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Received: 26 May 2021 | Accepted: 13 September 2021

DOI: 10.1002/eap.2539

ARTICLE

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

Aboveground carbon accumulation by second-growth forests after deforestation in Hawai'i

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Handling Editor: Tamara Jane Zelikova

Abstract

Successional processes ultimately determine and define carbon accumulations in forested ecosystems. Although primary succession on wholly new substrate occurs across the globe, secondary succession, often following storm events or anthropogenic disturbance, is more common and is capable of globally significant accumulations of carbon (C) at a time when offsets to anthropogenic carbon dioxide (CO_2) emissions are critically needed. In Hawai'i, prior studies have investigated ecosystem development during primary succession on lava flows, including estimates of C mass accumulation. Yet relatively little is known regarding secondary succession of Hawaii's native forests, particularly regarding C mass accumulation. Here we documented aboveground C mass accumulation by native- and nonnative-dominated second-growth forests following deforestation of mature native lowland rainforests in the Puna District of Hawai'i Island. We characterized species composition and stand structure of three distinct successional forest stand types: those dominated by the native tree, *Metrosideros polymorpha* ('Ōhi'a), and those dominated by invasive nonnative trees, *Falcataria moluccana* (albizia) and *Psidium cattleianum* (strawberry guava). We compared *M. polymorpha*-dominated and *F. moluccana*-dominated second-growth forests to adjacent mature *M. polymorpha*-dominated forests as well as young *M. polymorpha*-dominated forests undergoing initial stages of primary succession on 36-years-old lava fields. Aboveground carbon density (ACD) values of mature primary forest stands (171 Mg/ha) were comparable to those of mature continental tropical forests. *M. polymorpha*-dominated second-growth stands attained nearly 50% of ACD values of mature primary forests after less than 30 years of post-disturbance succession and exhibited aboveground carbon accumulation rates of ~3 Mg C·ha^{-1}·year^{-1}. Such rates were comparable to those of second-growth forests in continental tropics. Rates of ACD accumulation by second-growth forests dominated by nonnative *F. moluccana* stands were similar, or slightly greater than, those of *M. polymorpha*-dominated stands. However, *M. polymorpha* individuals were virtually absent from stands dominated by either *P. cattleianum* or *F. moluccana*. Taken together, results demonstrated that re-establishment and rapid accumulation of C mass by

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M. polymorpha stands during secondary succession is certainly possible, but only where populations of nonnative species have not already colonized areas during early stages of secondary succession.

KEYWORDS
deforestation, *Falcataria moluccana*, forest carbon mass, forest succession, Hawai'i, invasive species, *Metrosideros polymorpha*, *Psidium cattleianum*, second-growth forests

INTRODUCTION

Succession, whether primary succession occurring on wholly new or newly exposed substrate (e.g., lava flows, landslides, scoured riverbeds) or secondary succession following storm events or anthropogenic deforestation, determines and defines accumulations of carbon (C) and nutrients in forested ecosystems. Although primary succession occurs in many locations throughout the world, secondary succession is more common and capable of globally significant accumulations of C during a time when offsets to anthropogenic carbon dioxide (CO_2) emissions are critically needed (Pan et al., 2011; Poorter et al., 2016; Yang et al., 2010). C accumulation by secondary forests at local, regional, and global scales remains an essential yet poorly understood, and often unpredictable, phenomenon demanding increased insight (Norden et al., 2015). Secondary forest regrowth following deforestation encompassed nearly one-third (i.e., 2.4 million km^2) of all forested and agricultural land of tropical Latin America by 2008; such forests were estimated to accumulate 8.5 Pg C (i.e., petagrams of carbon) during the subsequent 40 years of succession (Chazdon et al., 2016).

In most cases, C accumulation during primary succession is slow relative to secondary succession, although direct comparisons are rare (Hughes et al., 2014). Early stages of primary succession are not usually complicated by competition with invasive, nonnative plant species; though noted exceptions include some N-fixing species (Potgieter et al., 2014; Vitousek et al., 1987). In contrast, post-disturbance secondary succession often provides opportunities for establishment and growth of a variety of nonnative plant invasions not otherwise likely under undisturbed conditions (Burke & Grime, 1996; Crawley, 1987; D'Antonio et al., 1993; Hobbs, 1989).

In Hawai'i, native forest succession typically involves the dominant native overstory tree, *Metrosideros polymorpha* ('Ōhi'a). Accounting for an estimated 290 million mature individuals on Hawai'i Island, *M. polymorpha* is an order of magnitude more numerous than any other native tree species (Owen et al., 2021). It typically dominates most of Hawaii's varied ecosystems, including early successional forest at sea level on newly formed lava substrates, tall stature and structurally complex sub-montane forests, and high-elevation, low-stature bog communities (Mueller-Dombois et al., 2013; Rock, 1974; Wagner et al., 1999). Further, *M. polymorpha* forests account for nearly 40% (i.e., 18.4 million tons) of all aboveground forest carbon stocks across the Hawaiian Islands (Asner et al., 2016; Johnson, 2019; Owen et al., 2021).

Numerous studies have systematically investigated community and ecosystem development during primary succession on Hawaiian lava flows (Drake, 1992; Kitayama et al., 1995; Vitousek et al., 1993), and some have documented C mass accumulation over time (Aplet & Vitousek, 1994; Mascaro et al., 2012; Raich et al., 1997). Primary succession in forests dominated by *M. polymorpha*, a species not capable of symbiotic N fixation, is gradual and highly constrained by N limitation on newly formed lava substrates that uniformly lack plant-available N (Raich et al., 1997; Vitousek et al., 1993). As such, *M. polymorpha* growth typically has been viewed through the lens of primary succession and considered slow-growing, particularly when compared to aboveground C mass accumulation rates exhibited by nonnative N-fixing tree species (e.g., *Falcataria moluccana*, *Casuarina equisetifolia*) in similar environmental settings (Hughes et al., 2014; Mascaro et al., 2012).

In contrast to primary succession, relatively less has been understood or documented regarding secondary succession in Hawaii's forests, particularly with respect to C mass accumulation by *M. polymorpha*-dominated second-growth forests. Prior studies of succession following fire in Hawaiian ecosystems focused on displacement of native woody species by nonnative grasses or herbaceous species rather than post-disturbance growth by native trees (Ainsworth & Kauffman, 2013; Hughes et al., 1991; Litton et al., 2006; Mack & D'Antonio, 2003). Perhaps most informative, studies initiated in the 1970s to investigate successional processes following extensive stand level dieback of *M. polymorpha* forests in wet montane zones of Hawai'i Island documented robust recovery of *M. polymorpha* overstory canopies through vigorous re-establishment and growth of young *M. polymorpha* trees (Boehmer et al., 2013; Mertelmeyer et al., 2019). These studies, however, did not estimate aboveground biomass or C mass accumulation associated with secondary succession in these scenarios.

An opportunity to understand and document dynamics of aboveground forest C accumulation during secondary succession in Hawai'i presented itself in the mid-1980s when portions of an intact, mature native lowland rainforest located in the Puna District of Hawai'i Island were deforested (Holden, 1985). The forest, composed of tall-statured overstories dominated by *M. polymorpha* trees and a diverse understory of native trees, ferns, and herbaceous plants, was cut to the ground and bulldozed. These actions created extensive areas of exposed, highly disturbed lava substrate across most of the clearcut region. Areas immediately adjacent to the deforestation event were left intact, providing mature, primary *M. polymorpha*-dominated reference forests with which to compare dynamics of forest composition, structure, and function during secondary succession in the clearcut areas. Grossman (1992) investigated early phases of secondary succession (i.e., 2 years post-disturbance) in the deforested area to evaluate the capacity of Hawaii's native lowland tropical forests to regenerate after deforestation and to provide baseline information for subsequent long-term monitoring of secondary succession. Widespread recruitment and growth of *M. polymorpha* seedlings occurred across large portions of the clearcut area. The nonnative tree, *Psidium cattleianum* (strawberry guava), also rapidly colonized large portions of the clearcut area (Grossman, 1992). *P. cattleianum* is considered a profound threat to native Hawaiian forests, and it has displaced native species across hundreds of thousands of hectares (Barbosa et al., 2017; Zimmerman et al., 2008). Stands of the large, fast-growing, nonnative tree, *Falcataria moluccana* (albizia), present but not widespread 2 years after the clearcut event (Grossman, 1992), eventually became well-established at specific locations across the study area. After nearly three decades of secondary succession, three distinct forest types, dominated by *M. polymorpha*, *P. cattleianum*, and *F. moluccana*, respectively, now occupy the majority of the clearcut area; together they provide an opportunity to investigate secondary successional processes, including C accumulation, with adjacent intact mature primary native forests serving as successional endpoints. Lastly, 'a'ā lavas flowed along the western boundaries of both mature intact forests and deforested areas in 1977 (i.e., prior to the deforestation event); these recent lava flows provided an opportunity to document C accumulation during early stages of primary succession and compare that to coincidental C accumulation rates during secondary succession in adjacent clearcut areas.

