Hemignathus munroi	EN	Hawai`i		Montane wet forest	7
Himantopus mexicanus knudseni	EN	All main islands	X	Lowland and coastal wetlands, mud flats	3
Loxops caeruleirostris	EN	Kaua`i		Montane wet forest, Montane bog	5
L. coccineus coccineus	EN	Hawai`i		Montane wet forest	7
L. coccineus ochraceus	EN	Maui		Montane forest	7
Megalagrion leptodemus	EN	O`ahu	X	Lowland wetland, freshwater streams	8
M. nesiotes	EN	Maui	X	Lowland wetland, freshwater streams	9
M. nigrohamatum nigrolineaum	EN	O`ahu	X	Lowland wetland, freshwater streams	8
M. oceanicum	EN	O`ahu		Lowland wetland, lowland mesic, montane wetland, wet cliff	8
M. pacificum	EN	All main islands	X	Lowland wetland, freshwater stream	9

Melamprosops phaeosoma	EN	Maui		Montane mesic and wet forest	7
Moho braccatus	EN	Kaua`i	X	Montane wet forest, montane bog	7
Myadestes lanaiensis rutha	EN	Moloka`i, Maui		Lowland and montane wet forests	7
M. myadestinus	EN	Kaua`i		Montane wet forest, montane bog	7
M. palmeri	EN	Kaua`i		Montane wet forest	7
Newcombia cumingi	EN	Lana`i, Maui, Moloka`i	X	Lowland wet forest	10
Hemignathus lucidus	EN	Kaua`i, Maui		Montane mesic and wet forest	7
Oreomystis bairdi	EN	Kaua`i		Montane mesic and wet forest	7
O. mana	EN	Hawai`i		Montane wet forest	7
Palmeria dolei	EN	Maui		Montane wet forest	7
Paroreomyza flammea	EN	Moloka`i		Montane wet forest	7
P. maculata	EN	O`ahu		Montane wet forest	7
Partulina semicarinata	EN	Lana`i,	X	Montane and lowland wet forest, wet cliff	10
P. variabilis	EN	Lana`i,	X	Montane and lowland wet forest, wet cliff	10
Pseudonestor xanthophrys	EN	Maui		Montane wet forest	7
Psittirostra psittacea	EN	Hawai`i, Kaua`i, Ni`ihau		Montane mesic and wet forest	7
Plants					
Acaena exigua	EN	Maui, Kaua`i	X	Montane bog	11
Adenophorus periens	EN	Hawai`i, Kaua`i, Moloka`i	X	Montane wet forest, lowland wet forest, wet cliff	12
Alectryon macrococcus	EN	Kauai, Maui, Moloka`i, O`ahu		Montane wet forest, lowland wet forest, dry cliff	12
Alsinidendron lychnoides	EN	Kaua`i	X	Montane wet forest	13
A. viscosum	EN	Kaua`i	X	Montane wet forest	13
Argyroxiphium kauense	EN	Hawai`i		Lowland wet forest, mesic shrubby forest	11
Astelia waialealae	EN	Kaua`i	X	Montane wet	5
Bidens campylotheca pentamera	EN	Maui		Montane mesic and montane wet, forest, wet and dry cliff	10
B. campylotheca waihoiensis	EN	Maui	X	Obligate, lowland wet, wet cliff, montane wet	10
B. conjuncta	EN	Maui	X	Obligate, lowland wet, wet cliff, montane wet	10
Calamagrostis hillebrandii	EN	Maui	X	Montane wet forest	10
Chamaesyce deppeana	EN	O`ahu	X	Wet cliff	14
C. remyi var. kauaiensis	EN	Kaua`i	X	Lowland wet forest, wet cliff	5
C. remyi var. remyi	EN	Kaua`i		Lowland mesic and wet forests, montane mesic and wet forests, wet cliff	5
C. rockii	EN	O`ahu	X	Lowland wet forests, cliffs	14
Charpentiera densiflora	EN	Kaua`i		Lowland mesic and wet forest	5

