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CHANGES IN MAUNA KEA DRY FOREST STRUCTURE 2000–2014

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ABSTRACT

Changes in the structure of the subalpine vegetation of Palila Critical Habitat on the southwestern slope of Mauna Kea Volcano, Hawaiʻi, were analyzed using 12 metrics of change in māmane (*Sophora chrysophylla*) and naio (*Myoporum sandwicense*) trees surveyed on plots in 2000 and 2014. These two dominant species were analyzed separately, and changes in their structure indicated changes in the forest's health. There was a significant increase in māmane minimum crown height (indicating a higher ungulate "browse line"), canopy area, canopy volume, percentage of trees with ungulate damage, and percentage of dead trees. No significant changes were observed in māmane maximum crown height, proportion of plots with trees, sapling density, proportion of plots with saplings, or the height distribution of trees. The only significant positive change was for māmane tree density. Significantly negative changes were observed for naio minimum crown height, tree height, canopy area, canopy volume, and percentage of dead trees. No significant changes were observed in naio tree density, proportion of plots with trees, proportion of plots with saplings, or percentage of trees with ungulate damage. Significantly positive changes were observed in naio sapling density and the height distribution of trees. There was also a significant increase in the proportion of māmane vs. naio trees in the survey area. The survey methods did not allow us to distinguish among potential factors driving these changes for metrics other than the percentage of trees with ungulate damage. Continued ungulate browsing and prolonged drought are likely the factors contributing most to the observed changes in vegetation, but tree disease or insect infestation of māmane, or naio, and competition from alien grasses and other weeds could also be causing or exacerbating the impacts to the forest. Although māmane tree density has increased since 2000, this study also demonstrates that efforts by managers to remove sheep (*Ovis* spp.) from Palila Critical Habitat have not overcome the ability of sheep to continue to damage māmane trees and impede restoration of the vegetation.

INTRODUCTION

From 14 December 1998 to 24 April 2001, the U.S. Geological Survey conducted vegetation surveys of 504 stations in the dry forest area of Mauna Kea Volcano on Hawaiʻi Island (Banko and Farmer 2014) hereafter referred to as the "2000 survey." From 13 August 2013 to 12 February 2014, the Hawaiʻi Division of Forestry and Wildlife conducted a follow-up survey (hereafter "2014 survey") at 60 stations, replicating the original methodology to look for changes in forest structure in the intervening time. The 2014 survey was focused on the southwestern slope of Mauna Kea, the habitat for the majority of the remaining population of the palila (*Loxioides bailleui*), an endangered endemic bird (Camp *et al*. 2014).

The palila is threatened with extinction primarily because this forest, which has been designated Critical Habitat, has been degraded by introduced sheep (*Ovis* spp.) and other ungulate species over many decades (Banko *et al*. 2009). The sheep population has been culled annually since 1980, and the response of the vegetation has been quantitatively monitored primarily within ungulate exclosures (Scowcroft and Giffin 1983, Reddy *et al*. 2012, Banko *et al*. 2014). The frequency and intensity of drought also has impacted the palila and its habitat since 2000, compounding the damage caused by browsing (Banko *et al*. 2013). Disease and other factors also affect Palila Critical Habitat (Banko *et al*. 2002, 2009), but for the first time, the 2000 and 2014 surveys permit an analysis of vegetation changes outside ungulate exclosures and following a period of severe drought. These results are intended to provide managers with

perspectives on the condition and trajectory of Palila Critical Habitat so that they can evaluate what actions are needed to expedite habitat recovery and protect the palila from extinction.

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METHODS

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Study Area

Mauna Kea is a dormant volcano on Hawaiʻi Island reaching to an elevation of 4,205 m above sea level. The subalpine dry forest surrounds the mountain between 1,800 to 2,900 m elevations. The remaining population of the palila is concentrated on the southwestern slope (Figure 1). The habitat there is a dry forest dominated from 1,800 to 2,200 m elevation by māmane (*Sophora chrysophylla*) and naio (*Myoporum sandwicense*) trees and solely by māmane from 2,200 m to tree line at about 2,900 m (Hess *et al.* 1999). Native shrubs, grasses, and other forbs are scattered throughout the woodland, whereas alien grasses and other herbaceous cover are particularly dense at mid and low elevations (Banko *et al.* 2002).

The subalpine forest of Mauna Kea generally lies above the trade wind inversion, resulting in a cool, dry climate throughout the year. Annual mean temperatures range between 9 and 13°C and are relatively stable, varying more during the day than they do seasonally (Juvik *et al.* 1993). Rainfall averages 511 mm annually and falls mostly during heavy winter storms. Monthly rainfall may vary by two orders of magnitude and other than the winter storms there is no distinct seasonal pattern (Juvik *et al.* 1993). Long-term (58-year) rainfall records from mid elevation on the western slope of Mauna Kea indicate that June receives the least amount of rain at 10–20 mm; July and September–December receive 20–30 mm; February, April, May, and August receive 30–40 mm; and January and March receive 40–50 mm (Juvik *et al*. 1993). Precipitation is not related to elevation in years of normal or higher rainfall, and isohyet maps indicate no clear rainfall gradient on the western slope; however, rainfall decreases with elevation in drier years (Juvik *et al*. 1993). Cloud water intercepted by vegetation ("fog-drip") contributes additional precipitation, resulting in nearly 50% more precipitation falling through tree canopies to the ground during droughts (Juvik and Nullet 1993).

Prospective Power Analysis

Prior to beginning the 2014 survey we conducted a preliminary power analysis to identify the sampling effort needed to detect a biologically meaningful difference in five potential changes in forest structure based on māmane trees only: a 10% change in the probability a tree suffered bark stripping, a 10% change in the probability a tree suffered browse damage, a 33% change in the number of māmane recruits <0.5 m tall, and both a 20 cm and a 30 cm change in minimum crown height. We simulated the results of a new survey by sub-sampling the stations from the 2000 survey on the southwestern slope of Mauna Kea at varying sampling efforts. We also accounted for smaller sampling plots (20 × 20 m rather than 40 × 40 m) and then adjusted the new sample by the biologically meaningful difference. We then compared the two samples with either logistic regression or a two-sample t-test as appropriate. The process was repeated 10,000 times, and power was estimated as the fraction of tests that were statistically significant at a 0.05 Type I error rate.

