Remote analysis of biological invasion and the impact of enemy release

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Abstract. Escape from natural enemies is a widely held generalization for the success of exotic plants. We conducted a large-scale experiment in Hawaii (USA) to quantify impacts of ungulate removal on plant growth and performance, and to test whether elimination of an exotic generalist herbivore facilitated exotic success. Assessment of impacted and control sites before and after ungulate exclusion using airborne imaging spectroscopy and LiDAR, time series satellite observations, and ground-based field studies over nine years indicated that removal of generalist herbivores facilitated exotic success, but the abundance of native species was unchanged. Vegetation cover <1 m in height increased in ungulate-free areas from 48.7% ± 1.5% to 74.3% ± 1.8% over 8.4 years, corresponding to an annualized growth rate of $\lambda = 1.05 \pm 0.01 \text{ yr}^{-1}$ (median ± SD). Most of the change was attributable to exotic plant species, which increased from 24.4% ± 1.4% to 49.1% ± 2.0%, ($\lambda = 1.08 \pm 0.01 \text{ yr}^{-1}$). Native plants experienced no significant change in cover (23.0% ± 1.3% to 24.2% ± 1.8%, $\lambda = 1.01 \pm 0.01 \text{ yr}^{-1}$). Time series of satellite phenology were indistinguishable between the treatment and a 3.0-km^2 control site for four years prior to ungulate removal, but they diverged immediately following exclusion of ungulates. Comparison of monthly EVI means before and after ungulate exclusion and between the managed and control areas indicates that EVI strongly increased in the managed area after ungulate exclusion. Field studies and airborne analyses show that the dominant invader was *Senecio madagascariensis*, an invasive annual forb that increased from <0.01% to 14.7% fractional cover in ungulate-free areas ($\lambda = 1.89 \pm 0.34 \text{ yr}^{-1}$), but which was nearly absent from the control site. A combination of canopy LAI, water, and fractional cover were expressed in satellite EVI time series and indicate that the invaded region maintained greenness during drought conditions. These findings demonstrate that enemy release from generalist herbivores can facilitate exotic success and suggest a plausible mechanism by which invasion occurred. They also show how novel remote-sensing technology can be integrated with conservation and management to help address exotic plant invasions.

Key words: exotic; functional trait; Hawaii; imaging spectroscopy; invasive species; LiDAR; MODIS; remote sensing; resource-use efficiency; tropical dry forest.

INTRODUCTION

A widely held generalization for the success of exotic plants is escape from natural enemies, a hypothesis known as the enemy-release hypothesis (ERH [Keane and Crawley 2002]). It is based on three assumptions. Enemies regulate plant populations, reduced enemy regulation facilitates population growth, and enemies have a greater impact on native than on exotic species (Keane and Crawley 2002). Although all three assumptions are controversial, the third assumption is the most fundamental to ERH. It follows from the observation that enemies can be either specialists or generalists, and that specialist enemies are unlikely to be introduced to

novel regions with their host species. The hypothesis assumes that native plants are regulated by both specialist and generalist enemies, whereas exotics are regulated only by generalists. Hence, the hypothesis predicts that generalist enemies have a greater impact on native competitors that are also burdened by specialists than on exotic plants lacking specialist enemies. The converse prediction from these assumptions is that removal of generalist enemies from an invaded region should facilitate the success of exotics more strongly than native plants, because natives should still be regulated by their own specialist enemies.

Understanding factors responsible for exotic success at relevant spatial scales is important to conservation and ecosystem management. Biological invasions, disturbance, and movement of species at higher trophic levels are three ecological processes that operate at spatial scales larger than typical field studies. They

impact both native and exotic species, and cut across levels of ecological organization by influencing populations, communities, and ecosystems (Vitousek et al. 1987, D'Antonio and Vitousek 1992, Asner and Vitousek 2005, Asner et al. 2009). Inability to observe and respond to these processes at appropriate scales will often fail to achieve management objectives (Cabin et al. 2000, Weller et al. 2010). Innovative approaches are required to confront these challenges.

We conducted a large-scale experiment to quantify impacts of exotic herbivore removal on plant growth and performance, and to test whether removal of a generalist herbivore facilitated exotic success. Our approach integrates airborne imaging spectroscopy and light detection and ranging (LiDAR) with time series of satellite phenology and field studies over a nine-year period. We focused on two large areas of subalpine tropical drylands on the island of Hawaii, dominated by the endemic tree species *Myoporum sandwicense* and *Sophora chrysophylla* (*Myoporum–Sophora* dry forest, MSDF). One area of 4.28 km^2 was fenced in 2001, followed by removal of exotic feral goats (*Capra hircus*) in 2003. Grazing and browsing by goats is a preeminent threat to dryland ecosystems in Hawaii, facilitating biological invasion and a persistent grass–fire cycle (Stone et al. 1992, Cabin et al. 2000). The second area is an unmanaged control site of 3.0 km^2 in which ungulate numbers were not manipulated. Both are of high conservation value as the last tracts of MSDF in the world, and are designated as "critical habitat" for the endangered Palila honeycreeper bird, *Loxoides bailleui* (Pratt et al. 1998).

To place these tracts of MSDF in the context of regional patterns and demonstrate the sensitivity of remote observations to vegetation structure and condition, we also examined two other endemic vegetation communities that occur in the same area. *Metrosideros polymorpha* woodlands (MPW) are intact native dry forest. *Dodonaea viscosa* shrublands (DVS) have a history of disturbance by fire, which has facilitated establishment of exotic grass species and extensive biological invasion (i.e., the grass–fire cycle [D'Antonio and Vitousek 1992]).

