

What follows fallow? Assessing revegetation patterns on abandoned sugarcane land in Hawai'i

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15 **Highlights:**

- 16 ● Revegetation on abandoned agricultural land remains poorly understood
- 17 ● Abandoned sugarcane fields in Hawai‘i offer a rich empirical opportunity
- 18 ● Grass was initially prominent, but woody vegetation increased over time
- 19 ● Non-native species dominated the composition of secondary vegetation
- 20 ● Vegetation recovered functional traits fastest, in ~53 years

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Abstract: Millions of hectares of agricultural land have been abandoned globally in recent decades, presenting opportunities for secondary vegetation growth and restoration. While abandoned fields have the potential to return to ecological communities with similar species diversity to their pre-agricultural state, they alternatively may transition to novel ecosystems or persist in degraded states that may have alternative functions that impact ecological and human communities. Yet we lack an understanding of how vegetation naturally recovers on disturbed lands. Using remote sensing and land survey data, we characterized the structure, composition, and function of secondary vegetation canopies on former sugarcane fields in Hawai'i that were abandoned between 4 and 117 years ago. We used a species distribution model to identify patches of uncultivated land with similar environmental conditions to abandoned sugarcane fields to serve as reference ecosystems. Using these reference ecosystems, we evaluated how secondary ecosystems at different ages since abandonment compare in terms of canopy structure, composition, and function. Grasses were prevalent in the years immediately following abandonment, but shrubs and trees dominated canopy structure on fields that had been abandoned more than 20 years. Non-native species constituted most of the secondary vegetation, but native vegetation cover increased on sugarcane fields that had been abandoned longer than 25 years. Secondary vegetation recovered canopy functional traits in ≤ 53 years since abandonment. Completely recovering the structural properties of reference ecosystems would require over a century. Abandoned sugarcane fields are unlikely to recover the native composition of reference ecosystems without active restoration. Our findings contribute to a growing body of literature that characterizes whether and when the globally increasing area of abandoned agricultural land may passively recover, which can direct restoration efforts on

abandoned lands to enhance ecosystem services or guide alternative management to achieve socio-cultural objectives.

1. Introduction

Agricultural land use change is a central component of global environmental change, with implications for both human and natural systems worldwide (Isbell et al., 2013; Vitousek et al., 1997). The expansion of agriculture drives land use change (Tilman et al., 2011), displacing natural systems and causing systematic losses of biodiversity both locally (Dornelas et al., 2014; Vellend et al., 2013) and globally (Murphy and Romanuk, 2014; Newbold et al., 2015). However, in many developed countries, including the U.S., agricultural areas are contracting; upwards of 385 million hectares have been abandoned in recent decades (Campbell et al., 2008). Here we consider a field to be abandoned if it is no longer cultivated and has not been urbanized or converted to an alternative land use. These abandoned fields have the potential to return to ecological communities like their pre-agricultural state, but they alternatively may transition to novel ecosystems or persist in degraded states that are often dominated by invasive vegetation with diminished structure and function (Cramer et al., 2008; Yang et al., 2020). Despite common perceptions, the literature is ambiguous as to whether, where, and when abandoned agricultural lands are beneficial to the recovery of biodiversity (Queiroz et al., 2014; Subedi et al., 2021) and ecosystem services (Bell et al., 2020; Lana-Renault et al., 2020).

As abandoned agricultural land becomes an increasingly common land cover type, interest has grown in understanding revegetation patterns on these lands (Jakovac et al., 2021). While decades of intense cultivation have led to local and global loss of biodiversity (Cardinale et al., 2012; Zabel et al., 2019), strategic abandonment of these agricultural lands could lead to the recovery of beneficial habitat for plants and animals (Beilin et al., 2014; Bourque et al., 2019;

Fischer et al., 2009; Kelsey et al., 2018; Lortie et al., 2018; Navarro and Pereira, 2015; Sojneková and Chytrý, 2015), if fields remain abandoned for a sufficient duration of time (Crawford et al., 2022). Vegetation recovery is often crucial to the return of species at higher trophic levels, not only providing habitat and food resources but also modifying environmental characteristics such as temperature and temperature fluctuations in ways that support various species (Chazdon et al., 2020; Cramer et al., 2008). Further, revegetation on retired lands can act as a buffer that insulates more pristine lands from disturbance (Wang et al., 2020). If abandoned lands revegetate to native vegetation, they may function as refugia from high intensity disturbances such as harvest or pesticide use and increase connectivity between suitable habitat patches (Crouzeilles et al., 2020; Molin et al., 2018). If instead they transition to weed patches or remain unvegetated, they may have limited habitat value and could degrade surrounding habitat, stressing flora, fauna, and human communities (Lasanta et al., 2017; Regos et al., 2016; van der Zanden et al., 2017; Vesk and Mac Nally, 2006). Thus, much of the biodiversity value of abandoned lands depends on whether they regenerate to suitable habitat, which is often tied to the type and extent of vegetation recovery (Pérez-Cárdenas et al., 2021).

Investigations of post-abandonment succession have focused primarily on fields with lower intensity cultivation histories such as pasture lands and experimental agricultural fields (Isbell et al., 2019; Letcher and Chazdon, 2009; Norden et al., 2015; Pérez-Cárdenas et al., 2021). As with succession following natural disturbance (Pang et al., 2018; Turner et al., 1998; Xi et al., 2019), the duration and intensity of cultivation influence the pace and trajectory of recovery on abandoned agricultural land (Flinn and Marks, 2007; Fraterrigo et al., 2006; Moran et al., 2000). Landscape context, such as proximity to forest fragments, can also influence revegetation patterns on abandoned fields (César et al., 2021; Molin et al., 2017). Few studies have examined secondary vegetation on intensely cultivated cropland, and most of those have focused on relatively small-

scale field studies (Grau et al., 1997; Isbell et al., 2019; Martínez and Lugo, 2008). Yet, a considerable amount of abandonment is likely to occur as groundwater limitations affect high value, intensely cultivated fields such as those in California and Australia (Brown et al., 2022; Bryant et al., 2020; Hanak et al., 2017; Millar and Roots, 2012). Additional abandonment is expected if policies promote intensive cultivation on a smaller area in accordance with the Shared Socioeconomic Pathway 1 (SSP1), which is geared toward a sustainable future (Leclère et al., 2020; Popp et al., 2017).

Extensive field measurements have enhanced our understanding of post-abandonment vegetation recovery across the Neotropics (Poorter et al., 2021, 2016; Rozendaal et al., 2019), but collecting field measurements across the anticipated extent of abandoned agricultural land is not feasible. For decades, satellite remote sensing data have been used to monitor regional and global changes in vegetation cover and land use (Beuchle et al., 2015; Cui et al., 2022; Hansen et al., 2013; Souza et al., 2020, 2013; Zhu, 2017). A growing number of studies have used remotely sensed data to identify agricultural land abandonment (Dara et al., 2018; de Castro et al., 2022; Estel et al., 2015; Kolečka and Kozak, 2019; Prishchepov et al., 2012; Suziedelyte Visockiene et al., 2019; Yin et al., 2018). However, few studies have leveraged these data to monitor vegetation recovery after abandonment at regional scales (César et al., 2021; Janus et al., 2021; Kolečka, 2021; Kolečka et al., 2015; Sačkov et al., 2020; Wuyun et al., 2022). A tradeoff of using vegetation indices and land cover classifications derived from optical remote sensing data is that these data are limited to characterizing the vegetation canopy (Glenn et al., 2008). Despite this limitation, analyses leveraging these data are valuable to develop scalable methods to monitor vegetation growth to complement field observations and improve our understanding of ecosystem recovery across the current and increasing expanse of abandoned agricultural land (Estoque et al., 2019; Gvein et al., 2023; Perpiña Castillo et al., 2020; Popp et al., 2017).