The power to detect a change using the smaller 20 x 20 m plots varied from 10 to 100 stations (Figure 1). At least 90% power was accrued at 60 stations for three of five test variables, and because 30 cm was deemed an acceptable threshold for detecting changes in minimum crown height ("browse line"), 60 stations was chosen as the target effort for the 2014 survey.
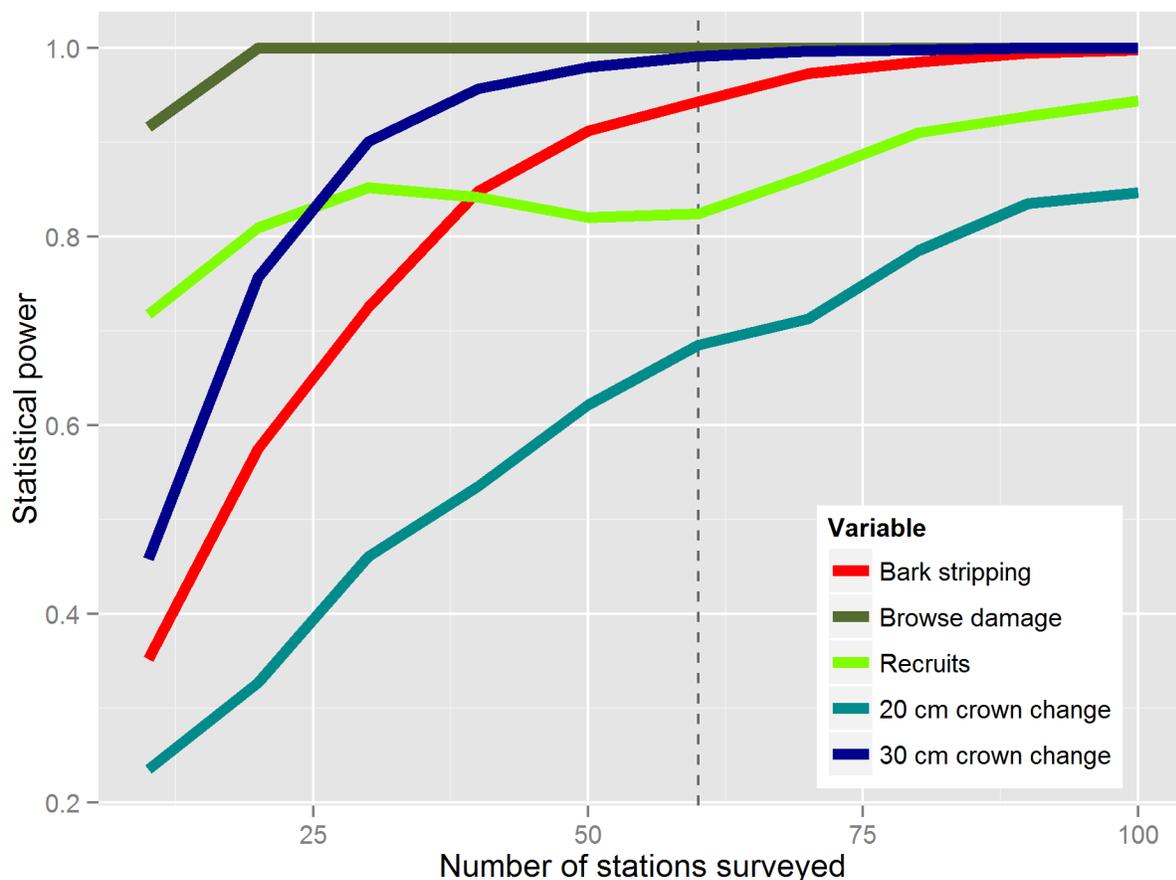
Figure 1. Power to detect a change as a function of sampling effort. Simulation-based estimates of power to detect a change in five different measures of forest structure with a Type I error rate of 0.05, based on the variation present in the original 2000 survey. The vertical dashed line represents a survey effort of 60 stations.

Sampling Design

The 2000 survey effort is described in Banko and Farmer (2014). They surveyed 40 × 40 m plots at 504 sampling stations on 32 transects around the dry forest zone of Mauna Kea, counting woody plants, measuring trees, and conducting point-intercept surveys of all ground cover.

The 2014 survey effort was constrained to core palila habitat on the southwest slope of Mauna Kea (Figure 2). To select stations for the 2014 survey, the 358 core habitat stations (as defined by Camp *et al*. 2014) from the 2000 survey were put in random order and the first 60 stations (as determined in the power analysis) selected. Because the random selection left gaps in spatial coverage (e.g., some transects had no stations selected) the random selection was then manually adjusted in an attempt to achieve a more even distribution. Stations in areas that, by chance, had a high density of points were dropped in favor of the next station in order from a transect without points. We assumed there was no bias introduced in the process and treated
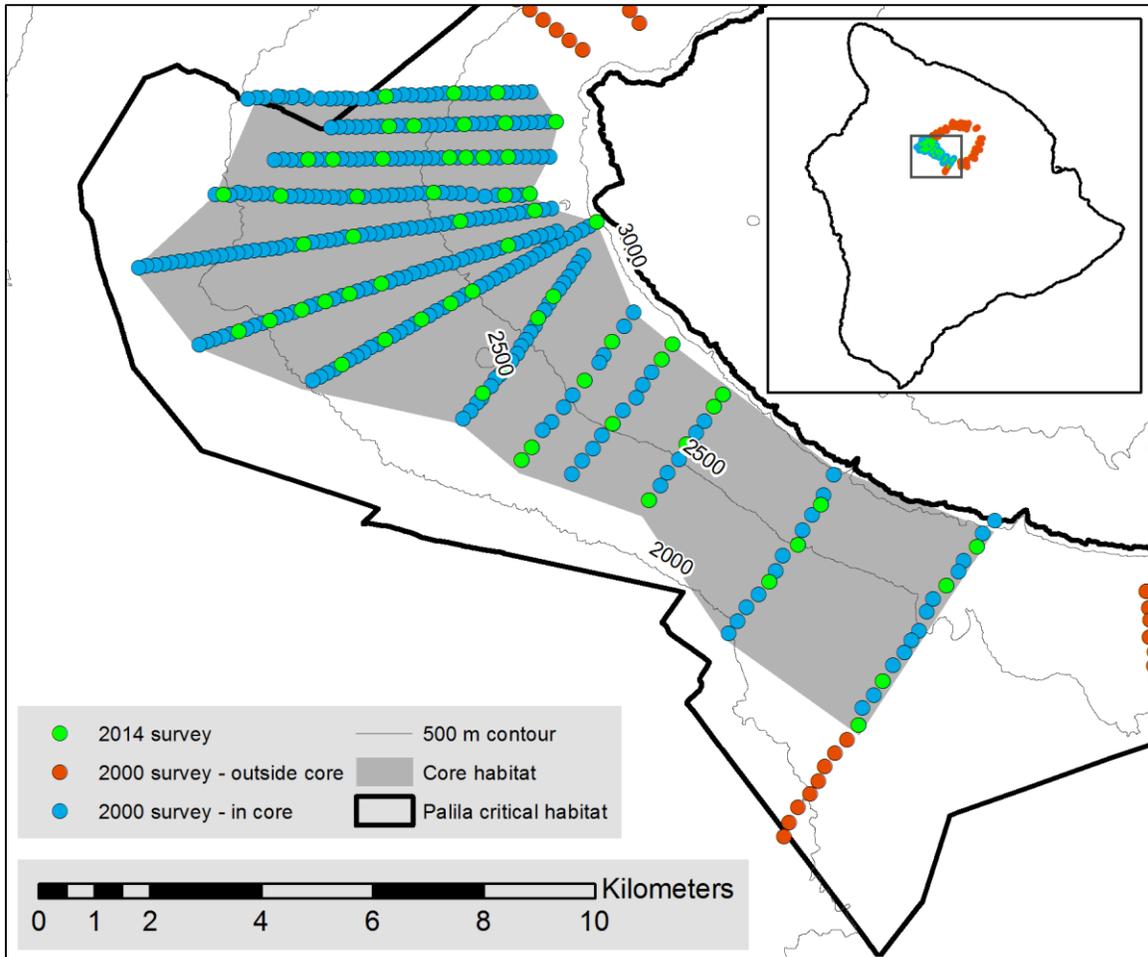
Figure 2. Survey stations and core palila habitat on Mauna Kea. The map shows stations surveyed in 2000, both inside and outside core palila habitat. Stations re-surveyed in 2014 are shown in green. The inset map shows the survey area in relation to Hawaiʻi Island.