METHODS

Site description

The analysis was conducted in the Pohakuloa Training Area (PTA), a 439-km^2 subalpine dryland ecosystem on the island of Hawaii. Annual precipitation from 2000 to 2009 was 171, 221, 226, 259, 949, 451, 497, 414, 228, and 274 mm/yr, respectively (daily records from weather station near 215 505E, 2 176 702N, UTM 5 N). Mean elevation is 1883 m and ranges from 1107 to 2877 m. The study site contains 24 unique vegetation communities and substrates from at least 13 volcanic eruptions. Volcanic substrates include both pahoehoe and a'a types of lava and volcanic cinder cones. We consider three vegetation communities that together

accounted for 52% of the landscape. MPW dominate on Mauna Loa substrates <3.0×10^3 yr old (Stemmermann and Ihsle 1993). They are intact native communities, and sometimes support understories with *D. viscosa* and *Styphelia tameiameiae*. DVS are on Pleistocene Mauna Loa and Mauna Kea flows that support extensive invasion by exotic plant species, including *Pennisetum setaceum* and *Senecio madagascariensis*. Ages of Pleistocene flows in this area are poorly constrained, but have been reported between 10.0×10^3 and 65.0×10^3 yr old. MSDF are dryland tree communities on substrates that are $0.75–10.0 \times 10^3$ yr old from Mauna Loa and Mauna Kea volcanoes.

The Kipuka Alala forest fragment of MSDF has been the focus of intensive management activity. Because exotic ungulates threaten regeneration of *S. chrysophylla* and other native and endangered plant species (Cuddihy and Stone 1990, Cabin et al. 2000), the area was fenced in 2001 to exclude exotic feral goats (*C. hircus*), which were subsequently hunted inside the fenced area. Systematic efforts are now underway to quantify ungulate density and movement, but a recent herding operation forced 1.8×10^3 animals out of a 2.1-km^2 management unit that was recently fenced (Kipuka Kalawamauna), corresponding to a mean density of 0.8 goats/ha^{-1}. The Kipuka Alala forest fragment was declared ungulate-free in 2003 and no reintroductions have occurred.

Experimental design

We used a combination of satellite and aircraft remote sensing to quantify impacts of ungulate removal on plant growth and performance. The approach is based on before–after control–impact methodology (BACI) that is modified for analysis of large areas (e.g., Underwood 1994, Oksanen 2001). It integrates data from multiple sources to characterize impacts of ungulate removal. Although there are numerous measurements in impact and control sites from both field and remote observations, the comparison is based fundamentally on two large samples in MSDF: a fenced site of 4.28 km^2 in which ungulates were excluded was compared to a 3.0-km^2 control site where ungulate numbers were not manipulated.

High-resolution surface cover mapping

The Carnegie Airborne Observatory (CAO) is an integrated airborne remote sensing and analysis system developed to acquire spatially detailed and extensive measurements of structural and biochemical properties of vegetation (Asner et al. 2007). In this analysis, it combined the airborne visible and infrared imaging spectrometer (AVIRIS) with a LiDAR sensor and three-dimensional navigation technology (i.e., the CAO Beta system [Asner et al. 2007]). We used height measurements from LiDAR to quantify vertical and horizontal vegetation structure, and reflectance observations from the imaging spectrometer to estimate the fractional

cover of photosynthetic vegetation (PV), nonphotosynthetic vegetation (NPV), and barren volcanic substrate (B) using methods detailed by Asner and Heidebrecht (2002) and Asner et al. (2005).

Airborne data were collected on 7 January 2008, which is 3–4 years after ungulate removal and during a relatively dry period in the context of 9-year EVI time series from satellite observations (see Fig. 2). The LiDAR system was configured to record the locations of up to four reflecting surfaces for every emitted laser pulse at 1.1-m laser spot spacing. Horizontal and vertical accuracy of the LiDAR system is discussed in detail in Asner et al. (2007). Laser ranges were combined with navigation information to determine the vertical and horizontal locations of reflecting surfaces. To estimate canopy height aboveground, LiDAR elevation measurements were processed to identify which laser pulses were likely to have penetrated vegetation and reached the ground surface. These points were then used to interpolate a raster digital terrain model (DTM) for the ground surface. The remaining points were used to interpolate a digital surface model (DSM) for the vegetation canopy (Fig. 1). Subtraction of the DTM from the DSM produced a model of canopy height aboveground (digital canopy model, DCM). Because the DSM and DCM estimate the height of the upper canopy, variability in canopy heights is related to differences in vegetation height and the openness of the canopy. The elevation models were generated using pixels of 2.2 m side length. Subsequent analyses were performed directly on the elevation models.

Low-resolution vegetation phenology

To quantify changes through time, we used satellite observations from the NASA Moderate Resolution Imaging Spectroradiometer (MODIS). At our Hawaiian study site, each MODIS pixel has a 463-m side length, and thus represents 21.4 ha of ground surface. Data were processed as 8-day image composites using MODIS product MOD09A1 from 26 February 2000 to 26 February 2009, and thus include 414 unique temporal observations. Occasional observations in some pixels are missing due to apparent cloud cover or volcanic haze, and one observation day is missing entirely (observation day 169 in 2001). All of the analyses that follow are based on subsets of pixels without missing data on the given observation date (i.e., missing values were ignored).

We used the enhanced vegetation index (EVI) to quantify vegetation phenology (Huete et al. 2002). EVI is a ratio between near-infrared and visible reflectance, providing a metric of vegetation greenness. It leverages the high reflectance of leaf tissues in near-infrared (NIR) wavelengths and low reflectance in the visible spectrum (Asner 1998, Huete et al. 2002). To identify forest structural or physiological sources of variation in the MODIS EVI time series, we used LiDAR height measurements to partition vegetation into 1-m vertical

height classes within the extent of each MODIS pixel. Each height class is a horizontal slab of forest whose dimensions are equal to the extent of a MODIS pixel, and whose thickness is 1 m. This analysis allowed us to quantify the distribution of vegetation height within each MODIS pixel, and to relate detailed biophysical properties of the landscape observed using the CAO to seasonal and longer-term patterns quantified by MODIS. We calculated the proportion of vegetation in each 1-m height class as follows:

$$V_{i,h} = \frac{\sum_{j=1}^{n_i} PV_{j,h} + NPV_{j,h}}{n_i} \qquad (1)$$

(i.e., the sum of the proportion of photosynthetic and nonphotosynthetic vegetation in MODIS pixel i and height class h, divided by the total number of CAO pixels in MODIS pixel i). To determine whether a particular vertical height class was correlated with patterns in seasonal and long-term phenology, we correlated fractional vegetation cover in each height class with the maximum EVI value over the 9-year record and with the EVI value closest in time to the date of airborne data collection (7 January 2008). Statistical significance of correlation coefficients was determined using a nonparametric bootstrap with 2000 iterations (Clark 2007).