Abandoned sugarcane fields in Hawai‘i present a rich empirical opportunity to enhance our conceptual understanding of vegetation recovery following abandonment. Once widely grown across Hawai‘i, over 46,582 hectares of sugarcane land were abandoned between 4 and 117 years ago. Using Hawai‘i as a case study, we evaluated the recovery of vegetation canopy properties on abandoned sugarcane land leveraging a combination of land surveys, vegetation data, and remotely sensed imagery. Specifically, we addressed the following three questions: What is the ecological structure, composition, and function of the secondary vegetation canopy on abandoned agricultural land? How do these properties of secondary vegetation canopies change with the time since a field was abandoned? After how long, if ever, do the characteristics of secondary vegetation converge to those of uncultivated ecosystems? We found that vegetation canopy structure categories progressed from grasslands to woody vegetation over several decades. Invasive species were prevalent in secondary vegetation canopies and exhibited similar functional traits to the canopies of reference ecosystems. Estimated timelines to recover the canopy properties of reference ecosystems varied from decades for functional traits to thousands of years for native vegetation representation.

2. Methods

2.1. Sugarcane in Hawai‘i

Sugarcane plantations in Hawai‘i expanded from 4,000 ha in 1867 to 38,500 ha in 1905 (MacLennan, 2004), driven by a combination of favorable trade conditions with the U.S. and aggressive agricultural intensification and extensification by American businesses (Kahane and Mardfin, 1987). While some plantations closed within a few years and remained uncultivated thereafter (Conde and Best, 1973), overall sugarcane cultivation expanded to more than 98,000 ha in 1969 (HSPA, 1995). The area cultivated with sugarcane began declining in the 1980s because

of competition with tourism for land and water resources (State of Hawaii Department of Planning and Economic Development, 1980), cheaper sugar production internationally (HSPA, 1995), and a shift in preference to high fructose corn syrup (Dorrance and Morgan, 2005). The last commercial sugar operation in Hawai'i closed in 2016 (Melrose et al., 2016). Some abandoned sugarcane land has been converted to commercial forestry, production of genetically modified seeds, diversified agriculture (e.g., lettuce, melons, tropical fruit), or suburban developments. However, 46,582 ha of former sugarcane land, abandoned between 4-117 years ago, are not currently used for agriculture and have not been converted to alternative land uses (Perroy et al., 2016).

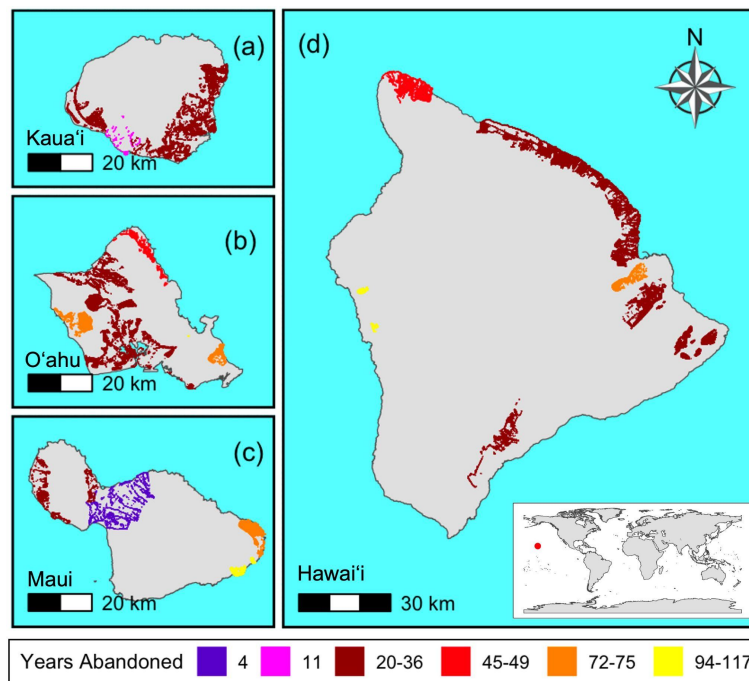


Figure 1. Abandoned sugarcane fields in Hawai'i total 46,582 ha across the islands Kaua'i (a), O'ahu (b), Maui (c), and Hawai'i (d). Abandoned fields are colored based on the number of years that they have been abandoned before the year 2020. Most of the abandonment occurred 20-36 years ago. Areas that have been abandoned longer (>72 years) occur primarily on O'ahu, Maui, and Hawai'i.

2.2. Identifying abandoned sugarcane land

We use a combination of historical and modern land surveys to identify abandoned sugarcane fields (Fig. 1). Sugarcane cultivation in Hawai'i was surveyed in 1900, 1920, 1937 and

1980, and documented on hand-drafted maps that have since been digitized into shapefiles (State of Hawaii Department of Agriculture Planning and Development Section and US Soil Conservation Service, 1980; Tetra Tech EM Inc., 2006). Two additional agricultural land cover surveys were completed in 2015 and 2020 using a combination of WorldView-2 high-resolution satellite imagery, GIS land use layers, and field visits (Melrose et al., 2016; Perroy and Collier, 2021). These six agricultural land cover shapefiles (years 1900, 1920, 1937, 1980, 2015, 2020) were used to determine where and when sugarcane fields were abandoned. A field was considered abandoned if it was designated as a sugarcane field in one land cover survey but was no longer used to grow sugarcane in any future land cover survey. We used *RStudio* software (RStudio Team, 2022) to calculate the difference between agricultural land use shapefiles to identify abandoned fields. Relevant code is available in our GitHub repository with additional details in the Supplementary Information.

Due to our focus on assessing the traits of recovering vegetation on abandoned sugarcane land, we filtered out former sugarcane fields that have been converted to other crops, tree plantations, or alternative anthropogenic uses according to the Carbon Assessment of Hawai'i (CAH) GIS dataset. The CAH provides the most recent detailed map of land use and cover across Hawai'i and was created by integrating previous land use maps and high-resolution imagery (Price et al., 2016). To refine estimates of when sugarcane land was abandoned between surveys, we used a variety of historical records that documented when plantations were initially cultivated and ultimately abandoned (Conde and Best, 1973; Meyers, 1999). Further details about the start and end dates for plantations can be found in the Supplementary Information.

2.3. Assessing revegetation patterns

In alignment with recent studies of vegetation recovery following agricultural land abandonment (Chazdon, 2014; Mata et al., 2022; Poorter et al., 2021), we assessed the canopy properties of secondary ecosystems on three axes: structure, composition, and function. Evaluating secondary ecosystems across multiple dimensions holistically captures revegetation patterns following intense cultivation. Canopy structure and canopy composition, hereafter, structure and composition, respectively, were categorically defined, and canopy functional traits, hereafter, functional traits, were quantitatively estimated with satellite-derived vegetation indices, as described below. These remotely sensed data were validated against ground observations of tree height and species as well as separate remotely sensed data that estimated vegetation height and biomass (see Supplementary Information). To develop an understanding of whether secondary ecosystems resembled uncultivated vegetation, we constructed reference plots that shared the biophysical characteristics of abandoned sugarcane fields to the extent possible but were not previously cultivated or grazed based on land use data dating back to 1900. We used the values of vegetation attributes extracted from the uncultivated ecosystems to estimate the recovery time for secondary ecosystem properties to reach reference levels.