Clermontia drepanomorpha	EN	Hawai`i	X	Montane wet forest	15
C. oblongifolia ssp. brevipes	EN	Moloka`i	X	Mid-elevation wet forest	16
C. oblongifolia ssp. mauiensis	EN	Maui	X	Montane wet forests	17
C. peleana	EN	Hawai`i, Maui	X	Montane wet forests	15
C. pyrularia	EN	Hawai`i	X	Montane wet forests	15
C. samuelii	EN	Maui	X	Montane wet forests	17
Cyanea acuminata	EN	O`ahu	X	Montane wet forest, lowland mesic and wet forest, wet cliff	14
C. asarifolia	EN	Kaua`i	X	Montane wet shrubland	13
C. asplenifolia	EN	Maui	X	Montane wet forests and wet cliffs	18
C. calycina	EN	O`ahu		Lowland mesic and wet forest, montane wet forest, wet cliff	14
C. copelandii ssp. copelandii	EN	Hawai`i	X	Montane wet forest	19
C. c.opelandii ssp. haleakalaensis	EN	Maui		Montane wet or mesic forest, freshwater stream	12
C. crispa	EN	O`ahu		Lowland mesic and wet forest, wet cliff	14
C. dolichopoda	EN	Kaua`i	X	Montane wet forest, waterfall margins	5
C. dunbarii	EN	Moloka`i	X	Montane wet forest	16
C. eleeleensis	EN	Kaua`i	X	Montane wet forest	5
C. glabra	EN	Maui	X	Lowland wet forest, freshwater stream	12
C. grimesiana ssp. grimesiana	EN	Maui, O`ahu	X	Lowland wet and mesic forest, wet cliff, freshwater stream	20
C. grimesiana ssp. obatae	EN	O`ahu		Lowland mesic and wet forest, wet and dry cliff	20
C. humboldtiana	EN	O`ahu	X	Lowland wet forest, wet cliff	20
C. kolekoleensis	EN	Kaua`i	X	Lowland wet forest	5
C. koolauensis	EN	O`ahu	X	Lowland wet forest	20
C. kuhihewa	EN	Kaua`i	X	Lowland wet forest	5
C. kunthiana	EN	Maui		Lowland wet forest, montane mesic and wet forest	10
C. lanceolata	EN	O`ahu		Lowland wet forest	20
C. lobata	EN	Maui, Lana`i	X	Freshwater streams	11
C. macrostegia ssp. gibsonii	EN	Lana`i	X	Lowland wet forest	21
C. mceldowneyi	EN	Maui	X	Montane wet forest	11
C. platyphylla	EN	Hawai`i	X	Lowland and montane wet forest	15
C. procera	EN	Maui, Moloka`i	X	Lowland wet forest	16
C. purpurellifolia	EN	O`ahu		Lowland wet forest, wet cliff	20
C. recta	TH	Kaua`i	X	Lowland wet forest	13
C. remyi	EN	Kaua`i	X	Lowland wet forest	13
C. st.-johnii	EN	O`ahu	X	Lowland wet forest, wet cliff	20
C. stictophylla	EN	Hawai`i		Montane mesic and wet forest	19

C. truncata	EN	O`ahu		Lowland mesic and wet forest, wet cliff	20
C. undulata	EN	Kaua`i	X	Montane wet forest	21
Cyrtandra cyaneoides	EN	Kaua`i	X	Montane wet forest	13
C. dentata	EN	O`ahu		Lowland mesic and wet forest, dry cliff	20
C. filipes	EN	Maui, Moloka`i	X	Lowland wet forest and wet cliff	10
C. gracilis	EN	O`ahu		Lowland wet forest	20
C. kaulantha	EN	O`ahu	X	Lowland wet forest and wet cliff	20
C. oenobarba	EN	Kaua`i	X	Lowland wet forest and wet cliff	5
C. oxybapha	EN	Maui, Moloka`i		Montane mesic and wet forest	10
C. paliku	EN	Kaua`i	X	Wet cliff	5
C. polyantha	EN	O`ahu		Lowland mesic and wet forest	20
C. sessilis	EN	O`ahu		Lowland wet forest	20
C. subumbellata	EN	O`ahu	X	Lowland wet forest and wet cliff	20
C. viridiflora	EN	O`ahu	X	Lowland wet forest and wet cliff	20
C. waiolani	EN	O`ahu		Lowland mesic and wet forest	20
C. crenata	EN	O`ahu		Montane mesic and wet forest	14
C. giffardii	EN	Hawai`i	X	Wet montane forest	15
C. limahuliensis	TH	Kaua`i	X	Lowland wet forest	13
C. munroi	EN	Lana`i, Maui	X	Lowland wet forest	21
C. tintinnabula	EN	Hawai`i	X	Lowland wet forest	15
Delissea rivularis	EN	Kaua`i	X	Montane wet forest	13
Diplazium molokaiense	EN	Maui		Lowland mesic and wet forest	20
Dryopteris crinalis var. podosorus	EN	Kaua`i	X	Montane wet forest	5
Dubautia imbricata imbricata	EN	Kaua`i	X	Lowland wet forest	5
D. kalalauensis	EN	Kaua`i	X	Montane wet forest	5
D. pauciflorula	EN	Kaua`i	X	Lowland wet forest	23
D. plantaginea ssp. humilis	EN	Maui	X	Wet cliff	24
D. plataginea ssp. magnifolia	EN	Kaua`i	X	Wet cliff	5
D. waialealae	EN	Kaua`i	X	Montane wet forest	5
Exocarpos luteolus	EN	Kaua`i	X	Lowland and montane wet forest	13
Gahnia lanaiensis	EN	Lana`i	X	Lowland wet forest	21
Gardenia manii	EN	O`ahu		Lowland mesic and wet forest	20
Geranium arboreum	EN	Maui		Montane wet forest, freshwater streams	24
G. hanaense	EN	Maui	X	Montane wet forest	10
G. hillbrandii	EN	Maui		Facultative, montane mesic, montane wet	10
G. Kauaiense	EN	Kaua`i	X	Montane wet forest	5
G. multiflorum	EN	Maui		Montane mesic and wet forest	24
Gouania vitifolia	EN	Hawai`i, Maui, O`ahu		Lowland dry, mesic, and wet forest, dry cliff	20