the 2014 survey as a simple random sample of the core palila habitat, comparable with the systematic survey of 2000.

Statistical Comparisons

Most hypotheses were two-sample comparisons between the population surveyed in 2000 and in 2014. Two-sample t-tests are appropriate where the sample populations meet the test assumptions, primarily normal error around the sample mean. Non-parametric Wilcoxon tests are less powerful than parametric tests, but they allow for a comparison where some parametric assumptions are violated, such as significant non-centrality (skew) or truncation. Non-parametric tests do have underlying assumptions but they are met so long as the distribution of observations in the two samples has approximately the same shape.

Density plots were used to depict the observed distributions with the measured quantity represented along the horizontal scale and the relative proportion of measurements with that value along the vertical scale. The exact value of the vertical scale is unimportant for comparing

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similar distributions, as it varies with the range of the horizontal scale. Instead, the shape of the curve (e.g., bell-like vs. skewed) is used to determine if a parametric t-test or a non-parametric Wilcoxon test was appropriate, and whether the shapes of the distribution were roughly similar (e.g., both unimodal vs. unimodal and bi-modal) as required by the Wilcoxon test.

Tests of similar categorical distribution (e.g., number of stations with māmane trees present) were compared with either a χ^2 with a Yates' continuity correction for 2 × 2 tables or a Fisher's exact test for larger tables. Tests of a binomial probability (e.g., the probability that a tree suffered ungulate damage) were modeled as a binomial regression with a single factor predictor. All tests were conducted in R version 3.1.1 (R Core Team 2014).

The 2000 surveys recorded all tree species found in plots, the 2014 survey recorded māmane, naio, and a selection of other native species (other tree species were only 5% of the total 2000 survey). For purposes of this analysis, only māmane and naio trees were considered, as they are by far the dominant species and both provide food resources to palila.

Comparisons Between Surveys

Minimum crown height
Heavy ungulate presence often results in a "browse line" on trees, marking the highest point animals can reach to browse the vegetation. The minimum crown height of māmane and naio trees was recorded in both surveys at the lower limit of the 95% estimate of the vegetated canopy volume. Treating all trees measured in a survey as a sample, we compared the lower crown height with a two-sample test.

Tree height
Height of a tree can often be treated as an indicator of tree maturity, size, and the resources available to foraging birds. The height of māmane and naio trees was recorded in the 2014 survey. In the 2000 survey, trees less than 2 m tall were recorded as three categories: 0–0.5, 0.5–1.0, and 1.0–2.0 m. To compare heights of all trees in both samples, the categories were treated as being the middle of the range: 0.25, 0.75, and 1.5 m. Treating all trees measured in a survey as a sample, we compared tree height with a two-sample test.

Canopy area
Canopy area provides a measure of the ground cover, shade, and area of fog intercept provided by a tree. While most tree canopies are irregular in shape, we approximated the area of each tree's canopy as an ellipse. The longest dimension of the canopy (projected onto a horizontal plane) was measured (the major axis, *a*) along with the longest canopy width on an axis perpendicular to the first (the semi-major axis, *b*). The elliptical area of the canopy was then calculated as п·a·b. The areas were compared with a two-sample test.

Canopy volume
The vegetated volume of a tree may be a better indicator of the amount of resources/habitat available to birds. The volume of each tree in each survey was calculated by multiplying the canopy area (as described above) by the thickness of the canopy determined as the difference between the tree height and the minimum crown height. Eleven trees, where the recorded minimum crown height was greater than the tree height (presumably due to measurement or recording error), were excluded from the analysis. The areas were then compared with a two-sample test.

Tree density
The density of trees on the landscape can be treated as a measure of a change in forest structure as well as the total number of trees available to provide resources to birds. The number of trees of each species ≥2 m tall per 40 × 40 m plot was used as a measure of tree density. For the 2014 survey stations, which were smaller (20 × 20 m plots), the number of trees per plot was multiplied by 4 to make them comparable. Two-sample tests were used to compare densities between the two surveys.

Proportion of survey stations with trees
Not all survey plots contained trees. The change in the probability of finding trees at a random spot on the landscape is a measure of a change in forest structure. We compared the relative proportion of stations in each survey where māmane and naio trees were present. The 2000 survey stations were 40 × 40 m plots, as opposed to the 20 × 20 m plots in the 2014 surveys. However the 2000 survey plots were subdivided into four 40 × 10 m sub-plots (labeled 1–4), so to compensate for the differing plot size we used only sub-plot number 1 at each 2000 survey station. We used χ^2 tests of homogeneity to test for similar distributions between the surveys.

Sapling density
The presence of young trees on the landscape is an important indicator of forest health. The lack of recruits indicates long-term non-viability. The numbers of saplings counted in each survey plot were compared with a two-sample test, after multiplying the 2014 survey counts by 4 to account for the smaller sampling plot.

Proportion of survey stations with saplings
Similarly to tree distribution across the landscape, a change in the distribution of saplings can be used as an indicator of forest structure. We compared the relative proportion of stations in each survey where māmane and naio saplings were present. We compensated for the differing plot size by using only sub-plot number 1 at each survey station. We used χ^2 tests of homogeneity to test for similar distributions between the surveys.

Māmane / naio proportion
A change in the relative prevalence of the two major species could be indicative of a change in forest structure, especially the expansion of one at the detriment of another, or in response to climate change. We tested the relative proportion of māmane and naio trees in the two surveys. Each station was treated as an independent sample, and the ratio of māmane and naio trees was tested with binomial regression to estimate the probability of a tree being māmane rather than naio (given it is one of the two).