2.3.1. Vegetation structure and composition

We first assessed trends in the structure of recovering vegetation on abandoned sugarcane fields by intersecting the abandoned sugarcane fields with the CAH dataset and extracting the major land cover (Maj_LC) attribute. Our analysis only considered the abandoned sugarcane fields where Maj_LC was one of four categories associated with vegetation structure: forest, shrubland, grassland, or bare ground. We first calculated the area of each abandoned parcel and then the percent of each parcel's area that was in each of the four structure categories. We grouped all parcels that have been abandoned for the same number of years and calculated the weighted

average of the percent cover in each structure category (Eq. 1) (National Institute of Standards and Technology, 2001a). For each structure category (e.g., forest cover), the weighted average (\bar{X}_w) is the sum of the product of percent forest cover in each parcel (X_i) and the abandoned parcel's area (w_i) divided by the sum of all the parcel areas. The subscript i represents each of the abandoned parcels and n is the total number of abandoned parcels. In some cases, parcels were entirely one structure cover type (e.g., 100% grassland), implying an observation of 0% cover for other structure categories (e.g., shrubland, forest, and bare ground) for that abandoned parcel. We included the implied observations to avoid artificially reducing sample sizes by calculating the weighted average only using instances where a given vegetation structure had non-zero percent cover.

$$\bar{X}_w = \frac{\sum_{i=1}^n w_i X_i}{\sum_{i=1}^n w_i} \quad (\text{Eq. 1})$$

The weighted standard deviation (SD_w) for each weighted average percent cover value was calculated using Equation 2 (National Institute of Standards and Technology, 2001b). All variables were the same as Equation 1 with the addition of a variable for the number of non-zero weights (N'). The weighted standard deviation was divided by the square root of the number of observations to yield a weighted standard error which was multiplied by 1.96 to define the 95% confidence interval for each of the weighted average calculations from Equation 1.

$$SD_w = \sqrt{\frac{\sum_{i=1}^n w_i (X_i - \bar{X}_w)^2}{(N' - 1) \frac{\sum_{i=1}^n w_i}{N'}}} \quad (\text{Eq. 2})$$

To assess the robustness of our metric for canopy structure, we extracted LANDFIRE's Existing Vegetation Height 30 m raster within abandoned sugarcane fields (LANDFIRE, 2020). LANDFIRE vegetation height increased with time since abandonment (Figure S1), which is consistent with our results using the structure metric derived from the CAH. We also determined

that these remotely sensed structure metrics are similar to field measurements of vegetation height (USDA Forest Service, 2021) (see Supplementary Information).

We leveraged a similar approach to measure the composition of secondary vegetation on abandoned sugarcane fields using habitat status (Hab_Status), another attribute of the CAH dataset that was intersected with the abandoned sugarcane fields. Habitat status differentiates the composition of secondary ecosystems across four categories: native dominated, non-native dominated, native/non-native mix, and bare ground. Using a more detailed land cover attribute in the CAH dataset (Det_LC), we determined that the native/non-native mix were primarily composed of non-native vegetation types, and these mixed native/non-native vegetation patches composed <1% of the abandoned area. Thus, we combined the native/non-native mix and non-native dominated composition classes into one non-native composition class, resulting in three categories to analyze vegetation composition: native dominated, non-native dominated, and bare ground. Following the approach used with the structure categories, we calculated the percent of each abandoned parcel's total area in each of the composition categories, grouped all parcels abandoned for the same number of years, and calculated the area-weighted average of the percent cover in each composition category (Eq. 1). The weighted standard deviation was also calculated as previously described (Eq. 2) and was used to calculate a 95% confidence interval for the weighted average of percent cover for each composition category. When compared to observations of tree composition in USDA Forest Service plots (USDA Forest Service, 2021), the remotely sensed canopy composition metric we derived from CAH distinguished plots dominated by native or non-native species with >82% accuracy (see Supplementary Information).

2.3.2. Vegetation function

We estimated functional characteristics of secondary vegetation using vegetation indices. Vegetation indices capitalize on how plants reflect different wavelengths of light to distinguish vegetation within a remotely sensed image (Roberts et al., 2018; Tucker, 1979; Verrelst et al., 2015; Xue and Su, 2017). Previous studies have utilized vegetation indices to classify adjacent vegetation based on their structural properties such as the differences in leaf area index between grass and tree canopies (Huete et al., 2002; Pôças et al., 2020) or phenology such as seasonal variations between annual and perennial vegetation (Brown et al., 2013; Gong et al., 2015; Wardlow et al., 2007; Zeng et al., 2020). Here we calculated three vegetation indices from Sentinel-2 Multispectral Instrument imagery (European Space Agency (ESA), 2015) to approximate the functional traits of secondary vegetation: the soil adjusted vegetation index (SAVI) (Huete et al., 2002), the normalized difference in red-edge index (NDRE) (Barnes et al., 2000), and the normalized difference in water index (NDWI) (Gao, 1996). SAVI is strongly correlated with gross primary productivity and is resistant to changes in soil brightness when vegetation cover is low (Huete et al., 2002; Ren et al., 2018; Tunca et al., 2023; Zhou et al., 2014). SAVI is sensitive to leaf area index (Gong et al., 2003; Zhen et al., 2021), so it also provides a measure of canopy structure (Roberts et al., 2018). NDRE is calculated using a ratio of two bands at red-edge wavelengths (705 and 783 nm in this study) to amplify the expression of chlorophyll absorption (Barnes et al., 2000; Evangelides and Nobajas, 2020). NDRE has been used to monitor crop maturity (Morlin Carneiro et al., 2020; Thompson et al., 2019), vegetative stress (Eitel et al., 2011; Poudel et al., 2023), and foliar nitrogen content (Bandyopadhyay et al., 2017; Crema et al., 2020). Finally, NDWI provides critical insight into canopy water content (Chai et al., 2021; Gao, 1996; Zhou et al., 2022) and live fuel moisture (Dennison et al., 2005; Lai et al., 2022; Roberts et al., 2006; Xie et al., 2022; Zacharakis and Tsihrintzis, 2023), which can capture the seasonal

phenology of secondary vegetation, particularly on abandoned sugarcane fields in dry climates. All three vegetation indices are correlated with aboveground biomass (Cho and Skidmore, 2009; Hidayatullah et al., 2023; Huang et al., 2009; Jin et al., 2014; Munyati, 2022; Na et al., 2018; Peng and Gitelson, 2012), which holds true in this context based on the correlation between all three vegetation indices and biomass estimates from the GEDI spaceborne-LIDAR sensor (Dubayah et al., 2022) (see Supplementary Information).

Using Sentinel-2 Surface Reflectance imagery collected between October 1, 2018 and October 1, 2021, we created two composite images that encompass 6-month seasons. We generated 6-month composite images to overcome any data gaps that result from cloud cover in individual images. The first season spanned October through March, roughly aligning with the Hawaiian season of Ho‘oilō, the wet season. The second season extended from April through September, matching the Hawaiian season of Kau, the dry season. For each composite image, we only included pixels with a cloud probability less than 50 percent based on the Sentinel-2 Cloud Probability image collection, which was generated using the sentinel2-cloud-detector algorithm (Copernicus Service Information, 2022a, 2022b). The value of each band in each pixel in the composite images was the median value of the cloud-free pixels at that location across all the images in each 6-month season for that year. A minimum of four images were used to calculate the value of a pixel in each composite image, but an average of 78 and 84 images were used to generate each pixel in the wet and dry season composites, respectively (Table S2). The three vegetation indices (SAVI, NDRE, and NDWI) were calculated using each of the seasonal composite images. Within each abandoned sugarcane parcel, we extracted the average value of each vegetation index in each season. We calculated the seasonal area-weighted mean value of each vegetation index in each season among fields that were abandoned for the same number of

years (Eq. 1). We also calculated the 95% confidence interval associated with each seasonal area-weighted mean vegetation index (Eq. 2).