Hedyotis cookiana	EN	Hawai`i, Kaua`i		Lowland mesic and wet forest, freshwater stream	23
Hesperomannia arborescens	EN	Maui, Moloka`I, O`ahu		Lowland mesic and wet forest	20
H. arbuscula	EN	Maui, O`ahu		Lowland mesic and wet forest	20
Hibiscus waimeae ssp. hannerae	EN	Kaua`i	X	Lowland wet forest	13
Huperzia mannii	EN	Hawai`i, Kaua`i, Maui		Montane mesic and wet forest	14
H. nutans	EN	Kaua`i, O`ahu	X	Lowland wet forest and wet cliff	20
Isodendrion longifolium	TH	Kaua`i, O`ahu,	X	Lowland mesic and wet forest	20
Keysseria erici	EN	Kaua`i	X	Montane wet forest	5
K. helenae	EN	Kaua`i	X	Montane wet forest	5
Korthalsella degeneri	EN	O`ahu		Lowland wet forest	20
Labordia cyrtandrae	EN	O`ahu		Lowland mesic and wet forest, montane wet forest, wet cliff	20
L. helleri	EN	Kaua`i		Lowland mesic and wet forest, montane mesic and wet forest	5
L. lydgatei	EN	Kaua`i	X	Lowland wet forest and lowland wet shrubland	13, 22
L. pumila	EN	Kaua`i	X	Montane wet forest	5
L. tinifolia var. wahiawaensis	EN	Kaua`i	X	Lowland wet forest	13
Lobelia gaudichaudii ssp. koolauensis	EN	O`ahu	X	Lowland wet forest	20
L. O`ahuensis	EN	O`ahu	X	Lowland wet forest, montane wet forest, wet cliff	20
Lysimachia daphnoides	EN	Kaua`i	X	Montane wet forest	5
L. filifolia	EN	Kaua`i, O`ahu	X	Wet cliff	20
L. iniki	EN	Kaua`i	X	Wet cliff	5
L. maxima	EN	Moloka`i	X	Montane wet forest	16
L. pendens	EN	Kaua`i	X	Wet cliff	5
L. venosa	EN	Kaua`i	X	Wet cliff	5
Melicope balloui	EN	Maui		Montane mesic and wet forest	24
M. christophersenii	EN	O`ahu	X	Montane wet forest and wet cliff	20
M. degeneri	EN	Kaua`i	X	Montane wet forest	25
M. hiiakae	EN	O`ahu	X	Lowland wet forest	20
M. lydgatei	EN	O`ahu		Lowland mesic and wet forest	20
M. makahae	EN	O`ahu		Lowland mesic and wet forest, dry cliff	20
M. munroi	EN	Lana`i, Moloka`i	X	Lowland wet shrubland	12
M. ovalis	EN	Hawai`i, Maui	X	Montane wet forest	11
M. paniculata	EN	Kaua`i	X	Montane wet forest	25
M. puberula	EN	Kaua`i	X	Montane wet forest, Montane bog	25
M. quadrangularis	EN	Kaua`i		Lowland mesic and wet forest	23
M. reflexa	EN	Moloka`i	X	Montane wet forest	16

