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Carbon storage landscapes of lowland Hawaii: the role of native and invasive species through space and time

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Abstract. Tropical forests are important storehouses of carbon and biodiversity. In isolated island ecosystems such as the Hawaiian Islands, relative dominance of native and nonnative tree species may influence patterns of forest carbon stocks and biodiversity. We determined aboveground carbon density (ACD) across a matrix of lava flows differing in age, texture, and vegetation composition (i.e., native or nonnative dominated) in wet lowland forests of Hawaii Island. To do this at the large scales necessary to accurately capture the inherent heterogeneity of these forests, we collected LiDAR data across areas of interest and developed relationships between LiDAR metrics and field-based estimates of forest ACD. This approach enabled us to inventory, rather than merely sample, the entire populations (i.e., forests) of interest. Native Hawaiian wet lowland forests exhibited ACD values similar to those of intact tropical forests elsewhere. In general, ACD of these forests increased with increasing lava flow age, but patterns differed between native and nonnative forest stands. On the youngest lavas, native-dominated forest ACD averaged <60 Mg/ha, compared to ~100 Mg C/ha for nonnative-dominated forests. This difference was due to the presence of the nonnative, N_2-fixing trees *F. moluccana* and *C. equisetifolia* in the nonnative-dominated forest stands, as well as the corresponding absence of N_2-fixing trees in native-dominated forest stands. Following ~500 years of primary succession and thereafter, however, both forest types exhibited ACD values averaging ~130 Mg C/ha, although it took nonnative forests only 75–80 years of post-establishment succession to reach those values. Given the large areas of early-successional *M. polymorpha*-dominated forest on young lava flows, further spread of *F. moluccana* and *C. equisetifolia* populations would likely increase ACD stocks but would constitute a significant erosion of the invaluable contribution of Hawaii's native ecosystems to global biodiversity.

Key words: aboveground carbon density; biodiversity; Hawaii; invasive trees and shrubs; lava; LiDAR; lowland wet forest; nonnative forests; Pacific Islands; primary succession; remote sensing.

Introduction

Forests are a global storehouse of both carbon (C) and biodiversity (Dixon et al. 1994, Houghton 2005). Tropical regions in particular account for ~40% of the world's forest carbon (Jobbagy and Jackson 2000, Lewis et al. 2006), 35% of earth's primary production (Melillo et al. 1993), and at least 66% of all known terrestrial species (Raven 1988). As forests develop, they typically increase in both C stocks and diversity (Brown and Lugo 1990, Letcher and Chazdon 2009, Mascaro et al. 2012*a*), but not always, as in plantations that are often monocultures (Putz and Redford 2009) or where introduced species replace native species (e.g., Carpenter et al. 2009, Dickie et al. 2011).

Variation in age-states of forest succession across broad landscapes, whether following disturbance (i.e., secondary succession) or through the origination of wholly new substrate (i.e., primary succession), largely determines both regional C sequestration and biodiversity (Aplet and Vitousek 1994, Marin-Spiotta et al. 2007). Prior conditions such as duration and intensity of land use (Zimmerman et al. 1995), soil conditions (Chazdon 2003), and the presence of introduced, nonnative species (D'Antonio and Vitousek 1992, Yoshida and Oka 2004, Sullivan et al. 2007, Murphy et al. 2008) may also provide controls on C accumulation and diversity during succession.

Previous studies of primary succession on Pacific Island volcanoes illustrate the control of time, temperature, precipitation, and soil substrate on species composition and forest C accumulation (Whittaker et al. 1989, Aplet et al. 1998, Kitayama et al. 1995, Zimmerman et al. 2008, Marler and del Moral 2011). Because biologically available nitrogen is universally scarce during early stages of primary succession and therefore limiting to primary production (Vitousek 2004), plants with nitrogen-fixing symbiotic partners

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often have a disproportionately large influence on forest C accumulation and compositional dynamics (Marrs et al. 1983, Kamijo et al. 2002, Walker et al. 2003). Where such N_2-fixers are introduced nonnative species, they may profoundly influence both native species diversity and collective C stocks accounted for by native species (Hughes and Denslow 2005, Mascaro et al. 2012*b*). Nonnative species that lack the capacity for N_2-fixation may also alter C stocks and community composition away from patterns of native-dominated succession; such divergence will be determined by their individual growth forms and functional traits (Asner et al. 2008*a*, *b*, Mascaro and Schnitzer 2011).