2.4. Constructing Reference Fields

To compare recovering vegetation on abandoned fields to ecosystems without a legacy of obvious canopy disturbance, we built a Maximum Entropy (Maxent) environmental niche model (Elith et al., 2011; Phillips et al., 2006) to identify locations in Hawai‘i that have similar climate, topography, and soil traits to former sugarcane fields but no history of being cultivated or urbanized. Maxent has been used extensively to model habitat ranges based on the environmental conditions for aquatic (Mafuwe et al., 2022; Silva et al., 2019; Wang et al., 2018) and terrestrial species (Molloy et al., 2014; Srivastava et al., 2021; Su et al., 2021; Zhang et al., 2021), including plants (Ab Lah et al., 2021; Adhikari et al., 2012; Remya et al., 2015). We implemented the Maxent model using *RStudio* software (RStudio Team, 2022) and the *Wallace* modular platform (Kass et al., 2018). We provided Maxent with 2,000 occurrence points that were randomly distributed across abandoned sugarcane fields. We provided 13 environmental rasters to characterize Hawai‘i in terms of climate (air temperature, surface temperature, precipitation, humidity) (Giambelluca et al., 2014, 2013), topography (elevation, slope percent, easting, northing) (LANDFIRE, 2022a, 2022b, 2022c), and soil (pH, cation exchange capacity, saturated hydraulic conductivity, organic matter, soil moisture) (Deenick et al., 2014). Climate rasters were available at a resolution of 250 m (0.00225°) (Giambelluca et al., 2014, 2013). Elevation, slope percent, and aspect rasters were downloaded from LANDFIRE (LANDFIRE, 2022a, 2022b, 2022c) and resampled from their native 30 m resolution to 250 m to align with the climate rasters. The aspect raster was additionally separated into northing and easting components. We converted individual attributes from the Soil Atlas of Hawai‘i (Deenick et al., 2014), a shapefile derived from the Natural Resources and

Conservation Service (NRCS) database, to 250 m rasters to match the resolution of the other environmental rasters. We randomly sampled ten thousand background points from the extent of the eight main Hawaiian Islands. It is uncommon to have known locations where a species was absent, so background points are used to capture the conditions that influence the geographic distribution of the species across the study region, which is consistent with recommendations for implementing Maxent (Phillips et al., 2009).

The occurrence points were spatially partitioned into four groups. The model was trained using 75 percent of the occurrence data and validated against the remaining 25 percent. We built environmental niche models using both linear and quadratic transformations of the 13 environmental predictor variables to capture potential non-linear relationships between environmental conditions and sugarcane habitat while avoiding a model that overfit the data (Merow et al., 2013). The optimal model, which had the lowest corrected Akaike information criterion value, only used linear transformations and included 10 of the 13 predictors: air temperature, surface temperature, and soil organic matter predictors had coefficients of zero and were excluded from the optimal model. We used the optimal Maxent model to predict habitat suitability for sugarcane across 250 m raster cells covering the extent of Hawai'i based on the underlying environmental conditions. We used a complementary log-log (cloglog) transformation to convert Maxent's raw relative occurrence rates to a probability of sugarcane having the potential to be grown at a location based on the environmental conditions (Phillips et al., 2017). We then reclassified the continuous range of habitat probability values to binary presence and absence values using the 10-percentile training presence threshold (p10). This threshold assumes that 10 percent of the occurrence points with the lowest habitat suitability are not representative of the environmental conditions for sugarcane (Kramer-Schadt et al., 2013; Radosavljevic and Anderson,

2014). Our model output and occurrence points yielded a 10-percentile training presence threshold of 0.36. Pixels in the habitat suitability raster with values greater than or equal to this p10 threshold were included as potential reference ecosystems, while the remainder were omitted. The reference ecosystem raster was vectorized, intersected with the CAH dataset, (Price et al., 2016) and filtered for locations where the land cover was forest, shrubland, grassland, or bare ground. Following the approach used for the abandoned sugarcane fields as described in Section 2.3.1, we calculated the proportion of the reference ecosystem area in each of the structural (e.g., grassland, shrubland, forest, bare) and compositional (e.g., native, non-native, bare) classes. To additionally compare the functional traits of post-sugarcane secondary vegetation to those of reference vegetation, we calculated the mean of the three vegetation indices (SAVI, NDRE, NDWI) in the wet and dry seasons within the reference ecosystems following the procedure in Section 2.3.2.

In order to assess whether or not the constructed reference ecosystems had similar environmental characteristics to abandoned sugarcane fields, we extracted the average value of key topographic (elevation, percent slope) (LANDFIRE, 2022c, 2022b), climatic (annual precipitation, relative humidity) (Giambelluca et al., 2014, 2013), soil (pH, CEC, soil moisture) (Deenick et al., 2014), and geological (substrate age) (Sherrod et al., 2021) variables. Other than the substrate age, all environmental variables were previously prepared as 250 m rasters, as described above. Using the Geological Map for the State of Hawai'i shapefile (Sherrod et al., 2021), we calculated the mean age of the volcanic substrates by taking the average of the upper and lower bounds provided by the AgeRange column. We isolated this new mean age column from the shapefile and rasterized it on a 250 m grid that aligned with the other environmental variables. We extracted the average characteristics of all eight environmental variables within reference ecosystems and abandoned sugarcane fields. Fields that were abandoned for the same number of

years were grouped, and the area-weighted average and 95% confidence interval of each environmental property was calculated. We compared the area-weighted average of environmental traits on abandoned fields to the average value of each environmental variable across reference ecosystems. A subset of the environmental traits is plotted below; the remainder are included in the Supplementary Information.

2.5. Visualizing Trends in Vegetation Outcomes

To visualize possible temporal relationships between vegetation structure, composition, and function, we regressed each outcome variable (Y), for example the mean percent forest cover in abandoned fields at a given time point, on the logarithmic transformation of the number of years those parcels had been abandoned (Time) (Eq. 3). Using these regression models, we specified the value of each structure, composition, and function trait in reference ecosystems as a target value (Y) and calculated the number of years required for secondary vegetation to recover to those values.

$$Y = \text{intercept} + \beta * \ln(\text{Time}) \quad (\text{Eq. 3})$$

Previous studies have observed logarithmic patterns in the recovery of several vegetation traits such as biomass (Poorter et al., 2016), nitrogen fixation (Gei et al., 2018), species richness (Rozendaal et al., 2019), and several other structural, compositional, and functional traits (Isbell et al., 2019; Poorter et al., 2021). Succession theory also generally predicts non-linear rates of ecological progression following disturbance with change initially occurring rapidly but slowing as space, nutrients, light and other resources become limited (Drury and Nisbet, 1973; Foster and Tilman, 2000).