We focused on two large areas of MSDF with distinct management histories. In fenced MSDF, we selected 20 contiguous MODIS pixels, representing 4.28 km^2. The sampled area is in the north of the Kipuka Alala fence unit. We selected this area because it is accessible in the field (sites in the south require helicopter access) and because we suspected that contemporary biological invasion occurred there during the previous decade. Our objective was to determine whether the timing of invasion corresponded with the impact of ungulate exclusion and removal. We excluded pixels that were not of the target community type. Mean elevation is 1757 ± 56 m (mean ± SD). In unfenced MSDF, we selected 14 contiguous MODIS pixels, representing 3.0 km^2. Mean elevation in unfenced MSDF is 2028 ± 24 m. Combined, the impact and control sites include most MSDF that remains in large enough fragments to be observed by MODIS. In MPW we selected 12 MODIS pixels representing 2.6 km^2 (mean elevation is 1594 ± 46 m), and in DVS we selected 25 MODIS pixels covering an extent of 5.4 km^2. Mean elevation in DVS is 1517 ± 68 m. We attempted to ensure that selected MODIS pixels represented unadulterated samples of the target community type for which field studies were underway.

Preliminary analyses of satellite EVI time series indicated that differences between impacted and control sites were expressed primarily during dry periods. We quantified this relationship by calculating the difference in mean EVI between the managed and control sites and the first derivative of the mean EVI time series for the managed area. The derivative was computed by

subtracting the EVI value at time t from the subsequent observation at time $t + 1$. We examined the correlation coefficient between the difference in mean EVI and the rate of change in vegetation greenness. A negative correlation coefficient would indicate that differences are expressed during periods of water limitation.

Field measurements

We conducted field studies to identify sources of quantitative phenology dynamics and changes in vegetation cover. Eighteen 25×10 m plots were sampled in 2001 and 2009 using point-intercept methods. All plots were randomly located and samples were collected using a 2-m measuring pole. In each plot, data were collected in 2001 using three transects placed along the sides and center of each plot (i.e., transects were 25 m long, and separated by 5 m). We determined vegetation presence along each transect in 0.5-m horizontal increments. For this study, vegetation was "present" if it touched the measuring pole at a height <1 m above ground. This same procedure was repeated in 2009, except that horizontal sample distances were 1 m, rather than 0.5 m. Below we discuss the implications of different sample sizes between years. Unmanaged MSDF was not sampled in 2001. Therefore we identified five locations for field sampling in unmanaged MSDF where data were collected from a single transect of 75 m in 1-m increments. Thus, field samples are based on 18 plots in managed MSDF, MPW, and DVS that were sampled in 2001 and 2009, and 5 plots in unmanaged MSDF that were sampled in 2009. There were 153 points per plot in 2001 and 78 points per plot in 2009.

We measured the water content of living leaves during a one-year period. Four species were sampled that are common in subalpine dryland ecosystems in Hawaii to quantify species contributions to ecosystem-level vegetation greenness: *D. viscosa, M. sandwicense, P. setaceum,* and *S. madagascariensis.* From 26 August 2008 to 22 July 2009, we collected leaf samples from 10 individuals for each species every 2–3 weeks from sites with similar substrates. Samples were collected for each species between 10:00 and 14:00, and were not collected during rainfall. Each sample contained ~5 g of leaf tissue, and most sample dates included 10 replicates per species. Wet mass was measured immediately after collection. Dry mass was measured after drying in a forced-air oven for ≥48 h at 70°C. Relative leaf water content was calculated as (wet mass–dry mass)/dry mass. Negative values were treated as zeros.

Quantifying vegetation dynamics

We conducted four analyses to quantify changes in species composition using plot data. Each analysis quantified changes in fractional vegetation cover between 2001 and 2009. In the first analysis, we calculated the realized population growth rate for each species across all transects in each plot. This allowed us to determine which species had significant changes in cover
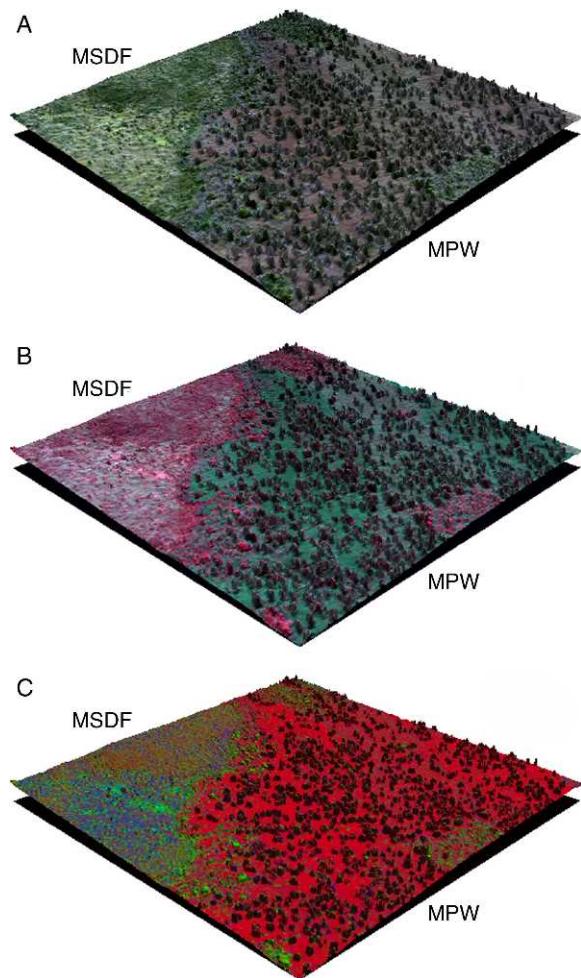

Fig. 1. Imaging spectroscopy and LiDAR show the vertical distribution of vegetation in a tropical dryland ecosystem. Each image is a 1-km^2 sample of tropical dry forest in Hawaii mapped at 2.2-m resolution. Data show samples of a managed area dominated by *M. sandwicense* and *S. chrysophylla* dry forest (MSDF) and adjacent *M. polymorpha* woodland (MPW). (A) The top image is a natural color composite resembling a traditional aerial photograph. (B) The middle image is color-infrared, and shows regions of high vegetation cover using NIR reflectance (pale reds and pinks). (C) The bottom image was processed to quantify photosynthetic vegetation (PV; green), nonphotosynthetic vegetation (NPV; blue), and barren substrate (red). Effects of substrate age and biological invasion are clearly distinguishable between MSDF and MPW.

in at least one plot. The second analysis pooled information across transects and plots to assess which species had significant changes among three community types. The third analysis was designed to test whether density-dependent population dynamics were influencing the local assembly process and outcome of biological invasions (Fargione et al. 2003). We grouped plant species into three functional types and asked whether there was a negative relationship between the change in fractional cover for a given functional type and its cover in 2001. A negative relationship is evidence of negative

TABLE 1. Fractional vegetation cover in 10 vertical height classes.