Myrsine juddii	EN	O`ahu	X	Lowland wet forest	20
M. linearifolia	TH	Kaua`i	X	Lowland wet forest	13
M. mezii	EN	Kaua`i	X	Montane wet forest	5
M. vaccinioides	EN	Maui	X	Montane wet forest	10
Nothocestrum peltatum	EN	Kaua`i		Montane mesic and wet forest	23
Peperomia subpetiolata	EN	Maui	X	Montane wet forest	10
Phlegmariurus nutans	EN	Kaua`i, O`ahu		Montane mesic and wet forest	14
Phyllostegia bracteata	EN	Maui		Lowland wet forest, montane mesic and wet forest, subalpine forest, wet cliff	10
P. hirsuta	EN	O`ahu		Lowland mesic and wet forest, montane wet forest, wet cliff	20
P. hispida	EN	Moloka`i	X	Montane wet forest	26
P. manii	EN	Moloka`i	X	Montane wet forest	16
P. mollis	EN	O`ahu, Maui		Lowland mesic and wet forest	20
P. parviflora var parviflora	EN	O`ahu		Lowland mesic and wet forest, wet cliff	20
P. racemosa	EN	Hawai`i		Montane mesic and wet forest	15
P. renovans	EN	Kaua`i	X	Montane wet forest	5
P. velutina	EN	Hawai`i		Montane dry, mesic, and wet forest	15
P. waimeae	EN	Kaua`i		Montane mesic and wet forest	13
P. warshaueri	EN	Hawai`i	X	Montane wet forest	15
P. glabra	EN	Lanai		Montane mesic and wet forest	21
Plantago princeps var longibracteata	EN	O`ahu	X	Lowland wet forest	20
P. princeps var princeps	EN	Kaua`i, O`ahu		Lowland mesic and wet forest, wet and dry cliff	20
Platanthera holochila	EN	Kaua`i, Maui, Moloka`I, O`ahu	X	Lowland wet forest	20
Platydesma cornuta cornuta	EN	O`ahu	X	Lowland wet forest	20
P. cornuta var. decurrens	EN	O`ahu		Lowland wet forest	20
P. rostrata	EN	Kaua`i		Lowland mesic and wet forest, montane mesic and wet forest, wet cliff	5
Pleomele fernaldii	EN	Lana`i		Lowland dry, mesic, and wet forest, wet and dry cliff	10
P. forbesii	EN	O`ahu		Lowland dry and wet forest, montane wet forest, and wet cliff	20
Poa manii	EN	Kaua`i		Wet cliff	13
P. sandvicensis	EN	Kaua`i	X	Montane wet forest, wet cliff	23
Pritchardia hardyi	EN	Kaua`i	X	Lowland wet forest and wet cliff	5
P. viscosa	EN	Kaua`i	X	Lowland wet forest	13
Psychotria grandiflora	EN	Kaua`i	X	Montane wet forest	5
P. hexandra ssp. oahuensis	EN	O`ahu	X	Lowland wet forest and wet cliff	20
Pteralyxia auaiensis	EN	Kaua`i		Lowland mesic and wet forest	13
P. macrocarpa	EN	O`ahu		Lowland mesic and wet forest, wet and dry cliff	20
Remya mauiensis	EN	Maui		Montane mesic and wet forest	24
Remya montgomeryi	EN	Kaua`i		Mid-elevation mesic and wet forest	23

Sanicula purpurea	EN	O`ahu	X	Lowland wet forest, wet cliff	20
Schiedea helleri	EN	Kaua`i	X	Montane wet forest	13
S. hookeri	EN	O`ahu		Lowland dry, mesic, and wet forest, dry and wet cliff	20
S. kaalae	EN	O`ahu		Lowland mesic and wet forest, wet cliff	20
S. kauaiensis	EN	Kaua`i	X	Montane wet forest	13
S. membranacea	EN	Kaua`i	X	Montane wet forest	13
S. trinervis	EN	O`ahu		Montane wet forest, dry and wet cliff	20
Sicyos alba	EN	Hawai`i	X	Montane wet forest	15
Stenogyne bifida	EN	Moloka`i		Montane mesic and wet forest	16
S. kealiae	EN	Kaua`i		Lowland wet forest, montane mesic forest, dry cliff	5
Tetramolopium capillare	EN	Maui		Montane dry forest, mesic or wet shrubland, wet cliff	24
Tetraplasandra bisattenuata	EN	Kaua`i		Lowland mesic and wet forest	5
T. flynni	EN	Kaua`i		Lowland wet forest, montane mesic and wet forest	5
T. gymnocarpa	EN	O`ahu		Lowland mesic and wet forest, wet cliff	20
Trematolobelia singularis	EN	O`ahu	X	Lowland wet forest and wet cliff	20
Urera kaalae	EN	O`ahu		Lowland mesic and wet forest	20
Viola helenae	EN	Kaua`i		Lowland mesic and lowland wet forest	22
V. lanaiensis	EN	Lana`i		Lowland mesic and wet shrubland	21
V. O`ahuensis	EN	O`ahu	X	Lowland wet forest, wet cliff	20
Wikstroemia villosa	EN	Maui		Lowland wet forest, montane mesic and wet forest	10
Xylosma crenatum	EN	Kaua`i	X	Montane wet forest	23
Zanthoxylum oaahuense	EN	O`ahu	X	Lowland wet forest	20

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