3. Results

3.1. Environmental characteristics of sugarcane fields and reference ecosystems

To assess the recovery of secondary vegetation on abandoned agricultural land, we used a Maxent model to identify reference ecosystems with similar environmental conditions to historical sugarcane fields in areas that were not previously cultivated. The reference ecosystems resembled abandoned sugarcane fields across several key environmental traits (Fig. 2). Average elevation was lowest among fields that were abandoned 73 years ago (66 m); however, there was no clear relationship between elevation and time since abandonment. Reference ecosystems were at an average elevation (257 m), which was higher than the average elevation across all abandoned sugarcane fields (203 m) (Fig. 2). Generally, fields that were abandoned longer had steeper slopes: fields abandoned 32, 72, and 97 years ago had the steepest average slopes ($\geq 25\%$). The slope of the reference ecosystems (17%) was slightly higher than the average slope across all abandoned sugarcane fields (16%). Many of the fields that have been abandoned for over 20 years received more than double the annual precipitation that occurred on recently abandoned fields, peaking at 3,427 mm on fields abandoned 36 years ago. Reference ecosystems received an average rainfall of 2,674 mm, which was higher than the average rainfall across abandoned fields (2,262 mm). Fields that have been abandoned longer tended to have more acidic soils compared to recently abandoned areas. Fields that had been abandoned 45 years ago had the most acidic soils (pH = 4.7) followed by fields abandoned 97 and 75 years ago (pH = 5.1). Reference ecosystems soils were acidic (pH = 5.4), which was slightly more acidic than the average soil pH among abandoned sugarcane fields (pH = 5.5). Additional environmental conditions observed in abandoned sugarcane fields and reference ecosystems are presented in the supplementary information (Fig. S1).

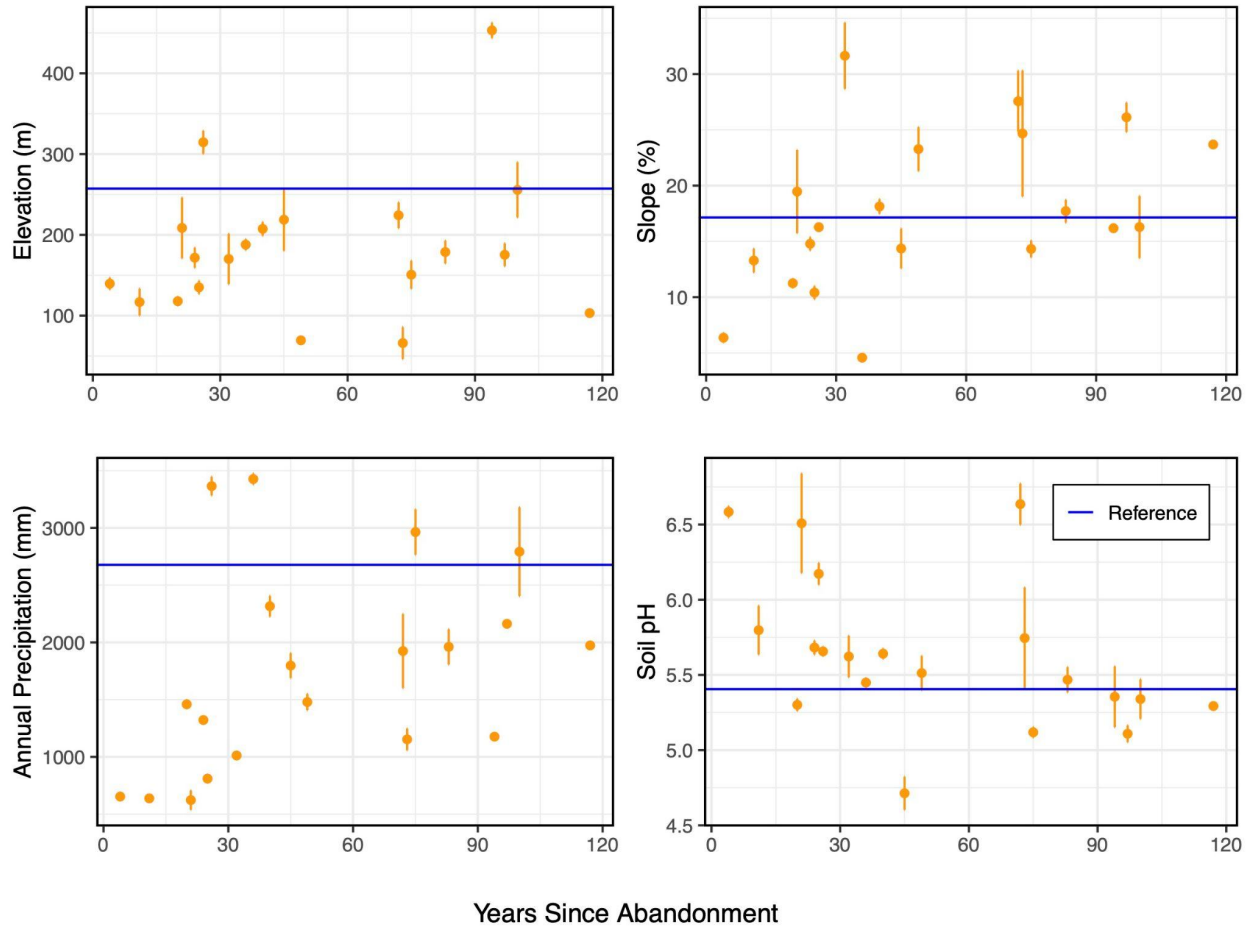


Figure 2. **Environmental traits of abandoned sugarcane fields and constructed reference fields.** Each point is the area-weighted mean of each environmental trait among fields that have been abandoned for the same number of years. Error bars represent the 95% confidence interval of each area-weighted mean. Blue lines represent the average conditions for each environmental trait in reference ecosystems. Across all ecosystem traits, the range of values observed on abandoned sugarcane fields consistently include the average value of reference ecosystems.

3.2. Vegetation structure

We first assessed temporal changes in vegetation structure on abandoned sugarcane fields and reference ecosystems. Grasslands constituted the highest proportion of secondary vegetation on sugarcane fields in the years immediately following abandonment (< 11 years); however, vegetation structure tended toward higher proportions of shrubs and trees on fields abandoned for a longer period (Fig. 3). Percent cover of shrub vegetation was initially low, peaking in fields that had been abandoned for 20 years, followed by a decrease in fields that had been abandoned longer.

After 40 years, tree species occupied a similar or higher percentage of abandoned area compared to shrubs. The percent cover of all structural categories approached the fractional composition of reference ecosystems with more time since abandonment. While no structure class had a significant relationship with the logarithmic transformation of time since abandonment, forest cover had a positive marginally significant relationship ($p = 0.06$) with the logarithmic transformation of time since abandonment (Table 1). Several sites abandoned for more than 40 years have similar forest and grass cover to those of reference ecosystems.

