

Monitoring native, non-native, and restored tropical dry forest with Landsat: A case study from the Hawaiian Islands

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ABSTRACT

Tropical dry forests are highly threatened at a global scale. Long-term monitoring of remaining stands is needed to assess forest health, efficacy of management practices, and potential impacts of climate change. Using a multi-seasonal Landsat time series, we examined Normalized Difference Vegetation Index (NDVI) patterns in native dry forest, non-native vegetation types, and dry forest restoration sites from 1999 to 2022 in the Hawaiian Islands. We calculated trends in median NDVI and robust coefficient of variation of NDVI for dry and wet seasons, and used Breaks for Additive Seasonal and Trend analysis to detect trend departures. To assess the impact of regional drying trends, NDVI trends were compared to the seasonal long-term precipitation anomaly and cumulative precipitation anomaly. We found that native dry forest was less green than non-native forest, particularly during the dry season, and that median NDVI increased in both native and non-native dry forests over the study period despite negative precipitation anomaly trends. This result differs from coarser-scale studies in Hawaii, but is supported by trends in other dry forest regions. Greening was also observed in restoration study sites, especially larger sites where native species establishment and recruitment has been reported. Non-native grassland NDVI exhibited a strong positive link to precipitation anomalies, suggesting that drier climate scenarios may exacerbate the invasive grass-wildfire cycle that threatens native dry forest. These results demonstrate that Landsat time series may be used to detect seasonal variation in dry forest plots and to support restoration site monitoring in a highly fragmented ecosystem.

1. Introduction

Tropical dry forest is a highly threatened ecosystem that continues to experience high rates of loss (Fremout et al., 2020; Hansen et al., 2013; Sanchez-Azofeifa et al., 2005). They tend to be severely fragmented (Miles et al., 2006) and to occur in areas with significant human influence (Riggio et al., 2020). In many regions, recovery requires assistance through active restoration and management (Dimson and Gillespie, 2020). Yet, dry forests are relatively under-protected and under-studied compared to temperate and tropical rainforests (Rivas et al., 2020; Schröder et al., 2021; Sunderland et al., 2015). The majority of dry forest field plots documented in the literature have only been surveyed once, and their geographic distribution is heavily biased toward North and Central America and the Caribbean (Ocón et al., 2021). The status of

much of the world's remaining tropical dry forest is thus relatively unknown, and a standard, repeatable method for monitoring long-term trends is needed (David et al., 2022).

Native dry forests of the Hawaiian Islands are extremely rare, fragmented, and limited in extent. It is estimated that less than 10 % of the region's original dry forest remains (Falk et al., 1996), and 45 % of dry forest tree species are federally threatened or endangered (Pau et al., 2009). Ongoing threats include competition with non-native plant species, feral ungulate activity, and, as is the case globally, an increase in fire frequency and intensity, which in Hawaii is largely driven by invasive pasture grasses (Ellsworth et al., 2014; Schröder et al., 2021). The result is a patchwork of flammable grasslands and small, isolated forests that are highly likely to experience continued fragmentation (Balzotti et al., 2020; Friday et al., 2015). Conservation of dry forest

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requires intensive, active restoration followed by sufficient monitoring to avoid misleading, short-term results (Ammondt et al., 2013; Burney and Burney, 2007; Herrick et al., 2006; Holl, 2017; Trauernicht et al., 2018). However, field monitoring is generally insufficient, due in part to perceived costliness, unclear objectives or criteria for success, and limited time or resources (Coppus et al., 2019; Höhl et al., 2020; Stanturf, 2021). A few long-term examples have been published (Burney and Burney, 2016; Faucette et al., 2008; A. C. Medeiros et al., 2014), but on average, active restoration studies in Hawaii are only monitored for approximately three years (Dimson and Gillespie, 2020).

Remote sensing data support a diverse range of applications in vegetation monitoring (Lechner et al., 2020). In particular, satellite-derived indices, such as the widely used Normalized Difference Vegetation Index (NDVI), and associated phenological metrics serve as indicators of properties such as photosynthetic activity and moisture content, and are used to delineate vegetation cover, track seasonal fluctuations in productivity, and understand the response of vegetation to environmental stress and change (Duarte et al., 2014; Gamon et al., 1995; Pettoirelli et al., 2005; Xue and Su, 2017; Zeng et al., 2022). NDVI and other vegetation indices (e.g. Vegetation Condition Index, Leaf Area Index, Enhanced Vegetation Index [EVI]) have been used to detect varying responses of vegetation to long-term climatic trends, including greening driven by warming and CO₂ fertilization (Xu et al., 2020; Zhu et al., 2016) and browning due to drought or reduced rainfall (Hilker et al., 2014; Zhou et al., 2014). Teng et al. (2023) showed that though global NDVI has increased in response to warmer temperatures, broad-leaf forests have greened more slowly and are predicted to experience declines in future. In tropical dry forest, drier conditions are likely to reduce productivity, increase tree mortality rates, and impede native species recruitment (Anderson-Teixeira et al., 2013; Dantas et al., 2020). But while drought periods have been linked to declines in NDVI and EVI, long-term trends indicate net greening in some dry forests (Castro et al., 2018; Venter et al., 2020; Verdugo et al., 2024).

The Hawaiian Islands have experienced significant warming and drying trends over the last century (Frazier and Giambelluca, 2017; McKenzie et al., 2019). On the island of Hawai'i, Barbosa and Asner (2016) used Moderate Resolution Imaging Spectroradiometer (MODIS) imagery (250 m spatial resolution) to link drying trends to a decrease in forest greenness in mesic to wet zones, with particularly strong declines in photosynthetic activity and canopy volume on the drier, leeward side. A study of the eight largest Hawaiian islands by Madson et al. (2022) using resampled Advanced Very High Resolution Radiometer (AVHRR) imagery (5.1 km spatial resolution) found significant browning in all land cover classes since the 1980s, and evidence of higher sensitivity to drought in leeward areas.

However, AVHRR or MODIS pixels that include native dry forest fragments are likely to contain spectral data from surrounding vegetation types as well. Approximately 71 % of remaining tropical dry forests on oceanic Pacific islands are smaller than 20 ha, while over 50 % of native fragments on the Hawaiian Islands are smaller than 3 ha (Gillespie et al., 2013). Higher spatial resolution data, such as Landsat imagery, may be needed to capture dry forest trends obscured at coarser resolutions (Yi et al., 2023), particularly in the environmentally heterogeneous Hawaiian landscape. Landsat imagery is freely accessible through multiple platforms, and its 30 m spatial resolution permits monitoring at the site-level (Caughlin et al., 2021; Davis et al., 2022). Though the Landsat revisit interval is longer than that of moderate resolution sensors like MODIS or AVHRR, it is still useful for detecting seasonal variation (Berviglieri et al., 2021). NDVI metrics derived from finer-scale spatial data could also be used to enhance the longevity and efficiency of conventional in situ restoration monitoring (de Almeida et al., 2020). Several studies have used MODIS or SPOT VEGETATION (1 km resolution) data to monitor post-restoration changes in NDVI for study sites greater than 1000 km² in area (Kim et al., 2015; Sun et al., 2011; Zhang et al., 2012). For finer-scale studies in fragmented forest landscapes, NDVI derived from aerial imagery (Reis et al., 2019; Tuxen

et al., 2008) or Landsat data (Hausner et al., 2018) is more appropriate.

Using a 23-year, multi-seasonal Landsat time series, we characterized NDVI trends in native versus non-native species-dominated dry forest, dry forest restoration sites, and non-native grassland in Hawaii. Many dry forests, including the restoration sites in this study, have been invaded by non-native grasses. Depending on restoration progress at a given site, greenness at a grass-invaded site would be expected to shift from typical grassland NDVI to values more characteristic of dry forest (i.e. higher NDVI, less seasonal variability) (Reis et al., 2019). Tropical dry forest phenology is closely linked to high precipitation seasonality (Castro et al., 2018; Pau et al., 2010), and woody vegetation is more accurately distinguished from herbaceous cover during the dry season (Van Passel et al., 2020). This within-year variation is obscured by annual NDVI metrics, which are currently used in the majority of dry forest time series analyses (David et al., 2022). We therefore used a seasonally-aggregated NDVI time series to separate wet and dry season trends.

This research investigated three primary questions related to tropical dry forest status, efficacy of management practices, and potential impacts of climate change, which have not yet been examined for Hawaiian dry forest at the Landsat spatial scale: 1) How do multi-seasonal NDVI trends differ between native dry forests and non-native vegetation types? We hypothesized that native dry forest NDVI would be higher and less variable than that of non-native dry grassland, and lower than that of non-native dry forest during the dry season. 2) How did native dry forest NDVI change from 1999 to 2022, and were long-term changes associated with precipitation anomalies? We hypothesized trends in dry forest NDVI would be negative over time, based on previous studies in the region, and that these declines would be positively correlated with regional drying trends. 3) Do trends in NDVI reflect reported outcomes in dry forest restoration sites? We hypothesized that, post-restoration, greenness at a given site would initially decrease, then gradually approach native dry forest values if successful outplant survival and establishment were reported.