Until recently, investigations into patterns and dynamics of tropical forest succession, including most referenced above, have been conducted at the plot scale. While this approach is highly informative in many ways, it may not effectively encompass the true variation of particular regions of interest we attempt to describe, and thus it risks introducing biases. Plot-based approaches may also miss broad-scale patterns that are critical determinants of ecosystem structure and function at the local scale and beyond (Porder et al. 2005, Vitousek et al. 2009). Inability to understand such patterns and process at relevant scales may hinder efforts to understand and portray reality (Biggs et al. 2009). In contrast, newly developed remote sensing approaches address these issues by characterizing landscapes and regions in a synoptic fashion that can reveal broad-scale patterns and variability. Airborne light detection and ranging (LiDAR) technology in particular provides an effective means to explicitly measure, as opposed to sample, structural characteristics of forests at hundred- to million-hectare scales (Asner et al. 2008*a*, 2010*a*, 2011, Vitousek et al. 2009). This approach, when calibrated against plot-based measures of aboveground C stocks and species composition, can provide a new understanding of how patterns of succession determine forest C stocks and the specific contributors, whether native or introduced nonnative species, to those stocks across time and space.

Lowland wet forests of the Puna district of Hawaii Island, USA, present a useful setting for investigations into how species composition interacts with, and affects, aboveground C density (ACD) of forests during primary succession. Lava flows varying in age and type occur across the region. They collectively span a successional range of 50–1500 years before present (yr BP) (Moore and Trusdell 1991), and primarily occur as either pāhoehoe lavas or ʻaʻā lavas. Pāhoehoe lava is generally smooth, with a ropy texture and frequent cracks. In contrast, ʻaʻā lava is characterized as rough, jagged or "clinker" rock piles generated where flows exhibit relatively low temperatures and high viscosities. Prior studies have documented notable differences in forest growth and succession between these two lava types (Raich et al. 1996, Aplet et al. 1998). Native-dominated lowland wet forests, characterized by monotypic stands of the endemic tree *Metrosideros polymorpha* (ʻŌhiʻa) during initial stages of primary succession and increasing compositional complexity (i.e., native tree, fern, forb, and vine species) as succession proceeds, are now rare and largely restricted to the far eastern portions of Hawaii Island (Hughes and Denslow 2005, Zimmerman et al. 2008). Because these forests consist of species endemic to Hawaiʻi, they are quite distinct from other tropical and subtropical wet lowland forests with regard to diversity, form, and function. Although much of the remaining protected forested areas continue to support native-dominated vegetation, significant portions of these forests have been invaded by introduced nonnative species (Feret and Asner 2012). These species dramatically alter the composition and function of the native forests they invade (Hughes and Denslow 2005, Zimmerman et al. 2008, Ostertag et al. 2009). Some have the capacity to fix nitrogen (e.g., *Falcataria moluccana* and *Casuarina equisetifolia*), while others do not (e.g., *Psidium cattleianum*, *Cecropia obtusifolia*), and such differences lead to distinct functional changes to the forests where they occur (Hughes and Denslow 2005, Zimmerman et al. 2008, Mascaro et al. 2012*b*). As such, this region provides an opportunity to investigate and contrast the influences of native and alien species on forest C sequestration patterns (Peltzer et al. 2010) within the context of primary succession across lava substrates of varying age. Through application of remote sensing approaches, we are able to determine C stocks across these forested landscapes rather than merely sampling discrete portions of the area. We addressed the following questions: How does aboveground forest carbon vary with increasing lava substrate (i.e., successional) age? Does lava substrate type (i.e., pāhoehoe vs. ʻaʻā) affect patterns of forest C accumulation throughout succession? Do native-dominated forests differ from nonnative-dominated forests with regard to forest C accumulation across successional states? Do forest stands dominated by nonnative N_2-fixing tree species differ from native-dominated stands with regard to C sequestration on substrates of equivalent age?

Given these questions, our objectives were to determine ACD across the matrix of lava flows occurring within state forest reserves of the Lower Puna District of Hawaii Island. To do so, we collected airborne LiDAR data across the targeted areas of interest and developed relationships between LiDAR metrics and field-based measures of forest ACD. We then related LiDAR-derived ACD values to plot-based measures of species composition to determine the respective roles of native and alien species in shaping broad-scale patterns of C sequestration across space and time.

Methods

Study area

Our study area encompasses Nanawale, Malama Ki, and Keauohana Forest Reserves as well as Lava Tree