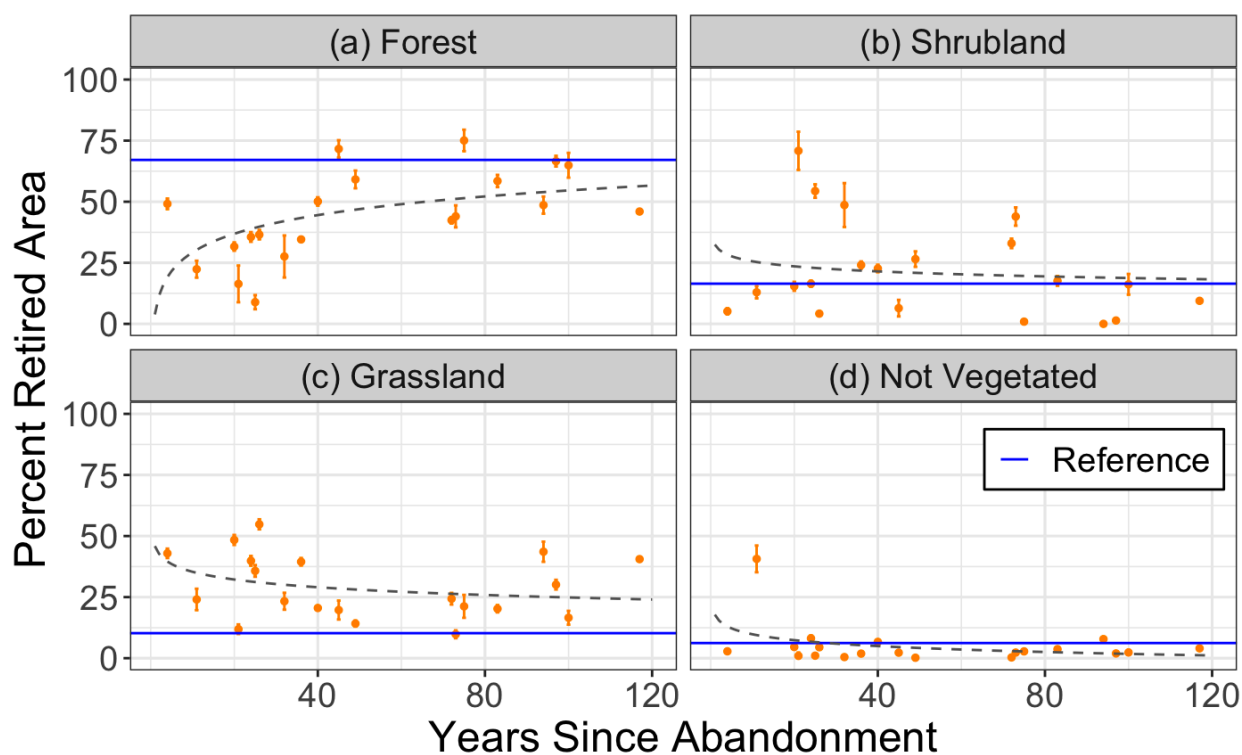


Figure 3. Vegetation structure by age of abandoned fields. While high proportions of grasses (c) were present immediately following abandonment, shrub (b) and tree (a) cover increased with time since abandonment. The proportion of abandoned fields that was not vegetated (d) decreased with more time since abandonment. Each point is the area-weighted mean of percent cover of each vegetation structure category among fields that have been abandoned for the same number of years. Error bars represent the 95% confidence interval of the area-weighted means. Blue lines represent the percent cover of each structure category across the reference ecosystem areas. Gray dashed lines reflect logarithmic models fit to the data to visualize possible temporal changes in vegetation structure. Additional model details are in Table 1.

Table 1. Effect of time since abandonment (log transformed) on various metrics of vegetation structure, composition, and function. Models take the form: outcome variable = intercept + $\beta \cdot \ln(\text{Time})$. We calculated heteroskedasticity-robust standard errors for the coefficient estimates. Significant p values ($p < 0.05$) are indicated with ** and marginally significant p values ($p < 0.1$) are indicated with *. We only estimate recovery times for outcome variables that have a marginally significant or significant relationship with time. The model results for the % Not Vegetated outcome variable related to structure and composition properties are equivalent because they consider the same abandoned parcels.

Outcome	Property	Intercept Estimate	Coefficient (β)	Coefficient Standard Error	p	Adjusted R^2	Estimated Recovery Time (Years)
% Forest	Structure	3.9	11	5.6	0.064*	0.22	311
% Shrubland	Structure	32	-3.0	5.3	0.58	-0.038	–
% Grassland	Structure	46	-4.6	2.8	0.12	0.037	–
% Not Vegetated	Structure	18	-3.5	3.4	0.32	0.14	–
% Native	Composition	-12	5.1	1.9	0.017**	0.18	3900
% Invasive	Composition	94	-1.6	3.5	0.66	-0.042	–
NDRE (Wet)	Function	0.12	0.092	0.017	<0.001***	0.40	27
NDRE (Dry)	Function	0.048	0.010	0.017	<0.001**	0.40	47
NDWI (Wet)	Function	-0.15	0.12	0.019	<0.001**	0.42	42
NDWI (Dry)	Function	-0.18	0.12	0.021	<0.001**	0.40	53
SAVI (Wet)	Function	0.39	0.17	0.033	<0.001**	0.40	34
SAVI (Dry)	Function	0.21	0.20	0.035	<0.001**	0.41	50

3.3. Vegetation Composition

To further understand vegetation recovery on abandoned sugarcane fields, we assessed the composition of secondary vegetation in terms of whether native or non-native species were dominant. Independent of the amount of time since a field was abandoned, non-native species dominated the composition of secondary vegetation. The proportion of native vegetation on former fields typically increased with more time since abandonment; however, native vegetation cover was variable across fields abandoned over 20 years from a high of 27% on fields abandoned for 100 years to nearly 0% on fields abandoned for either 73 or 117 years (Fig. 4). While native vegetation cover had a significant positive relationship ($p = 0.016$) with the logarithmic transformation of time (Table 1), this model predicted that abandoned fields would require 3,900 years to recover the native composition of reference ecosystems. This recovery time horizon suggests that secondary ecosystems on abandoned sugarcane fields will remain compositionally distinct from reference ecosystems without active restoration.

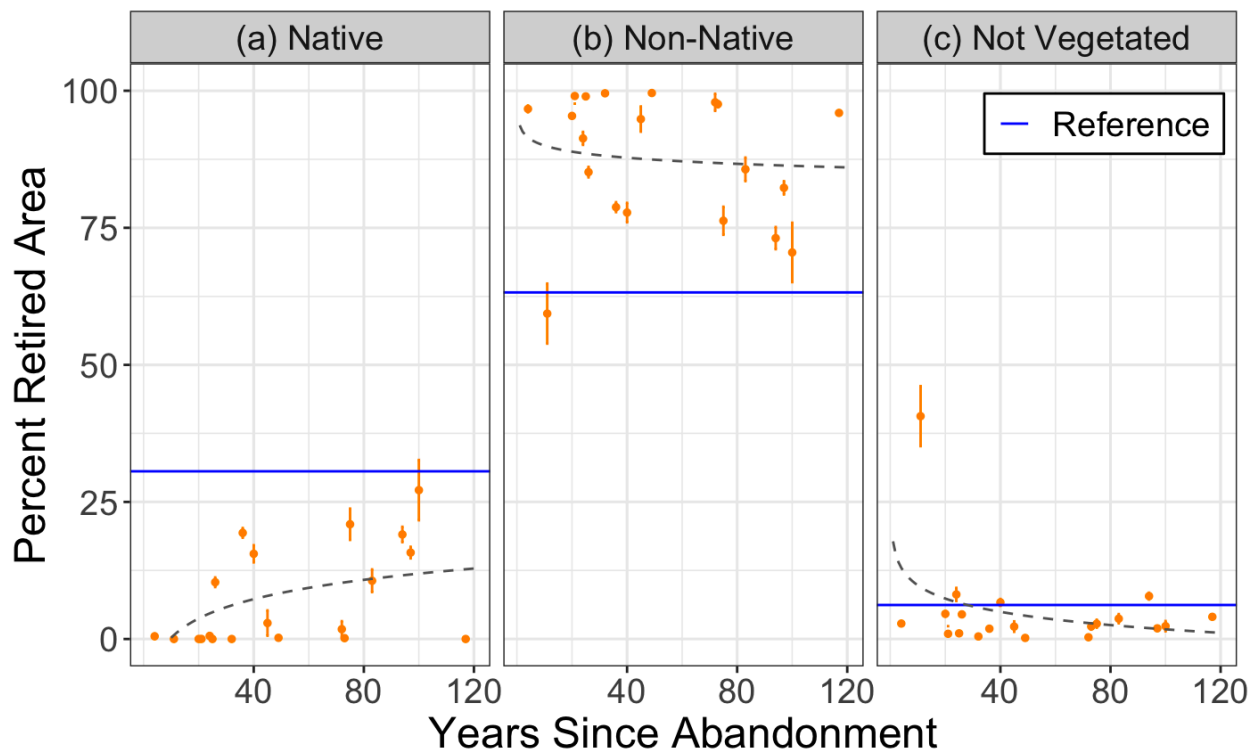


Figure 4. Vegetation composition by age of abandoned fields. While the percent cover of native vegetation (a) increased with time since abandonment, non-native species (b) consistently

composed most of the secondary vegetation. Each point is the area-weighted mean of percent cover of each vegetation composition type among fields that have been abandoned for the same number of years. Error bars represent the 95% confidence interval of the area-weighted means. Blue lines represent the percent cover of each composition category across the reference ecosystem areas. Gray dashed lines reflect logarithmic models fit to the data to visualize possible temporal changes in vegetation composition. Additional model details are in Table 1.

