

1 **What follows fallow? Assessing revegetation patterns on abandoned sugarcane land in**
2 **Hawai‘i**

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13 **Keywords:** Land abandonment; vegetation structure; vegetation composition; vegetation function

14

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

21

22 **Abstract:** Millions of hectares of agricultural land have been abandoned globally in recent
23 decades, presenting opportunities for secondary vegetation growth and restoration. While
24 abandoned fields have the potential to return to ecological communities with similar species
25 diversity to their pre-agricultural state, they alternatively may transition to novel ecosystems or
26 persist in degraded states that may have alternative functions that impact ecological and human
27 communities. Yet we lack an understanding of how vegetation naturally recovers on disturbed
28 lands. Using remote sensing and land survey data, we characterized the structure, composition,
29 and function of secondary vegetation canopies on former sugarcane fields in Hawai‘i that were
30 abandoned between 4 and 117 years ago. We used a species distribution model to identify
31 patches of uncultivated land with similar environmental conditions to abandoned sugarcane
32 fields to serve as reference ecosystems. Using these reference ecosystems, we evaluated how
33 secondary ecosystems at different ages since abandonment compare in terms of canopy structure,
34 composition, and function. Grasses were prevalent in the years immediately following
35 abandonment, but shrubs and trees dominated canopy structure on fields that had been
36 abandoned more than 20 years. Non-native species constituted most of the secondary vegetation,
37 but native vegetation cover increased on sugarcane fields that had been abandoned longer than
38 25 years. Secondary vegetation recovered canopy functional traits in ≤ 53 years since
39 abandonment. Completely recovering the structural properties of reference ecosystems would
40 require over a century. Abandoned sugarcane fields are unlikely to recover the native
41 composition of reference ecosystems without active restoration. Our findings contribute to a
42 growing body of literature that characterizes whether and when the globally increasing area of
43 abandoned agricultural land may passively recover, which can direct restoration efforts on

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

46 **1. Introduction**

47 Agricultural land use change is a central component of global environmental change, with
48 implications for both human and natural systems worldwide (Isbell et al., 2013; Vitousek et al.,
49 1997). The expansion of agriculture drives land use change (Tilman et al., 2011), displacing natural
50 systems and causing systematic losses of biodiversity both locally (Dornelas et al., 2014; Vellend
51 et al., 2013) and globally (Murphy and Romanuk, 2014; Newbold et al., 2015). However, in many
52 developed countries, including the U.S., agricultural areas are contracting; upwards of 385 million
53 hectares have been abandoned in recent decades (Campbell et al., 2008). Here we consider a field
54 to be abandoned if it is no longer cultivated and has not been urbanized or converted to an
55 alternative land use. These abandoned fields have the potential to return to ecological communities
56 like their pre-agricultural state, but they alternatively may transition to novel ecosystems or persist
57 in degraded states that are often dominated by invasive vegetation with diminished structure and
58 function (Cramer et al., 2008; Yang et al., 2020). Despite common perceptions, the literature is
59 ambiguous as to whether, where, and when abandoned agricultural lands are beneficial to the
60 recovery of biodiversity (Queiroz et al., 2014; Subedi et al., 2021) and ecosystem services (Bell et
61 al., 2020; Lana-Renault et al., 2020).

62 As abandoned agricultural land becomes an increasingly common land cover type, interest
63 has grown in understanding revegetation patterns on these lands (Jakovac et al., 2021). While
64 decades of intense cultivation have led to local and global loss of biodiversity (Cardinale et al.,
65 2012; Zabel et al., 2019), strategic abandonment of these agricultural lands could lead to the
66 recovery of beneficial habitat for plants and animals (Beilin et al., 2014; Bourque et al., 2019;

67 Fischer et al., 2009; Kelsey et al., 2018; Lortie et al., 2018; Navarro and Pereira, 2015; Sojneková
68 and Chytrý, 2015), if fields remain abandoned for a sufficient duration of time (Crawford et al.,
69 2022). Vegetation recovery is often crucial to the return of species at higher trophic levels, not
70 only providing habitat and food resources but also modifying environmental characteristics such
71 as temperature and temperature fluctuations in ways that support various species (Chazdon et al.,
72 2020; Cramer et al., 2008). Further, revegetation on retired lands can act as a buffer that insulates
73 more pristine lands from disturbance (Wang et al., 2020). If abandoned lands revegetate to native
74 vegetation, they may function as refugia from high intensity disturbances such as harvest or
75 pesticide use and increase connectivity between suitable habitat patches (Crouzeilles et al., 2020;
76 Molin et al., 2018). If instead they transition to weed patches or remain unvegetated, they may
77 have limited habitat value and could degrade surrounding habitat, stressing flora, fauna, and human
78 communities (Lasanta et al., 2017; Regos et al., 2016; van der Zanden et al., 2017; Vesk and Mac
79 Nally, 2006). Thus, much of the biodiversity value of abandoned lands depends on whether they
80 regenerate to suitable habitat, which is often tied to the type and extent of vegetation recovery
81 (Pérez-Cárdenas et al., 2021).