Height distribution of trees
A change in the distribution of tree height classes could indicate recruitment from the under-2-m saplings or overall growth in the population in the intervening 14 years. Because trees less than 2 m were recorded as height categories (rather than exact heights) in the 2000 survey only four categories (2–4, 4–6, 6–8, and >8 m) were used in the comparison. The relative distribution for each species was tested with a Fisher's exact test of homogeneity.

Percentage of trees with ungulate damage
Ungulates can damage trees, reducing their vitality and ability to provide food resources for palila, or killing them outright. In both surveys māmane and naio trees (≥2.0 m tall) were scored for the presence of animal sign: digging under the tree, fresh droppings, bark stripping, or browse damage. Trees with fresh browse damage or bark stripping were classified as having

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ungulate damage, while the other two factors were classified as ungulate sign and not considered in this analysis. Each survey station was treated as a separate sample of the proportion of trees affected by ungulate damage, and a binomial regression was used to test for a difference of the probability of a tree being damaged between the two surveys.

Percentage of dead trees
A change in the proportion of dead trees is another potential indicator of a change in forest structure. Trees were recorded as being alive or dead. We tested for a difference in the proportion of dead trees between the two surveys using binomial regression. Each survey station was treated as an independent sample of some probability that a tree was dead, rather than alive, and we tested if that probability was different between the two surveys.

RESULTS

Comparisons Between Surveys

Minimum crown height
Māmane minimum crown height averaged 0.74 m in 2000 and 1.48 m in 2014. Naio minimum crown height averaged 0.91 m in 2000 and 1.52 in 2014. The distribution of heights was right-skewed (Figure 3) and truncated at zero, indicating a non-parametric test is preferred. A Wilcoxon test showed significant differences for both species ($P < 0.001$ in both cases).

Tree height
Māmane trees averaged 2.23 m in height in 2000 and 2.20 m in 2014; naio trees averaged 3.82 m in 2000 and 3.35 m in 2014. The distribution of heights was right-skewed and truncated at 0 m (Figure 4), indicating a non-parametric test was appropriate. A non-parametric Wilcoxon test showed the difference in māmane height to be not statistically significant ($P = 0.969$), but the decrease in naio tree height was significant ($P < 0.001$).

Canopy area
The mean canopy area of māmane trees was 47.1 m^2 in 2000 and 40.4 m^2 in 2014. Naio canopy area decreased from 58.6 m^2 to 43.8 m^2. For both species, the right-skewed, truncated data led us to prefer a non-parametric test. Decreases in canopy area were significant for both species (māmane $P = 0.022$; naio $P < 0.001$).

Canopy volume
As with canopy area, the crown areas were right-skewed and truncated at zero (Figure 6). The mean canopy volume of māmane trees averaged 186.0 m^3 in 2000 and 132.0 m^3 in 2014. Naio canopy volume decreased from 245.0 m^3 to 143.3 m^3. For both species, the right-skewed, truncated data indicated a non-parametric test, and non-parametric Wilcoxon tests were significant for both species ($P < 0.001$).

Tree density
The mean number of māmane trees per survey plot increased from 18.4 in 2000 to 47.7 in 2014. Naio density ranged from 20.0 to 39.0. Because tree density showed a strong right skew and truncation at zero (Figure 7) a non-parametric Wilcoxon test is the appropriate comparison. The increase in māmane tree density was statistically significant ($P < 0.001$), but the difference in naio density was not significant ($P = 0.137$).
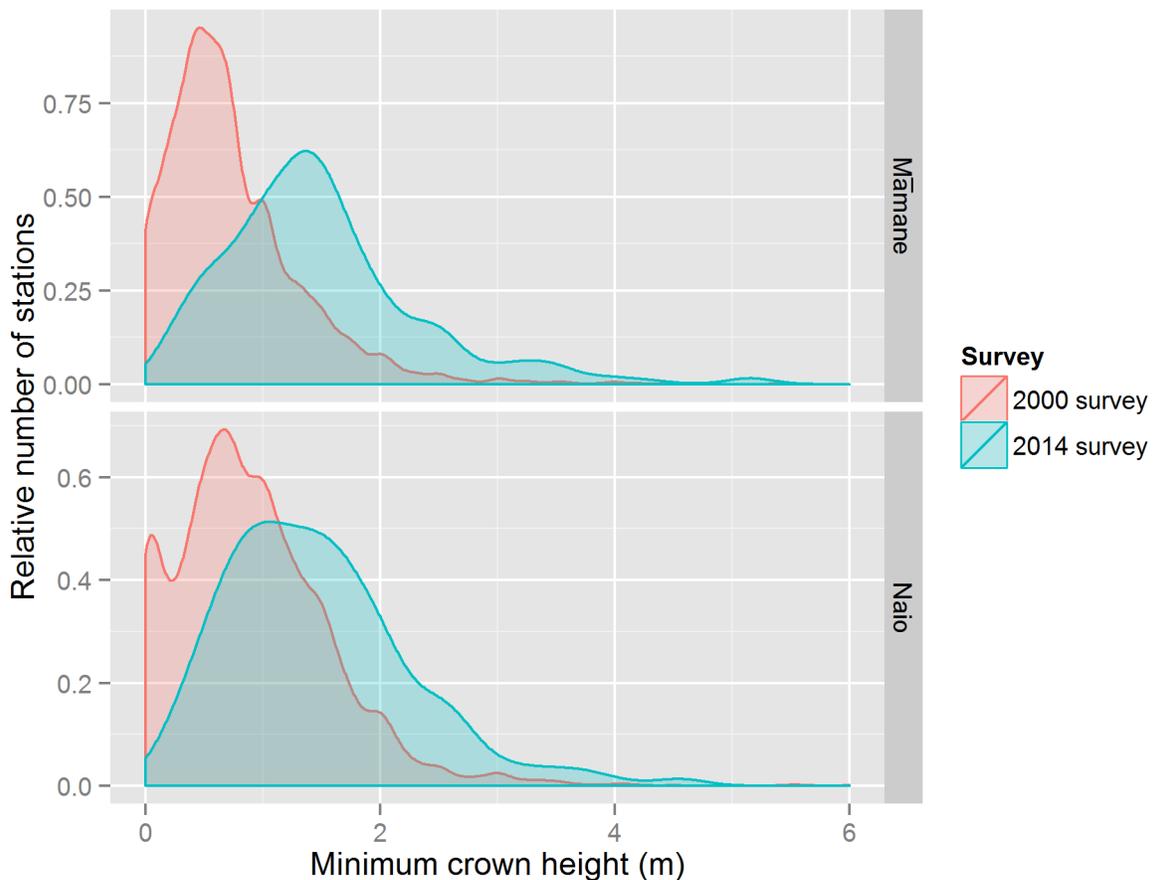
Figure 3. Relative density of minimum crown heights for māmane and naio trees in the 2000 and 2014 surveys.