3.4. Vegetation Function

We used vegetation indices as approximate measures of vegetation function. The mean values of all three vegetation indices in abandoned sugarcane fields generally increased on fields that had been abandoned longer. Mean values of the vegetation indices increased fastest in the first 20 years following abandonment, and the rate of increase slowed on fields that were abandoned longer (Fig. 5). The mean values of all three vegetation indices exceeded the respective mean values in reference ecosystems. Older forests in reference ecosystems are often more structurally complex, which increases shadows and may explain the lower average vegetation index values for reference ecosystems. While there were limited differences between mean values for the vegetation indices in the wet and dry seasons, most of the wet season values were higher than their dry season counterparts among fields abandoned for the same length of time. Seasonal differences were also minimal when calculating these vegetation indices in the reference ecosystems. The mean value of all three vegetation indices during both the wet and dry seasons had significant positive relationships with the logarithmic transformation of time (Table 1). The logarithmic models estimated that vegetation indices reached average reference values between 27 and 53 years depending on the vegetation index and season.

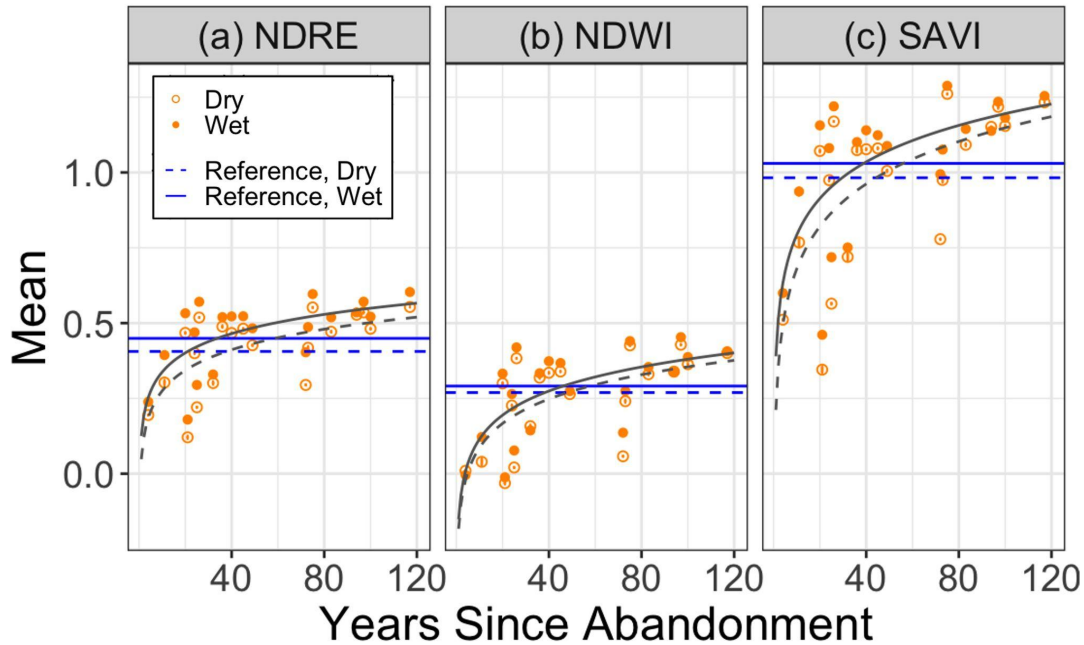


Figure 5. **Vegetation indices by age of abandoned fields and season.** These vegetation indices captured foliar chlorophyll content and stress (NDRE), canopy-scale water content (NDWI), and greenness and canopy structure (SAVI). Each point is the area-weighted mean of each vegetation index in the dry (hollow) and wet (solid) seasons among fields that have been abandoned for the same number of years. Error bars represent the 95% confidence interval of the area-weighted means for each vegetation index in each season. Blue lines represent the percent cover of each vegetation index across the reference ecosystem areas during the dry (dashed) and wet (solid) seasons. Gray dashed lines reflect logarithmic models fit to the data to visualize possible temporal changes in vegetation indices during the dry (dashed) and wet (solid) seasons. Additional model details are in Table 1.

4. Discussion

Globally, the area of abandoned agricultural land exceeds 385 million hectares (Campbell et al., 2008) with substantial increases in abandonment expected in the future (Leclère et al., 2020; Popp et al., 2017). Understanding how these lands contribute to ecosystem functions such as native species cover and carbon sequestration can inform the future management of abandoned agricultural land. Here we characterized the structure, composition, and function of secondary vegetation canopies on abandoned sugarcane fields in Hawai‘i. We assessed how those properties varied with time since a field was abandoned between 4 and 117 years ago and estimated after how

long, if ever, these secondary vegetation properties converged to those of uncultivated reference ecosystems. We found that non-native grasses and trees dominated secondary vegetation, but these novel ecosystems still resembled reference ecosystem canopies in terms of functional traits associated with carbon and water storage. These attributes varied with the time since a field was abandoned, trending toward woody vegetation and higher levels of functional traits with time. While the secondary vegetation canopy structure and function converged across many sites that had been abandoned for less than a century, secondary ecosystems are predicted to remain compositionally distinct from reference ecosystems.

Weedy forbs and grasses represented most of the vegetation immediately following abandonment likely due to the ease with which they disperse and grow (Funk, 2013; Levine et al., 2003), especially in heavily disturbed environments (Cramer et al., 2008; D'Antonio and Vitousek, 1992; Ellsworth et al., 2014; Xavier and D'Antonio, 2017). Non-native grasses were brought to Hawai'i primarily for livestock grazing (Ellsworth et al., 2014; Motooka et al., 2003; Williams and Baruch, 2000), but they have unintentionally modified ecosystem structure, composition, and function (Asner et al., 2008; Hamilton et al., 2021; Vitousek et al., 1997). Indigenous tree species in Hawai'i such as 'ōhi'a (*Metrosideros polymorpha*) and koa (*Acacia koa*) are accustomed to growing in relatively open canopy environments (Mertelmeyer et al., 2019), so they struggle to compete with invasive grasses (D'Antonio and Vitousek, 1992). Grasses have similarly dominated abandoned agricultural land elsewhere, including sites in Panama (Hooper et al., 2005), Spain (Grigulis et al., 2005), and Australia (Standish et al., 2008). We found that shrub and tree canopies successfully established on some abandoned sugarcane fields in Hawai'i (Fig. 3); however, non-native species constituted most of the woody vegetation (Fig. 4). While both 'ōhi'a and koa were likely present in some areas prior to sugarcane cultivation, substantial distances between

abandoned fields and intact forests limit the success of wind-dispersed ‘ōhi‘a seeds (Drake, 1992) and practically eliminate vegetative regeneration of koa (Spatz and Mueller-Dombois, 1973). Even in the absence of native vegetation, secondary vegetation on abandoned sugarcane fields exhibited functional traits related to carbon storage and canopy water content as approximated with vegetation indices (Fig. 5).