2. Materials and methods

2.1. Study sites

2.1.1. Native dry forest sites

We used OpenNahale, a community-level forest plot database for the Hawaiian Islands (Craven et al., 2018), to identify nine native dry forest plots across Hawai'i, Kaua'i, Lana'i, Maui, and O'ahu (Gillespie et al., 2011; Pau et al., 2012). We chose ≥ 0.1 ha plots in which a minimum of 80 % of inventoried plants were native species and at least 30 total plants were inventoried. Selected plots (0.1 ha) contained 7 to 21 tree and shrub species. Stand densities (165–279 stems ≥ 2.5 cm), basal areas (3.6 to 6.3 m²), and mean tree height (7.1–11.9 m) were highest at Kokee (Kaua'i) and Manuka (Hawai'i), while Kanepuu (Lana'i) and Kanaio (Maui) had lower stand densities (33–61 stems ≥ 2.5 cm), basal areas (1.2–2.6 m²), and mean tree heights (4.1–6.8 m) (Appendix 1, Table A.1). For each site, a 3 × 3 Landsat pixel window (90 m × 90 m) centered on the point location provided in OpenNahale was included in this analysis (i.e. 9 pixels per native dry forest site).

2.1.2. Non-native vegetation classes

Native and restored dry forest sites were compared to non-native species-dominated dry forest (i.e. non-native dry forest) and non-native species-dominated dry grassland (i.e. non-native grassland). We selected nine non-native dry forest and nine non-native grassland sites that were located within 1) the elevation range of the native and restored sites (Appendix A, Fig. A.1); 2) continuous areas (≥ 10 ha) of non-native grassland and non-native dry forest; and 3) the potential extent of dry forest as defined by Murphy and Lugo (1986): areas with mean annual temperature > 17 °C, mean annual precipitation of 250–2000 mm, and a potential evapotranspiration (PET) to

precipitation ratio > 1. To identify this extent, we used this definition and 250 m spatial resolution temperature, precipitation, and PET data (Giambelluca et al., 2013, 2014) to generate a climatic envelope in ArcGIS Pro version 2.9.

To identify continuous areas (≥10 ha) of non-native grassland and non-native dry forest, we used the Carbon Assessment of Hawaii land cover map, which provides detailed plant community classifications at 30 m spatial resolution (Jacobi et al., 2017). From these continuous areas, we selected two non-native grassland and two non-native dry forest sites on each of Hawaii’s four largest islands (Hawai’i, Maui, O’ahu, and Kaua’i), plus an additional site on the island of Hawai’i for a total of nine non-native dry forest and nine non-native grassland sites. Sites were manually selected in order to exclude structures, bare ground, and non-target vegetation (e.g. trees and shrubs within non-native grassland) as much as possible. These features were identified using World Imagery in ArcGIS Pro version 2.9. A 3 × 3 Landsat pixel window over each site was included in analysis (i.e. 9 pixels per non-native study site).

2.1.3. Restoration sites

Our analysis included four dry forest restoration sites—Auwahi, Makauwahi, Keaau, and Ohikilolo—greater than the area of a single Landsat pixel (≥ 0.1 ha). A pixel was included in analysis if the majority (>50 %) of its footprint was located inside the restored area. Overlap was calculated in ArcGIS Pro version 2.9 by computing the Union between each restoration site perimeter and the vectorized footprint of any Landsat pixels intersecting the site. A total of 42 pixels were used for the Auwahi site, 14 for Makauwahi, 5 for Keaau, and 10 for Ohikilolo.

Auwahi forest is located on private ranch land on the leeward side of Maui (Fig. 1). The native understory was degraded by 19th-century

grazing and burning practices and became densely covered by introduced kikuyu grass (*Cenchrus clandestinus*) by the mid-20th century (A. C. Medeiros et al., 2014). Restoration of a 4-ha plot began in 1997 through a combination of ungulate exclusion, herbicide control of non-native grass mats, and mass outplanting (i.e. transplanting of seedlings) of *Dodonaea viscosa* and other native species. By 2012, native plant cover had increased by 58 %. Since then, several thousand additional native plants have been planted, with ongoing minimal weed management.

Makauwahi Cave is a non-profit coastal reserve in Kaua’i (Fig. 1). Prior to restoration of an abandoned sugar cane field, the property supported few native species and was dominated by invasive species, including guinea grass (*Urochloa maxima*) and the small woody tree *Leucaena leucocephala* (Burney and Burney, 2016). In 2005, invasive vegetation was cleared using hand removal and rotary tillage, and over 3000 native and Polynesian plants were outplanted. Mean survival rate for tree and shrub species was 64 % after 5 years, with most mortality occurring immediately after outplanting or withdrawal of supplemental irrigation.

Keaau and Lower Ohikilolo are located in the Waianae range of O’ahu (Fig. 1) and managed by the Department of Forestry and Wildlife and the O’ahu Army Natural Resources Program (OANRP). Lower Ohikilolo is highly fire-prone and dominated by invasive grasses (including guinea grass and *Melinis repens*), *L. leucocephala*, and various herbaceous non-natives (Oahu Army Natural Resources Program, 2021). A fence was constructed in 2000 to prevent grazing, and regular grass control has taken place since 2001. Periodic outplanting of rare and common native species began in 2014, and native shrub cover doubled in certain parts of Ohikilolo after just three years. The Keaau management unit was fenced in 2014 (Oahu Army Natural Resources Program, 2020). The rocky terrain was dominated by guinea grass, and invasive *L.*

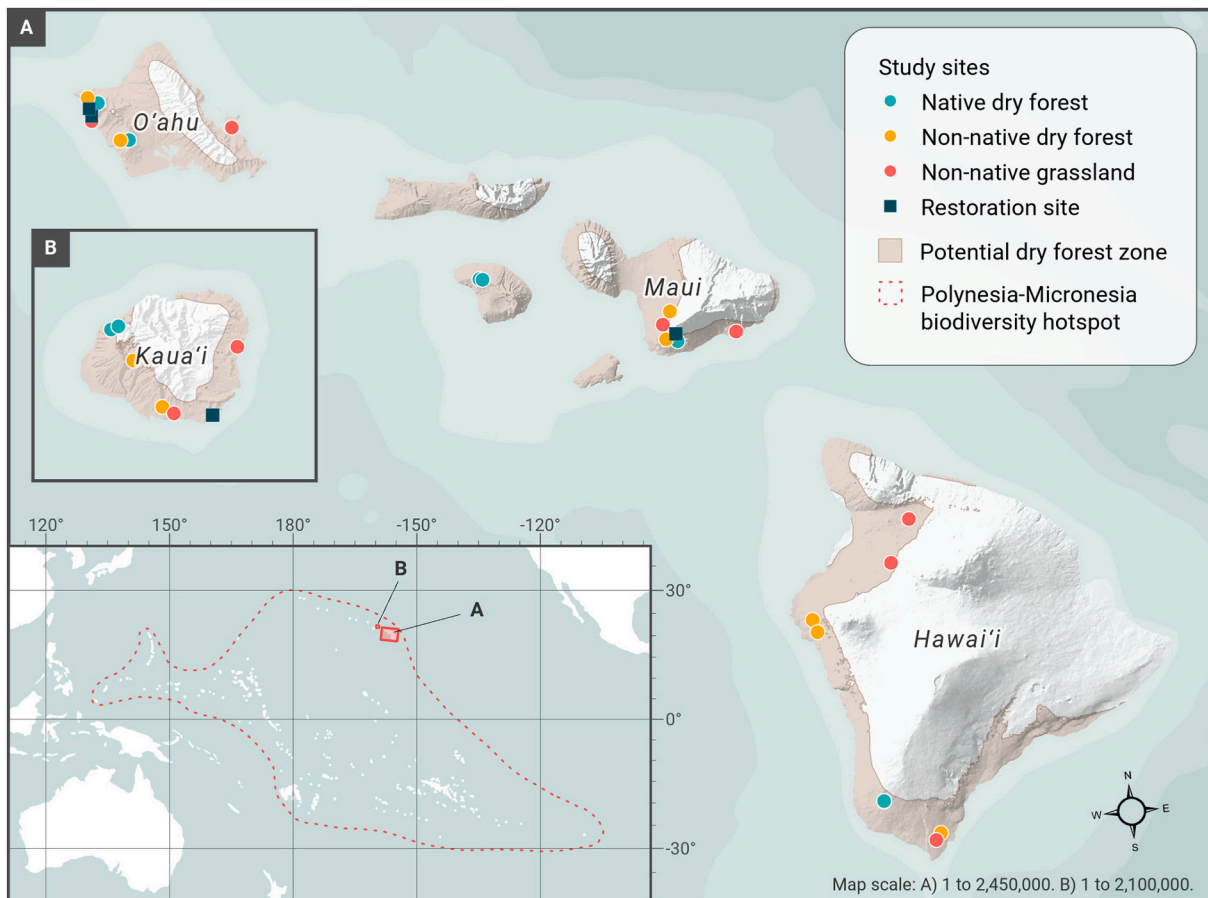


Fig. 1. Locations of native dry forest, non-native dry forest and grassland, and dry forest restoration sites in the Hawaiian Islands.

leucocephala and *Mesosphaerum pectinatum* were also widespread. Weeding of invasive plants and reintroductions of native species began in late 2015 and in 2016, respectively. We restricted analysis to areas where outplanting has occurred.