Vegetation type	LiDAR height class (m)										
	<1	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	>9	Total
MPW	31.4	2.0	1.8	1.7	1.4	1.1	0.8	0.5	0.3	0.3	41.3
MSDF (managed)	49.2	3.2	2.0	0.9	0.3	0.1	0.0	0.0	0.0	0.0	55.9
MSDF (control)	54.9	2.7	2.4	2.5	1.6	0.7	0.2	0.0	0.0	0.0	65.1
DVS	73.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	73.2

Notes: Numbers are the percentage of vegetation cover of photosynthetic and nonphotosynthetic vegetation from airborne imaging spectroscopy for subalpine tropical drylands in Hawaii. Communities differ in total vegetation cover, but across communities most vegetation is <1 m in height.

density dependence. The three functional types were forbs, C3 grasses and sedges, and C4 grasses and sedges. Finally, we compared changes in fractional vegetation cover among native and exotic species in managed MSDF. A complete list of species, their functional types and relative abundances is in Appendix A.

We quantified fractional cover of vegetation and barren ground in 2001 and 2009 using the multinomial distribution (Clark 2007). Multinomial probabilities correspond to traditional interpretations of fractional cover, which is calculated by dividing the number of observations for each species by n. However, we depart from the traditional approach for four reasons. First, it allows ready assessment of precision in fractional cover estimates. Second, it is straightforward to account for differences in sample size between years. Third, uncertainty in cover estimates can be propagated through statistical computations. Finally, it allows us to deal with zeros that are inherent in fractional cover data. For example, a species that was unobserved in a given plot was absent from that plot, but did not have a strictly 0% chance of occurring. Estimates of precision enable a test of the null hypothesis that species (or functional types) and barren ground did not change in cover. We estimated multinomial probabilities in a Bayesian framework using uninformative Dirichlet priors (Clark 2007). Unless otherwise stated, estimates are medians from the conditional posterior for each fractional cover parameter and the corresponding Bayesian standard error from 2000 simulations (Clark 2007).

To quantify changes in fractional cover, we calculated the realized population growth rate (Caswell 2000):

$$\lambda_{k,i} = \frac{\theta_{2,k,i}}{\theta_{1,k,i}} \quad (2)$$

where $\theta_{t,k,i}$ is the parameter estimate at time t for class k and iteration i of the conditional posterior distribution. Classes correspond to species or functional types. If λ_k is not significantly different from 1, it indicates that no significant change occurred. If $\lambda_k > 1$ there has been an increase in fractional cover for class k, and $\lambda_k < 1$ indicates a decrease. Values of λ_k are reported as annualized rates (Caswell 2000). This does not assume λ_k was constant over the duration of the study, but instead places all λ_k on the same scale to facilitate comparison. Tests of significance were computed by

calculating the 95% Bayesian confidence interval (Gelman et al. 2004, Clark 2007). To test whether there is evidence of negative density dependence among functional types, we estimated λ_k for each functional type in each plot, and calculated the linear relationship between λ_k and fractional cover in 2001. Statistical significance and standard errors of regression parameters were assessed by computing the 95% Bayesian confidence interval (Gelman et al. 2004, Clark 2007).

RESULTS

Field studies and remote observations indicate that managed areas were invaded by exotic plant species following exclusion of ungulates and a large precipitation event. Because our conclusions about biological invasion and its functional consequences depend on the sensitivity of remote observations to plant structure and condition, we first summarize canopy structure and condition in MSDF, MPW, and DVS from satellite observations, airborne imaging spectroscopy, and LiDAR, and then describe management impacts in MSDF.