We found that all the vegetation properties changed with time since abandonment, but not all properties had a significant relationship with time (Table 1). Vegetation structure trended from grasses to shrubs and trees, which generally aligned with classic succession theory in temperate forests (Clements, 1916; Egler, 1954) and succession following slash and burn agriculture in the Neotropics (Guariguata and Ostertag, 2001). However, this succession pathway is unusual for native vegetation in Hawai‘i. For example, following volcanic disturbances, ‘ōhi‘a, a dominant tree species in native forests, is among the earliest colonizers on recent lava flows in Hawai‘i (Drake, 1992). A variety of other trees (e.g., ‘ōlapa (*Cheirodendron trigynum*), ‘ōhelo (*Vaccinium rhyncocarpa*), kōlea (*Myrsine lanaiensis*)) and ferns (e.g., uluhe (*Dicranopteris linearis*), hāpu‘u tree ferns (*Cibotium* spp)) form the understory of the montane rainforests in subsequent decades to centuries (Aplet and Vitousek, 1994; Clarkson, 1998). Similarly, after forest dieback, native species recover over time through recruitment into canopy gaps and multiple mechanisms of natural regeneration (Jacobi et al., 1988; Mertelmeyer et al., 2019). However, unlike natural disturbances such as volcanic eruptions, intensive cultivation isolates land from seed sources for regeneration and dramatically changes the microhabitat to favor fast dispersing invasive species with minimal establishment requirements (Arroyo-Rodríguez et al., 2017; Cramer et al., 2008). Furthermore, invasive trees, such as the species introduced to tree plantations in Hawai‘i, typically do not facilitate the development of native forest understory (Ostertag et al., 2008). Thus, native

trees would likely struggle to recover in the understory of non-native forest or a densely grass-filled field without adequate substrates for regeneration such as native tree trunks, tree-fern trunks, and bryophytes (Rehm et al., 2021, 2019). In contrast with the slow recovery of native canopy composition on abandoned sugarcane fields, secondary vegetation quickly recovered carbon and water storing capacities. Interestingly, we found all the vegetation indices on abandoned fields frequently exceeded reference values on fields that have been abandoned more than ~50 years. Reference ecosystems are likely to have more complex canopy structures that generate shadows and may reduce vegetation index values compared to those measured in less structurally complex secondary vegetation (Jiang et al., 2006; Zhang et al., 2015). The novel ecosystems that form on fragmented post-agricultural land in Hawai'i (Barton et al., 2021) may indeed store more carbon and water than reference ecosystems, but further research would be necessary to test that hypothesis.

Lastly, we analyzed whether and when the properties of secondary vegetation on abandoned sugarcane land converged to those of reference ecosystems. Secondary vegetation canopies recovered the approximated functional traits fastest (≤ 53 years) after abandonment (Figure 5). Neotropical secondary forests recovered functional traits such as wood density and specific leaf area over similar timelines (Poorter et al., 2020). When considering vegetation structure, we found that tree cover in secondary vegetation converged to that of reference ecosystems despite decades of intensive cultivation (Figure 3). While several sites had similar forest and grassland cover to reference ecosystems less than a century after abandonment, complete recovery of canopy vegetation structure seems to take slightly longer than the 60-100 years required to recover the structural heterogeneity of old growth stands on abandoned agricultural land in the Neotropics (Poorter et al., 2021). Forests have also been found to recover

structure in a matter of decades following less severe disturbances (Moran et al., 2000; Rappaport et al., 2018). The abandoned sugarcane fields in this study have a more intense disturbance history than many abandoned fields that have been previously studied, which may account for this prolonged recovery of canopy structural traits observed here. While native vegetation cover increased over time, abandoned fields were projected to never recover the native composition of reference ecosystems on a relevant time horizon ($>3,900$ years) (Figure 4; Table 1). Neotropical secondary forests have previously recovered species richness in the canopy and subcanopy within a few decades, but recovering species composition required between many decades and a few centuries depending on the intensity of previous disturbances (Isbell et al., 2019; Letcher and Chazdon, 2009; Martin et al., 2013; Pérez-Cárdenas et al., 2021; Poorter et al., 2021; Rozendaal et al., 2019). Abandoned fields in Hawai‘i may never recover their composition due to the lower diversity of native tree species in Hawai‘i compared to many other tropical settings (Inman-Narahari et al., 2013). Low diversity of native tree species in American Samoa has contributed to secondary forests on abandoned agricultural land remaining compositionally distinct from mature forests (Webb et al., 2021). Thus, agricultural disturbance has the potential to play an outsized role in changing the composition of Hawai‘i’s landscapes despite secondary vegetation recovering the basic structure and function of a tropical forest. Recovering native-dominated ecosystems on Hawai‘i’s abandoned sugarcane fields would likely require active restoration (Friday et al., 2015). Alternatively, non-native vegetative stands may be restored to agroforestry systems composed of a mixture of native and non-native species to yield social and cultural benefits as has been explored on former pastures in Hawai‘i (Hastings et al., 2023).

While this study provides insight into patterns of secondary succession in terms of canopy structure, composition, and function following intensive cultivation, it has some limitations. First,

we relied on categorical variables that are inherently limited in their ability to capture the dynamic, mixed states that are common in semi-natural secondary ecosystems. Future studies could spectrally unmix satellite imagery to calculate the fractional cover of fine and woody vegetation in each pixel, providing a continuous metric for structural succession. However, publicly available remote sensing data lacks the spectral or spatial resolution to discern vegetation composition with the detail of the categorical composition variable we used. Future field observations of species composition would provide more nuanced insight into compositional succession but would require time and resources that may not be feasible when assessing revegetation across large swaths of abandoned land. Second, the vegetation indices used here serve as a proxy rather than direct measure of ecosystem functional traits and were unable to evaluate the recovery of functional traits in the understory of closed-canopy forest. While our current approach provides useful insight into top of canopy vegetation, future studies could leverage increasingly available LIDAR data that penetrates vegetated canopies to better characterize understory structure, composition, and function (Almeida et al., 2021; Caughlin et al., 2016; de Almeida et al., 2020). Lastly, our approach uses a chronosequence to analyze the recovery of secondary vegetation canopy properties in relation to the time fields have been abandoned rather than measuring secondary vegetation properties in each field over time. As with other studies that have applied chronosequences to study vegetation recovery following abandonment, our study sites cover a range of precipitation, elevation, and soil conditions. While we determined that the average recovery of vegetation traits is consistent across the sources of environmental heterogeneity in our study sites, chronosequences necessarily have limitations relative to following individual fields over time.

5. Conclusion

Despite recent increases in agricultural land abandonment globally, we still have a limited understanding of whether and when secondary vegetation can recover the biodiversity and ecosystem services of uncultivated ecosystems. We explored the canopy structure, composition, and function of secondary vegetation on sugarcane fields in Hawai‘i that were abandoned between 4 and 117 years ago. Our results suggest that even after prolonged, intense cultivation, secondary vegetation on abandoned sugarcane land recovered the structure and functional traits of reference ecosystems across sites that were abandoned less than a century but remained compositionally distinct from reference ecosystems in perpetuity. Given that abandonment is expected to increase on high-value, intensively cultivated land, further research is necessary to consider how cultivation intensity and the diversity of species pools affect secondary vegetation development on abandoned agricultural land. This study highlights the variable time required for secondary vegetation to passively recover several attributes, which can guide decisions to restore or otherwise manage abandoned agricultural land to promote biodiversity or a variety of ecosystem services.

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Appendix A. Supplementary Information

The GitHub repository for this project can be found at:
https://github.com/nakoafarrant/what_follows_follow.

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