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

91 scale field studies (Grau et al., 1997; Isbell et al., 2019; Martínez and Lugo, 2008). Yet, a
92 considerable amount of abandonment is likely to occur as groundwater limitations affect high
93 value, intensely cultivated fields such as those in California and Australia (Brown et al., 2022;
94 Bryant et al., 2020; Hanak et al., 2017; Millar and Roots, 2012). Additional abandonment is
95 expected if policies promote intensive cultivation on a smaller area in accordance with the Shared
96 Socioeconomic Pathway 1 (SSP1), which is geared toward a sustainable future (Leclère et al.,
97 2020; Popp et al., 2017).

98 Extensive field measurements have enhanced our understanding of post-abandonment
99 vegetation recovery across the Neotropics (Poorter et al., 2021, 2016; Rozendaal et al., 2019), but
100 collecting field measurements across the anticipated extent of abandoned agricultural land is not
101 feasible. For decades, satellite remote sensing data have been used to monitor regional and global
102 changes in vegetation cover and land use (Beuchle et al., 2015; Cui et al., 2022; Hansen et al.,
103 2013; Souza et al., 2020, 2013; Zhu, 2017). A growing number of studies have used remotely
104 sensed data to identify agricultural land abandonment (Dara et al., 2018; de Castro et al., 2022;
105 Estel et al., 2015; Kolecka and Kozak, 2019; Prishchepov et al., 2012; Suziedelyte Visockiene et
106 al., 2019; Yin et al., 2018). However, few studies have leveraged these data to monitor vegetation
107 recovery after abandonment at regional scales (César et al., 2021; Janus et al., 2021; Kolecka,
108 2021; Kolecka et al., 2015; Sačkov et al., 2020; Wuyun et al., 2022). A tradeoff of using vegetation
109 indices and land cover classifications derived from optical remote sensing data is that these data
110 are limited to characterizing the vegetation canopy (Glenn et al., 2008). Despite this limitation,
111 analyses leveraging these data are valuable to develop scalable methods to monitor vegetation
112 growth to complement field observations and improve our understanding of ecosystem recovery
113 across the current and increasing expanse of abandoned agricultural land (Estoque et al., 2019;
114 Gvein et al., 2023; Perpiña Castillo et al., 2020; Popp et al., 2017).

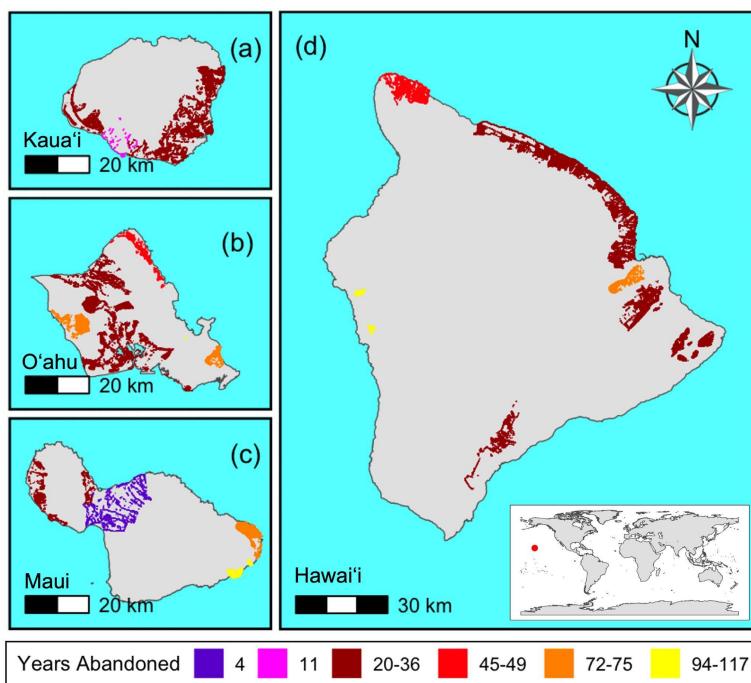
115 Abandoned sugarcane fields in Hawai‘i present a rich empirical opportunity to enhance our
116 conceptual understanding of vegetation recovery following abandonment. Once widely grown
117 across Hawai‘i, over 46,582 hectares of sugarcane land were abandoned between 4 and 117 years
118 ago. Using Hawai‘i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

130 **2. Methods**

131 **2.1. Sugarcane in Hawai‘i**

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

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



146
147 **Figure 1. Abandoned sugarcane fields in Hawai‘i total 46,582 ha across the islands Kaua‘i**
148 **(a), O‘ahu (b), Maui (c), and Hawai‘i (d).** Abandoned fields are colored based on the number
149 of years that they have been abandoned before the year 2020. Most of the abandonment occurred
150 20-36 years ago. Areas that have been abandoned longer (>72 years) occur primarily on O‘ahu,
151 Maui, and Hawai‘i.