Canopy structure and condition

Vegetation communities showed large differences in remotely sensed fractional vegetation cover and phenology (Figs. 1 and 2, Table 1). Managed areas in MSDF contained 56% vegetation cover, with remaining areas covered by exposed rock or soil substrates. Unmanaged control sites in MSDF had 65% vegetation cover. Enhanced vegetation index (EVI) time series in MSDF responded to recent precipitation events (Fig. 2). In contrast, MPW are on young volcanic substrates with little to no soil development. Fractional vegetation cover was 41%. EVI time series in MPW revealed a regular annual pattern that was largely decoupled from the magnitude of precipitation events. This is consistent with previous studies of water use among canopy trees, which indicate that canopy individuals can access deep water resources that may be well buffered from irregular precipitation inputs (Cordell and Sandquist 2008). DVS were extensively vegetated, as fractional vegetation cover was 73%. DVS have a history of fire disturbance, which has facilitated establishment of exotic grass species and a persistent grass–fire cycle. Observations of vegetation greenness in DVS indicate rapid green-up
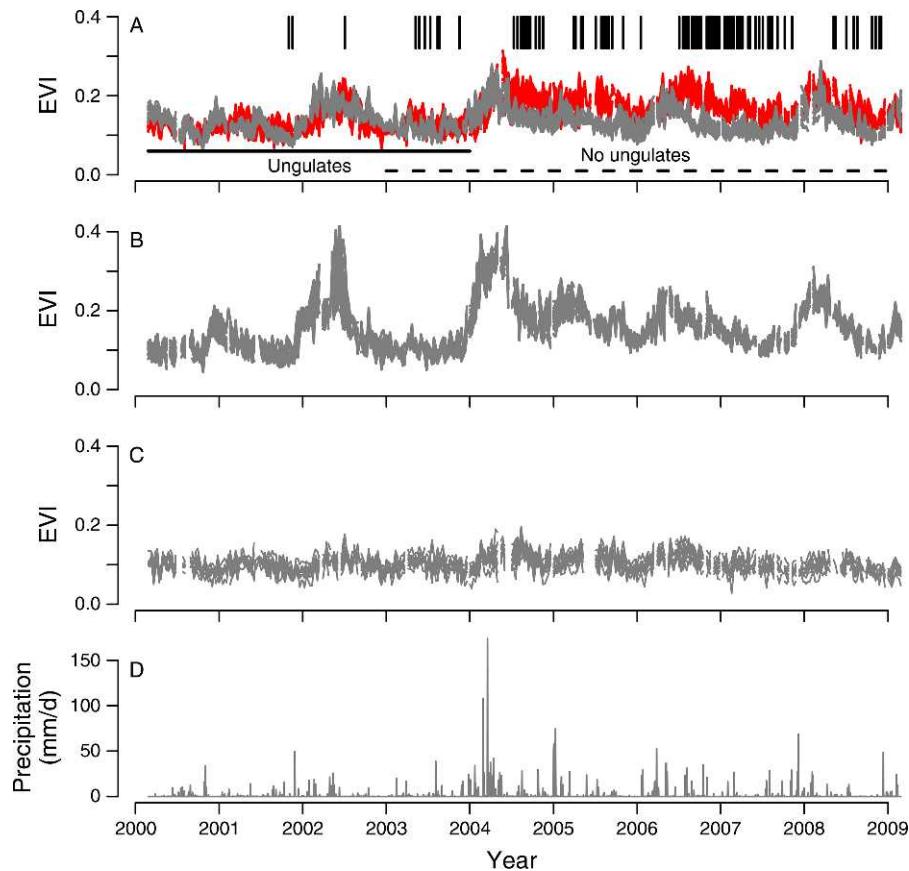
FIG. 2. Enhanced vegetation index (EVI) time series from MODIS for three vegetation communities. The data represent (A) *M. sandwicense* and *S. chrysophylla* dry forest (MSDF), (B) *D. viscosa* shrubland (DVS), (C) *M. polymorpha* woodland (MPW), and (D) daily precipitation. Panel A contrasts a 4.28-km^2 fenced area (red lines) in which exotic ungulate herbivores were removed and excluded in 2003 (indicated by the transition from solid to dashed lines, just above the axis) with a 3.0-km^2 control site (gray lines) where ungulate numbers were not manipulated. Solid and dashed horizontal lines overlap because the date when the last ungulate was exterminated is not precisely known. Vertical bars above the data are days when distributions of EVI in managed and control sites did not overlap.

events characteristic of grass phenology in dryland systems (Fig. 2 and Elmore et al. 2005).

Despite broad differences in species composition and fractional vegetation cover, 90% of vegetation was <1 m in height throughout the 439-km^2 landscape. This conclusion is based on partitioning proportions of PV and NPV measured using imaging spectroscopy into 1-m vertical compartments using canopy height measurements from LiDAR. In MSDF, fractional vegetation cover <1 m in height was 49% and 55% in managed and control sites, corresponding to 88% and 84% of vegetated surface area (Table 1). Because MPW are on historic lava flows still undergoing primary succession, fractional cover <1 m in height was 31%. This is 76% of the total vegetation cover in MPW. In DVS, fractional cover <1 m in height was 73%, which represents >99% of the vegetated surface area (Table 1).

Observations of satellite phenology were strongly correlated with vegetation cover <1 m in height (maximum EVI vs. fractional cover, $r = 0.918$, $P <$ 0.001, $n = 2044$), but the strength of this relationship broke down at higher canopy positions (Fig. 3). There was a similar positive relationship between EVI and vegetation cover using the EVI observation closest in time to the date of airborne spectroscopic measurements (EVI vs. fractional cover <1 m in height, $r = 0.912$, $P <$ 0.001, $n = 2037$; Appendix B). Taken together, analyses of canopy phenology and three-dimensional structure and function of tropical dry-forest canopies indicate that broad differences exist in the quantity, type, and vertical distribution of vegetation among three community types. Satellite-derived EVI depends linearly on fractional vegetation cover, and thus EVI time series in this dryland system are tracking the quantity of vegetation <1 m in height.

Management impacts in Myoporum–Sophora *dry forest*

Comparison of EVI time series between managed and control sites in MSDF indicates that the managed area experienced an abrupt increase in vegetation greenness
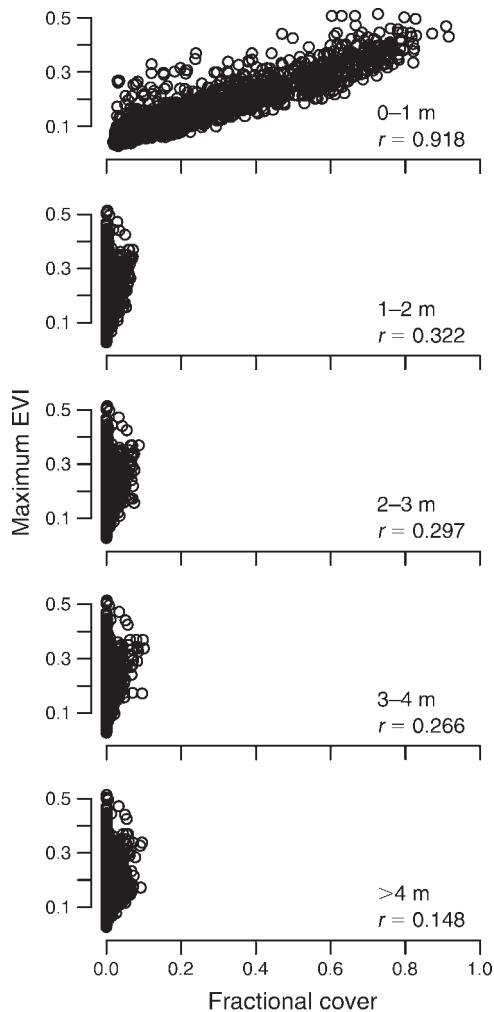
FIG. 3. Relationships between fractional vegetation cover and maximum enhanced vegetation index (EVI) from MODIS over nine years. Each point is from a single MODIS pixel 21.4 ha in area. Vegetation cover within MODIS pixels was quantified using airborne imaging spectroscopy and partitioned among height classes using LiDAR. Most of the variability in maximum EVI can be attributed to vegetation <1 m in height.

in 2004 following exclusion of ungulates (Fig. 2). This is apparent as a bifurcation among EVI time series in managed and control sites that appeared in 2004 and persisted for most of the duration of the study. Daily distributions of EVI were different in 10 out of 146 nonmissing observation days prior to 2004, but in 73 of 181 days after. The proportion of nonoverlapping days was 5.9 times greater after 2004. Most differences were expressed during periods of water limitation (Fig. 2, correlation between difference in mean EVI between managed and control sites and the rate of change in mean EVI for the managed area; $r = -0.286$, $P < 0.001$, $n = 370$). Comparison of monthly EVI means before and after ungulate exclusion and between the managed and control areas indicates that EVI strongly increased in the managed area after ungulate exclusion (Appendix C).