Given the available matrix of lava flows, stand types, and successional states in these Hawaiian lowland wet forests, our objectives were to document aboveground C mass across the range of forests in the context of primary and secondary successional processes. Our questions included the following: After several decades of succession since disturbance, to what degree have second-growth forests in clearcut areas accumulated C mass relative to adjacent intact mature primary forests? Do rates of C accumulation differ among stands dominated by *M. polymorpha* and *F. moluccana*, respectively? How do rates of C accumulation in second-growth forests dominated by *M. polymorpha* differ from those undergoing primary succession? More broadly, we hoped to learn the extent to which Hawaii's dominant native tree, *M. polymorpha*, may be a viable candidate for reforestation efforts both in the wake of stand-level mortality induced by the fungal pathogen, *Ceratocystis lukuohia*, and in future carbon-market based efforts to increase forest carbon across the Hawaiian Archipelago. To address these questions, we used established methods to estimate aboveground C mass of woody species encountered in forest inventory plots established in both primary and second-growth forest types located in the Kalapana region of the Puna District of Hawai'i Island.

METHODS

Study site location and characteristics

All forest inventory plots were located within a 6-km^2 area approximately 6 km upslope and northwest of the town of Kalapana in the Puna District of Hawai'i Island (UTM 5Q 0288419 E 2145932 N; Figure 1). The region exists as a matrix of relatively young 'a'ā and pāhoehoe lava flows emanating from the East Rift Zone of Kilauea Volcano (Wolfe & Morris, 1996); lava flows in this area range from very young (i.e., 20–40 years old) to those 1500–3000 years old (Grossman, 1992; Wolfe & Morris, 1996). The climate of the area is warm and wet; annual temperatures average 20.6°C (Giambelluca et al., 2014) and annual precipitation averages 3150 mm (Giambelluca et al., 2013).

Undisturbed lowland wet forest vegetation on older 'a'ā lava substrates in intact portions of the study area were dominated by mature stands of the native tree, *M. polymorpha*, with young cohorts of scattered *M. polymorpha* individuals becoming established in early stages of primary succession on younger lava flows (Grossman, 1992). Primary succession by native vegetation in these areas typically begins with colonization of barren 'a'ā and pāhoehoe lava substrates by cohorts of *M. polymorpha* that develop as monotypic forest stands during the first 100–200 years of succession (Atkinson, 1970; Mueller-Dombois & Fosberg, 1998). *M. polymorpha*-dominated stands ultimately develop into more diverse and structurally complex forests as additional species become established during subsequent

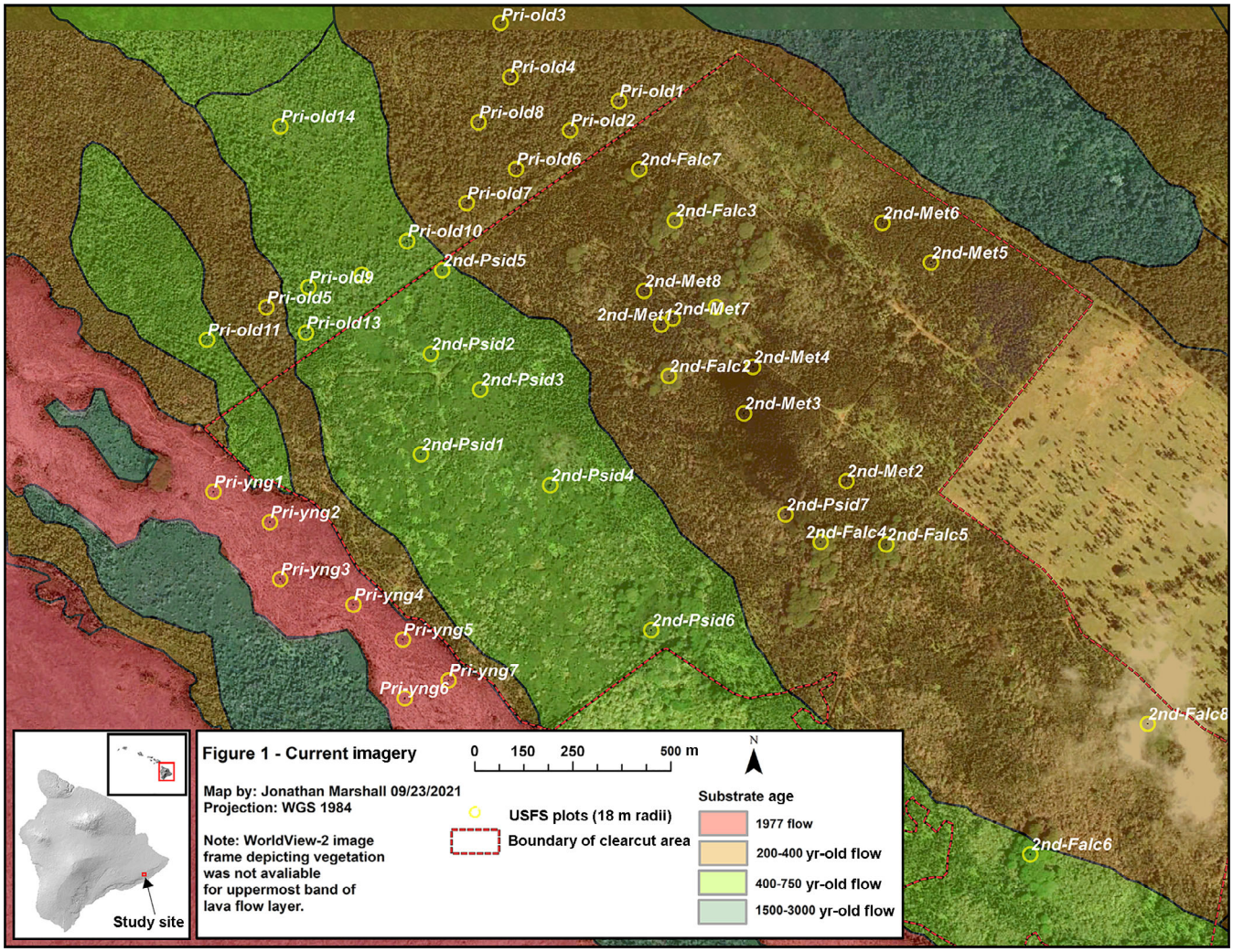

FIGURE 1 The Kalapana forest study region located on Kilauea Volcano in the Puna District of Hawai'i Island, HawaiI, USA. Yellow dots indicate location of each forest inventory plot; associated labels denote forest stand type and correspond to information presented in Table 1. Lava flow age (Wolfe & Morris, 1996) is indicated by different color shading. I mage Source: Google Earth Pro (v 7.3.3.7786) 64bit (January 21, 2013 image date), Kalapana, Hawai'i 19°23′ 37.76″ N, 155° 00/39.52″ W, Eye Alt 11,714 feet. Georeferenced by authors. Digital Globe 2013

centuries (i.e., 200–700 years; Zimmerman et al., 2008). Common subcanopy species in mature forests include the native tree, *Psychotria hawaiiensis* (Kopiko), native tree fern species in the genus *Cibotium* (Hapu'u), the nonnative tree *Psidium cattleianum* (strawberry guava), and the nonnative shrub, *Clidemia hirta* (Koster's curse). Mueller-Dombois (1985) characterized forests occupying the study area as among the few remnants of tall-statured, native-dominated lowland forest in Hawai'i, noting that these forests contained the full spectrum of species richness and successional states of this ecosystem type. Lamoureux (1985) noted their geographic uniqueness as part of continuous native forest spanning lowland to upland regions.

During 1984 and into 1985, approximately 400 ha of previously intact, mature *M. polymorpha*-dominated forest in the study area was deforested. The objective of the logging operation was to cut down all *M. polymorpha* trees in the area, grind them into wood chips, and burn those chips to generate electric power at a nearby sugar mill (Holden, 1985). Large tree shears mounted on bulldozers cut tree boles that were subsequently chipped on site; a process that leveled virtually all vegetation of the deforested area (Figure 2). The landowner and biofuel company initially planned to deforest the entirety of a 1300-ha tract, but public opposition and concerted efforts of scientists and conservation groups (e.g., Friends of Hawai'i's Forests) prematurely halted the operation and limited the scope of deforestation to less than a third of the proposed area (Grossman, 1992). The clearcut area occurred on two 'a'ā lava flows, one aged 200–400 years and the other 400–750 years, respectively