152
153 **2.2. Identifying abandoned sugarcane land**

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

156 1980, and documented on hand-drafted maps that have since been digitized into shapefiles (State
157 of Hawaii Department of Agriculture Planning and Development Section and US Soil
158 Conservation Service, 1980; Tetra Tech EM Inc., 2006). Two additional agricultural land cover
159 surveys were completed in 2015 and 2020 using a combination of WorldView-2 high-resolution
160 satellite imagery, GIS land use layers, and field visits (Melrose et al., 2016; Perroy and Collier,
161 2021). These six agricultural land cover shapefiles (years 1900, 1920, 1937, 1980, 2015, 2020)
162 were used to determine where and when sugarcane fields were abandoned. A field was considered
163 abandoned if it was designated as a sugarcane field in one land cover survey but was no longer
164 used to grow sugarcane in any future land cover survey. We used *RStudio* software (RStudio Team,
165 2022) to calculate the difference between agricultural land use shapefiles to identify abandoned
166 fields. Relevant code is available in our GitHub repository with additional details in the
167 Supplementary Information.

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

177 **2.3. Assessing revegetation patterns**

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

193 **2.3.1. Vegetation structure and composition**

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

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

$$211 \quad \bar{X}_w = \frac{\sum_{i=1}^n w_i X_i}{\sum_{i=1}^n w_i} \quad (\text{Eq. 1})$$

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

$$218 \quad SD_w = \sqrt{\frac{\sum_{i=1}^n w_i (X_i - \bar{X}_w)^2}{\frac{(N' - 1) \sum_{i=1}^n w_i}{N'}}} \quad (\text{Eq. 2})$$

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

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

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

244 **2.3.2. Vegetation function**

245 We estimated functional characteristics of secondary vegetation using vegetation indices.
246 Vegetation indices capitalize on how plants reflect different wavelengths of light to distinguish
247 vegetation within a remotely sensed image (Roberts et al., 2018; Tucker, 1979; Verrelst et al.,
248 2015; Xue and Su, 2017). Previous studies have utilized vegetation indices to classify adjacent
249 vegetation based on their structural properties such as the differences in leaf area index between
250 grass and tree canopies (Huete et al., 2002; Pôcas et al., 2020) or phenology such as seasonal
251 variations between annual and perennial vegetation (Brown et al., 2013; Gong et al., 2015;
252 Wardlow et al., 2007; Zeng et al., 2020). Here we calculated three vegetation indices from
253 Sentinel-2 Multispectral Instrument imagery (European Space Agency (ESA), 2015) to
254 approximate the functional traits of secondary vegetation: the soil adjusted vegetation index
255 (SAVI) (Huete et al., 2002), the normalized difference in red-edge index (NDRE) (Barnes et al.,
256 2000), and the normalized difference in water index (NDWI) (Gao, 1996). SAVI is strongly
257 correlated with gross primary productivity and is resistant to changes in soil brightness when
258 vegetation cover is low (Huete et al., 2002; Ren et al., 2018; Tunca et al., 2023; Zhou et al., 2014).
259 SAVI is sensitive to leaf area index (Gong et al., 2003; Zhen et al., 2021), so it also provides a
260 measure of canopy structure (Roberts et al., 2018). NDRE is calculated using a ratio of two bands
261 at red-edge wavelengths (705 and 783 nm in this study) to amplify the expression of chlorophyll
262 absorption (Barnes et al., 2000; Evangelides and Nobajas, 2020). NDRE has been used to monitor
263 crop maturity (Morlin Carneiro et al., 2020; Thompson et al., 2019), vegetative stress (Eitel et al.,
264 2011; Poudel et al., 2023), and foliar nitrogen content (Bandyopadhyay et al., 2017; Crema et al.,
265 2020). Finally, NDWI provides critical insight into canopy water content (Chai et al., 2021; Gao,
266 1996; Zhou et al., 2022) and live fuel moisture (Dennison et al., 2005; Lai et al., 2022; Roberts et
267 al., 2006; Xie et al., 2022; Zacharakis and Tsirhrintzis, 2023), which can capture the seasonal