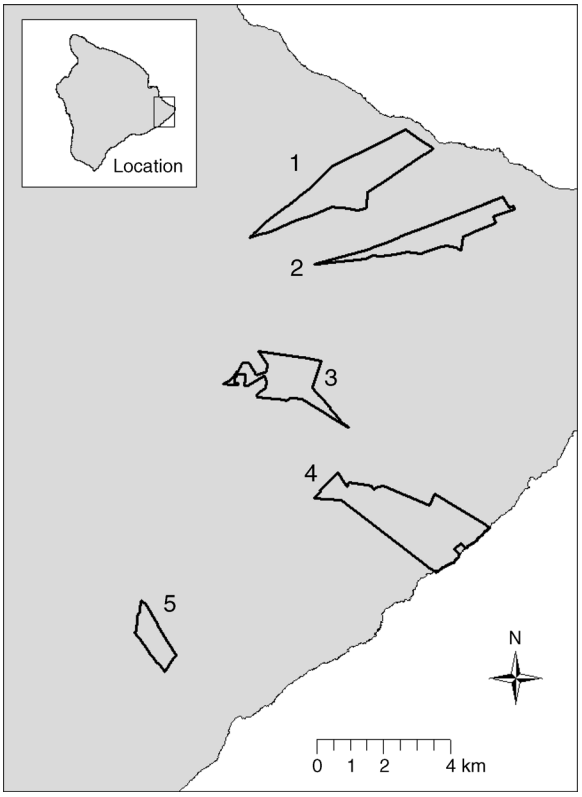

FIG. 1. Hawaii State Forest Reserves in the Puna District of Hawaii Island. Polygons 1 through 5 correspond to (1) the Kahuwai section of Nanawale Forest Reserve (FR), (2) the Halepuaa section of Nanawale FR, (3) the Kaniahiku section of Nanawale FR, (4) Malama Ki FR, and (5) Keauohana FR.

State Park located in the lower east rift zone of Kilauea Volcano in the Puna District of Hawaii Island (Fig. 1). These forest reserves are managed by the Hawaii Island Branch of the Division of Forestry and Wildlife (DOFAW) in the state of Hawaii's Department of Land and Natural Resources (DLNR); Lava Tree State Park is managed by the Hawaii State Parks Division. Collectively, these Forest Reserves contain some of the best remaining examples of lowland wet forests in Hawaii (Mueller-Dombois and Fosberg 1998, Wagner et al. 1999), as most of this forest type was converted to agriculture or for human habitation following Polynesian colonization and, to a greater extent, following European contact in the 1700s (Kirch 1982, Cuddihy and Stone 1990). The lowland wet forests now designated as state forest reserve lands have remained relatively intact because most of the area consists of young lava substrate (Moore and Trusdell 1991) previously deemed unsuitable for agriculture. They were originally set aside by successive proclamations of the territorial governors of Hawaii prior to statehood in the early 1900s; the Forest Reserves of Keauohana, Malama Ki, and Nanawale were established in 1918, 1926, 1928, respectively (Table 1). Protective status was granted with the specific intent to preserve the unique native plants and animals contained within these low-elevation forests.

The climate of the study region is generally warm and wet; mean annual temperature averages 23°C and mean annual rainfall ranges from ~2600 mm/yr near the coast to 3200 mm/yr at the highest elevation of the reserves (Table 1). Soils across each forest reserve are derived from lava flows emanating from the lower East Rift Zone of the active shield volcano, Kilauea. Parent material is tholeiitic basalt that varies little among lava flows with regard to initial chemical composition (Moore and Trusdell 1991), but varies substantially with substrate age (i.e., from 55 to 1500 years before present) and texture. Soils typically consist of soil organic matter overlaying relatively unweathered lava beds of either the smooth pāhoehoe type or the rough ʻaʻā type. Ash substrates, derived from explosive volcanic events, also occur in localized pockets across the study areas; they may overlay either pāhoehoe or ʻaʻā, and have been shown to increase N availability (Kitayama et al. 1995).

Vegetation within the Forest Reserves is generally characterized as wet lowland forest (Zimmerman et al. 2008). Primary succession by native vegetation in these areas typically manifests as colonization of barren pāhoehoe and ʻaʻā lava substrates by a single cohort of *M. polymorpha*, which grow as a monotypic forest stand during the first 100 to 200 years (Mueller-Dombois and Fosberg 1998). These monotypic stands ultimately

TABLE 1. Name, location, environmental variables, and stewardship of Hawaii Island Forest Reserves where study was conducted.

Forest area name	Location	Elevation range (above sea level in m)	Mean annual rainfall (mm)	LiDAR coverage (ha)	Land stewardship	Year established
Malama Ki FR	19°26′46″ N, 154°52′29″ W	0–195	2556	607	DOFAW, DLNR	1926
Nanawale FR, Kahuwai section	19°32′26″ N, 154°53′27″ W	18–108	3023	408	DOFAW, DLNR	1928
Nanawale FR, Halepuaa section	19°31′29″ N, 154°51′58″ W	30–113	2682	257	DOFAW, DLNR	1928
Keauohana FR	19°24′59″ N, 154°57′06″ W	187–305	2871	111	DOFAW, DLNR	1918
Nanawale FR, Kaniahiku section and Lava Tree State Park	19°29′08″ N, 154°54′39″ W	174–223	3188	245	DOFAW and State Parks, DLNR	1928

Notes: FR denotes Forest Reserve; DOFAW, DLNR denotes Division of Forestry and Wildlife, Department of Land and Natural Resources, State of Hawaii. Year established indicates year that said area was designated part of the Forest Reserve System. Rainfall is from Giambelluca et al. (2011).

TABLE 2. Areal extent, (i.e., number of pixels and hectares) and aboveground C density (mean ± SE) across state forest reserves of the Puna District of Hawaii Island.