2.2. NDVI parameters

NDVI is calculated as a difference ratio between red and near-infrared (NIR) reflectance $[(\text{NIR} - \text{Red}) / (\text{NIR} + \text{Red})]$, as chlorophyll absorbs visible light while the cell structure of healthy leaf tissue strongly reflects NIR (Rouse et al., 1974). Values range from -1 to $+1$, where negative values correspond to clouds or water and higher values signify denser vegetation and greater photosynthetic activity.

Landsat 5 Thematic Mapper (TM), Landsat 7 Enhanced Thematic Mapper Plus (ETM+), Landsat 8 Operational Land Imager (OLI), and Landsat 9 OLI Tier 1 collections were accessed through Google Earth Engine (GEE), a cloud computing platform that facilitates processing and analysis of remote sensing data (Gorelick et al., 2017). We used the Collection 2, Level-2 surface reflectance product (courtesy of the U.S. Geological Survey), which is atmospherically corrected and meets the solar zenith angle constraint of <76 degrees, and applied a cloud mask using the QA_PIXEL band. NDVI values were computed in GEE, then extracted for the study pixels and exported for analysis. Only values greater than zero were retained, in order to reflect the typical NDVI of soil and vegetated surfaces (Roy et al., 2016). As no Landsat 5 TM images satisfied these criteria for our study area, this collection was not included in the analysis.

Valid Landsat images were available for July 1999 through September 2022. Though individual Landsat sensors have a revisit interval of 16 days, temporal coverage of Hawaii during this period was inconsistent, mainly due to cloud cover. The number of unique image dates over the study period ranged from 163 to 775 per site, with a median of 247 (Appendix A, Table A.2). We aggregated NDVI observations into a multi-seasonal time series, in which quarterly seasons—November–January (NDJ), February–April (FMA), May–July (MJJ), and August–October (ASO)—aligned with Hawaii’s wet (November–April) and dry seasons (May–October) (Frazier and Giambelluca, 2017). The resulting time series spanned ASO 1999 to MJJ 2022.

Median NDVI and robust coefficient of variation (RCV) of NDVI were calculated for each season in R version 4.2.2 (R Core Team, 2022). We chose median rather than mean NDVI because the annual distribution of NDVI values was often moderately to highly skewed (Bulmer, 1979). For skewed data, RCV is a preferred alternative to the mean-based coefficient of variation, and is calculated by dividing the median absolute deviation by the median value (Arachchige et al., 2022). RCV provides a measure of seasonality and may capture the response of NDVI to climatic variations and other potential disturbances that cannot be detected by the median alone (Barbosa et al., 2006). Higher RCV signifies greater variability within a season.

2.3. Statistical analysis

2.3.1. NDVI analysis

To characterize general NDVI conditions in each vegetation class (native dry forest, non-native dry forest, and non-native grassland), pixel-wise median and RCV of NDVI were calculated within each season over the 1999–2022 study period. Kruskal-Wallis and post-hoc Wilcoxon rank sum tests were used to make pairwise comparisons and identify significant differences between groups within seasons (McDonald, 2009). All statistical analyses were performed in R version 4.2.2 (R Core Team, 2022).

Within-season NDVI trends in the native dry forest class, non-native vegetation classes, and individual restoration sites were characterized using non-parametric Sen’s slope and Mann-Kendall tests (Hirsch et al., 1982; Kendall, 1975; Mann, 1945). The slope and strength of potential monotonic trends was first measured with Sen’s slope estimator, and the

significance of the trend was then determined using the Mann-Kendall test, which is suitable for the detection of upward or downward monotonic trends in environmental data that may not necessarily be linear. Autocorrelation and partial autocorrelation functions were applied to time series of each vegetation class and restoration site; if autocorrelation was observed, Mann-Kendall tests were used with the block bootstrap method to improve estimates of significance.

2.3.2. Study site environment

Though all study sites were located in the potential dry forest zone (Fig. 1), mean elevation ranged from 7 to 1156 m (mean 466 ± 339) and annual rainfall from 650 to 1385 mm (mean 907 ± 202). To examine the potential influence of site elevation and annual site rainfall on NDVI, we calculated the Pearson’s correlation coefficient (Akoglu, 2018) between each of these environmental variables and four NDVI metrics for each site: median NDVI and RCV of NDVI, summarized over the full study period, and change in median NDVI and RCV of NDVI, represented by the Kendall coefficient of each parameter over time (calculated by Mann-Kendall tests).

2.3.3. NDVI and restoration

Changes in NDVI at the restoration sites were evaluated in two ways. First, pre- and post-restoration pixel-wise parameters (seasonal median and RCV of NDVI) were calculated for each site. For Makauwahi, Keaau, and Ohikilolo, the year that native plant reintroductions began was used as a threshold, as this is when sites became actively managed. Pre-restoration NDVI was not calculated for Auwahi, where outplanting began prior to 1999. For comparison, pixel-wise NDVI parameters in the native and non-native vegetation classes were also calculated for each pre- and post-restoration period. Kruskal-Wallis and post-hoc Wilcoxon rank sum tests were used to make pairwise comparisons and identify significant differences between groups within seasons.

Second, we identified potential breakpoints in the 1999–2022 NDVI time series. Breakpoints signify shifts in a time series and divide it into segments. The Breaks for Additive Seasonal and Trend (BFAST) framework (Verbesselt et al., 2010a) has been used to detect vegetation changes, including forest disturbances and NDVI response to drought, with minimal influence from seasonal amplitudes and in spite of time series irregularity (DeVries et al., 2015; Forkel et al., 2013; Xu et al., 2020). In this study, we tested the utility of BFAST in monitoring post-restoration changes in Landsat-derived NDVI parameters, and examined whether breakpoints in restoration time series coincided with changes in site management. Because breakpoints could potentially be caused by broader climatic trends, we also used BFAST analysis to check for concurrent breaks in the native and non-native vegetation classes. The `bfast()` function in the R package ‘bfast’ was applied using a frequency of 4 (representing the quarterly seasonal cycle) and the harmonic seasonal model, which requires fewer observations and is less sensitive to short-term variations (Verbesselt et al., 2010b). For minimum segment size (a parameter defining the minimum length of time allowed between potentially detected breaks), we tested two values of 0.08 and 0.13, which are equal to trend departures of at least 2 and 3 years, respectively. Overlap was determined using each breakpoint’s 95 % confidence interval.

2.3.4. Precipitation data and analysis

The relationship between NDVI and precipitation trends was examined using data from the Rainfall Atlas of Hawaii, a 250 m resolution, gridded monthly and annual rainfall product that was recently expanded to span 1920–2019 (Giambelluca et al., 2013). Total rainfall was extracted using the center of each study site, and seasonal time series were created by summing monthly precipitation for NDJ, FMA, MJJ, and ASO. We then calculated the seasonal long-term precipitation anomaly (PA_t) (Eq. (1)) and cumulative precipitation anomaly (CPA_t) (Eq. (2)). As a baseline, we selected the widely-used 1978–2007 period as per Frazier and Giambelluca (2017), who found that adjusting the 30-

year window had little effect on rainfall trend estimates. We then calculated the seasonal long-term precipitation anomaly (PA_t) and cumulative precipitation anomaly (CPA_t) as:

$$PA_t = \frac{Precipitation_t - Precipitation_{1978-2007}}{Precipitation_{1978-2007}} \quad (1)$$

$$CPA_t = PA_t + PA_{t-1} \quad (2)$$

PA_t is precipitation change in the year 't' relative to the baseline mean, calculated using $Precipitation_t$ (total rainfall in the year 't') and $Precipitation_{1978-2007}$ (mean precipitation of the 1978–2007 baseline period). CPA_t depicts the accumulation of relative changes in precipitation by summing PA in the year 't' and 't-1'. The significance of 1978–2019 seasonal precipitation trends at each study site were determined using Sen's slope estimator and the non-parametric Mann-Kendall test (Frazier and Giambelluca, 2017).

To evaluate the relationship between changes in seasonal rainfall and greenness from 1999 to 2019, correlation coefficients were calculated between PA_t and CPA_t and median and RCV of NDVI in each vegetation class and restoration site. As Shapiro-Wilk tests determined that PA_t , CPA_t , median NDVI, and RCV of NDVI were not normally distributed, we used the non-parametric Spearman rank correlation (Akoglu, 2018).

3. Results

3.1. NDVI of native and non-native classes

When summarized by site and season over the study period, median NDVI of native dry forest sites ranged from 0.4 to 0.84 (Appendix B, Table B.1). Median NDVI differed significantly between vegetation classes ($p < 0.05$, Appendix B, Table B.2) and tended to be highest in non-native dry forest, followed by native dry forest (Fig. 2). In all vegetation classes, median NDVI was significantly higher during the early wet season (NDJ) than the dry quarters (MJJ and ASO) ($p < 0.01$, Appendix B, Table B.3). Seasonal median NDVI and RCV of NDVI were

strongly negatively correlated in each site class ($p < 0.001$), suggesting that greener sites experience less within-season variation. This relationship was weaker (though still significant) for non-native grassland. RCV of NDVI was highest in non-native grassland in all seasons ($p < 0.001$), and peaked during the late dry season (ASO) (Fig. 2). There was no significant difference between native and non-native dry forest RCV of NDVI (Appendix B, Table B.2).