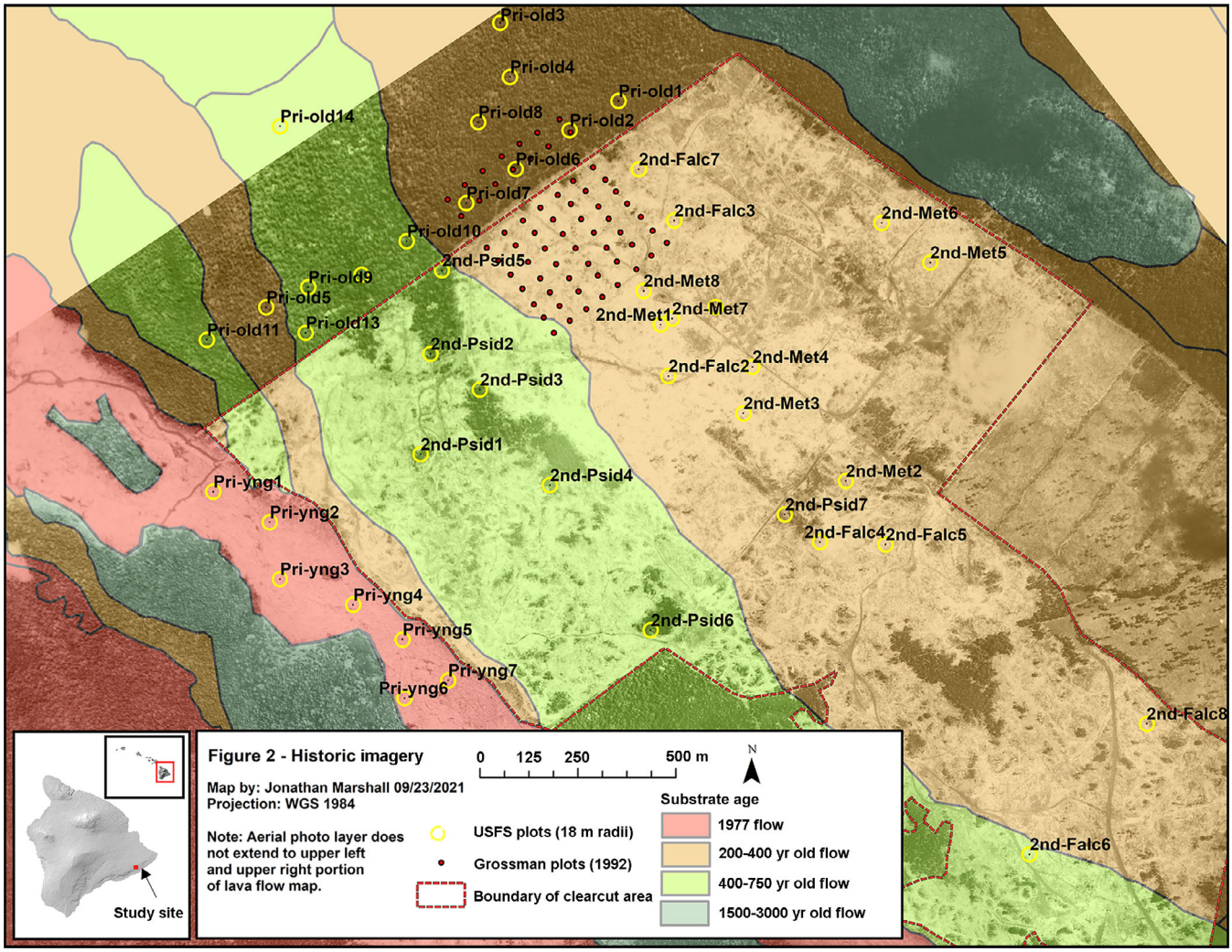

FIGURE 2 Historical aerial photograph of the deforested region of the Kalapana forest study region located on Kilauea Volcano in the Puna District of Hawai'i Island, Hawai'i. Photograph was taken in 1985, a few months after the clearcutting operations had ceased. Note extant patches of *Psidium cattleianum* throughout the deforested area; such patches were not cut down and bulldozed during the operations and so continued to develop throughout subsequent years of succession. Image Source: R. M. Towill Corporation, Honolulu. Aerial photo. (August 10, 1985 image date). Image number 8381-4. Approximate scale is 1 inch = 400 feet (1 foot = 0.30 m). Georeferenced by authors in 2021 for this study

(Figure 1). Both lava flows extended upslope from the deforested area into relatively undisturbed mature forests dominated by mature *M. polymorpha* trees (Figures 1 and 2). Following nearly three decades of post-disturbance succession, vegetation in the clearcut area consisted of three distinct second-growth forest stand types defined by their respective dominant tree species: *M. polymorpha*-dominated stands, *P. cattleianum*-dominated stands, and *F. moluccana*-dominated stands. Approximately 2 years after the clearcut event, Grossman (1992) conducted a significant investigation into the patterns and dynamics of early-stage forest succession; he compared recovering vegetation and microclimate variables (e.g., solar insolation, air and soil temperature, soil moisture, relative humidity, and rainfall) in areas of the region that had been clearcut and bulldozed with immediately adjacent areas supporting intact, mature, native-dominated forests (Figure 2).

Sampling methods

Our objectives were to characterize patterns and rates of aboveground C accumulation by dominant forest types that were present in clearcut areas. We compared aboveground C mass of those second-growth forests with developing forest stands on both 1977 lava flows and mature forests on the 200–400-years-old and 400–750-years-old lava flows. The study area was stratified into subregions distinguished by lava flow age (Wolfe & Morris, 1996), forest status (i.e., primary or second-growth; Grossman, 1992), and

dominant canopy tree type (Google Earth, 2012) (Figure 1). Study sites were selected and established by identifying 7–11 locations of each lava age, forest status, and dominant canopy tree type to obtain UTM coordinates for each designated plot location before visiting them on the ground (Google Earth, 2012) (Table 1, Figure 1). We subsequently navigated on foot to designated flow age/forest status/dominant tree locations where we established a center point for each respective plot. All *M. polymorpha*-dominated second-growth forest plots occurred on 200–400-years-old lava flows; nearly all *P. cattleianum*- dominated second-growth forest plots occurred on 400–750-years-old lava flows. All but one of *F. moluccana*-dominated second-growth forest plots occurred on 200–400-years-old lava flows (Wolfe & Morris, 1996). All second-growth forest plots were inventoried 26–28 years after the clearcut event (Table 1). Young primary forests were inventoried 36 years after the deposition of the 1977 'a'ā lava flow (Table 1) (Wolfe & Morris, 1996).

Forest inventory plots were circular and 36 m in diameter, encompassing an ~0.10-ha area. We identified all woody species, measured (i.e., diameter at breast height, or dbh), and characterized as live or dead all stems ≥5 cm dbh rooted within the boundary of each inventory plot. Additionally, we identified all woody species, measured (dbh), and characterized as live or dead all woody stems ≥0.3 cm and <5 cm at dbh and rooted within a 12 m diameter subplot nested within each 36 m diameter plot. Due to relative sparseness of vegetation in plots located on the 1977 lava flow (i.e., primary young forests), all woody stems ≥0.3 cm present within such plots were characterized and measured across the entirety of the 0.10 ha area. Plot-scale measures of species-specific stem density and basal area were expanded to a hectare basis using appropriate multipliers for overall plot and nested subplot dimensions. We conducted measurements within 14 plots in mature primary forest, 7 plots in young primary forest, 11 plots in second-growth forests dominated by *M. polymorpha*, 8 plots in second-growth forests dominated by *F. moluccana*, and 7 plots in second-growth forests dominated by *P. cattleianum* (Table 1, Figure 1).

Biomass of all live stems encountered in each plot was estimated using allometric equations from Asner et al. (2011); we used species-specific equations for *M. polymorpha* stems ≤33 cm dbh, all *P. cattleianum* stems, and tree ferns (i.e., *Cibotium* spp.). When species-specific equations were not available for particular species such as *F. moluccana* and *P. hawaiiensis*, as well as *M. polymorpha* stems ≥33 cm dbh, aboveground biomass was calculated using a wet forest allometric model employing independent variables of stem dbh (cm), wood density (g/cm^3), and height (m) to predict aboveground biomass (kg; Chave et al., 2005). Tree-specific dbh values were used throughout. Species-specific wood density values (Asner et al., 2011) were applied where possible. Where species-specific values were unavailable, we applied genera-specific values. In rare instances where genera-specific values were unavailable, we applied a default wood density value of 0.50 g/cm^3. Tree height estimates were obtained from species-specific allometric models relating height to diameter (Asner et al., 2011). Aboveground C mass values for all trees on all plots were calculated by multiplying aboveground biomass values by 0.48 (Losi et al., 2003). Aboveground C mass was not determined for dead stems encountered in any plot. Consequently, forest C mass values presented here include only live trees. However, dead stems were recorded and included in stem density and basal area values of each plot.

Statistical analyses

Mean and standard error values were determined for each measured parameter (e.g., stem density, basal area, and aboveground C mass) within each forest type by averaging the respective values for all plots measured within each forest type. We estimated aboveground C mass accumulation rates for young primary forests and *M. polymorpha* and *F. moluccana* second-growth forest types by dividing C mass estimated in each respective forest plot by the number of years between the disturbance event and the year in which each plot was measured in the field (Table 1). Accumulation rates were calculated for both total stand C mass as well as C mass of the dominant tree species of each stand type. Following establishment and measurement of *P. cattleianum*-dominated second-growth forest plots, we discovered that the majority of said plots likely contained substantial numbers of stems of that tree species that had not been cut down and/or bulldozed to the ground during the deforestation event and which remained standing at the beginning of the nearly three-decade-long successional period (Figure 2). Therefore, we could not consider these plots as having initiated secondary succession from a completely disturbed state. Consequently, we excluded *P. cattleianum*-dominated second-growth forest plots from our analysis of C mass accumulation over time, although we retained them in analyses of forest composition and structure.