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

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

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

293 **2.4. Constructing Reference Fields**

294 To compare recovering vegetation on abandoned fields to ecosystems without a legacy of
295 obvious canopy disturbance, we built a Maximum Entropy (Maxent) environmental niche model
296 (Elith et al., 2011; Phillips et al., 2006) to identify locations in Hawai‘i that have similar climate,
297 topography, and soil traits to former sugarcane fields but no history of being cultivated or
298 urbanized. Maxent has been used extensively to model habitat ranges based on the environmental
299 conditions for aquatic (Mafuwe et al., 2022; Silva et al., 2019; Wang et al., 2018) and terrestrial
300 species (Molloy et al., 2014; Srivastava et al., 2021; Su et al., 2021; Zhang et al., 2021), including
301 plants (Ab Lah et al., 2021; Adhikari et al., 2012; Remya et al., 2015). We implemented the Maxent
302 model using *RStudio* software (RStudio Team, 2022) and the *Wallace* modular platform (Kass et
303 al., 2018). We provided Maxent with 2,000 occurrence points that were randomly distributed
304 across abandoned sugarcane fields. We provided 13 environmental rasters to characterize Hawai‘i
305 in terms of climate (air temperature, surface temperature, precipitation, humidity) (Giambelluca et
306 al., 2014, 2013), topography (elevation, slope percent, easting, northing) (LANDFIRE, 2022a,
307 2022b, 2022c), and soil (pH, cation exchange capacity, saturated hydraulic conductivity, organic
308 matter, soil moisture) (Deenick et al., 2014). Climate rasters were available at a resolution of 250
309 m (0.00225°) (Giambelluca et al., 2014, 2013). Elevation, slope percent, and aspect rasters were
310 downloaded from LANDFIRE (LANDFIRE, 2022a, 2022b, 2022c) and resampled from their
311 native 30 m resolution to 250 m to align with the climate rasters. The aspect raster was additionally
312 separated into northing and easting components. We converted individual attributes from the Soil
313 Atlas of Hawai‘i (Deenick et al., 2014), a shapefile derived from the Natural Resources and

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

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

337 2014). Our model output and occurrence points yielded a 10-percentile training presence threshold
338 of 0.36. Pixels in the habitat suitability raster with values greater than or equal to this p10 threshold
339 were included as potential reference ecosystems, while the remainder were omitted. The reference
340 ecosystem raster was vectorized, intersected with the CAH dataset, (Price et al., 2016) and filtered
341 for locations where the land cover was forest, shrubland, grassland, or bare ground. Following the
342 approach used for the abandoned sugarcane fields as described in Section 2.3.1, we calculated the
343 proportion of the reference ecosystem area in each of the structural (e.g., grassland, shrubland,
344 forest, bare) and compositional (e.g., native, non-native, bare) classes. To additionally compare
345 the functional traits of post-sugarcane secondary vegetation to those of reference vegetation, we
346 calculated the mean of the three vegetation indices (SAVI, NDRE, NDWI) in the wet and dry
347 seasons within the reference ecosystems following the procedure in Section 2.3.2.

348 In order to assess whether or not the constructed reference ecosystems had similar
349 environmental characteristics to abandoned sugarcane fields, we extracted the average value of
350 key topographic (elevation, percent slope) (LANDFIRE, 2022c, 2022b), climatic (annual
351 precipitation, relative humidity) (Giambelluca et al., 2014, 2013), soil (pH, CEC, soil moisture)
352 (Deenick et al., 2014), and geological (substrate age) (Sherrod et al., 2021) variables. Other than
353 the substrate age, all environmental variables were previously prepared as 250 m rasters, as
354 described above. Using the Geological Map for the State of Hawai‘i shapefile (Sherrod et al.,
355 2021), we calculated the mean age of the volcanic substrates by taking the average of the upper
356 and lower bounds provided by the AgeRange column. We isolated this new mean age column from
357 the shapefile and rasterized it on a 250 m grid that aligned with the other environmental variables.
358 We extracted the average characteristics of all eight environmental variables within reference
359 ecosystems and abandoned sugarcane fields. Fields that were abandoned for the same number of