Plot-based field studies confirmed that fractional vegetation cover <1 m in height increased in the managed area from 48.7% ± 1.5% to 74.3% ± 1.8% (mean ± SD) over 8.4 years, corresponding to an exponential annualized growth rate of $\lambda = 1.05 \pm 0.01$ yr^{-1}, which is significantly different from zero growth (95% CI = 1.04–1.06 yr^{-1}). However most of the change was attributable to exotic plant species, which increased from 24.4% ± 1.4% to 49.1% ± 2.0%, ($\lambda = 1.08 \pm 0.01$ yr^{-1}, 95% CI = 1.07–1.10 yr^{-1}). In contrast, native plants experienced no significant change in cover (23.0% ± 1.3% to 24.2% ± 1.8%, $\lambda = 1.01 \pm 0.01$ yr^{-1}, 95% CI = 0.98–1.03 yr^{-1}). The dominant invader was S. madagascariensis, an invasive nongraminoid herb recently introduced to the Hawaiian Islands. This species was present in 2001, but not detected in plot samples because of its rarity. It now represents 14.7% ± 1.4% fractional cover across all plots in managed MSDF ($\lambda = 1.89 \pm 0.34$ yr^{-1}, 95% CI = 1.55–2.81 yr^{-1}, $n = 6$). Several other exotic and native species had localized changes in cover, but no other species changed significantly in all plots in managed MSDF. Notably, S. chrysophylla, a dominant tree species that is browsed heavily by goats, had no significant change in fractional cover in any plot (all CI contained 1), and M. sandwicense decreased significantly in one plot (95% CI = 0.638–0.932, all remaining CI contained 1). The persistent and extensive increase in vegetation cover in managed MSDF cannot therefore be attributed to regeneration of endemic dry-forest trees and is instead due almost completely to increases in exotics. In contrast, unmanaged MSDF had smaller changes in quantitative phenology dynamics (Fig. 2; Appendix C), and field studies indicated that S. madagascariensis occupied a very small fraction of vegetation cover in unmanaged MSDF (1.4% ± 0.5%; Appendix A).

To confirm that invasion by S. madagascariensis was responsible for changes to EVI dynamics in managed MSDF, we measured plant traits in the field. Since EVI at the scale of a MODIS pixel is sensitive to both leaf area index and functional properties of plant tissues (Asner 1998, Huete et al. 2002), vegetation with high canopy water content can influence EVI signals. This is especially true in low-LAI environments like PTA, where LAI, leaf water content, and PV are strongly interdependent (Asner et al. 2005). Although most of the variation in EVI is attributable to fractional vegetation cover <1 m in height, remaining variation is likely driven by functional plant traits such as LAI and canopy water (Asner 1998, Asner et al. 2005). Measurements of leaf water content in dominant species indicate that S. madagascariensis has greater concentrations of leaf water than other plant species during wet conditions, but lower water content during dry periods, and demonstrated capacity to abruptly increase water content (Fig. 4). These characteristics were expressed in satellite phenology time series for managed MSDF,
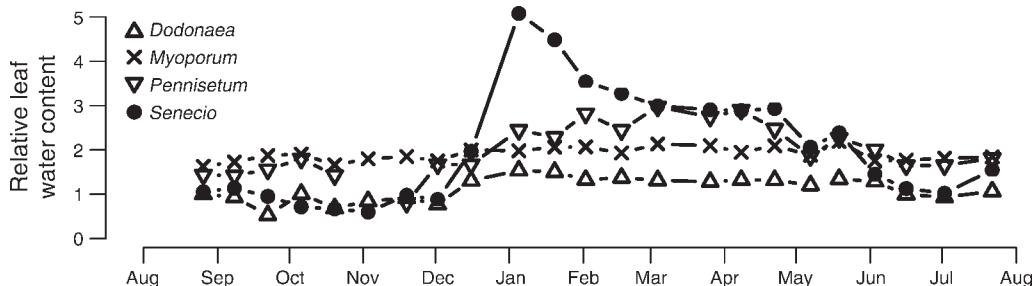
FIG. 4.   Mean relative leaf water content in dominant plant species in a subapline tropical dryland ecosystem in Hawaii. Leaf water content is (wet mass − dry mass)/dry mass. The time series is from August 2008 to August 2009.

but not in the control site where *S. madagascariensis* was rare (Fig. 2; Appendix A).

Density dependence

We tested whether density-dependent population dynamics were contributing to management outcomes and patterns of biological invasion by quantifying changes in the cover of three functional types using ground-based field studies. Forbs had the most significant change in cover (Appendix D). They increased from <1% to 6.4% across communities (Appendix D; Fig. 5; $\lambda = 1.29 \pm 0.02$, 95% CI = 1.25–1.33 yr^{-1}, $n = 18$). Despite widespread exotic grass invasion there were no significant changes to C3 or C4 grasses and sedges (Appendix D; Fig. 5; $\lambda = 0.99 \pm 0.01$, 95% CI = 0.97–1.03 yr^{-1}, and 1.02 ± 0.01, 95% CI = 1.00–1.03 yr^{-1}, $n = 18$). Strong negative density dependence limited the dominance of forbs, but no such patterns characterized other functional types (Fig. 5, Table 2). These findings cannot be attributed to available ground space or competition between functional types, because realized population growth rates for all functional types were unrelated to the amount of barren ground cover in 2001 or to the fractional cover of other functional types (95% CI on all slope parameters contained 0).