Regarding each measured parameter, we analyzed differences among forest types using one-way ANOVA tests ($p < 0.05$) at the 0.95 confidence level; we employed Tamhane's T2 Tests to execute pairwise comparisons between forest types ($p < 0.05$; Sokal & Rohlf, 1969). This conservative pairwise comparisons test is appropriate when variances of sample groups were unequal. Additionally, we analyzed differences between mature

TABLE 1 Descriptions, labels, locations, and characteristics of primary and second-growth forest stand types in the Kalapana forest study region of the Puna District of Hawai'i Island, Hawai'i

Stand type/dominant species	Plot no.	UTM 5 Q (m E)	UTM (m N) 5 Q (m N)	Elevation (m)	Lava age (YBP)	Time since disturbance (year)
Primary old/*Metrosideros*	Pri-old1	288,539	2,146,455	427	200–400	n.a.
	Pri-old2	288,420	2,146,382	428	200–400	n.a.
	Pri-old3	288,256	2,146,657	452	200–400	n.a.
	Pri-old4	288,278	2,146,519	447	200–400	n.a.
	Pri-old5	287,683	2,145,940	435	200–400	n.a.
	Pri-old6	288,289	2,146,285	431	200–400	n.a.
	Pri-old7	288,169	2,146,200	432	200–400	n.a.
	Pri-old8	288,200	2,146,405	442	200–400	n.a.
	Pri-old9	287,785	2,145,991	437	400–750	n.a.
	Pri-old10	288,024	2,146,105	429	400–750	n.a.
	Pri-old11	287,539	2,145,860	432	400–750	n.a.
	Pri-old12	287,914	2,146,021	430	400–750	n.a.
	Pri-old13	287,758	2,145,958	436	400–750	n.a.
	Pri-old14	287,722	2,146,400	457	400–750	n.a.
Primary young/*Metrosideros*	Pri-yng1	287,550	2,145,474	419	36	36
	Pri-yng2	287,685	2,145,395	413	36	36
	Pri-yng3	287,708	2,145,250	404	36	36
	Pri-yng4	287,884	2,145,183	393	36	36
	Pri-yng5	288,002	2,145,093	385	36	36
	Pri-yng6	288,005	2,144,944	381	36	36
	Pri-yng7	288,111	2,144,988	377	36	36
Second-growth/*Metrosideros*	2nd-Met1	288,634	2,145,886	402	200–400	26
	2nd-Met2	289,076	2,145,483	367	200–400	26
	2nd-Met3	288,831	2,145,658	384	200–400	26
	2nd-Met4	288,854	2,145,776	388	200–400	26
	2nd-Met5	289,286	2,146,036	376	200–400	26
	2nd-Met6	289,170	2,146,138	387	200–400	26
	2nd-Met7	288,470	2,146,167	415	200–400	27
	2nd-Met8	288,594	2,145,972	405	200–400	27
	2nd-Met9	n.a.	n.a.	n.a.	200–400	27
	2nd-Met10	n.a.	n.a.	n.a.	200–400	26
	2nd-Met11	n.a.	n.a.	n.a.	200–400	26
Second-growth/*Psidium*	2nd-Psid1	288,051	2,145,563	404	400–750	n.a.
	2nd-Psid2	288,078	2,145,818	414	400–750	n.a.
	2nd-Psid3	288,196	2,145,726	407	400–750	n.a.
	2nd-Psid4	288,362	2,145,481	391	400–750	n.a.
	2nd-Psid5	288,108	2,146,030	420	400–750	n.a.
	2nd-Psid6	288,601	2,145,110	363	400–750	n.a.
	2nd-Psid7	288,928	2,145,400	367	200–400	n.a.
Second-growth/*Falcataria*	2nd-Falc1	288,767	2,145,929	398	200–400	26
	2nd-Falc2	288,651	2,145,755	398	200–400	26

(Continues)

TABLE 1 (Continued)

Stand type/dominant species	Plot no.	UTM 5 Q (m E)	UTM (m N) 5 Q (m N)	Elevation (m)	Lava age (YBP)	Time since disturbance (year)
	2nd-Falc3	288,670	2,146,150	409	200–400	26
	2nd-Falc4	289,012	2,145,329	361	200–400	26
	2nd-Falc5	289,170	2,145,321	357	200–400	28
	2nd-Falc6	289,508	2,144,530	292	400–750	27
	2nd-Falc7	288,586	2,146,281	416	200–400	26
	2nd-Falc8	289,795	2,144,858	306	200–400	27

Notes: YPB denotes years before present, that is, at the time of the study. Time since disturbance values of second-growth/*Psidium* sites were not available and are thus not included. The "n.a." denotes that the data were not available.

primary forests occurring on 200 to 400 years old lavas and those on 400–750-years-old lavas using two-sample t tests at the 0.95 confidence level (pooled variance, $p < 0.05$; Sokal & Rohlf, 1969).

RESULTS

Aboveground live C mass varied substantially among forest types, largely as a function of both successional state and dominant canopy tree species. Among the five forest types (i.e., mature primary, young primary, *M. polymorpha*-dominated second-growth, *F. moluccana*-dominated second-growth, and *P. cattleianum*-dominated second-growth), total aboveground live C mass was highest in mature primary forest (171 Mg C/ha) and lowest in young primary forest (2.4 Mg C/ha; Table 2). *M. polymorpha* trees accounted for 77% and 100% of total C mass in mature and young primary forest stands, respectively (Table 2). Total C mass of *M. polymorpha*-dominated second-growth forests (80 Mg C/ha) was intermediate between young and mature primary forests and did not differ significantly from *F. moluccana*-dominated stands (123 Mg C/ha) and *P. cattleianum*-dominated stands (108 Mg C/ha). *F. moluccana*-dominated stands also did not differ significantly from mature primary forests (Table 2). In each second-growth forest stand, respective dominant canopy trees accounted for between 83 and 90% of total live C mass (Table 2). Further, total live C mass of second-growth forests represented 47% (*M. polymorpha*-dominant) to 72% (*F. moluccana*-dominant) of total C mass of mature primary forests, and C mass values were 33 to 51 times greater in second-growth forests compared to total stand C mass of the sparse young primary forest stands (Table 2).

Regarding dominant canopy trees in each respective forest type, and excluding *P. cattleianum*-dominated stands for reasons elaborated previously, aboveground C mass of *M. polymorpha* trees in mature primary forests (132 Mg/ha) was greater than that of *M. polymorpha* trees in second-growth forest dominated by those trees (i.e., 72 Mg/ha). In contrast, C mass of *F. moluccana* trees in stands dominated by that species (i.e., 101 Mg/ha) did not differ from that of *M. polymorpha* trees in mature primary forests or in second-growth stands dominated by that species (Figure 3). Aboveground C mass of *M. polymorpha* trees in young primary forest stands was substantially lower than all other forest stand types (Figure 3); values were only 0.02% of the C mass of that species in mature primary forests (Figure 3). Dominant trees of second-growth forests represented between 54% (*M. polymorpha*-dominant) and 77% (*F. moluccana*-dominant) of *M. polymorpha* C mass in mature primary forests, and they were 29–41 times greater in second-growth forests compared to total live C mass of young primary forests (Figure 3).

Variation in C mass values of subcanopy tree species and species that were not dominant in a given forest stand (e.g., *M. polymorpha* trees in the *P. cattleianum*-dominated second-growth stand) occurred among the different forest types. *M. polymorpha* C mass, which accounted for 77%–100% of total stand C mass in forests dominated by that tree, was significantly lower in second-growth forests dominated by *F. moluccana* and *P. cattleianum*, representing only 7% and 15% of total stand C mass, respectively (Table 2). *P. cattleianum* accounted for 18% of total stand C mass of primary mature forests (Table 2). C mass values of native subcanopy species *P. hawaiianensis* and *Cibotium* spp. accounted for 5% and 1% of total stand C mass values in mature primary forests, values substantially greater than any other forest stand type (Table 2). C mass values of nonnative trees other than *P. cattleianum*, largely consisting of *Aleurites moluccana*, *Psidium guajava*, and *Melochia umbellate*, were greater in *F. moluccana*-dominated second-growth forests than in any other forest stand type; collectively, they accounted for 3% of total stand C mass in that stand type (Table 2). In stark contrast to all other forest types, nonnative woody species were completely absent from

TABLE 2 Stem density, basal area, and aboveground live C mass of common plant species and structural components in primary and second-growth forest stand types of the Kalapana forest study region of the Puna District of Hawai'i Island, Hawaii