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

365 **2.5. Visualizing Trends in Vegetation Outcomes**

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

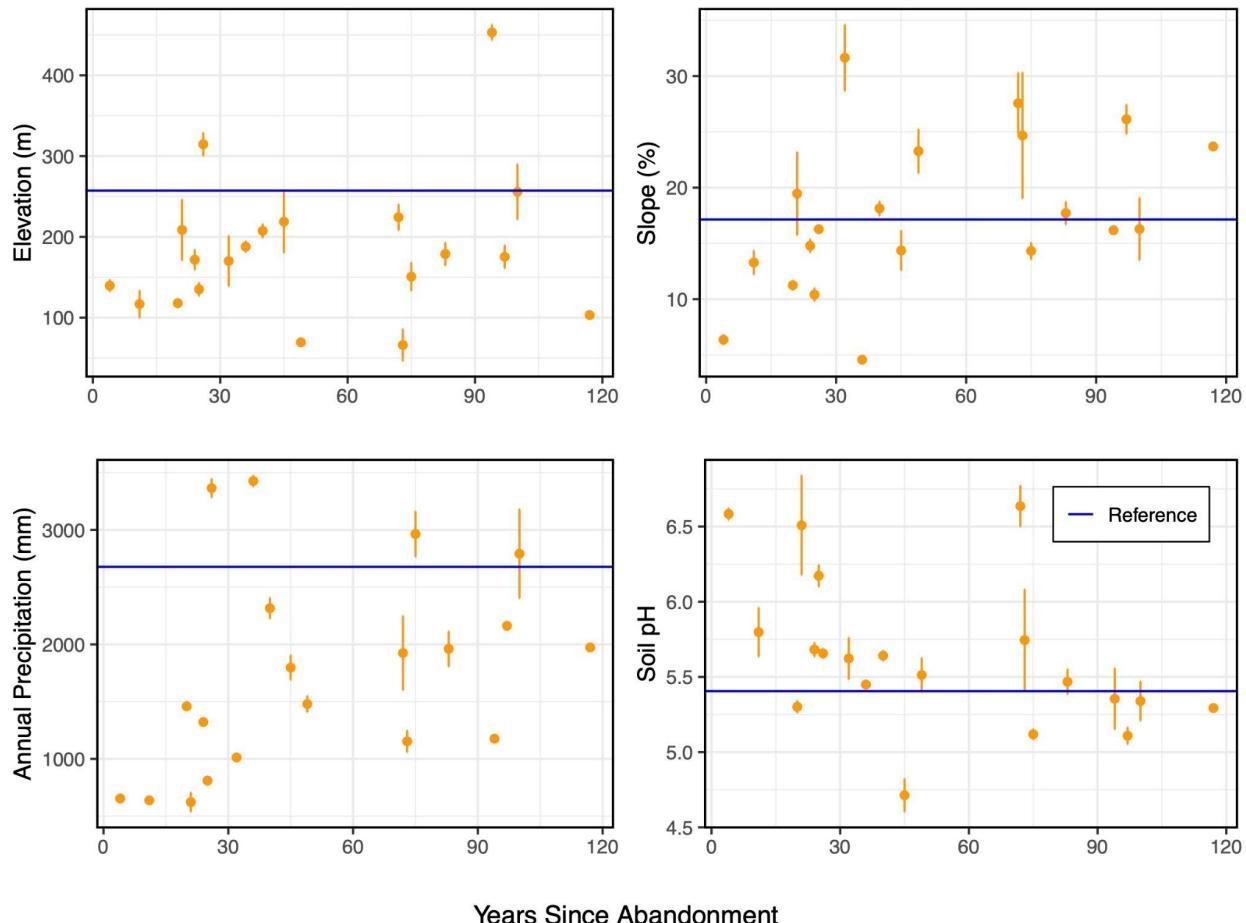
373
$$Y = \text{intercept} + \beta * \ln(\text{Time}) \quad (\text{Eq. 3})$$

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

381 **3. Results**

382 **3.1. Environmental characteristics of sugarcane fields and reference ecosystems**

383 To assess the recovery of secondary vegetation on abandoned agricultural land, we used a
384 Maxent model to identify reference ecosystems with similar environmental conditions to historical
385 sugarcane fields in areas that were not previously cultivated. The reference ecosystems resembled
386 abandoned sugarcane fields across several key environmental traits (Fig. 2). Average elevation
387 was lowest among fields that were abandoned 73 years ago (66 m); however, there was no clear
388 relationship between elevation and time since abandonment. Reference ecosystems were at an
389 average elevation (257 m), which was higher than the average elevation across all abandoned
390 sugarcane fields (203 m) (Fig. 2). Generally, fields that were abandoned longer had steeper slopes:
391 fields abandoned 32, 72, and 97 years ago had the steepest average slopes ($\geq 25\%$). The slope of
392 the reference ecosystems (17%) was slightly higher than the average slope across all abandoned
393 sugarcane fields (16%). Many of the fields that have been abandoned for over 20 years received
394 more than double the annual precipitation that occurred on recently abandoned fields, peaking at
395 3,427 mm on fields abandoned 36 years ago. Reference ecosystems received an average rainfall
396 of 2,674 mm, which was higher than the average rainfall across abandoned fields (2,262 mm).
397 Fields that have been abandoned longer tended to have more acidic soils compared to recently
398 abandoned areas. Fields that had been abandoned 45 years ago had the most acidic soils (pH = 4.7)
399 followed by fields abandoned 97 and 75 years ago (pH = 5.1). Reference ecosystems soils were
400 acidic (pH = 5.4), which was slightly more acidic than the average soil pH among abandoned
401 sugarcane fields (pH = 5.5). Additional environmental conditions observed in abandoned
402 sugarcane fields and reference ecosystems are presented in the supplementary information (Fig.
403 S1).