Multi-seasonal time series of median NDVI were primarily positive over the 1999–2022 study period. Significant trends were observed at 22 out of 31 study sites and were stronger in native and non-native dry forest sites than non-native grassland (Fig. 3). The strength and significance of the correlation varied by site and season, but the mean slope of each class did not differ significantly. Trends in RCV of NDVI were more variable (Fig. 4). For the majority of sites, trends over time were insignificant, though declines were more common in forest, and increases more common in grassland.

3.2. Pre- and post-restoration NDVI

Restoration sites generally exhibited lower vegetation greenness and greater seasonal variability than native and non-native dry forest (Fig. 5). Pre- and post-restoration median NDVI was consistently lower than that of native and non-native dry forest across seasons ($p < 0.05$), with a few exceptions where there was no statistical difference between the restoration site and native dry forest. RCV of NDVI was significantly higher than or statistically similar to native and non-native dry forests both pre- and post-restoration ($p < 0.05$).

Relationships between restoration sites and non-native grassland were more varied. Atuwahi was greener than non-native grassland during the dry season, and less variable within seasons (Fig. 5). Pre-restoration, Makauwahi NDVI parameters were similar to those of non-native grassland. Post-restoration, median NDVI at Makauwahi was consistently significantly higher ($p < 0.05$) and RCV of NDVI was significantly lower ($p < 0.05$) than non-native grassland values. NDVI parameters for Ohikilolo and Keauu (both pre- and post-restoration) were generally similar to those of non-native grassland in most seasons.

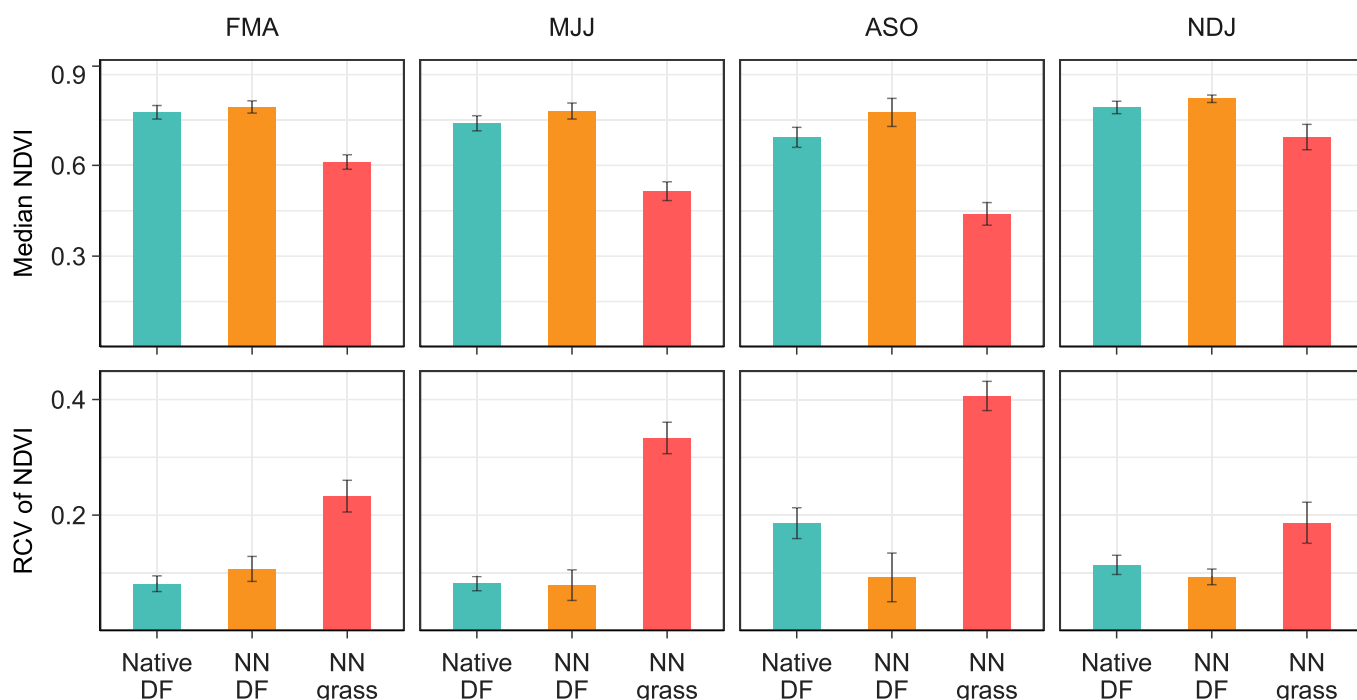


Fig. 2. Pixel-wise median and RCV of NDVI summarized within seasons over the 1999–2022 study period. Error bars indicate 95 % confidence interval of the median. See Appendix B, Table B.1 for individual study sites, and Table B.2 for significant differences between classes. DF = dry forest; NN = non-native.

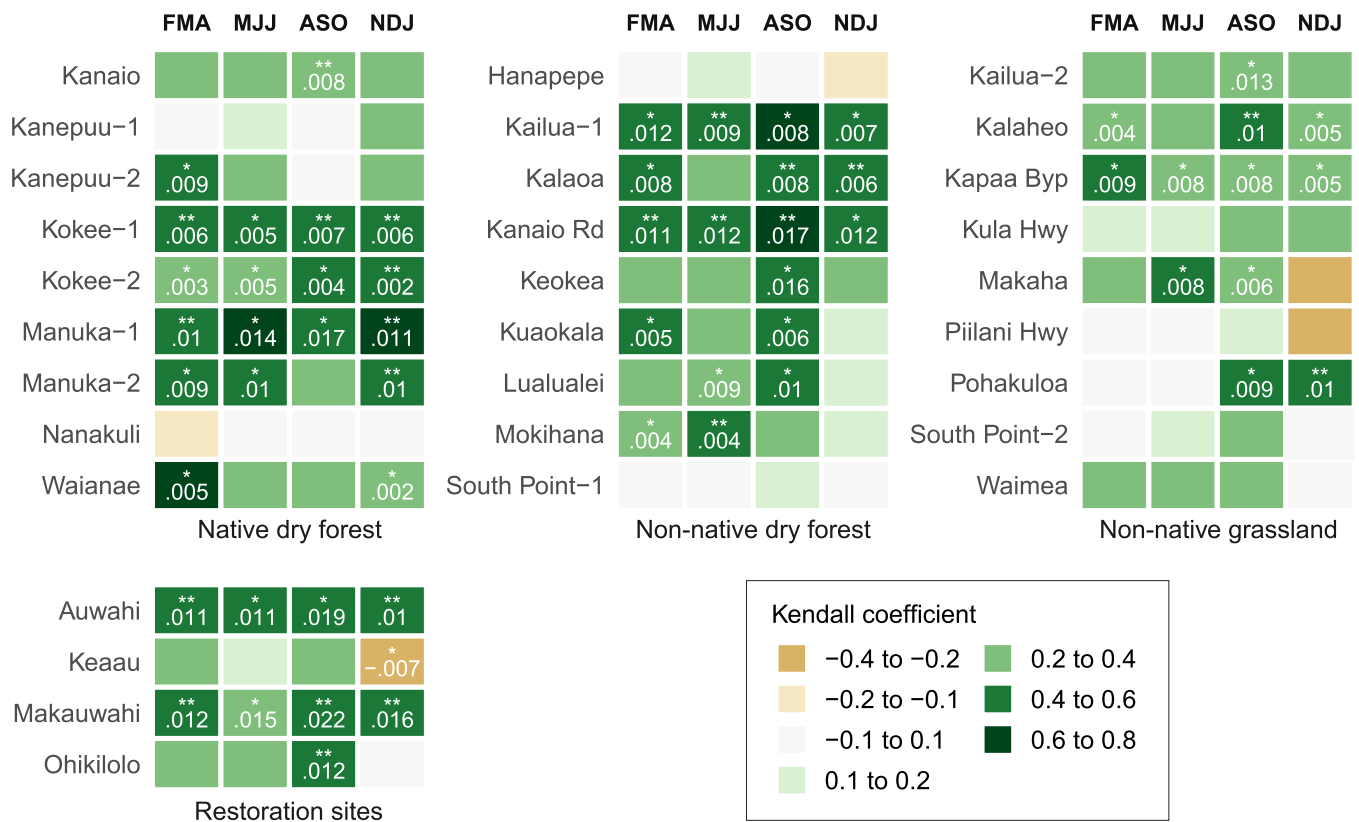


Fig. 3. Correlation of seasonal median NDVI and year from 1999 to 2022 (* $p < 0.05$, ** $p < 0.01$). Sen's slope given for significant relationships. Brown and green tiles indicate a decrease or increase in median NDVI over time, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The greatest post-restoration shift in NDVI parameters occurred at Makauwahi. After restoration, its median NDVI significantly increased ($p < 0.05$) and RCV of NDVI decreased ($p < 0.001$) in all seasons (Fig. 5). Post-restoration changes at Keaau and Ohikilolo were similar in some ways, but less consistent. Keaau experienced a significant decrease in RCV of NDVI ($p < 0.05$) and increase in median NDVI ($p < 0.05$) during dry quarters, but also a slight decrease in median NDVI during NDJ ($p < 0.05$). At Ohikilolo, significant increases in median NDVI occurred in every season but NDJ ($p < 0.05$), while RCV made non-significant decreases in every season but ASO, during which it increased ($p < 0.05$).