Stand type/dominant species	*Metrosideros polymorpha*	*Psidium cattleianum*	*Falcataria moluccana*	*Psychotria hawaiianensis*	*Cibotium* spp.	Other natives	Other nonnatives	Dead	Total
Stem density (stems/ha)									
Primary old	$461^{a,b} \pm 56$	$7543^{a} \pm 2159$	$0^{a} \pm 0$	$1611^{a} \pm 447$	$184^{a} \pm 32$	$149^{a} \pm 85$	$291^{a} \pm 145$	$349^{a} \pm 52$	$10{,}589^{a} \pm 1845$
Primary young	$808^{b} \pm 110$	$0^{a} \pm 0$	$0^{a} \pm 0$	$0^{b} \pm 0$	$0^{b} \pm 0$	$0^{a} \pm 0$	$0^{a} \pm 0$	$0^{b} \pm 0$	$808^{b} \pm 110$
Second/Metrosideros	$2962^{c} \pm 329$	$1115^{a} \pm 366$	$0^{a} \pm 0$	$700^{a} \pm 186$	$23^{b} \pm 8.6$	$19^{a} \pm 16$	$138^{a} \pm 85$	$252^{a} \pm 52$	$5209^{a} \pm 509$
Second/Psidium	$79^{a} \pm 35$	$41{,}344^{b} \pm 4276$	$0^{a} \pm 0$	$143^{ab} \pm 60$	$44^{b} \pm 15$	$0^{a} \pm 0$	$39^{a} \pm 15$	$208^{ab} \pm 78$	$41{,}856^{c} \pm 4371$
Second/Falcataria	$274^{a} \pm 106$	$1316^{a} \pm 486$	$566^{b} \pm 123$	$125^{ab} \pm 107$	$6^{b} \pm 3.2$	$1^{a} \pm 1$	$311^{a} \pm 81$	$280^{a} \pm 77$	$2880^{d} \pm 373$
Basal area (m^2/ha)									
Primary old	$36.4^{a} \pm 2.7$	$11.0^{a} \pm 2.9$	$0.0^{a} \pm 0.0$	$6.1^{a} \pm 1.1$	$4.9^{a} \pm 0.9$	$0.1^{a} \pm 0.04$	$0.1^{a} \pm 0.0$	$3.8^{a} \pm 0.5$	$62.4^{a} \pm 3.0$
Primary young	$1.3^{b} \pm 0.2$	$0.0^{b} \pm 0.0$	$0.0^{a} \pm 0.0$	$0.0^{b} \pm 0.0$	$0.0^{b} \pm 0.0$	$0.0^{a} \pm 0.00$	$0.0^{a} \pm 0.0$	$0.0^{b} \pm 0.0$	$1.3^{b} \pm 0.2$
Second/Metrosideros	$24.9^{c} \pm 1.2$	$2.1^{ab} \pm 0.6$	$0.0^{a} \pm 0.0$	$2.0^{c} \pm 0.5$	$0.7^{b} \pm 0.3$	$0.1^{a} \pm 0.04$	$0.3^{a} \pm 0.1$	$1.0^{b} \pm 0.4$	$31.0^{c} \pm 1.4$
Second/Psidium	$4.2^{b} \pm 1.9$	$39.4^{c} \pm 2.2$	$0.0^{a} \pm 0.0$	$0.6^{bc} \pm 0.2$	$1.1^{b} \pm 0.4$	$0.0^{a} \pm 0.00$	$0.^{a}2 \pm 0.2$	$2.3^{ab} \pm 0.8$	$47.8^{d} \pm 3.0$
Second/Falcataria	$2.6^{b} \pm 0.9$	$3.5^{ab} \pm 1.7$	$34.8^{b} \pm 4.5$	$0.4^{bc} \pm 0.3$	$0.3^{b} \pm 0.1$	$0.0^{a} \pm 0.00$	$2.8^{b} \pm 0.5$	$1.6^{b} \pm 0.5$	$46.0^{acd} \pm 4.6$
Aboveground live carbon mass (Mg/ha)									
Primary old	$131.8^{a} \pm 9.7$	$30.4^{a} \pm 8.3$	$0.0^{a} \pm 0.0$	$8.0^{a} \pm 1.5$	$1.1^{a} \pm 0.2$	$0.3^{a} \pm 0.1$	$0.0^{a} \pm 0.0$	n.a.	$170.9^{a} \pm 9.0$
Primary young	$2.4^{b} \pm 0.4$	$0.0^{b} \pm 0.0$	$0.0^{a} \pm 0.0$	$0.0^{b} \pm 0.0$	$0.0^{b} \pm 0.0$	$0.0^{a} \pm 0.0$	$0.0^{a} \pm 0.0$	n.a.	$2.4^{b} \pm 0.4$
Second/Metrosideros	$71.5^{c} \pm 3.9$	$5.2^{ab} \pm 1.6$	$0.0^{a} \pm 0.0$	$2.5^{c} \pm 0.7$	$0.2^{b} \pm 0.1$	$0.2^{a} \pm 0.1$	$0.3^{a} \pm 0.1$	n.a.	$79.7^{c} \pm 4.4$
Second/Psidium	$15.3^{b} \pm 6.9$	$91.4^{c} \pm 4.2$	$0.0^{a} \pm 0.0$	$0.7^{bc} \pm 0.2$	$0.2^{b} \pm 0.1$	$0.0^{a} \pm 0.0$	$0.6^{a} \pm 0.5$	n.a.	$108.1^{c} \pm 9.2$
Second/Falcataria	$7.3^{b} \pm 2.5$	$10.1^{ab} \pm 5.2$	$101.1^{b} \pm 17.2$	$0.5^{bc} \pm 0.4$	$0.1^{b} \pm 0.0$	$0.0^{a} \pm 0.0$	$3.5^{b} \pm 0.6$	n.a.	$122.5^{ac} \pm 18.9$

Note: Values are mean ± SE. "n.a." denotes that the data were not available. Within each measurement parameter (i.e., density, basal area, C mass) and species, stand type mean values that share the same letter did not differ significantly (Tamhane's T2 test of pairwise comparisons; $p < 0.05$).

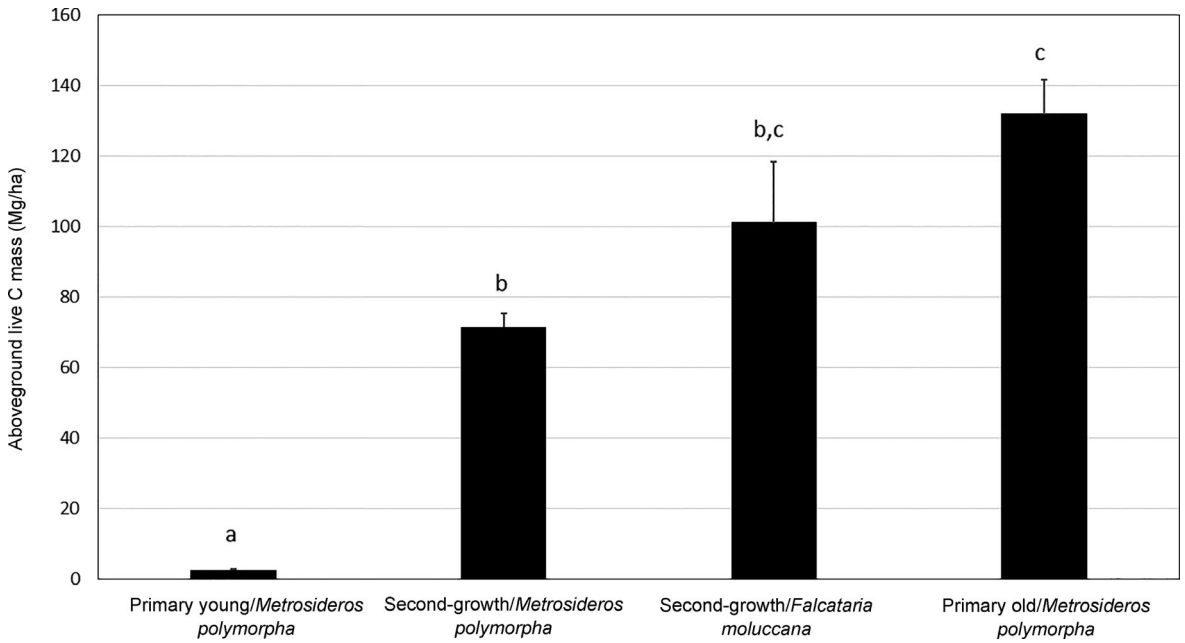

FIGURE 3 Aboveground live C mass of dominant species of each forest type in primary and second-growth forest stand types in the Kalapana forest study region of the Puna District of Hawai'i Island, Hawai'i. Values (mean and SE) are presented for each stand type and dominant species. Dominant tree species of respective stand types that shared the same lowercase letter did not differ significantly from one another (Tamhane's T2 Test of pairwise comparisons; $p \leq 0.05$)

young primary successional stands dominated by *M. polymorpha* (Table 2).

Regarding contrasting mature primary forests growing on 200–400-years-old and 400–750-years-old lava flows, respectively, neither total aboveground C mass nor C mass of the canopy dominant *M. polymorpha* differed between the two forest types (Table 3). However, stem density and C mass of the two common understory trees,

TABLE 3 Stem density, basal area, and aboveground live C mass of common plant species and structural components in primary forests on 200–400 yr-old and 400–750 yr-old lava flows in the Kalapana forest study region of the Puna District of Hawai'i Island, Hawaii

Stand type	*Metrosideros polymorpha*	*Psidium cattleianum*	*Psychotria hawaiianensis*	*Cibotium* spp.	Other natives	Other nonnatives	Dead	Total
Stem Density (stems/ha)								
Primary; 200–400 yr-old lava	**593 ± 31**	**1832 ± 644**	**2665 ± 529**	187 ± 31	257 ± 140	265 ± 152	**443 ± 64**	**6242 ± 868**
Primary; 400–750 yr-old lava	**285 ± 80**	**15,157 ± 2686**	**206 ± 27**	180 ± 66	6.5 ± 5	324 ± 289	**226 ± 57**	**16,384 ± 2735**
Basal area (m^2/ha)								
Primary; 200–400 yr-old lava	39.7 ± 3.3	**2.5 ± 0.9**	**8.8 ± 1.1**	5.0 ± 1.0	0.1 ± 0.1	0.1 ± 0.0	4.3 ± 0.5	60.4 ± 4.5
Primary; 400–750 yr-old lava	32.0 ± 4.2	**22.3 ± 2.1**	**2.5 ± 0.9**	4.9 ± 1.8	0.1 ± 0.0	0.0 ± 0.0	3.1 ± 0.7	64.5 ± 3.9
Aboveground live carbon mass (Mg/ha)								
Primary; 200–400 yr-old lava	144.6 ± 12.1	**5.8 ± 2.2**	**11.5 ± 1.6**	1.0 ± 0.3	0.3 ± 0.1	0.1 ± 0.0	n.a.	162.6 ± 13.3
Primary; 400–750 yr-old lava	114.7 ± 14.1	**63.3 ± 6.0**	**3.4 ± 1.2**	1.1 ± 0.4	0.2 ± 0.2	0.0 ± 0.0	n.a.	182.0 ± 10.8

Note: Values are mean ± SE. "n.a." denotes that the data were not available. Boldface denotes mean values that differed significantly between lava flow age types (two sample t-tests, pooled variance, $p < 0.05$).

the native tree, *P. hawaiiensis*, and the nonnative tree, *P. cattleianum*, differed substantially between lava flows; average *P hawaiiensis* stem density and C mass values were greater on the 200–400-years-old flow relative to the 400–750-years-old flow, and the opposite was true for average values of *P. cattleianum* stem density and C mass.