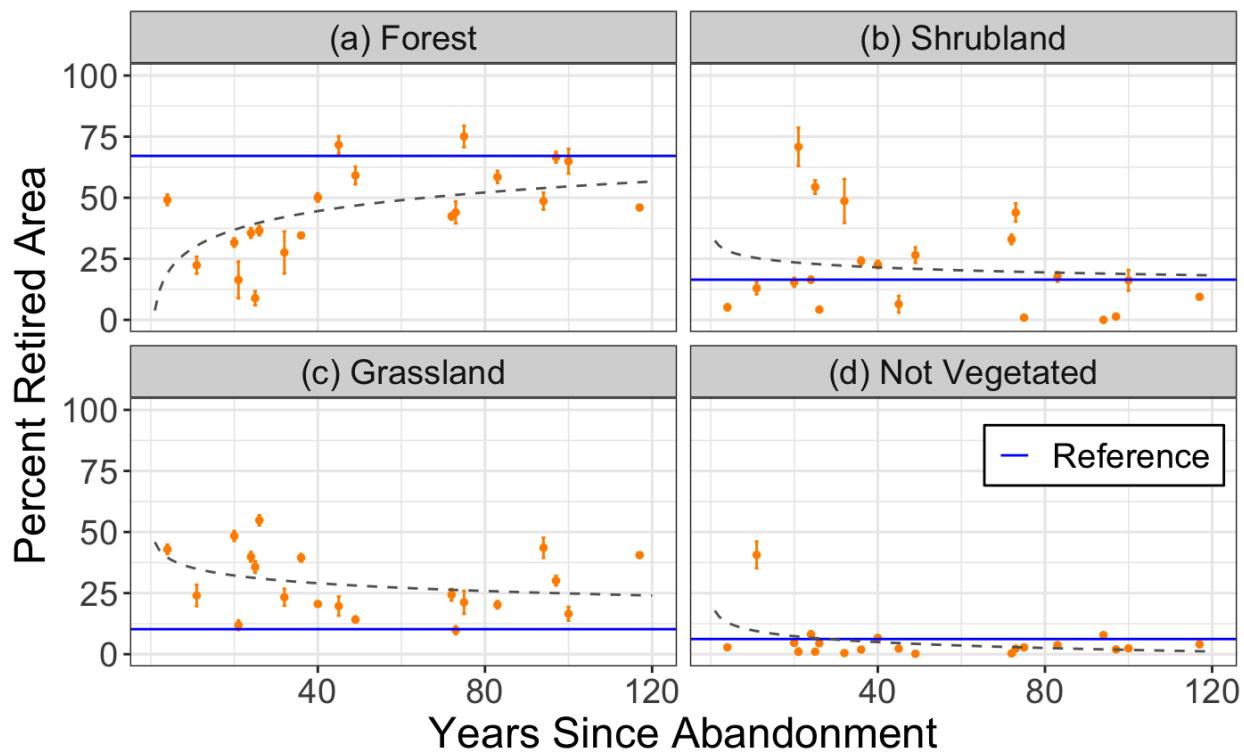
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Figure 2. Environmental traits of abandoned sugarcane fields and constructed reference fields. Each point is the area-weighted mean of each environmental trait among fields that have been abandoned for the same number of years. Error bars represent 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.

412 **3.2. Vegetation structure**

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

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



426

427 **Figure 3. Vegetation structure by age of abandoned fields.** While high proportions of grasses
 428 (c) were present immediately following abandonment, shrub (b) and tree (a) cover increased with
 429 time since abandonment. The proportion of abandoned fields that was not vegetated (d) decreased
 430 with more time since abandonment. Each point is the area-weighted mean of percent cover of each
 431 vegetation structure category among fields that have been abandoned for the same number of years.
 432 Error bars represent the 95% confidence interval of the area-weighted means. Blue lines represent
 433 the percent cover of each structure category across the reference ecosystem areas. Gray dashed
 434 lines reflect logarithmic models fit to the data to visualize possible temporal changes in vegetation
 435 structure. Additional model details are in Table 1.
 436