Category	Pixels (25 m^2)	Area (ha)	Total C (Gg)	C (Mg/ha)	
				Mean	SE
Reserve					
Keauohana	43 954	110	13.46	123	69
Malama Ki	231 461	579	51.97	90	56
Nanawale-Halepuaa	102 831	257	33.21	129	45
Nanawale-Kahuwai	163 634	409	26.16	64	55
Nanawale-Kaniahiku	97 965	245	24.03	98	73
Total	639 845	1600	148.83	93	62
Lava flow type					
ʻAʻā	191 793	479	56.09	117	51
Pāhoehoe	447 407	1119	92.54	83	64
Cinder	645	2	0.20	125	52
Total	639 845	1600	148.83	93	62
Lava flow age class (yr BP)					
55	9 274	23	1.27	55	42
170	171 441	429	24.94	58	49
220	237 370	593	51.86	87	56
200–400	54 835	137	18.04	132	51
335	18 682	47	1.24	27	26
400–750	111 902	280	39.83	142	54
750–1500	36 341	91	11.64	128	59
Total	639 845	1600	148.83	93	62
Dominant vegetation					
Native	519 107	1298	106.86	82	58
Nonnative	118 184	295	41.11	139	60
Unknown	2 554	6	0.86	135	43
Total	639 845	1600	148.83	93	62

Notes: Areal extent and C values are variously categorized by Forest Reserve section, lava flow type and age, and dominant vegetation. Total C is expressed in gigagrams (Gg) or 1×10^9 g.

develop into more diverse and structurally complex forests as species establish during subsequent centuries of succession (i.e., 200 to 700 years) (Zimmerman et al. 2008). Such species include the following: *Diospyros sandwicensis*, *Psychotria hawaiiensis*, *Psydrax odorata*, and *Pandanus tectoris* (Wagner et al. 1999). A third phase noted by Zimmerman et al. (2008) involves declines in *M. polymorpha* stem density and basal area and corresponding increased dominance by mid-to-late successional species. Atkinson (1970) characterized three relatively distinct successional trends in lowland wet forests, all of which begin with dominance by pioneer cohorts of *M. polymorpha* through the first 400 years of succession, and either remain as such or are eventually replaced by *P. tectorius*-dominated forest or forest co-dominated by *M. polymorpha* and *D. sandwicensis*.

Although native-dominated vegetation still occurs across much of the area, significant portions are now occupied by nonnative tree and shrub species purposefully introduced as part of a massive nonnative tree-planting effort that took place across Hawaii throughout the 1900s. Over 10 000 nonnative species were introduced into Hawaii and more than 13 million individuals were planted in what has been characterized as the largest environmental project ever conducted in Hawaii (Woodcock 2003). Of the ~100 species now considered invasive in Hawaii, half were introduced during this tree-planting period. In the Forest Reserves of Puna, an area totaling ~2000 ha, nearly 35 000 individuals of 114 different species, 74 distinct genera, and 38 plant families were planted between 1906 and 1960 (Skolmen 1963, Nelson 1965; also see Appendix A). Most commonly planted species include: *Casuarina equisetifolia*, *Albizia* (various species including *Falcataria moluccana*, a former member of the *Albizia* genus), *Eucalyptus robusta*, *Melaleuca quinquenervia*, *Grevilia robusta*, and *Cocos nucifera* (Appendix A). Of 35 000 individuals planted in forest reserves of the Puna District, exactly 7 were native species (Appendix A). While many plantings did not survive, many have persisted and/or proliferated beyond where they were planted (e.g., N_2-fixing trees *F. moluccana* and *C. equisitifolia*). As a result, the present vegetation of the Reserves exists as a mosaic of native- and nonnative-dominated forest stands.

Methodological approach

Our primary objective was to inventory, as opposed to merely sample, ACD in a "wall-to-wall" fashion across the Forest Reserves. We did this by relating plot-based estimates of ACD to forest canopy metrics derived from LiDAR data (Asner et al. 2012*a*). LiDAR data were acquired by the Carnegie Airborne Observatory Alpha System (CAO; Asner et al. 2007) across a total of 1628

ha of the five forest reserve sections (Table 2). LiDAR has the capacity to detect at sub-meter resolution the various components of forest structure, including ground, subcanopy, and canopy layers (Asner et al. 2012*a*). The CAO LiDAR was operated at 70 kHz, with a maximum half-scan angle of 17 degrees (after a 2-degree cutoff) and 50%-overlap between adjacent flight lines. The sensor-to-target range was maintained at 1000 m above ground level, with a standard deviation of <100 m throughout the data collection. LiDAR spot size at ground level ranged from 0.5–0.65 m from nadir to the edge of each scan line (17° off-nadir), with two laser shots per location due to the adjacency of flight line overlap.