Rates of aboveground C mass accumulation differed substantially between young primary forest stands and second-growth stands but did not differ between second-growth forest stand types. The total stand C mass accumulation rate of young primary forests (0.1 $Mg{\cdot}ha^{-1}{\cdot}year^{-1}$) represented just 2% of stand level accumulation rates for second-growth stands dominated by *M. polymorpha* (3.0 $Mg{\cdot}ha^{-1}{\cdot}year^{-1}$) and *F moluccana* (4.7 $Mg{\cdot}ha^{-1}{\cdot}year^{-1}$; Figure 4). Considering second-growth forest types, rates of total stand C mass accumulation did not differ between *F. moluccana*-dominated stands and *M. polymorpha*-dominated stands. Similarly, regarding only aboveground C mass accumulation rates of the respective canopy dominant tree in each forest stand (i.e., for *M. polymorpha* and *F. moluccana* individuals, and as opposed to total stand values), values did not differ significantly between the two second-growth forest dominant trees species (2.7 and 3.8 $Mg{\cdot}ha^{-1}{\cdot}year^{-1}$), and both were substantially higher than accumulation rates of *M. polymorpha* in young primary forests of the 1977 lava flow (Figure 4).

Stem density values varied greatly among species and forest types, and they contrasted with patterns of C mass and basal area values in several notable instances. Total stand stem density values were by far greatest in *P. cattleianum*-dominated forest plots (41,856 stems/ha), which dwarfed values for all other species and forest types (Table 2). *P. cattleianum* stems were solely responsible for total stand stem densities in this forest stand type, accounting for 99% of all stems (Table 2). *P. cattleianum* also accounted for 71% and 46% of total stem density values in mature primary forests and *F. moluccana*-dominated second-growth forests, respectively (Table 2). In contrast, this species accounted for only 18% and 8% of total stand C mass values, respectively, in those forest types (Table 2). Similarly, although aboveground C mass and basal area values for *M. polymorpha* trees were highest in mature primary forests, stem density values of this tree species were significantly higher in *M. polymorpha*-dominated second-growth forests compared to any other forest type (Table 2).

DISCUSSION

Mature primary forest ACD

Aboveground carbon density (ACD) values of mature primary forest stands in the Kalapana region of Hawai'i (i.e., 171 Mg/ha) were similar to other mature *M. polymorpha*-dominated forests across Hawai'i as well as those of continental tropical forests. ACD of mature *M. polymorpha*-dominated stands located in nearby lowland wet forests in the Puna district of Hawai'i Island were 110–125 Mg/ha; such values were only slightly lower than Kalapana forest stands measured here (Hughes et al., 2014; Mascaro et al., 2012). Aplet and Vitousek (1994) estimated ACD values of 150 and 175 Mg/ha for *M. polymorpha*-dominated forests growing on 3400-years-old lava flows of Mauna Loa at 914 and 1524 m elevations, respectively. Hughes et al. (2018) reported estimated ACD values of

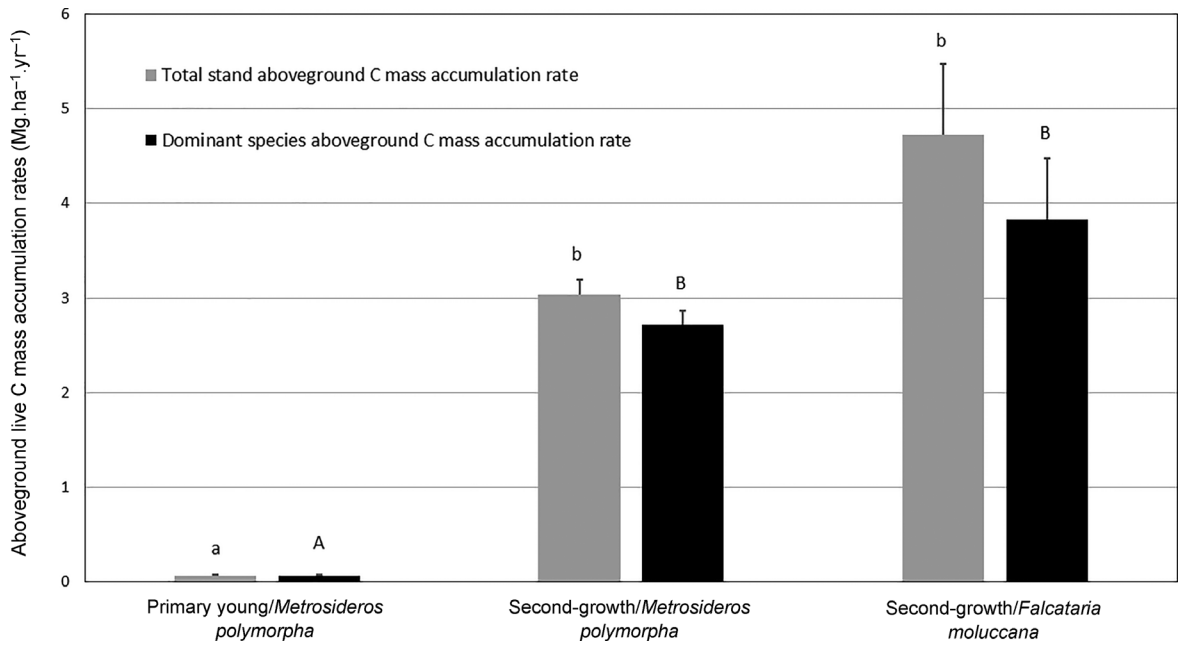

FIGURE 4 Total aboveground live C mass accumulation rates in primary and second-growth forest stand types as well as in the dominant tree species of each forest type in the Kalapana forest study region of the Puna District of Hawai'i Island, Hawai'i. Values (mean and SE) are presented for each stand type and dominant species. Stand types that shared the same lowercase letter did not differ from one another; dominant tree species of respective stand types that shared the same uppercase letter did not differ significantly from one another (Tamhane's T2 Test of pairwise comparisons; $p \leq 0.05$)

~205 Mg/ha for *M. polymorpha*-dominated stands growing at 1150 m above sea level on 5000-years-old lava flows of Mauna Kea volcano; they likely represent the highest values for any native Hawaiian forests, and ACD values of mature primary forests in Kalapana were not substantially lower than those values. More broadly, mature lowland tropical forests of Panama, the Peruvian Amazon, and the Brazilian Amazon exhibited ACD values as high as 130, 125, and 175, respectively (Asner et al., 2010; Chave et al., 2003; Malhi et al., 2006); ACD of tropical forests in Africa ranged widely from 76 to 398 Mg C/ha (Lewis et al., 2009). In addition, ACD values of mature *M. polymorpha*-dominated forests in Kalapana, Hawai'i were somewhat higher than those developed and used for tropical wet forests (126 Mg C/ha) in Tier 1 carbon assessments of the Intergovernmental Panel on Climate Change (IPCC, 2006). Although not remarkably tall statured compared to continental tropical or subtropical forests, mature *M. polymorpha*-dominated forests exhibited relatively high ACD values due to the dense wood of individual trees (i.e., 0.7 g/cm^3), high stand-level density (i.e., stems/ha) and high basal area values relative to forests found elsewhere in the tropics and subtropics (e.g., 260 stems >20 cm dbh per hectare; Zimmerman et al., 2008). Basal area values exhibited by mature primary forests measured in this study (i.e., 62 m^2/ha) were nearly 1.7 times average values exhibited by comparable tropical and subtropical wet forests of Asia, Africa, South America, and the Caribbean (Ostertag et al., 2014). Ostertag et al. (2014) also noted greater stand level basal area values in Hawaii's wet forests compared to those of forests located elsewhere in the tropics; they attributed the relatively high basal area values to an abundance of subcanopy endemic tree ferns (*Cibotium* spp.) of forests measured in their study. In contrast, our results indicated that *Cibotium* spp. stems accounted for only 2% of total stand stem densities, 8% of total stand basal area, and 1% of total stand aboveground C; clearly tree ferns were not responsible for elevated basal area values of the lowland wet forests of Kalapana studied here. Rather, *M. polymorpha*, as the canopy dominant tree of these forests, accounted for 69% of total stand basal area along with the subcanopy trees *P. hawaiiensis* (10% of stand basal area) and *P. cattleianum* (18% of stand basal area). Further, the majority of ACD in mature native forests of Kalapana was accounted for by native species (83% of total), and *M. polymorpha* accounted for the vast majority that percentage (77% of total).