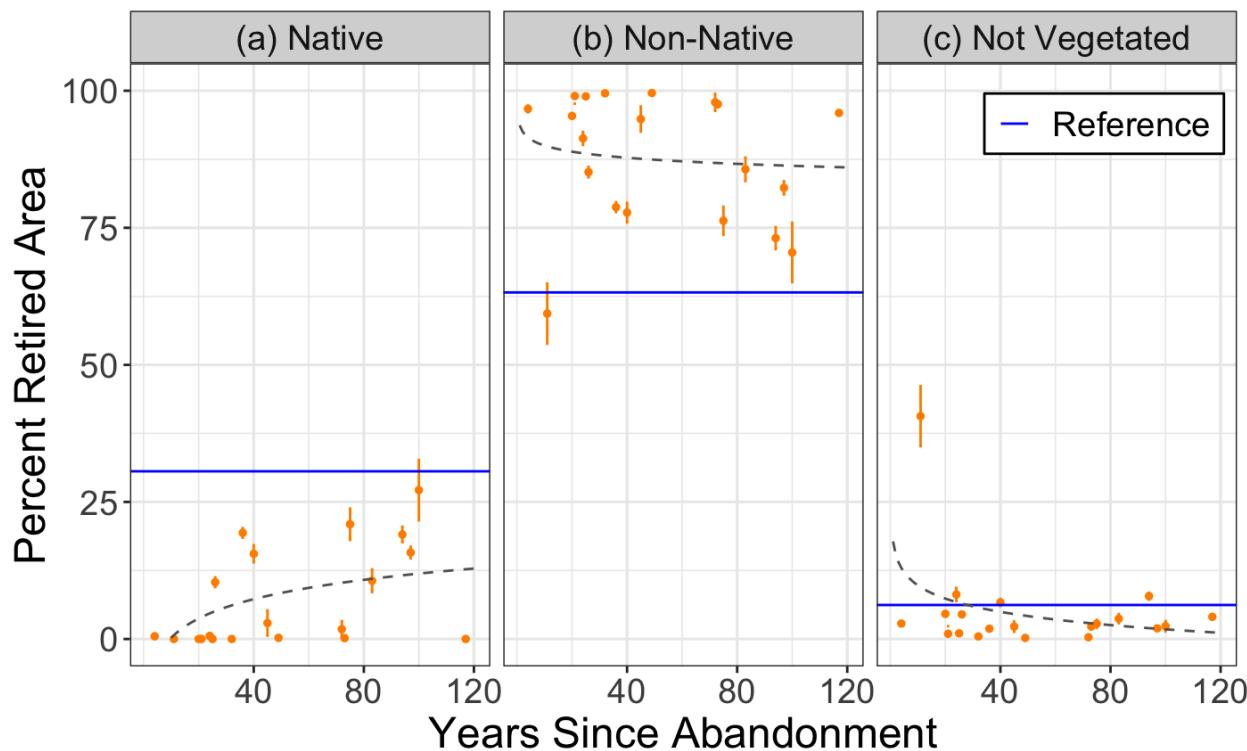
437 Table 1. **Effect of time since abandonment (log transformed) on various metrics of vegetation**
 438 **structure, composition, and function.** Models take the form: outcome variable = intercept +
 439 $\beta^* \ln(\text{Time})$. We calculated heteroskedasticity-robust standard errors for the coefficient estimates.
 440 Significant p values ($p < 0.05$) are indicated with ** and marginally significant p values ($p < 0.1$)
 441 are indicated with *. We only estimate recovery times for outcome variables that have a marginally
 442 significant or significant relationship with time. The model results for the % Not Vegetated
 443 outcome variable related to structure and composition properties are equivalent because they
 444 consider the same abandoned parcels.

Outcome	Property	Intercept Estimate	Coefficient (β)	Coefficient Standard Error	<i>p</i>	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

445
 446

3.3. Vegetation Composition

447 To further understand vegetation recovery on abandoned sugarcane fields, we assessed the
 448 composition of secondary vegetation in terms of whether native or non-native species were
 449 dominant. Independent of the amount of time since a field was abandoned, non-native species
 450 dominated the composition of secondary vegetation. The proportion of native vegetation on former
 451 fields typically increased with more time since abandonment; however, native vegetation cover
 452 was variable across fields abandoned over 20 years from a high of 27% on fields abandoned for
 453 100 years to nearly 0% on fields abandoned for either 73 or 117 years (Fig. 4). While native
 454 vegetation cover had a significant positive relationship ($p = 0.016$) with the logarithmic
 455 transformation of time (Table 1), this model predicted that abandoned fields would require 3,900
 456 years to recover the native composition of reference ecosystems. This recovery time horizon
 457 suggests that secondary ecosystems on abandoned sugarcane fields will remain compositionally
 458 distinct from reference ecosystems without active restoration.



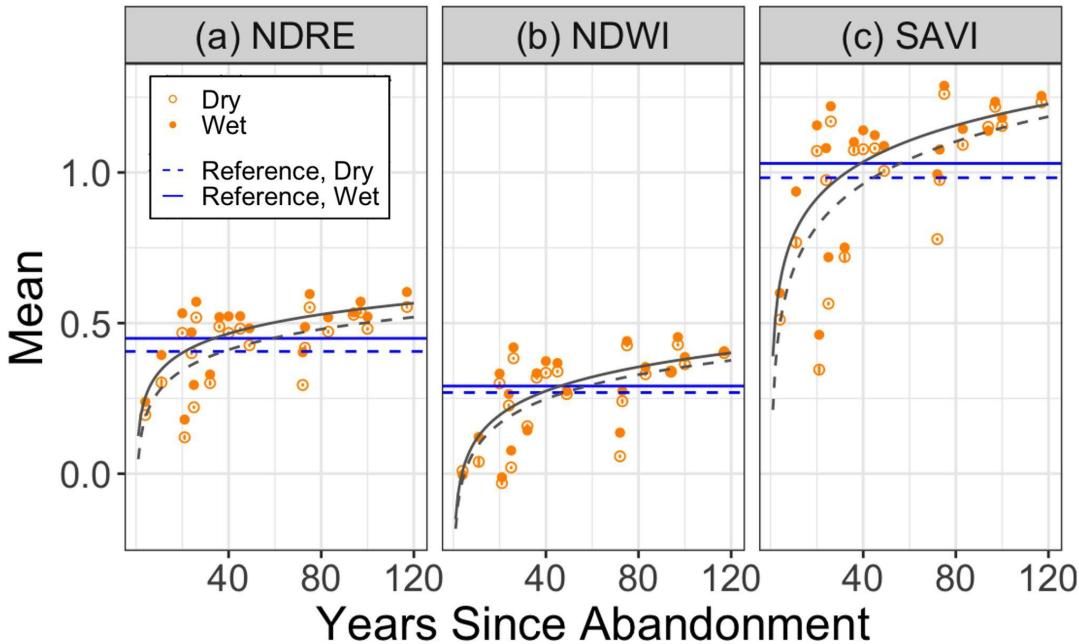
459
 460 **Figure 4. Vegetation composition by age of abandoned fields.** While the percent cover of native
 461 vegetation (a) increased with time since abandonment, non-native species (b) consistently