The LiDAR point cloud data were analyzed in two steps: (1) A physical model was used to derive surface (top-of-canopy) and ground digital elevation models (DEM). Vertical errors in ground DEM were previously estimated to be 0.12 ± 0.14 m; mean ± SE (Asner et al. 2009). (2) The vertical distribution of LiDAR points was calculated by binning them into volumetric pixels (voxels) of 5 × 5 m spatial resolution with 1-m vertical resolution. The DEM of ground elevation was used to standardize the vertical datum of each voxel. Therefore, the heights of each vertical "slice" of a vegetation canopy were defined relative to the ground at the horizontal center of each voxel. After the LiDAR points were binned in each volume cube, each vertical cube was divided by the total number of LiDAR points in that column, yielding the percentage of LiDAR points that occurred in each voxel. This approach has the positive effect of decreasing our sensitivity to localized variations in canopy leaf density or tree branch characteristics and flight line overlap pattern (major component of absolute variation), which can result in a different number of LiDAR returns from voxel to voxel. From these data, the Mean Canopy Profile Height (MCH) was calculated as the weighted height of the LiDAR point cloud in each 5 × 5 m kernel (Lefsky et al. 2002), and MCH was subsequently related to ACD (Asner et al. 2012*a*).

We estimated ACD across the reserves at a 5-m^2 pixel resolution using relationships developed by Asner et al. (2011) that related MCH to field-based estimates of ACD for 126 field plots that were 30 m in radius and located across a wide variety of environmental conditions and forest types of Hawaii Island. Many of these plots were located in the Forest Reserves studied here. In each 30 m radius plot, we measured and identified to species all woody stems ≥5 cm in diameter at breast height (i.e., dbh; 1.37 m above the ground). We measured tree ferns (i.e., *Cibotium* spp.) that had stems ≥1.37 m tall within a 9 m radius plot nested in the larger plot. We used a combination of local and generalized allometric equations to estimate the aboveground C density of each plot (Appendices B, C, and D). Biomass of stems <5 cm in diameter, grasses, forbs, coarse woody debris, and fine litter was not measured and not included in ACD estimates. We used a global positioning system receiver (Leica GS-50 with differential correction; Leica Geosystems Incorporated, Norcross, Georgia, USA) to locate all field plots within the LiDAR data. This LiDAR/ACD relationship, where LiDAR-derived measures of mean canopy profile height predict forest ACD (Asner et al. 2011), was then applied to each 25-m^2 pixel across the entirety of LiDAR coverage acquired for the Reserve parcels

$$\mathrm{ACD} = 6.3745 \times \mathrm{MCH}^{1.2404}$$

where $n = 126$, adjusted $r^2 = 0.83$, RMSE = 32.55 Mg C/ha. For a given plot, field-based ACD values represent the total, allometric-estimated tree biomass for each plot. Within the LiDAR imagery, plot-average MCH is determined using all pixels for which the center point falls within the plot footprint (e.g., a circular polygon in the imagery). Real ACD is something that can only be determined by direct harvest of whole plots, that is, without the aid of allometric models (Clark and Kellner 2012, Colgan et al. 2013). The disparity between plot size and mapping resolution is important to consider for uncertainty, but uncertainty in MCH-ACD predictions propagates close to the inverse of the square root of the pixel size as shown by Mascaro et al. (2011). Thus, on individual 25-m^2 pixels, uncertainty was high, but at a 1-ha resolution it declines to ~10%-of the predicted ACD value. Given the large size of the target areas considered within this study, we have confidence that comparisons among them are robust.

Preliminary analysis of relationships between field-based estimates of ACD and LiDAR-derived measures of mean canopy profile height revealed poor conformity of *F. moluccana*-dominated forest stands relative to other forest types. This was due to the tendency of *F. moluccana* stands to maintain very tall canopies with relatively low basal area and wood density. We addressed this by identifying and separating the LiDAR coverage of *F. moluccana* stands from other forest types. To these *F. moluccana*-dominated areas, we applied an *F. moluccana*-specific relationship that we derived from inventory plots located in *F. moluccana* stands and their associated LiDAR measures of mean canopy profile height

$$\mathrm{ACD} = 4.3915 \times \mathrm{MCH}^{1.025}$$

where $n = 20$, adjusted $r^2 = 0.63$, RMSE = 31.43 Mg C/ha. The lower adjusted r^2 value of the *F. moluccana* stand LiDAR/ACD relationship relative to that of the generalized Asner et al. (2011) model was likely attributable to the structure of *F. moluccana* stands. In such forest stands, individual crown sizes and large tree spacing is substantially greater than in other forest types found on Hawaii Island; that is, even in stands containing very large *F. moluccana* trees, the overall stand basal area tends to be relatively small. As a consequence, canopy or crown areas are also much greater within *F. moluccana* forests. This leads to a

larger disagreement between field and LiDAR protocols regarding which trees are inside or outside of a plot area. Field protocols followed here call for trees to be included if a given tree bole is at least 50%-within the plot, i.e., as bisected by the plot edge (Asner et al. 2009, 2011) Regarding LiDAR data, pixels contributing to MCH do not isolate individual crowns, and thus, portions of crowns are included or excluded depending on the position of the plot edge (Mascaro et al. 2011).