Metrosideros polymorpha-dominated second-growth forest ACD

Our results documenting that *M. polymorpha*-dominated second-growth stands attained nearly 50% of ACD values for mature primary forests of Kalapana, Hawai'i and exhibited aboveground carbon accumulation rates of ~3 Mg C·ha^{-1}·year^{-1} were surprising given the conventional

wisdom that *M. polymorpha* is a slow-growing species. Accumulation rates exhibited by these second-growth forests were similar to those of second-growth forests in continental tropical and subtropical ecosystems; Poorter et al. (2016) documented biomass recovery during secondary succession across a robust set of 45 Neotropical forest sites; rates of aboveground C accumulation averaged 3.05 Mg C·ha^{-1}·year^{-1}, leading the authors to characterize studied secondary forests as highly productive and resilient. Based on essentially equivalent C accumulation values for *M. polymorpha*-dominated second-growth forests measured here, we may characterize them as comparably resilient and highly productive as well.

Reasons for robust accumulations of aboveground C mass by *M. polymorpha*-dominated second-growth forests measured here included relatively high average stand-level basal area values as well as the high wood specific-gravity values exhibited by *M. polymorpha*. Total stand basal area and *M. polymorpha*-only basal area values (i.e., 31 m^2/ha and 25 m^2/ha, respectively) were comparable to stand-level basal areas values of tropical wet second-growth forests of similar age documented elsewhere. Intermediate-aged (i.e., 20–40-years-old) second-growth forests of Panama exhibited stand basal area values of ~23 m^2/ha (Denslow & Guzman, 2000). In 25–35-years-old second-growth tropical forests of southern Brazil, total stand basal area values ranged from 23 to 26 m^2/ha (Dalmaso et al., 2020). Similarly, basal area values were approximately 27 m^2/ha in 35-years-old second-growth forests of Southern Mexico (Aryal et al., 2014). Additionally, and perhaps more importantly, wood specific-gravity values of the dominant tree, *M. polymorpha* (i.e., 0.70 g/cm^3) were substantially greater than aggregates of common pioneer trees in second-growth forests documented elsewhere. Community-weighted wood specific-gravity values of trees species within a chronosequence of second-growth forests in Costa Rica ranged from 0.40 to 0.49 g/cm^3 (Plourde et al., 2015). In a similar subsequent study, community-weighted wood specific-gravity values of tree species along an elevation gradient of second-growth forests in Costa Rica ranged from 0.28 to 0.57 g/cm^3 (Muñoz et al., 2020).

Further, direct comparison of primary and secondary successional trajectories in this region of Hawai'i Island revealed that aboveground C accumulations in *M. polymorpha*-dominated second-growth forests were an impressive 43 times greater than those documented in adjacent young primary successional forest stands on 36-years-old lavas also dominated by *M. polymorpha*. ACD accumulation rates on these latter sites were expected to be low because *M. polymorpha* stands established on young and barren 'a'ā lava fields were previously well characterized as lacking plant-available N, a constraint that severely limits primary productivity (Harrington et al., 2001; Vitousek et al., 1993). In their systematic study of controls on primary succession on Mauna Loa volcano, Hawai'i, Aplet and Vitousek (1994) documented aboveground biomass accumulations by primary successional *M. polymorpha*-dominated forest stands on 47-years-old 'a'ā lava flows at 914 and 1219 m elevations that were 6.5 and 4.6 Mg/ha, respectively. Aboveground C accumulation rates of these 914 and 1219 m sites calculated to 0.07 and 0.05 Mg·ha^{-1}·year^{-1}, respectively; values similar to those of young primary forest stands of Kalapana reported here (i.e., 0.07 Mg·ha^{-1}·year^{-1}). The greater C accumulation rates exhibited by *M. polymorpha*-dominated second-growth forests relative to young primary forest stands can likely be best explained by accretion of both biomass and plant available nutrients, particularly nitrogen, during the 200–400 years of primary succession prior to the clearcut disturbance of 1985 (Hughes & Denslow, 2005). It may be supposed that documented high rates of C accumulation were at least partially due to coppicing from *M. polymorpha* stumps. However, Grossman (1992) did not note coppicing of this species in surveys conducted 2 years after the clearcut event, a period presumably sufficient for coppicing to be expressed. Instead, we attributed *M. polymorpha* ACD accumulations to vigorous regeneration from seed rather than by coppicing from stumps, as seen elsewhere in the tropics (Guimaraes Mesquita et al., 2015). Grossman (1992) reported *M. polymorpha* seedling densities averaging 800 individuals/ha across the study site during early stages of secondary succession (i.e., 2 years post-disturbance), and expressed hope that such seedlings would grow to maturity. To the contrary, our results documented *M. polymorpha* stem densities (i.e., 3000 stems/ha) that were three times greater than initial seedling densities reported by Grossman (1992), indicating substantial seedling recruitment and growth during subsequent years of secondary succession.

It is important to note that relatively rapid rates of C accumulation by second-growth *M. polymorpha* stands occurred on 'a'ā lavas rather than pāhoehoe lavas. Prior studies in Hawai'i documented substantially higher rates of biomass accumulation on 'a'ā lavas compared to pāhoehoe lavas on the wet, windward side of Hawai'i Island (Aplet et al., 1998; Hughes et al., 2014; Raich et al., 1996); these authors attributed higher accumulation rates for 'a'ā lavas to greater surface area and subsequent increased weathering and nutrient availability. As such, second-growth *M. polymorpha* stands in our study likely would have exhibited lower C mass accumulation had they established and developed on pāhoehoe lavas rather than 'a'ā lavas.

It is also important to note that *M. polymorpha*-dominated second-growth forests occurred exclusively on 200–400-years-old lavas in the area and not on 400–

750-years-old substrates. This pattern was apparent to Grossman (1992), who documented a strong east-to-west gradient of decreasing *M. polymorpha* stem and seedling densities 2 years after the clearcut event; he attributed this pattern to proximity to intact *M. polymorpha* forest stands from which propagules would be sourced. Grossman (1992) also acknowledged that distinct pre-disturbance successional stages of forests determined by substrate age differences likely manifested in contrasting post-disturbance secondary successional patterns.

Results here indicate that pre-disturbance states were paramount in controlling patterns of *M. polymorpha* recruitment and growth during secondary succession. The east-to-west gradient of decreasing seedling density documented by Grossman (1992) 2 years post-disturbance coincided with locations of the two lava substrates of the clearcut area; 200–400-years-old lavas occurred in the eastern portion of the area and 400–750-years-old lavas occurred in the western portion of the clearcut region; upslope mature primary forests were oriented similarly (Figures 1 and 2). In light of higher *M. polymorpha* stem density values and lower *P. cattleianum* stem density and C mass values in mature primary forests on the 200–400-years-old lavas relative to those on 400–750-years-old lavas, initial conditions, particularly regarding the relative paucity of *P. cattleianum* stems, likely provided favorable conditions for initial recruitment and growth of *M. polymorpha*, an acknowledged shade-intolerant tree species (Burton & Mueller-Dombois, 1984), on the 200–400-years-old lavas. Two years after the deforestation event, *P. cattleianum* remained abundant and well established in the western portions of both mature forest and clearcut areas (i.e., on 400–750-years-old lava flows); Grossman (1992) noted *P. cattleianum* survival in clearcut areas through coppicing, a well-known trait of this species (Huenneke & Vitousek, 1990). As such, well established *P. cattleianum* stands in mature primary forests on 400–750-years-old lava flows likely led to prompt establishment of this species through coppicing soon after the clearcut event (Grossman, 1992). This, combined with the widespread presence of *P. cattleianum* stands on 400–750-years-old lava flows that were not significantly disturbed during the deforestation event (Figure 2), effectively preempted significant post-disturbance *M. polymorpha* seedling recruitment on the older 400–750-years-old substrate.

Falcataria moluccana-dominated second-growth forest structure, composition, and dynamics

Whether growing on 200–400-years-old or 400–750-years-old lavas, high aboveground C mass values exhibited by *F. moluccana* stands after 27 years of succession were to be expected given the tree's N-fixation capacity, acknowledged rapid growth rates, and prior documentation of stand dynamics in Hawai'i (Hughes et al., 2014; Hughes & Denslow, 2005; Mascaro et al., 2012). Grossman (1992) noted the initial invasion of multiple nonnative tree species, including *F. moluccana*, in areas around his original sampling site two years following the clearcut event, and he anticipated that this species would play an important role in shaping subsequent forest succession across the area. Although invasion and stand establishment did occur, distribution of *F. moluccana*-dominated second growth forest stands was relatively patchy, likely a result of initial colonization limited to open, high-sunlight areas required by this shade-intolerant, pioneer tree species (Hughes et al., 2012; Soerianegara et al., 1994). Where *F. molucanna* stands were present across the clearcut landscape, their high average rate of aboveground C mass accumulation (3.8 $Mg \cdot ha^{-1} \cdot year^{-1}$), resulted in stand-level stocks of aboveground C mass (i.e., 102 Mg/ha) that approached those of intact mature *M. polymorpha* forests after less than three decades of succession. This provides further evidence regarding the capacity of *F. moluccana* to rapidly capture, invade, and dominate, in part through its nitrogen-fixing ability, significant suburban, agricultural, and forested areas of the Hawaiian Archipelago and other Pacific Islands (Hughes et al., 2012; 2013; 2014; Hughes & Denslow, 2005).