DISCUSSION

Escape from natural enemies is a leading hypothesis to explain the success of exotic plants. Because both specialist and generalist enemies should have differential impacts on the success of native and exotic plants, and the hypothesis assumes that specialist enemies of exotics will be rare in the introduced range, the hypothesis predicts that generalist enemies will have a greater impact on native than exotic species (Keane and Crawley 2002). This prediction follows from the assumption that native species are regulated by specialist and generalist enemies, but that exotics are regulated mainly by generalists. We used a large-scale field experiment to test whether release from generalist herbivores (exotic feral ungulates) facilitated the success of exotics in a subalpine tropical dryland ecosystem in Hawaii. Assessment of impacted and control sites before and after ungulate exclusion using airborne imaging spectroscopy and LiDAR, time series satellite observa-

tions, and ground-based field studies over nine years indicated that removal of generalist herbivores facilitated exotic success, but the abundance of native species was unchanged.

In managed MSDF, removal and exclusion of ungulates was associated with a 53% increase in fractional vegetation cover <1 m in height over 8.4 years. Cover in 2001 before ungulate exclusion was 48.7% ± 1.5%. But five years after fencing and ungulate removal in 2004, vegetation cover was 74.3% ± 1.8%. This 53% increase corresponds to an annual exponential growth rate of $\lambda = 1.05 \pm 0.01$ yr^{-1} (95% CI = 1.04–1.06
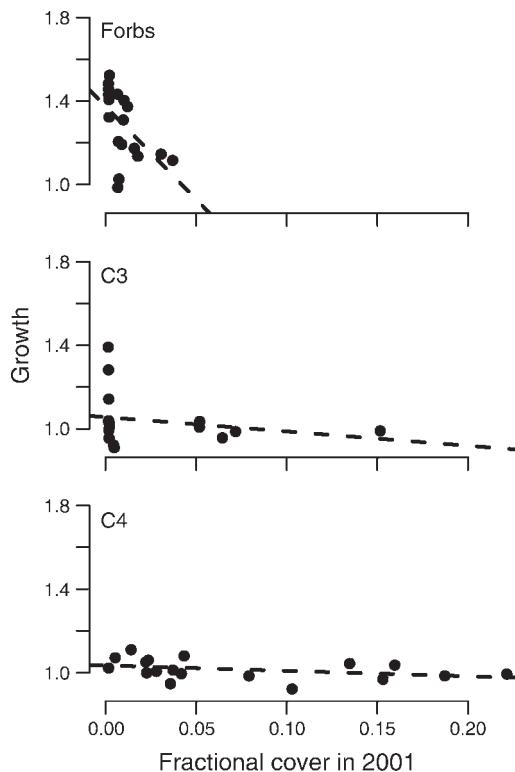

FIG. 5.   Effects of functional plant type on the relationship between initial fractional cover and subsequent change in annualized population growth rates. Lines are the best-fit simple linear regression. Forbs showed a significant negative relationship. Parameter estimates are in Table 2.

TABLE 2. Parameter estimates from linear regressions relating the annualized change in fractional vegetation cover over 8.4 years to initial fractional vegetation cover.

Parameter	b_0	Bayesian SE	Bayesian CI	b_1	Bayesian SE	Bayesian CI	r^2	n
Forbs	1.43	0.07	1.32 to 1.60	−11.38	4.07	−27.77 to −6.09	0.29	18
C3	1.08	0.07	0.97 to 1.24	−1.11	0.72	−2.75 to 0.09	0.04	18
C4	1.04	0.04	0.98 to 1.12	−0.32	0.25	−0.90 to 0.10	0.09	18

Notes: A negative value for the slope (b_1) is evidence of negative density dependence. Estimates are posterior medians and corresponding Bayesian standard error and 95% interval.

yr^{-1}). However, removal of exotic ungulate herbivores had differential impacts on native and exotic species. Nearly all of the increase in vegetation cover was attributable to increases in exotic plants, which increased from 24.4% ± 1.4% to 49.1% ± 2.0%, ($\lambda = 1.08 \pm 0.01$ yr^{-1}, 95% CI = 1.07–1.10 yr^{-1}). Native plants had no significant change in cover (23.0% ± 1.3% to 24.2% ± 1.8%, $\lambda = 1.01 \pm 0.01$ yr^{-1}, 95% CI = 0.98–1.03 yr^{-1}). The dominant invader was *S. madagascariensis*, which represented 14.7% ± 1.4% fractional cover across all plots in managed MSDF after ungulate exclusion ($\lambda = 1.89 \pm 0.34$ yr^{-1}, 95% CI = 1.55–2.81 yr^{-1}, $n = 6$). This species is native to southern Africa and Madagascar (Le Roux et al. 2006). It is a prolific seed producer and capable of rapid population growth (Sindel and Michael 1988). It also produces pyrrolizidine alkaloids that are toxic to most herbivores, but 20 times less toxic to goats, which were excluded from managed MSDF, and have been used for effective biological control of *S. madagascariensis* in Australia (Bull 1955, Dollahite 1972, Sindel and Michael 1988). In contrast, unmanaged MSDF experienced much smaller differences in quantitative phenology dynamics (Fig. 2; Appendix C), and field studies indicated that exotic plants occupied less fractional cover in unmanaged MSDF (Appendix A).

Although ERH can partly explain the increase in exotics in managed MSDF where generalist ungulates were excluded, the large increase in vegetation cover that was observed using satellite observations also coincided with a period of greater than average precipitation (Fig. 2). Whether this provides support for some other hypothesis depends on whether exotic success required both enemy release and increased water availability, or only one. Our data suggest that exclusion of feral ungulates (ERH) is the more likely causal explanation for exotic success and invasion of *S. madagascariensis* for two reasons. First, field studies demonstrate that most of the increase in vegetation cover was attributable to exotic plant species, consistent with the prediction of ERH that release from generalists will facilitate the success of exotics more strongly than native species (Keane and Crawley 2002). In the control site where ungulate numbers were not manipulated, fractional cover of exotic plants was 31.3% ± 2.2% and *S. madagascariensis* was rare, representing just 1.4% ± 0.5% of fractional vegetation cover. Therefore, precipitation alone was insufficient to facilitate exotic success in the presence of ungulate herbivores. Dispersal limitation is also an unlikely explanation for the absence of *S. madagascariensis* in unmanaged MSDF, because it produces very large numbers of small, wind-dispersed seeds (Sindel and Michael 1988).