3.3. Restoration site trends and breakpoints

Increases in median NDVI were observed at Makauwahi and Auwahi in all seasons (Fig. 3). During the dry season in particular, the slope of the trend was relatively larger than that observed in native and non-native dry forest. At Ohikilolo, median NDVI increased significantly during the ASO quarter, while Keaau's median NDVI showed a significant negative trend during NDJ. Like the native dry forest and non-native vegetation sites, the direction of the RCV of NDVI trend was weaker and more variable (Fig. 4). The exception was Makauwahi, where RCV of NDVI decreased significantly over time.

Breakpoints were detected in median NDVI and/or RCV of NDVI time series at each restoration site (Fig. 6). Both breakpoints in median NDVI at Auwahi coincided with breakpoints in native dry forest, and the direction of the trend departures was similar. Median and RCV of NDVI breakpoints at Makauwahi had the clearest overlap with the site's restoration start date. The 95 % confidence interval of the Ohikilolo break, estimated to occur in 2005, overlapped a native dry forest breakpoint. Restoration at Keaau began after breaks detected in RCV of NDVI, which highlighted a steep rise in RCV between NDJ 2012 and MJJ

2014.

3.4. Site environment and NDVI

Mean annual rainfall was positively associated with median NDVI and negatively associated with RCV of NDVI in all three vegetation classes (Appendix B, Table B.4). This relationship was strongest for native dry forest ($r = 0.74$, $p < 0.001$; $r = -0.79$, $p < 0.001$). Median NDVI was highest at the wettest native sites (Waianae and Nanakuli, O'ahu; Kokee-1 and Kokee-2, Kaua'i) and lowest at the driest (Kanaio, Maui). In native dry forest, mean site elevation was also positively correlated with median NDVI ($r = 0.47$, $p < 0.01$) and negative correlated with RCV of NDVI ($r = -0.63$, $p < 0.001$).

Change in median NDVI was positively associated with site rainfall in non-native grassland ($r = 0.47$, $p < 0.01$), and with site elevation in non-native dry forest ($r = 0.46$, $p < 0.01$). Otherwise, change in NDVI parameters was not correlated with site elevation nor mean rainfall. No correlation was observed between any NDVI or site environment variables for the restoration class.

3.5. Precipitation anomalies

Mann-Kendall tests indicated weak to moderate negative trends in the seasonal long-term precipitation anomaly (PA_t) and cumulative precipitation anomaly (CPA_t) from 1978 to 2019, and statistically significant trends at 11 out of 31 study sites (Appendix B, Table B.5). Some positive trends occurred during the FMA, MJJ, and ASO quarters, but these were not significant and coefficients were low (mean $r = 0.07 \pm 0.05$). During the dry season, the PA_t and CPA_t trends were positively correlated with site elevation (MJJ CPA_t $r = 0.39$, $p < 0.05$; ASO CPA_t $r = 0.49$, $p < 0.01$; ASO PA_t $r = 0.43$, $p < 0.05$) and negatively correlated

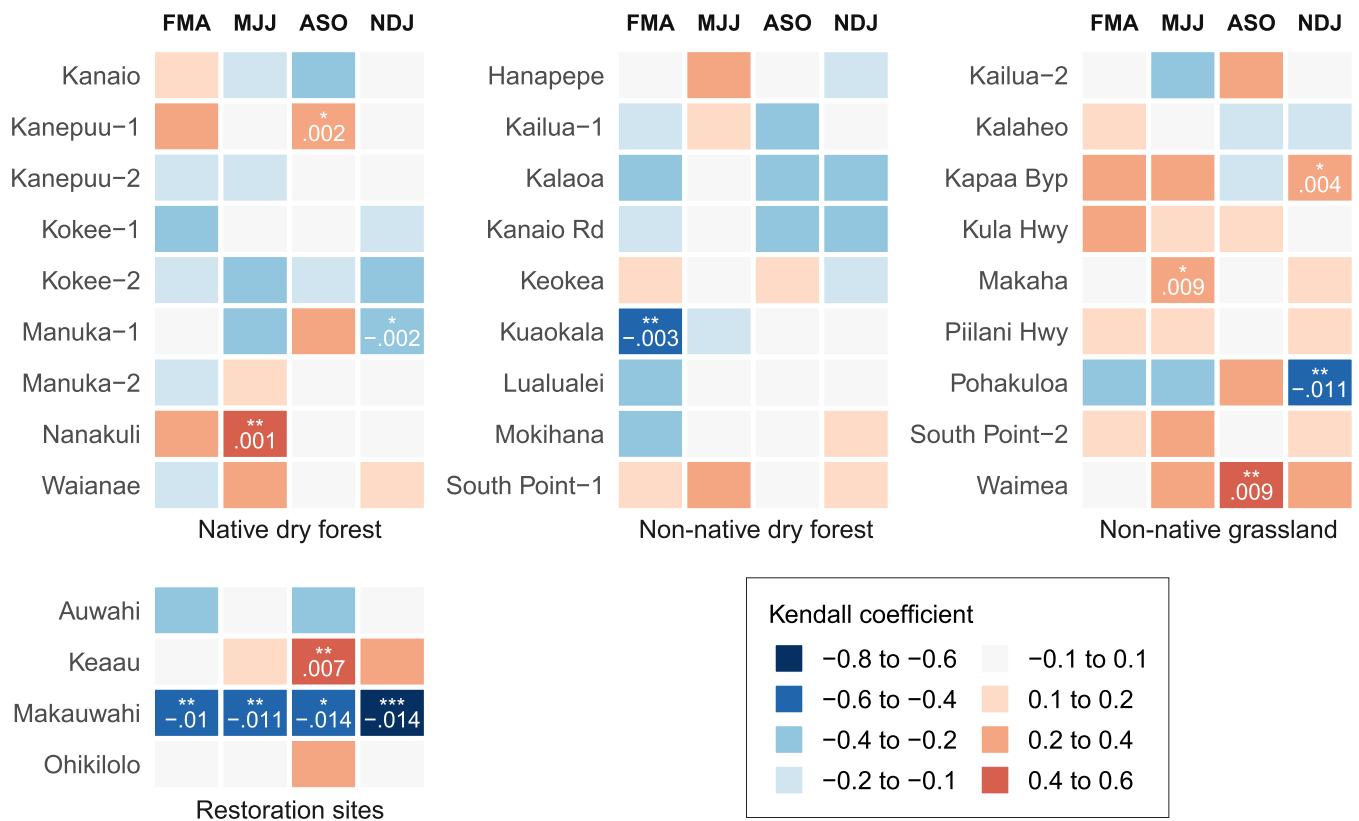


Fig. 4. Correlation of seasonal RCV of NDVI and year from 1999 to 2022 (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Sen's slope given for significant relationships. Blue and red tiles indicate a decrease or increase in RCV over time, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

with site rainfall (MJJ $PA_t r = -0.37, p < 0.05$; ASO $CPA_t r = -0.39, p < 0.05$). During the NDJ quarter, PA_t coefficients were positively associated with site rainfall ($r = 0.40, p < 0.05$).

At the majority of study sites, seasonal PA_t and CPA_t were positively associated with median NDVI (Fig. 7). The strength and significance of the correlation were most consistent in non-native grassland sites and during the ASO quarter. Native and non-native dry forest study sites and the NDJ quarter in general showed more variation. The relationship between each seasonal precipitation anomaly and RCV of NDVI was primarily negative, but varied widely among study sites and seasons (Appendix B, Table B.7). Trends were relatively weak, and statistical significance was observed for only a few sites.

4. Discussion

4.1. NDVI in native and non-native dry forest

Hawaiian dry forests experience exceptionally long dry seasons compared to dry forests globally (Barton et al., 2021). In both native and non-native species-dominated dry forest, we observed significantly lower median NDVI during the dry season, and lower overall greenness and greater within-season variation at sites with relatively lower mean annual rainfall. It is well understood that dry forest vegetation dynamics are highly influenced by precipitation seasonality (Huang et al., 2021). Studies in dry forest have found that precipitation is the strongest predictor of variation in NDVI (Ruiz-Díaz et al., 2024), and, though the relationship between wet season duration and vegetation productivity can be non-linear, lower total rainfall is associated with lower NDVI (Souza et al., 2016), and higher wet season rainfall is associated with higher NDVI (Verduzco et al., 2015). Our observations provide further support for the strong link between dry forest greenness and seasonal

and spatial variation in water availability.

Although inter- and intra-seasonal variability in NDVI was similar in native and non-native dry forest, drier conditions had a relatively stronger influence on native sites. Median NDVI was consistently lower in native dry forest than in non-native dry forest, particularly during the late dry season (ASO) when native site greenness was the most variable. The relationship between site environment (mean annual rainfall and mean elevation) and NDVI was also stronger in native dry forest; lower rainfall was likely to yield lower and more variable within-season NDVI in native dry forest than in non-native sites. This could reflect species-level differences in resource use, for native Hawaiian trees demonstrate more conservative growth and water use than invasive trees in both wet (Asner et al., 2006; Cavaleri et al., 2014) and dry forest (Stratton and Goldstein, 2001). Asner et al. (2006) detected higher NDVI for invasive *Morella faya* than for native *Metrosideros polymorpha*, and higher growth rates for *M. faya* during periods of lower rainfall in rainforest. Our results suggest that the dry season and drier environments have a similar effect on native versus non-native dry forest productivity as well. Understanding native and non-native resource-use strategies under different climate conditions is critical to conservation planning, as invasion by non-native woody species has been observed to negatively impact forest ecosystem hydrology (e.g. groundwater recharge and availability, soil water content), which could in turn limit native species growth or recovery (Cavaleri et al., 2014; Dudley et al., 2020; Hata et al., 2016; Takahashi et al., 2011).