Establishment of *F. moluccana* stands largely excluded *M. polymorpha* re-establishment and growth in clearcut areas. Results agree with those of Hughes and Denslow (2005), who found that invasion by *F. moluccana* into *M. polymorpha*-dominated stands led to wholesale mortality and subsequent suppression of that native tree species. Although still present in *F. moluccana*-dominated second-growth stands, *M. polymorpha* C mass values averaged <10% of those in *M. polymorpha*-dominated second-growth stands. Based on prior studies in Hawai'i (Asner et al., 2008; Hughes et al., 2014; Mascaro et al., 2012), we had expected, and subsequently documented, *M. polymorpha*-dominated and *F. moluccana*-dominated secondary succession to be mutually exclusive.

Psidium cattleianum-dominated second-growth forest composition and structure

Psidium cattleianum is a widely acknowledged threat to the integrity of native Hawaiian forests; it is capable of invading understories of intact forests in the absence of overstory disturbance (Asner et al., 2008; Barbosa et al., 2017; Zimmerman et al., 2008) where it forms dense clonal thickets (Huenneke & Vitousek, 1990). To date, *P. cattleianum* has invaded, and continues to invade, hundreds of thousands of hectares, displacing endemic

and endangered native Hawaiian species in the process (Asner et al., 2009; Smith, 1985; Zimmerman et al., 2008). At present, it is Hawaii's most abundant tree, constituting ~41% of all woody stems in the Archipelago's forests (Owen et al., 2021). Although *P. cattleianum* establishment on very young lava substrates (i.e., less than 300 years old) of Hawai'i Island is constrained due to inherent soil N limitation during early stages of primary succession (Hughes & Denslow, 2005), it often exhibits high stem densities on lava flows >200 years old where soil N availability is sufficient. It also forms dense subcanopy stands on younger lavas where well-established, nonnative, N-fixing, canopy-dominant trees (e.g., *F. moluccana* and *Casuarina* spp.) prematurely increase soil N availability (Hughes et al., 2014; Hughes & Denslow, 2005; Zimmerman et al., 2008). Results regarding species composition on young verses mature primary forests inventoried in Kalapana support ideas regarding constraints of substrate age on *P. cattleianum* invasion; while *P. cattleianum* trees were abundant in subcanopies of mature primary forests on older lava flows, they were completely absent from young primary forests growing on 36-years-old lava flows. Very young lava flows may represent among the most favorable substrates for establishment and persistence of native-dominated ecosystems in Hawai'i.

Nearly all second-growth stands dominated by *P. cattleianum* were located on 400–750-years-old lava substrate that had been heavily invaded by *P. cattleianum* prior to the clearcut event, as borne out by observed high densities of *P. cattleianum* in mature primary forest growing on that same aged lava substrate immediately adjacent to the clearcut area. Given this tree's proclivity to coppice following disturbance (Grossman, 1992) and establish large numbers of clonal shoots (Huenneke & Vitousek, 1990), the exceedingly high stem densities (i.e., >41,000 stems/ha) and relatively large ACD values exhibited by *P. cattleianum* in the clearcut area were not unexpected and agree with prior findings of Barbosa et al. (2017). Although *P. cattleianum* is a subcanopy tree and not considered tall to any degree, high stem densities combined with a relatively high wood density (0.70 g/cm^3; Asner et al., 2011), resulted in relatively high ACD values of *P. cattleianum* stands. Although several previous studies investigating displacement of mature *M. polymorpha*-dominated forests by *P. cattleianum* have documented or predicted overall reductions in biomass, and C mass (Asner et al., 2008; Hughes et al., 2014, 2018), our results documented that *P. cattleianum* exhibited approximately 64% of C mass values in adjacent intact mature *M. polymorpha* forests. It remains to be seen whether *P. cattleianum* stands will continue to accumulate and store aboveground C in this area. However, as also seen in second-growth stands dominated by *F. moluccana* and in contrast to clearcut areas on 200–400-years-old lava flows dominated by *M. polymorpha* stands, *M. polymorpha* individuals were virtually absent from *P. cattleianum*-dominated stands. This finding underscored the capacity of *P. cattleianum*, once established, to exclude *M. polymorpha* during secondary succession (Asner et al., 2008). Findings support assertions by Zimmerman et al. (2008) that *P. cattleianum* establishment, whether into disturbed areas or intact native forest understories, leads ultimately to replacement of native wet lowland forests formerly dominated by *M. polymorpha*.

CONCLUSIONS

Keeping in mind that our study sampled a single forested region in the eastern portion of Hawai'i Island that experienced a single contiguous deforestation event in 1985 within and around which we sampled, our results present a carbon mass-based counterpoint to conceptions that *M. polymorpha* is inherently a slow-growing species. Such conceptions were predominantly supported by observations of primary successional stands established and developing on new lava flows (Aplet et al., 1998; Hughes et al., 2014; Raich et al., 1996) or mature stands that had reached their zenith with respect to C accumulation. Somewhat surprisingly, aboveground C accumulation rates by *M. polymorpha*-dominated second-growth forests of this study were on par with neotropical second-growth forests characterized as highly productive and resilient to disturbance (Poorter et al., 2016). Our results documenting C mass accumulation by *M. polymorpha* during secondary succession largely agree with Mertelmeyer et al. (2019), who documented that 80% of forest inventory plots that underwent severe *M. polymorpha* stand dieback in the 1970s recovered much of their *M. polymorpha*-dominated canopy by 2015 through recruitment and growth of new generations of *M. polymorpha* individuals. Similarly, Boehmer et al. (2013) found that, following the collapse of *M. polymorpha* stands in the 1970s, dieback plots experienced a wave of seedling and sapling establishment resulting in new *M. polymorpha* cohort stands. The Kalapana deforestation event differed from these prior studies in that mature *M. polymorpha* overstory canopies were completely eliminated, resulting in substantial aboveground C losses averaging 132 Mg/ha. In contrast to the complete canopy recovery of *M. polymorpha* following 38 years of post-dieback succession documented previously by Mertelmeyer et al. (2019), aboveground C mass accumulation values exhibited by *M. polymorpha*-dominated second-growth stands following three decades of succession at Kalapana averaged just over one-half

(i.e., 71 Mg/ha) those exhibited by adjacent mature *M. polymorpha* stands in undisturbed forests. These patterns of, and potential for, post-disturbance *M. polymorpha* stand biomass and C mass recovery were distinct from measurements of stand-level canopy recovery documented elsewhere, and they were not necessarily proportional to stand-level canopy recovery.

Our results agree with assertions by Mertelmeyer et al. (2019) that *M. polymorpha* stands were readily capable of replacing themselves rather quickly as long as other factors such as nonnative plant invasion did not disrupt their establishment and development through competition. In the deforested areas of Kalapana, aboveground C mass accumulation by *M. polymorpha* stands during secondary succession was limited to areas that had not been colonized by nonnative invasive species such as *P. cattleianum* and *F. molucanna*. Somewhat paradoxically, the catastrophic deforestation via clearcutting of large portions of intact, diverse, native forests of Kalapana (Holden, 1985) may have ultimately created post-disturbance site conditions favorable for *M. polymorpha* establishment and stand development, but only in areas free of initial competition from nonnative shrub and tree species.

Given recent increased levels of *M. polymorpha* mortality across many forested regions of Hawai'i caused by the fungal pathogen *Ceratocystis lukuohia* (Barnes et al., 2018; Mortenson et al., 2016, Vaughn et al., 2018), results presented here may offer both encouragement and guidance to land managers desiring to reestablish *M. polymorpha* populations in areas that have suffered significant recent mortality, as well as in future market-based efforts to increase forest C sequestration in targeted regions across Hawai'i (Koh et al., 2021; Pichancourt et al., 2014). Our study demonstrated that re-establishment and rapid aboveground C accumulation by *M. polymorpha*-dominated second-growth forests of Hawai'i was possible even in highly disturbed areas and following a massive loss of mature *M. polymorpha* individuals and stands. However, this will likely only occur where populations of nonnative species can be effectively controlled during early stages of secondary succession to allow for successful recruitment and growth of *M. polymorpha* (i.e., ʻŌhiʻa).

ACKNOWLEDGMENTS

We sincerely thank K. Hiraoka, M. Murphy, L. Bufil, E. Bufil, A. Cantan, A. Kaha, N. Wilhoite, I. Sagaga, Z. Winter, C. Rogers, J. Puni, N. Friday, N. Zimmerman for their invaluable assistance collecting and processing field data used in this study. We thank the Hawai'i Island Branch of the Division of Forestry and Wildlife, Department of Land and Natural Resources (DOFAW-DNLR), and the Office of Hawaiian Affairs (OHA) for permission to conduct field work in the Kalapana Forest landscapes. We also thank E. Lee for helpful assistance and access to study sites through his property. We are also very grateful to J. Jacobi, J. Baldwin, J. Mascaro, and G.P. Asner for providing helpful comments that improved earlier versions of the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Hughes et al., 2021) are available from the U.S. Forest Service Research Data Archive at https://doi.org/10.2737/RDS-2021-0089s.

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How to cite this article: Hughes, Richard Flint, Dennis Grossman, Travis G. Sowards, Jonathan D. Marshall, Dieter Mueller-Dombois. 2022. "Aboveground Carbon Accumulation by Second-Growth Forests after Deforestation in Hawai'i." *Ecological Applications* 32(4): e2539. https://doi.org/10.1002/eap.2539