Proportion of survey stations with trees
Māmane trees were recorded on 302 of 358 stations (84%) in 2000 and 56 of 60 stations (93%) in 2014. Naio trees were recorded on 175 of 358 (49%) stations in 2000 and 35 of 60 (58%) stations in 2014. χ^2 tests of homogeneity with Yates' continuity correction did not reveal significant differences in the distribution between surveys for either māmane ($P = 0.102$) or naio ($P = 0.224$).

Sapling density
The number of māmane saplings per survey station averaged 4.7 in 2000 and 8.8 in 2014. Naio numbers increased from 20.4 to 39. Because of the large number of stations with no saplings and positive skew (Figure 8), we used a non-parametric Wilcoxon test. This test showed no difference for māmane sapling density ($P = 0.127$), but a significant increase in naio sapling density ($P = 0.040$).

Proportion of survey stations with saplings
Māmane saplings were recorded on 141 of 358 stations (39%) in 2000 and 28 of 60 stations (47%) in 2014. Naio saplings were found on 211 of 358 (59%) stations in 2000 and 35 of 60
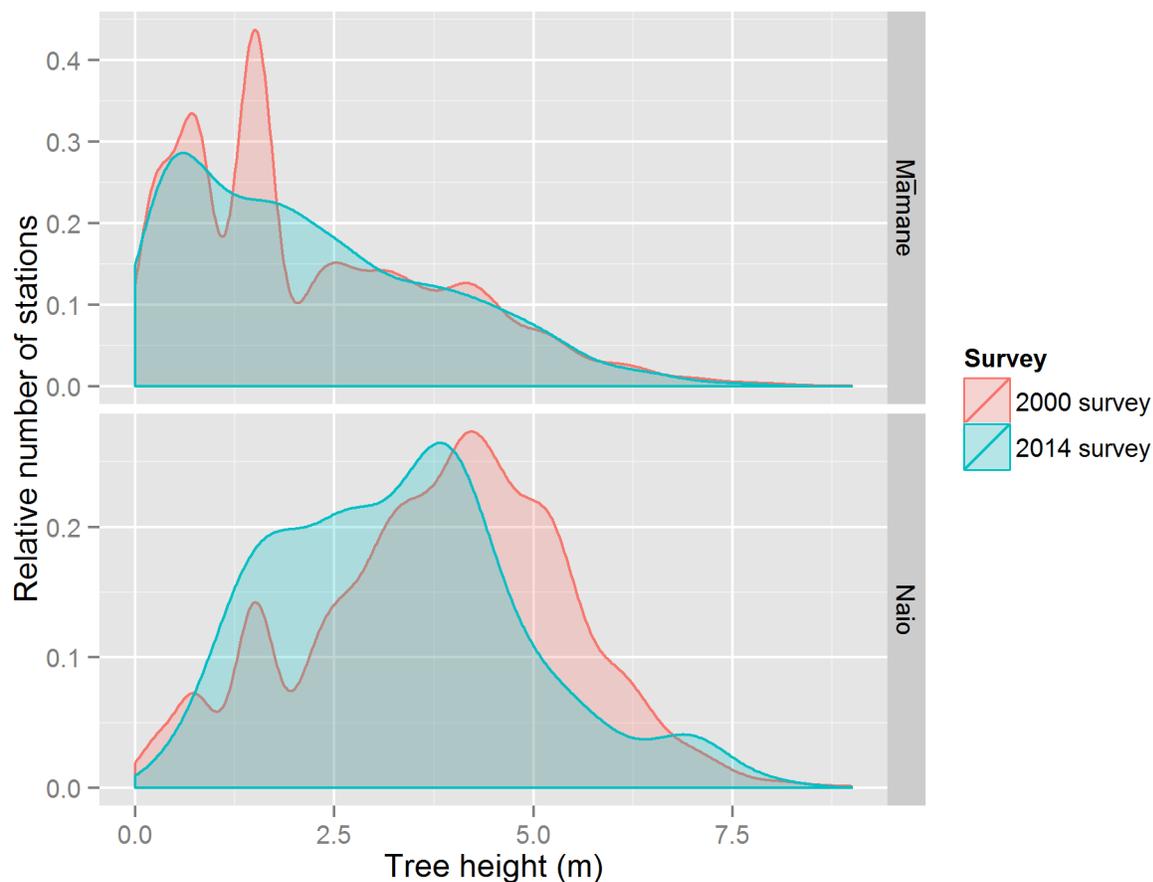
Figure 4. Relative distribution of tree height for māmane and naio in the 2000 and 2014 surveys. Sharp peaks in the 2000 survey curves are the result of heights of trees less than 2 m tall being recorded as categories during that survey.

(58%) stations in 2014. χ^2 tests of homogeneity with Yates' continuity correction did not reveal significant differences in the distribution between surveys for either māmane ($P = 0.357$) or naio ($P = 1.000$[1]).

Māmane / naio proportion
The proportion of māmane trees in the population increased from 47.7% in 2000 to 55.5% in 2014. Binomial regression revealed the increase to be statistically significant ($P < 0.001$).

Height distribution of trees
Small trees (2–6 m tall) predominated in the 2000 and 2014 surveys (Table 1). Examination of the residuals (Table 2) suggested an increase in the number of māmane trees in the 2–4 m category with slight decreases in the remaining height categories, however this change was not