We used maps of lava flow age and type to characterize and distinguish among lava flows across each of the Forest Reserves (Trusdell et al. 2005, Natural Resources Conservation Service 2010). We also classified each lava flow as to whether the vegetation was native dominated, *F. moluccana* dominated, or nonnative (but not *F. moluccana*) dominated. We used compositional data from Hughes and Denslow (2005), Carlson et al. (2007), Zimmerman et al. (2008), and Mascaro et al. (2012*b*) to inform vegetation designation for each lava flow age and type. In some cases vegetation was relatively evenly distributed between native and nonnative species, and in these instances we classified the area based on the simple majority of the aboveground biomass components (i.e., >50%). In many cases, all three vegetation types were present on a single lava flow type. Where that occurred, vegetation types were separated and each was classified as a distinct map unit (Appendix E). In subsequent figures, map units classified separately as *F. moluccana* dominated and nonnative (but not *F. moluccana*) dominated were consolidated under the term "nonnative-dominated."

Statistical analysis

In order to assess uncertainty with regard to the LiDAR-to-C relationship and in terms of the number of field plots measured, Asner et al. (2011) tested the potential variability of the regression results by randomly excluding 5%-of the samples from the regression and calculating the standard error of the estimate (SEE) for the resulting regression equation. The authors conducted 1000 iterations, removing and adding a random set of six field plots to characterize the error inherent in the model with larger sample numbers. The SEE initially increased with data point addition to the regression model (Asner et al. 2011), and attained a plateau at about 12, suggesting that additional samples did not markedly improve the relationship between the LiDAR metric and aboveground C estimates. The predictive capacity of the regression was then assessed by calculating the root mean squared error (RMSE) of a set of independent ($n = 7$) samples not used to develop the regression equation. Asner et al. (2011) conducted 1000 iterations of regression model versions that increased in sample size from 5%-to 95%-of the original data set. The authors documented a decline in RMSE values from 38 Mg C/ha when 5%-(seven plots) are used in the regression to 31 Mg C/ha when 20%-(24 plots) are used; additional increases in plot number let to only slight decreases in the predictive error (i.e., 30.5 Mg C/ha [Asner et al. 2011]).

As our objectives included discerning patterns and differences in forest ACD with respect to lava age, lava type (i.e., 'a'ā or pāhoehoe), and forest composition (i.e., native or nonnative), we derived trend lines for the various combinations of the above parameters as they varied with lava flow age. Our analysis is distinctive to some degree in that it represents a complete aboveground carbon inventory, rather than a sampling, of each of the forest reserves. Thus, in comparing given parameters, we employ the totality of pixels that contribute to those parameters along the axis of lava age (i.e., period of forest succession). Carbon values (Mg/ha) were obtained for 639 845 pixels on a 5-m^2 grid for each of the five Forest Reserve sections. We treated these pixels as representing the complete population of interest rather than a sample. Each Reserve was divided into a varying number (and size) of polygons classified by lava type ('a'ā and pāhoehoe), lava age class (lava flows in 1790, 1840, and 1955, and lava ages of 200–400 years, 200–750 years, 400–750 years, and 750–1500 years, and vegetation type (i.e., *F. moluccana*, nonnative but not *F. moluccana*, native, and unknown). The exception to this was that very small map units (i.e., those constituting <100 pixels), as well as map units that were exceedingly "edgy" (i.e., long, slender map units between two larger map units), were excluded from the hypothesis-testing analysis, although they were included in the overall summation of aboveground C mass in each Forest Reserve. Trend lines were derived from the collection of pixels of a given parameter distributed across time and represent the mean value of the entire population with 95%-confidence intervals bracketing those mean values.

When looking at relationships between mean ACD and time, we used either the historically observed age of the polygon's associated lava flow (i.e., 220, 170, and 55 yr BP, respectively, for the 1790, 1840, and 1955 flows) or the median age for polygons dated by stratigraphy (i.e., 300 for 200–400 years, 475 for 400–750 years, 575 for 400–750 years, and 1125 for 750–1500 years).