4.2. Greening and long-term precipitation trends

Based on previous climate and vegetation index studies, we expected to observe a decline in dry forest NDVI over the 1999–2022 period. However, median NDVI showed significant, albeit low magnitude,

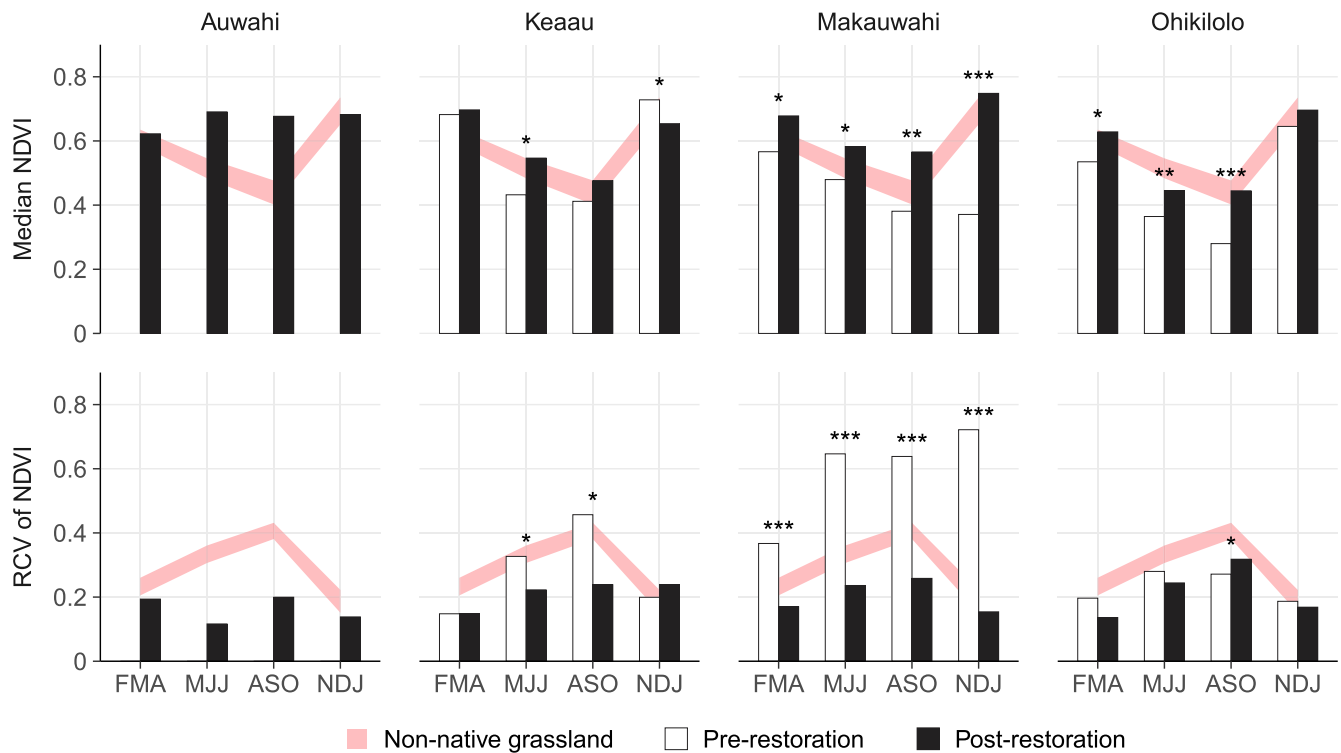


Fig. 5. Pixel-wise median and RCV of NDVI summarized within seasons for pre- and post-restoration periods (determined by the year that native outplanting began; Auwahi post restoration period = 1999–2022). Asterisks indicate significant differences between pre- and post-restoration values, as determined by Wilcoxon rank sum tests (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). 95 % confidence interval of non-native grassland median and RCV of NDVI (1999–2022) is included for comparison.

increases at the majority of native and non-native dry forest sites in at least one quarter. This Landsat-based trend deviates from MODIS- and AVHRR-based studies that observed browning in some regions of Hawaii, which were linked to declines in precipitation and or intensified drought conditions (J. M. Barbosa and Asner, 2016; Madson et al., 2022). It is possible that our study sites did not overlap the locations where Madson et al. (2022) detected decreases in NDVI, and that our results are therefore not representative of broader trends that are indeed affecting dry forests. For instance, at the two native dry forest sites (Kanepuu-1 and Nanakuli) where significant greening did not occur, trends in RCV of NDVI suggest that dry season variability in greenness has significantly increased. However, at Nanakuli, this could potentially be attributed to forest cover loss following a 2500-acre fire at the site in 2016 (Hidden Victims of The Nanakuli Fire, 2016).

Alternatively, dry forests may be an exception to broader browning trends in neighboring vegetation types that are more strongly correlated with precipitation anomalies, such as non-native grassland. Forest NDVI trends vary across datasets of different spatial resolutions (Arjasakusuma et al., 2018; Fensholt and Proud, 2012), and discrepancies between our results and time series of coarser spatial scale could be attributed to spatial aggregation of multiple vegetation types within larger pixels (Munyati and Mboweni, 2013). Native Hawaiian dry forest fragments are small, limited in distribution, and thus unlikely to occupy the full area of an AVHRR pixel (Jacobi et al., 2017). Furthermore, our findings corroborate dry forest greening trends in South Africa, where areas receiving more annual rainfall (>200 mm) demonstrate stronger trends (Venter et al., 2020), and Costa Rica and Mexico, which have been linked to increases in temperature (Huang et al., 2021; Verdugo et al., 2024). Though declines in dry forest greenness have been observed following extended drought periods (Castro et al., 2018; Verdugo et al., 2024), Huang et al. (2021) noted that this effect may be temporary, and the drought tolerance traits exhibited by many dry forest

species likely facilitate recovery even after exceptional drought conditions (C. D. Medeiros et al., 2019; Souza et al., 2016; Sunderland et al., 2015).

We found that significant increases in median NDVI occurred despite an overall downward trend in precipitation and a positive relationship between greenness and annual site rainfall. Though few significant trends were detected, seasonal trends in precipitation anomalies were primarily negative from 1978 to 2019. Across the Hawaiian Islands, dry season rainfall has declined more rapidly above 1500 m elevation (Frazier and Giambelluca, 2017). We found that the strength of negative dry season PA_t and CPA_t trends was greater at lower elevations; but as all of our study sites occurred below 1200 m, this may constitute an insufficient number of samples. We also observed weak but significant correlations between site mean annual rainfall and precipitation anomaly trends in certain quarters, which suggest drying trends have been relatively stronger at historically wetter sites during the dry season, and at drier sites during the wet season—i.e., rainfall seasonality has increased (Konapala et al., 2020).

Warmer, drier conditions in the Hawaiian Islands have been previously associated with declines in NDVI (J. M. Barbosa and Asner, 2016). At the majority of study sites, median NDVI was positively correlated with precipitation anomalies in at least one season, usually ASO (Fig. 7). While it seems counterintuitive that sites are becoming greener while the climate is drying, temperature, which we did not examine, is potentially a stronger driver of vegetation greenness in dry forest regions (Huang et al., 2021; Verdugo et al., 2024; Zhao et al., 2021). Additionally, native dry forest NDVI may be more stable due to drought tolerance traits in Hawaiian species. The deeper root systems of native woody species can access soil water during the dry season and, perhaps, anomalous dry periods (Calder and Dye, 2001). This could explain why native sites like Manuka-1 and Manuka-2 became greener despite experiencing the most significant regional drying trends on Hawai'i