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[1] Naio proportions were so similar that Yates' continuity correction rounded down to no difference.
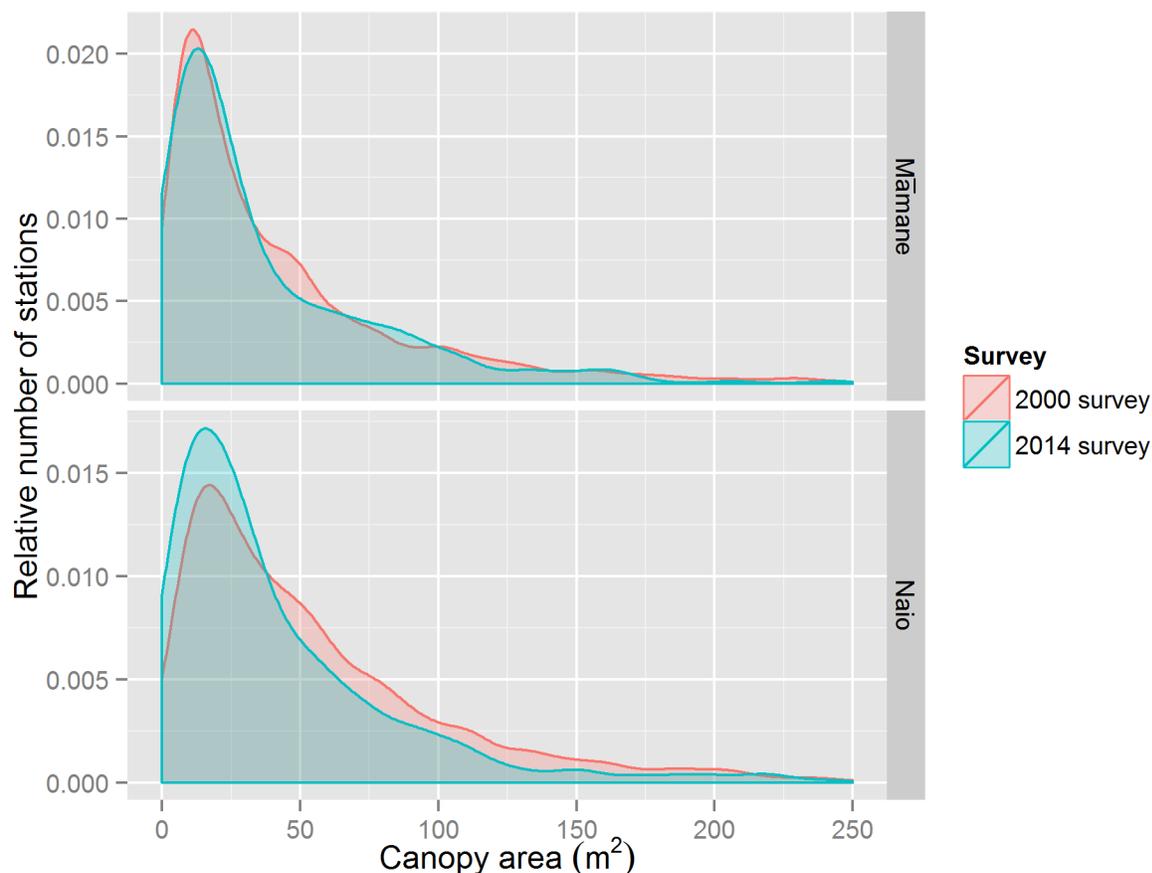
Figure 5. Relative density of canopy areas for māmane and naio trees in the 2000 and 2014 surveys.

significant (Fisher's exact test; $P = 0.181$). Naio trees increased in the 2–4 m category in 2014 while decreasing in the 4–6 m height category (Fisher's exact test; $P < 0.001$).

Percentage of trees with ungulate damage
For māmane trees, the mean proportion of surveyed trees with ungulate damage was 8.4% in the 2000 survey and 12.2% in the 2014 survey. For naio the proportion of damaged trees was 6.7% and 9.1%. Binomial regression showed that the increase in the probability of a tree being damaged was significant for māmane ($P = 0.015$) but not significant for naio ($P = 0.0502$).

Percentage of dead trees
For māmane trees, 1,095 of 6,573 trees (17%) were dead in 2000, and 163 of 715 trees (23%) were dead in 2014. For naio trees the proportions were 1,055 of 7,181 (15%) and 254 of 585 (43%), respectively. Binomial regression found that the increase in the proportion of dead trees was statistically significant ($P < 0.001$) in both cases.
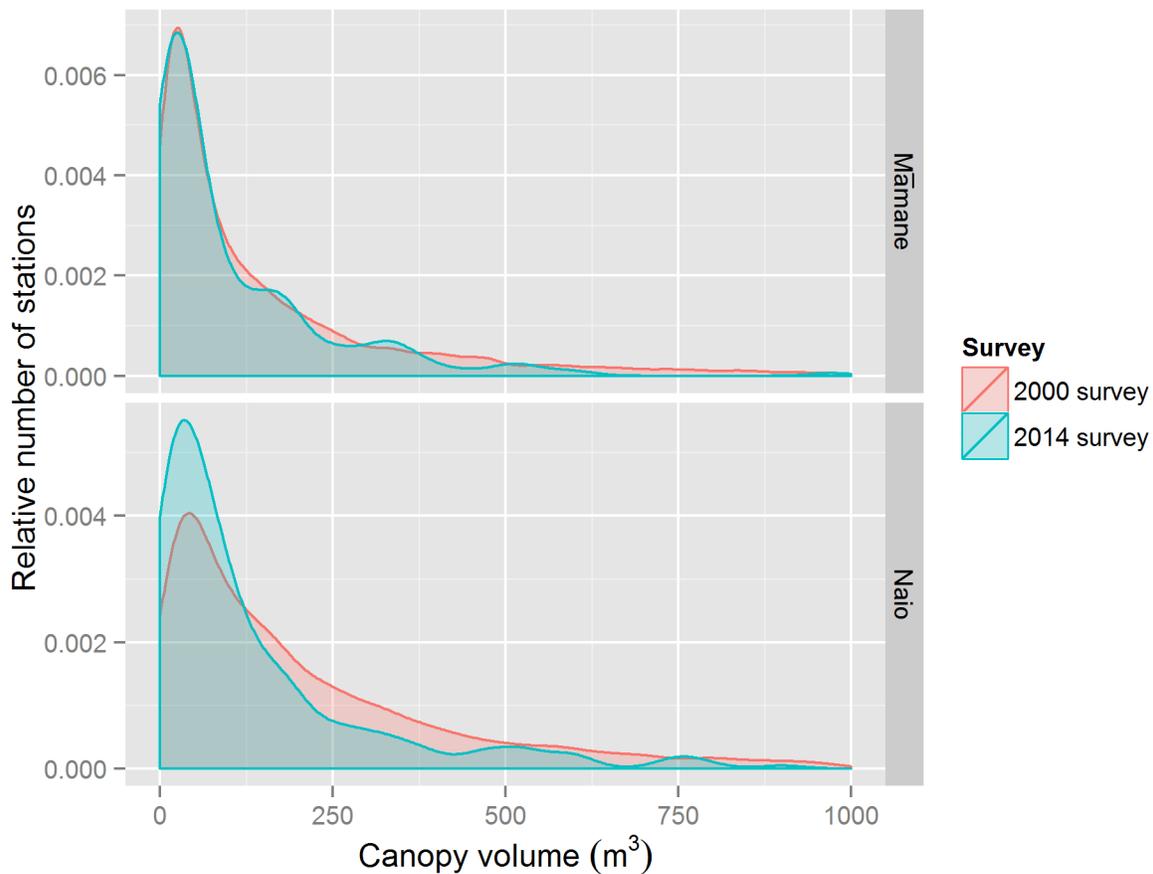
Figure 6. Distribution of tree canopy volume for māmane and naio trees in the 2000 and 2014 surveys.

DISCUSSION

We compared 12 metrics characterizing possible changes in forest structure between the 2000 and 2014 vegetation surveys on the southwest slope of Mauna Kea. Eleven of these metrics were separately applied to māmane and naio trees. Of the 22 metrics that can be generalized to reflect a positive or negative change in forest structure (Table 3). Note that "positive" and "negative" refer to general forest health (e.g., an increase change in minimum crown height would be a negative change for the forest structure). Ten metrics would be classified as negative, 3 as positive, and 9 as not significantly different across the two surveys. The final metric, the relative prevalence of māmane vs. naio trees showed significant increase in the proportion of māmane trees.