Because direct plotting of ages and class midpoints with 639 845 pixels did not result in clearly interpretable figures, we used a technique called "jittering" that added random noise to the age of each individual pixel (Chambers et al. 1983). Specifically, we added a random number from −50 to +50 years (the same for all age classes) to each pixel's age. If, for a specific figure, there were >1000 pixels to be plotted, we plotted only a random sample of 1000 points. This gives the reader a better feel for the density of where the data resides, as opposed to plotting just the midpoint of the lava age class. This technique is known by the name "jittered strip plots" (Robbins 2005). To aid observation of relationships over time, we fit loess smoother (a type of nonparametric regression) to each set of pixels over the jittered age values using a loess function in the statistical

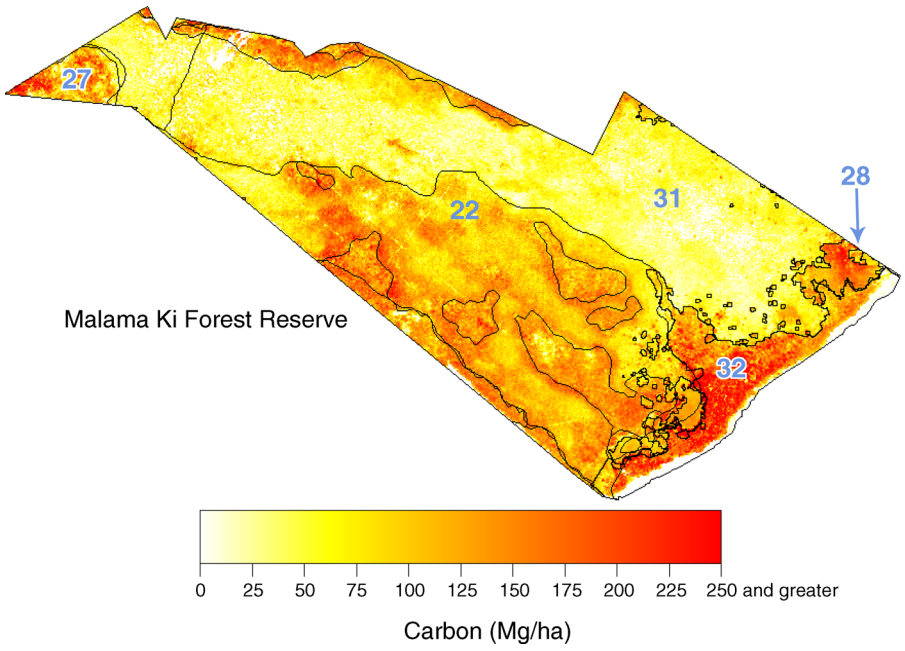

FIG. 2. Aboveground carbon density across Malama Ki forest reserve in the Puna District of Hawaii Island. Black boundaries delineate lava flows defined by lava age or type. Specific numbers in blue correspond to lava flows and or dominant vegetation types on lava flows (Appendix E).

package R (Cleveland et al. 1992, R Development Core Team 2012). The 95% confidence bands demonstrate how well the random sample of 1000 pixels estimated the loess curve of the complete set of pixels.

RESULTS

Forest ACD estimated across 1600 ha of Puna's Forest Reserves totaled 149 Gg (1 Gg = 10^9 grams), or an average of 93 Mg C/ha (Table 1; Figs. 2– 4). Not surprisingly, total ACD on an area basis was lowest (14 Gg) in the smallest Forest Reserve (Keauohana; 110 ha) and highest (52 Gg) in the largest Forest Reserve (Malama Ki; 579 ha). On an average per hectare basis, however, ACD was comparatively high in Keauohana Forest Reserve (123 Mg/ha) along with Nanawale-Halepuaa (129 Mg/ha); Nanawale-Kahuwai exhibited the lowest average ACD values (64 Mg/ha). Across all substrate ages and Reserve sections, ʻaʻā lavas averaged greater ACD (117 Mg/ha) than pāhoehoe lavas (83 Mg/ha). However, because pāhoehoe lavas were far more prevalent than ʻaʻā lavas (i.e., 1119 ha and 479 ha, respectively), total ACD was nearly two times greater for pāhoehoe flows (93 Gg) compared to ʻaʻā flows (56 Gg). On a per hectare basis, cinder substrates supported the highest ACD (125 Mg/ha), but their areal extent was quite limited (i.e., 2 ha) and their contribution to landscape-scale ACD was minor (Table 2).

Considering lava flow age alone (i.e., regardless of lava flow and vegetation type), two of the youngest lava flows (i.e., 220 and 170 yr BP) accounted for nearly two-thirds of the total area inventoried in the Forest Reserves, and accounted for over half of the total ACD (Table 2). In general, ACD on a per hectare basis tended to increase with increasing lava flow age; the highest average values (i.e., 128–142 Gg C) were found in 200–400, 400–750, and 750–1500 yr BP lava age classes (Table 2). Exceptions were the 335 yr BP lava flows, which supported an average of only 27 Mg C/ha. Of the older flows, only the 400–750 yr BP lava flows covered an area (280 ha) that approached the extent of the younger lava flows. Because these flows exhibited relatively large average C mass (i.e., 142 Mg/ha), they accounted for more than a quarter (280 Gg) of overall ACD at the landscape scale (Table 2).