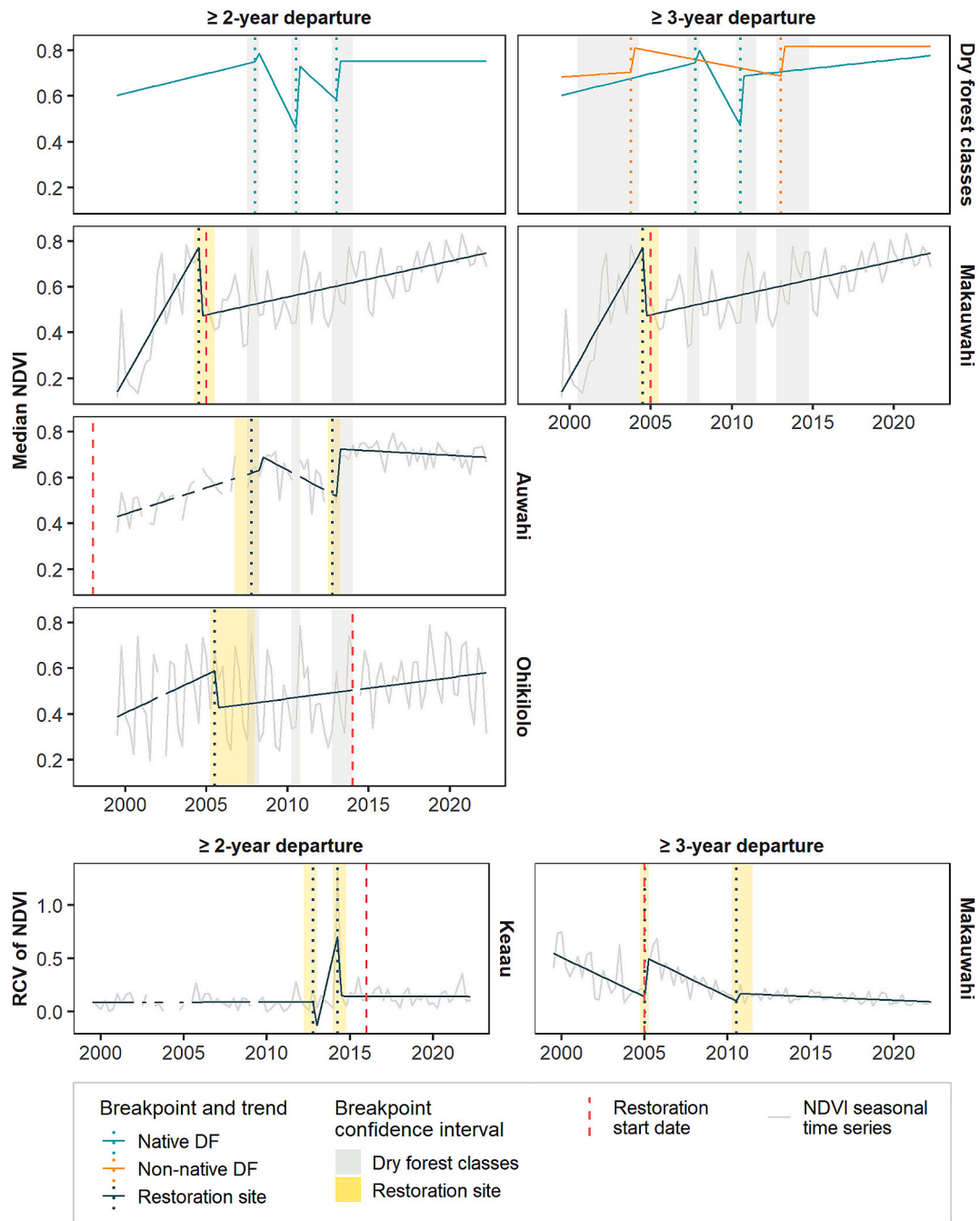


Fig. 6. Significant breakpoints (dotted lines) and trends (solid lines) in NDVI time series indicated by BFAST, for minimum trend departure lengths of 2 and 3 years. For reference, breakpoints in native and non-native dry forest are shown in the top panels, and red dashed lines show initial outplanting dates at restoration sites. Sites/metrics for which breakpoints were not detected were excluded from this fig. DF = dry forest. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Frazier and Giambelluca, 2017). However, it is important to consider that encroachment of woody non-natives could also be responsible for greening trends in both native and non-native dry forest. This is difficult to determine using just NDVI alone.

Though rainfall projections for the Hawaiian Islands are uncertain (Mizukami et al., 2022), tropical dry forests are expected to be highly sensitive to increased drought frequency and precipitation variability under potential climate scenarios (Allen et al., 2017). The productivity of native and restored dry forests sites, amid anomalous declines in precipitation, is an encouraging testament to dry forest resilience and the value of conservation and restoration efforts, but dry forests are not invulnerable to extended periods of drought, and interactions with non-

native species will likely influence native species recovery. The 2007–2011 departure from the positive trend in native dry forest median NDVI (Fig. 6) coincided with Hawaii’s longest and most intense drought since 2000 (<https://droughtmonitor.unl.edu/>). A concurrent break was not detected in non-native dry forest productivity, which may be less sensitive to dry periods (Asner et al., 2006). Meanwhile, non-native grassland had the strongest and most consistent relationship with precipitation anomalies (Fig. 7). Under drier climate scenarios and intensified drought conditions, non-native plant species are likely to impede the recovery and persistence of native dry forest through intensification of the invasive grass-wildfire cycle (Trauernicht, 2019) and negative effects on water availability (Z. Chen et al., 2023; Dudley

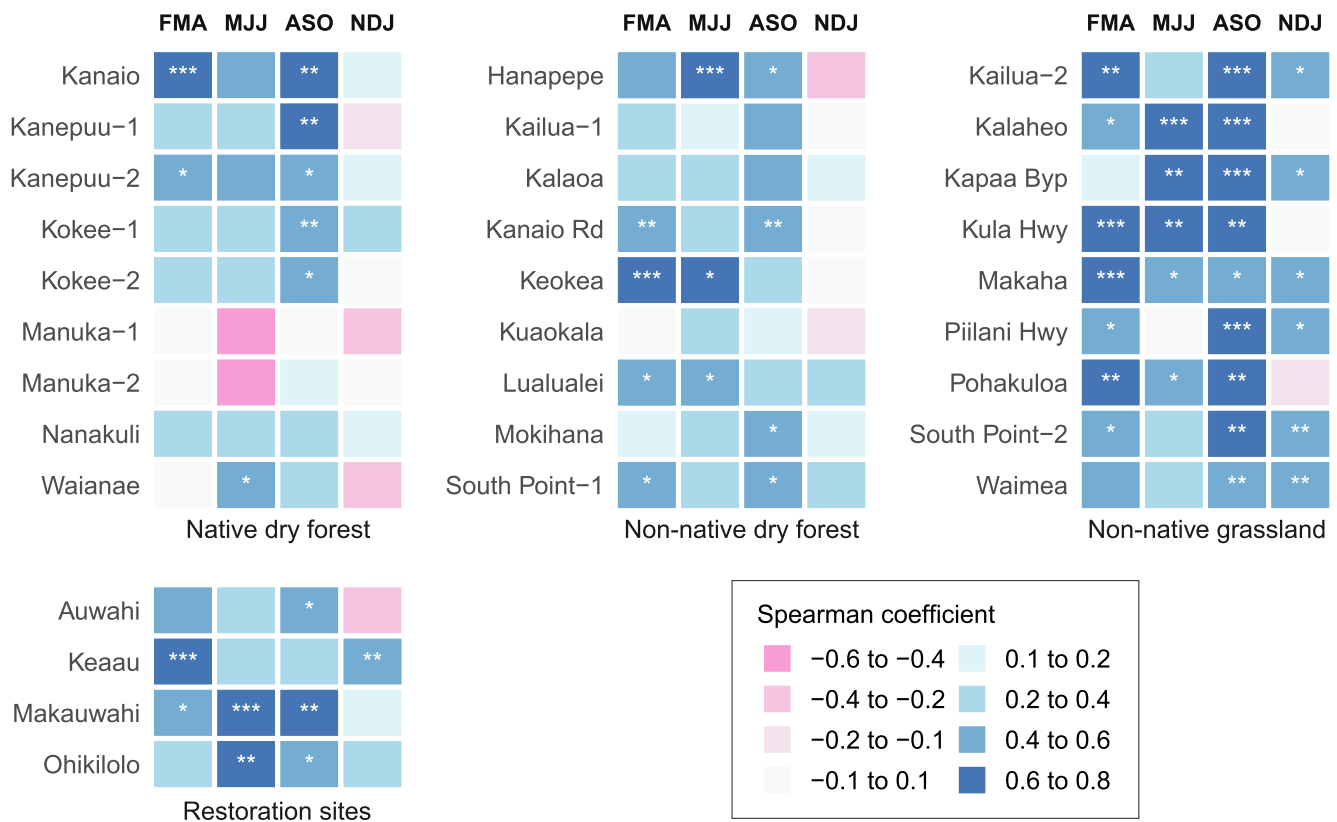


Fig. 7. Spearman correlation of PA_i and median NDVI (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) from 1999 to 2019. Pink and blue tiles indicate a negative or positive relationship, respectively. See Appendix B, Table B.6 for correlation coefficient values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al., 2020).

This highlights the importance of active management and monitoring of existing dry forest, and the need for further analysis of the drivers of native and non-native vegetation response to long-term climate trends. Our results suggest that medium-resolution Landsat time series data can be used to monitor changes in ≥ 1 ha tropical dry forest plots at local (Craven et al., 2018), regional (Gillespie et al., 2013), and global (Ocón et al., 2021) spatial scales from 2000 to present. A “dashboard” of individual dry forest stands (e.g. Fig. 3) could update scientists and conservation practitioners on well-protected, managed, healthy dry forests, while flagging disturbed sites like Nanakuli.

4.3. Post-restoration NDVI trends

We found that most restoration sites, like native and non-native dry forests, greened during the study period. Greening and browning trends could signal a number of different landscape changes, depending on geographic context, rates of change, and the target vegetation being monitored (Venter et al., 2020). Large-scale land conversions, including urban development in former cropland or concerted afforestation or reforestation efforts in severely degraded landscapes, are readily detected with NDVI as a proxy of vegetation cover (Abbas et al., 2023; Y. Chen et al., 2024; Zhao et al., 2021). But in dry forest, signals from the evergreen, woody canopy must be distinguished from those of the deciduous, herbaceous understory (Van Passel et al., 2020). Finer-scale active restoration projects, like the sites in our study, present an opportunity to match remotely-sensed NDVI trends to in situ observations and considerations.