There are a variety of factors potentially affecting the structure of the Mauna Kea dry forest (Banko *et al.* 2013), complicating interpretation of the observed changes. The 2000 survey was conducted during a period of relatively sparse rainfall, whereas the 2014 survey was conducted after an extended drought (Banko *et al.* 2013) had been broken by significant rainfall.
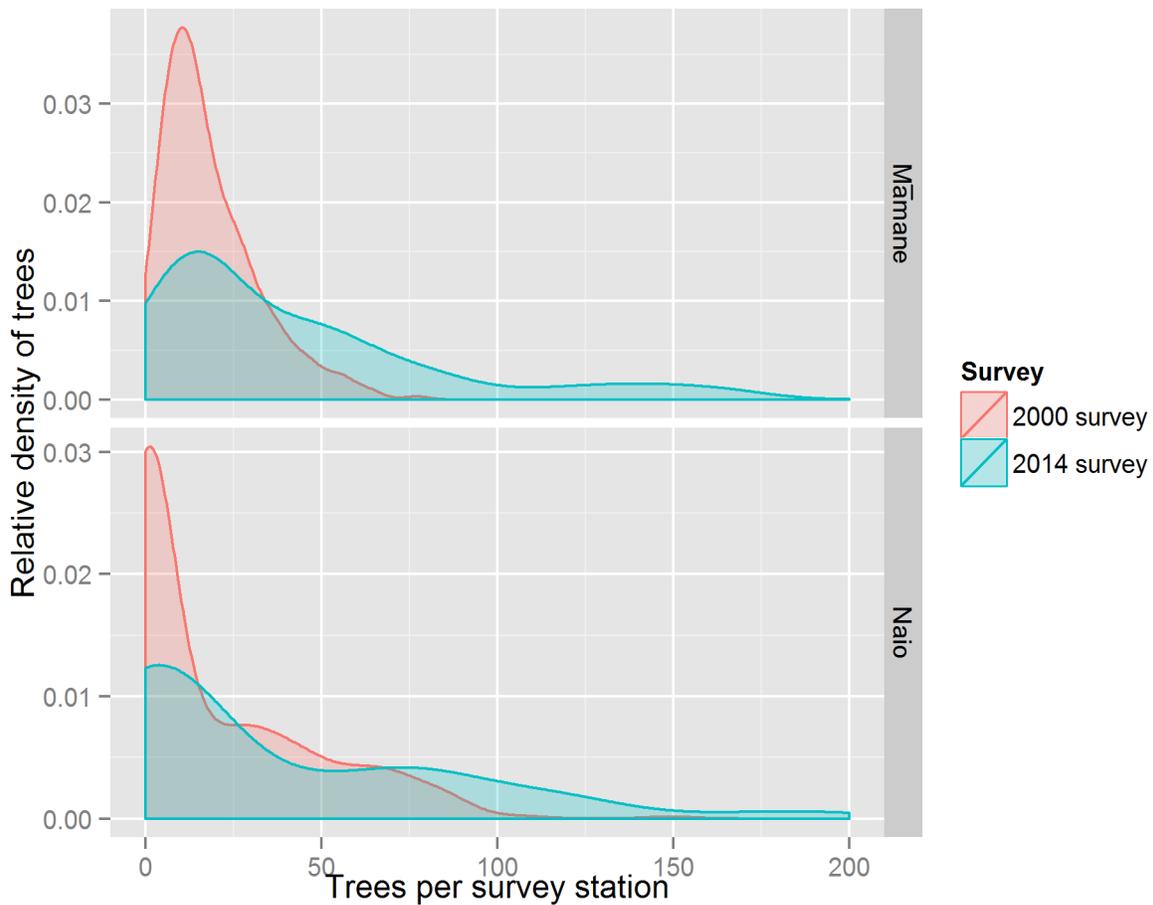
Figure 7. Relative number of trees per station for māmane and naio trees in the 2000 and 2014 surveys.

Ungulates continued to occupy the forest during the period between surveys (though numbers have been significantly reduced beginning in 2013). The only metric with an unambiguous cause, the probability of a tree displaying ungulate damage, increased significantly for māmane trees between the surveys, but there was no significant change for naio trees. The remaining effects upon forest structure are confounded with possible drought damage. Although comparing the two surveys does not allow us to account separately for the potential effects of ungulates, drought, and other factors on changes in vegetation structure, future studies could be designed to distinguish between factors if potential interactions among the drivers of vegetation dynamics were considered.

The minimum crown height increased (i.e., foliage is higher above the ground) for both species across the two surveys, suggesting greater ungulate browsing, age-related shifts in tree architecture (e.g., increased prevalence of tall, upright trees that produce few branches close to the ground), or increased shading and subsequent thinning of lower branches due to the denser distribution of trees. We observed an increase in the incidence of ungulate damage to māmane trees, but not to naio trees. Māmane tree height did not change, but naio tree height
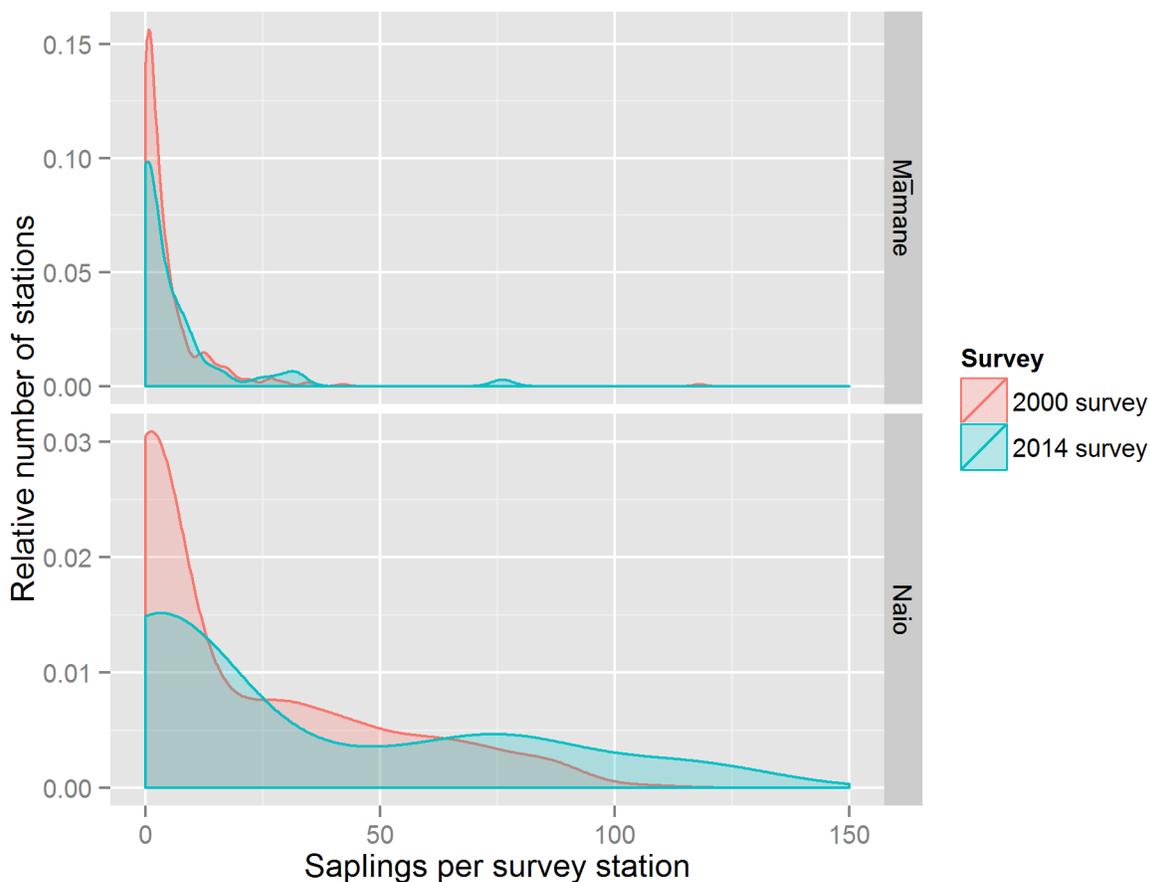
Figure 8. Relative densities of saplings per survey plot in 2000 and 2014 surveys for māmane and naio.