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

468
469

3.4. Vegetation Function

470 We used vegetation indices as approximate measures of vegetation function. The mean
471 values of all three vegetation indices in abandoned sugarcane fields generally increased on fields
472 that had been abandoned longer. Mean values of the vegetation indices increased fastest in the first
473 20 years following abandonment, and the rate of increase slowed on fields that were abandoned
474 longer (Fig. 5). The mean values of all three vegetation indices exceeded the respective mean
475 values in reference ecosystems. Older forests in reference ecosystems are often more structurally
476 complex, which increases shadows and may explain the lower average vegetation index values for
477 reference ecosystems. While there were limited differences between mean values for the
478 vegetation indices in the wet and dry seasons, most of the wet season values were higher than their
479 dry season counterparts among fields abandoned for the same length of time. Seasonal differences
480 were also minimal when calculating these vegetation indices in the reference ecosystems. The
481 mean value of all three vegetation indices during both the wet and dry seasons had significant
482 positive relationships with the logarithmic transformation of time (Table 1). The logarithmic
483 models estimated that vegetation indices reached average reference values between 27 and 53
484 years depending on the vegetation index and season.



485

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

496

497 **4. Discussion**

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

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

513 Weedy forbs and grasses represented most of the vegetation immediately following
514 abandonment likely due to the ease with which they disperse and grow (Funk, 2013; Levine et al.,
515 2003), especially in heavily disturbed environments (Cramer et al., 2008; D'Antonio and Vitousek,
516 1992; Ellsworth et al., 2014; Xavier and D'Antonio, 2017). Non-native grasses were brought to
517 Hawai'i primarily for livestock grazing (Ellsworth et al., 2014; Motoooka et al., 2003; Williams
518 and Baruch, 2000), but they have unintentionally modified ecosystem structure, composition, and
519 function (Asner et al., 2008; Hamilton et al., 2021; Vitousek et al., 1997). Indigenous tree species
520 in Hawai'i such as 'ōhi'a (*Metrosideros polymorpha*) and koa (*Acacia koa*) are accustomed to
521 growing in relatively open canopy environments (Mertelmeyer et al., 2019), so they struggle to
522 compete with invasive grasses (D'Antonio and Vitousek, 1992). Grasses have similarly dominated
523 abandoned agricultural land elsewhere, including sites in Panama (Hooper et al., 2005), Spain
524 (Grigulis et al., 2005), and Australia (Standish et al., 2008). We found that shrub and tree canopies
525 successfully established on some abandoned sugarcane fields in Hawai'i (Fig. 3); however, non-
526 native species constituted most of the woody vegetation (Fig. 4). While both 'ōhi'a and koa were
527 likely present in some areas prior to sugarcane cultivation, substantial distances between

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

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

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

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

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

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

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

618 **5. Conclusion**

619 Despite recent increases in agricultural land abandonment globally, we still have a limited
620 understanding of whether and when secondary vegetation can recover the biodiversity and
621 ecosystem services of uncultivated ecosystems. We explored the canopy structure, composition,
622 and function of secondary vegetation on sugarcane fields in Hawai‘i that were abandoned between
623 4 and 117 years ago. Our results suggest that even after prolonged, intense cultivation, secondary
624 vegetation on abandoned sugarcane land recovered the structure and functional traits of reference
625 ecosystems across sites that were abandoned less than a century but remained compositionally
626 distinct from reference ecosystems in perpetuity. Given that abandonment is expected to increase
627 on high-value, intensively cultivated land, further research is necessary to consider how cultivation
628 intensity and the diversity of species pools affect secondary vegetation development on abandoned
629 agricultural land. This study highlights the variable time required for secondary vegetation to
630 passively recover several attributes, which can guide decisions to restore or otherwise manage
631 abandoned agricultural land to promote biodiversity or a variety of ecosystem services.

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642 Appendix A. Supplementary Information

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

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