Second, although ERH predicts the success of exotics in general, and not any one exotic species in particular, the fact that more than half of the increase in exotic plants in managed MSDF was due to one species cannot be ignored. *S. madagascariensis* now represents about 20% of vegetated surface area in ungulate-free areas of MSDF, and its functional properties may be expressed in remote observations. At the scale of a MODIS pixel, EVI in low LAI environments is confounded with LAI, lateral vegetation cover, and canopy water content, but is mostly driven by fractional cover changes (Asner 1998, Asner et al. 2005). *S. madagascariensis* is an annual to short-lived perennial that experiences cycles of leaf flushing and physiology (Fig. 4). It has greater concentrations of leaf water than other plant species during wet conditions, but lower water content during dry periods, and demonstrated capacity to abruptly increase water content (Fig. 4). These characteristics were expressed in satellite time series for managed MSDF, but not in control sites where *S. madagascariensis* was rare (Fig. 2; Appendix A). Although EVI differences between managed and control sites were maintained after ungulate removal, most differences occurred on days when the landscape was drying (i.e., at times when the slope of EVI time series was negative), but not during green-up events (i.e., at times when the slope of EVI time series was positive; Fig. 2). This indicates that effects of enemy release and increases in exotics were expressed mainly during periods of water limitation. The ability of exotics to maintain canopy greenness during dry conditions demonstrates that abundant resources are not a necessary condition for invasion and persistence by enemy release to occur. Whether this is a characteristic of all exotics in managed MSDF or only a subset of species requires further investigation, but it suggests that resource-use efficiency may contribute to the success of *S. madagascariensis* and other exotics. This mechanism has been locally demonstrated for other exotic species in dryland systems of Hawaii (Funk and Vitousek 2007).

There are caveats to our interpretation that increases in the dominance of exotic plants in managed MSDF is attributable to ERH. Our comparison between impacted and control sites is based on two large samples, each of which is replicated through time and separated in space by 18 km. These two areas were chosen because they

represent significant portions of the only remaining tracts of MSDF in the world, and because each has inherent conservation value. Nonetheless, because our study is fundamentally unreplicated, there remains a possibility that inherent site differences have confounded the treatment effect and that we have misinterpreted these findings.

Our conclusion is based on five results. First, remotely sensed vegetation cover increased in ungulate-free areas (Fig. 2). This pattern was corroborated using field measurements. Second, phenology time series indicate that the timing of increased EVI corresponds to the impact of ungulate exclusion and removal (Fig. 2; Appendix C). Third, partitioning subpixel variability from MODIS into vertical components using LiDAR indicates that vegetation <1 m in height is most strongly correlated with EVI signals (Fig. 3; Appendix B). Fourth, field studies indicate that ungulate-free MSDF had increases in the dominance of exotic plants, but the integrated cover of native species did not change significantly. Fifth, phenological characteristics of the dominant invader measured in the field were apparent in satellite EVI time series (Figs. 2 and 4). Thus, inferences are based on a range of evidence from disparate sources, all of which point toward the conclusion that enemy release facilitated exotic success, and that key functional traits of the dominant invader (persistent high leaf water content and rapid uptake following rainfall) were expressed in satellite EVI time series. The alternative interpretation, that inherent site differences confound management impacts, is inconsistent with known effects of ungulates in dryland ecosystems of Hawaii (Cuddihy and Stone 1990, Cabin et al. 2000, Weller et al. 2010), and with the observation that differences in the mean EVI between managed and control areas were different after ungulate removal but similar before the impact occurred (Appendix C).

An assumption to our interpretation is that specialist enemies are regulating populations of native species, and that generalists are having greater impacts on native species than on exotics. We lack data to validate this assumption. However, the dominant invader is well defended by pyrrolizidine alkaloids that are toxic to most herbivores, so it at least is likely to be free from most specialist herbivores. Native species in Hawaii may be particularly poorly defended, because the Hawaiian Islands lack entire enemy guilds found on continents (Wagner and Funk 1995). This has produced an endemic flora that notably lacks defense structures (Wagner and Funk 1995). Thus, an alternative to the interpretation of differential impacts of generalist enemies on native and exotic species is that historical herbivore pressure has decimated native populations to the point where rapid recovery is no longer possible.

Even though ERH might explain invasion outcomes between managed and unmanaged MSDF, it cannot explain why some exotic plant species failed to increase following ungulate removal, or why some exotics increased in DVS and MPW (Appendix A). We addressed whether density-dependent population dynamics were contributing to species success by quantifying changes in three functional types. Negative density dependence limited the dominance of forbs, but relationships among C3 and C4 grasses and sedges were weak and marginally significant (Fig. 5, Table 2). This suggests that competition is shaping the local assembly process among species of forbs, because areas with greater forb dominance had lower realized population growth rates than sites where forbs were rare. We were surprised to discover that there was no significant relationship among C3 or C4 grasses and sedges, because conventional views hold that herbivore browsing suppresses grass dominance (Cabin et al. 2000), and the grass–fire cycle predicts a positive relationship between dominance of grasses and sedges and subsequent changes in cover (D'Antonio and Vitousek 1992). Neither pattern was observed. This indicates that ungulate removal and exclusion did not increase grass dominance at the level of functional types, despite the finding that it permitted increases in exotic species generally.

These findings show how powerful remote sensing tools can be integrated with field studies of tropical dryland ecosystems to confront challenging conservation and management problems. They also provide insight into the mechanisms and historical contingencies that influence exotic species success. Robust planning will require evaluation of competing interests and evaluating the consequences of management action. Removal of exotic feral ungulates is widely considered to be an important first step in conservation and restoration efforts, but its benefits must weighed against the potential cost of subsequent plant invasion if large-scale control is impractical.

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APPENDIX A

A complete list of species, functional types, and fractional cover values in three community types in a Hawaiian subalpine dry forest (*Ecological Archives* A021-094-A1).

APPENDIX B

Relationships between fractional vegetation cover and the enhanced vegetation index (*Ecological Archives* A021-094-A2).

APPENDIX C

Before–after control–impact analysis of exotic feral ungulate removal and exclusion in a subalpine tropical dry forest in Hawaii (*Ecological Archives* A021-094-A3).

APPENDIX D

Fractional vegetation cover <1 m in height for three functional types and barren ground in 2001 and 2009 (*Ecological Archives* A021-094-A4).