Table 1. Number of māmane and naio trees in four height (m) categories in 2000 and 2014.

Height	Māmane		Naio	
category	2000	2014	2000	2014
2–4	3,457 (59%)	215 (64%)	2,352 (40%)	254 (56%)
4–6	2,048 (35%)	106 (32%)	2,933 (50%)	158 (35%)
6–8	348 (6%)	15 (0.5%)	560 (10%)	37 (8%)
8+	32 (1%)	0 (0%)	32 (0.5%)	1 (0.2%)

decreased. The density of māmane (but not naio) trees increased. Because of these mixed results, the cause of the increase of minimum crown height in māmane and naio is unclear.

Changes in mean tree height could be due to tree growth (positive change), an increase of short (2–4 m) trees in the population (negative change; potentially due to the transition of a

Table 2. Standardized residuals of māmane and naio trees in four height categories in 2000 and 2014. Their value shows the relative degree of departure from the null hypothesis of identical distributions across height categories and survey.

Height	Māmane		Naio	
category	2000	2014	2000	2014
2–4	-0.28	1.18	-1.40	5.04
4–6	0.23	-0.96	1.15	-4.17
6–8	0.25	-1.04	0.23	-0.84
8+	0.31	-1.31	0.24	-0.88

Table 3. Summary of positive and negative interpretations of measured metrics. Dashes indicate metrics that were not statistically significantly different between the 2000 and 2014 surveys.

Metric	Māmane	Naio
Minimum crown height	negative	negative
Tree height	-	negative
Canopy area	negative	negative
Canopy volume	negative	negative
Tree density	positive	-
Proportion of survey stations with trees	-	-
Sapling density	-	positive
Proportion of survey stations with saplings	-	-
Height distribution of trees	-	positive
Percentage of trees with ungulate damage	negative	-
Percentage of dead trees	negative	negative

large cohort of saplings into trees), or high mortality of tall trees (negative change). Māmane tree height did not change significantly, and though there was a suggestion of an increase in māmane trees that were 2–4 m tall, the difference was not significant. Naio tree height decreased, possibly due in part to the increase of small (2–4 m) trees. Māmane and naio tree mortality increased between the two surveys, and greater mortality of larger trees could reduce mean tree height, but the mortality data were not analyzed with respect to tree height.

Canopy area and volume, both of which exhibited negative changes in māmane and naio, are a function of tree height, and changes could indicate shifts in the proportions of size classes. We did not detect a significant change in the height distribution of māmane trees, so losses in canopy area and volume may have been influenced by drought-induced mortality of branch tips (affecting both canopy area and volume), browsing (mostly affecting volume), or other factors such as disease and insect infestation. The size distribution of naio shifted to the smallest size class, which may explain some of the decrease in canopy area and volume. Additionally, the naio thrips (*Klambothrips myopori*), a pest that invaded subalpine Mauna Kea sometime after 2009 (Conant *et al.* 2009), may have contributed to the reduction of naio canopies.

Changes in māmane and naio tree and sapling density and the proportion of plots with each size category were generally not significant. Nevertheless, the changes that were recorded are especially difficult to interpret because they depend mainly on sapling growth and survival and on tree survival, which could be affected by many factors. Sapling density, which increased for naio but not māmane, and occurrence on plots could change based on the rate of transition to the tree size class and recruitment of seedlings to the sapling size class, neither of which was measured. Naio tree density did not change, despite an increase in the number of 2–4 m trees. On the other hand, māmane tree density increased significantly, even though the size distribution did not change significantly. Sapling and tree density would be expected to eventually reach an asymptote due to competition even in the absence of ungulates, drought, disease, and other factors; nevertheless, forest stands on Mauna Kea are unlikely to experience overcrowding for decades, based on low forest cover across the landscape currently (Hess *et al*. 1999, Banko and Farmer 2014, Banko *et al*. 2014).

Changes in the height distribution of trees indicate interactions between regeneration and tree growth and survival. With low mortality due to ungulates, drought, disease, competition, and other factors, the height distribution should eventually skew toward taller trees as regeneration slows and trees fill in the open spaces. Differences in the height distribution of māmane were not significant, although more naio were recorded in the 2–4 m size class in 2014.

The subalpine vegetation of Mauna Kea is highly dynamic due to interactions between ungulates, drought, and other factors (Hess *et al*. 1999; Banko *et al*. 2013, 2014; Banko and Farmer 2014). Recovering the palila depends largely on the restoration of its critical habitat on the southwestern slope of Mauna Kea, and vegetation monitoring provides a vital means for tracking the effects of management actions on habitat quality. The results of the 2000 and 2014 surveys indicate that the condition of Palila Critical Habitat has improved in terms of an increase in māmane density, but overall the forest has deteriorated in many important ways, including increased browsing damage to māmane trees. Following the surge in ungulate removal in 2013–2014, we expect that habitat conditions will begin to improve more dramatically. Nevertheless, habitat recovery will likely be slow if the frequency and intensity of drought continues as it has since 2000 and unless measures are taken to quickly and permanently eliminate sheep and accelerate the increase of māmane and other native vegetation.

LITERATURE CITED

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