Makauwahi experienced the most significant and apparent changes in NDVI. Seasonal NDVI parameters at the site pre-restoration resembled those of non-native dry grassland (lower values, higher seasonal and

annual variation), then shifted toward those of native dry forest (higher values, lower variation) (Fig. 5). These shifts were visible in the NDVI time series as well, which were positive for median NDVI and negative for RCV of NDVI (Figs. 3–4). Trend departures coincided with the Makauwahi restoration start date in 2005, when median NDVI briefly dropped, then increased, while RCV of NDVI rose, then decreased (Fig. 6). Consistent with our hypothesis regarding post-restoration greenness, the Makauwahi breaks and trends likely reflect the removal of non-native guinea grass and *L. leucocephala*, and the subsequent, gradual establishment and unassisted recruitment of outplanted species reported for the site. A second breakpoint in RCV of NDVI occurred in 2010, after which the decline in RCV was more gradual. This may be another indication of native species progress; Burney and Burney (2016) reported that by 2010, native plant size and dominance had increased to the point that less intense weeding was needed and supplemental water was withdrawn.

Median NDVI at Auwahi, the longest established of the restoration sites, exhibited a roughly five-year departure from the positive trend from late 2007–2012 (Fig. 6). Breakpoints coincided with those detected in native dry forest and the aforementioned period of prolonged drought, which was more severe on Maui and Hawai'i than on Kaua'i and O'ahu (<https://droughtmonitor.unl.edu/>). Nonetheless, median NDVI has increased significantly at Auwahi since 1999 and is approaching values typical of native dry forest. While additional plantings have been conducted at the site since 2014, unassisted recruitment has also occurred for the majority of native woody species (A. C. Medeiros et al., 2014). Establishment of native dry forest plants, like the removal of non-natives, can generate positive feedbacks on soil hydrology that are likely to favor native growth, including increased soil moisture content and infiltration rates (Hata et al., 2016; Perkins et al., 2012, 2014).

For Ohikilolo and Keaau, interpretation of the NDVI time series is less straightforward, and additional monitoring is likely needed to reveal clearer post-restoration trends. Management of these smaller sites differed from Auwahi and Makauwahi in several ways: native outplanting occurred in waves and in smaller, more widely dispersed patches; irrigation for outplants was only provided at the time of planting; and removal of non-native vegetation, though extensive, was performed more gradually, sometimes without complete eradication as the end goal. Results of these efforts appear more difficult to track at Landsat resolution. At Ohikilolo, post-restoration median NDVI was still similar to that of non-native grassland. Dry season median NDVI increased slightly, but the trend did not change significantly after outplanting (Fig. 6). Keaau was the only site to experience a significant decline in median NDVI, and one of the few sites where RCV of NDVI increased significantly, with the steepest change occurring prior to site restoration (Fig. 6). These results are unsurprising, as outplanting took place relatively more recently, and each site experienced notable disturbance events during the study period. In 2018, a fire at Keaau burned through stands of wild and reintroduced native plants. Ohikilolo experienced a wildfire in 2003 and multiple fence breaches by feral goats from 2003 to 2008. These factors may have been more influential on the median NDVI trend departure, identified in 2005 (Fig. 6), than the significant long-term decline in rainfall at Ohikilolo (Appendix B, Table B.5) (Zewdie et al., 2017). Additionally, establishment of *Myoporum sandwicense* outplants could be affected by invasive *Myoporum* thrips, which were discovered at the site in 2020. Nonetheless, OANRP surveys have observed a significant increase in native shrub cover at the oldest Ohikilolo outplanting, as well as post-fire native recruitment at Keaau (Oahu Army Natural Resources Program, 2020, 2021). Both sites may require more time before these changes can be detected at 30-m resolution.

These results demonstrate that, given sufficient time post-restoration, Landsat time series could provide a cost-effective, efficient complement to conservation efforts by extending restoration monitoring periods and capturing management-related breaks in >20 year greenness trends. Trends in NDVI agreed with reported restoration outcomes (e.g. native establishment at Auwahi and Makauwahi), and BFAST analysis identified breakpoints corresponding to management activities as well as disturbance events at several sites. The median NDVI trends at these sites, and RCV trend at Makauwahi, were also stronger than those observed for native and non-native dry forest, which highlights the value of intensive restoration practices that are necessary to the conservation of dry forests threatened by wildfire and non-native plant invasions (Trauernicht et al., 2018; Wolfe and Van Bloem, 2012).

4.4. Limitations

A critical shortcoming of our NDVI approach is that we cannot reliably distinguish native from non-native vegetation, which restricts the inferences that can be made about greening trends. We interpreted greening as increased productivity in native dry forest, and the establishment of woody native species in restoration sites previously dominated by non-native grasses. The steady transition from grassland to dry forest is more apparent from NDVI metrics, but in heterogeneous native/non-native landscapes, an increase in non-native species cover could also contribute to the rise in median NDVI. For example, at Auwahi, the small invasive tree *Bocconia frutescens* was common in restoration plots (A. C. Medeiros et al., 2014), and though native dry forest sites were dominated by native species at the time of survey, they have not been re-inventoried since then (Craven et al., 2018). Without updated in situ observations, higher spatial and spectral resolution data, together with species classification models, are needed to identify species-level differences (see Balzotti et al., 2020; Lin et al., 2024). Furthermore, tropical dry forests are characterized by a simple, typically open canopy structure (Barton et al., 2021; Murphy and Lugo, 1986); only two native sites in this study are classified as closed canopy (Kokee-1, Nanakuli) (Jacobi

et al., 2017). With NDVI, it is difficult to distinguish between greening in the canopy versus the understory, where non-native grasses or other herbaceous species that might be present (Van Passel et al., 2020). Because invasive grasses are deciduous and native dry forest species are primarily evergreen in Hawaii, we attempted to mitigate this limitation by using multi-seasonal analysis and RCV of NDVI for intra-seasonal variability. However, our analysis cannot distinguish between native vegetation and evergreen non-natives.

The strength of NDVI trends in this study is limited by the length and temporal resolution of the Landsat time series. The Landsat spatial resolution enables detection of site-level variations in NDVI, but its 16-day revisit interval required observations to be seasonally aggregated (for highly seasonal tropical dry forests, this is still preferable to annual time series). However, cloud cover reduced the number of valid image dates available for each site, which tended to be lowest for native dry forest (Appendix A, Table A.2). Using an inconsistent number of data points to calculate quarterly metrics could potentially bias median NDVI values and misrepresent seasonal site variations (Venter et al., 2020). Cloud cover is a prevalent issue for optical remote sensing in tropical regions, but could be addressed by integrating data from synthetic aperture radar (SAR) sensors, which can penetrate cloud, into Landsat analyses (David et al., 2022). Sparse coverage prior to 1999 truncated the time series as well, limiting detection of trends that might become more apparent over a longer observation period. Here again, the Landsat time series might be extended and augmented through the use of additional remote sensing products, such as The Harmonized Landsat and Sentinel-2 project produced by the National Aeronautics and Space Administration (Wulder et al., 2021).

5. Conclusion

Using a 1999–2022 Landsat time series, we observed significant increases in median NDVI in native dry forest, non-native dry forest, and non-native grassland, with stronger trends in forests. Though coarser-scale studies have observed browning in the Hawaiian Islands, our results corroborate observations from other dry forest regions. The discrepancy between our study and previous research in Hawaii could therefore be attributed, at least in part, to improved isolation of native dry forest pixels using Landsat. Median NDVI was positively associated with precipitation anomalies in all vegetation classes, particularly in non-native grassland. Despite this relationship and long-term declines in precipitation, positive NDVI trends have occurred in dry forest, highlighting the ability of dry forest to remain productive when non-native grasslands are not. Nevertheless, a break in the positive median NDVI trend was detected for native dry forest and Auwahi that coincided with a prolonged period of drought across the Hawaiian Islands. Tropical dry forest species are adapted to drought, but they are likely to experience stress in longer, more intense conditions under future climate scenarios, which may also exacerbate the hydrologic and wildfire effects of non-native vegetation. Further investigation of drought, temperature, and other potential drivers is needed to better understand the relationship between NDVI and long-term climatic trends in tropical dry forest.

These results underscore the significance of dry forest restoration and the need for consistent, long-term site monitoring. Trends were more variable at Keaau and Ohikilolo, where outplanting began relatively recently, management has been relatively more passive, and several disturbance events have occurred. However, we observed significant greening trends at the more established Makauwahi and Auwahi restoration sites. For fragmented dry forest patches and local-scale restoration efforts, we suggest that Landsat imagery is better suited to the detection of multi-seasonal NDVI trends than coarser-scale sensors. Future work could explore additional remote sensing metrics, and finer spatial resolution imagery (e.g. Sentinel-2) (Benhammou et al., 2022), to improve our understanding of vegetation conditions and recovery in this rare and threatened ecosystem.

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CRedit authorship contribution statement

Monica Dimson: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Kyle C. Cavanaugh:** Writing – review & editing. **Erica von Allmen:** Writing – review & editing, Resources. **David A. Burney:** Writing – review & editing, Resources. **Kapua Kawelo:** Writing – review & editing. **Jane Beachy:** Resources. **Thomas W. Gillespie:** Writing – review & editing, Methodology.

Declaration of competing interest

None.

Data availability

Data and scripts that support the findings of this study are openly available in the Dryad Digital Repository at <https://doi.org/10.5061/dryad.15dv41p5p>.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoinf.2024.102821>.

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