Across all lava flow ages and types, native-dominated vegetation (with "dominated" defined here as >50% of aboveground biomass) averaged only 82 Mg C/ha, a value just over half that of nonnative vegetation (139 Mg C/ha; Table 2). However, since native-dominated forest occupied >80% of the Reserve landscapes, they accounted for >70% of collective ACD of the Forest Reserves (107 Gg; Table 2). Vegetation not classified as either native or nonnative accounted for 6 of the 1600 hectares inventoried; these areas averaged 135 Mg C/ha and accounted for 0.5% of total ACD (Table 2).

Patterns of ACD with increasing lava flow age were distinctly different between native and nonnative forest stands (Fig. 5). Considering ʻaʻā and pāhoehoe lava flows together, native-dominated forest ACD averaged <60 Mg/ha on the youngest lavas, a value substantially less than the ~100 Mg C/ha of nonnative-dominated forests on similarly aged lava flows (Fig. 5). Map units 5, 82,

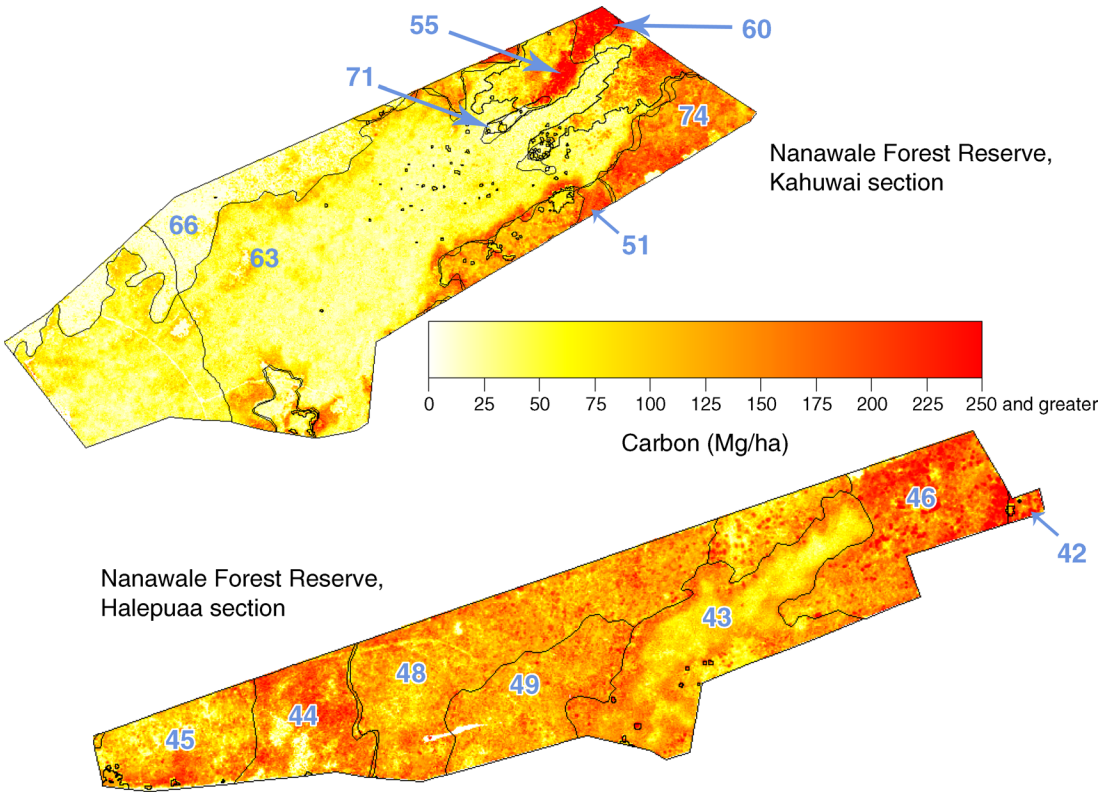

FIG. 3. Aboveground carbon density across Kahuwai and Halepuaa sections of Nanawale forest reserve in the Puna District of Hawaii Island. Black boundaries delineate lava flows defined by lava age and type. Specific numbers in blue correspond to lava flows and or dominant vegetation types on lava flows (Appendix E).

and 31 (Figs. 2 and 4) exemplify the low ACD of native forest occurring on young lava flows; flows aged 55, 170, and 220 supported average ACD of 20, 48, and 48 Mg/ha, respectively (Appendix E). In contrast, nonnative forests on comparably young lava flows such as map units 1, 32, and 75 supported average ACD between 88 and 160 Mg C/ha (Figs. 2 and 4; Appendix E).

ACD of native-dominated forest increased with increasing lava age to a plateau of ~130 Mg/ha on 400–750 yr BP flows, values that carried through to lava flows 750–1500 yr BP (Fig. 5). Examples of this trend were provided by map units 5, 63, 22, 9, and 74 (Figs. 3 and 4) which spanned flow ages of 55, 170, 220, 200–400, and 750–1500 yr BP and ACD values of 20, 48, 107, 140, and 152 Mg/ha, respectively (Appendix E). The pattern of relatively high average ACD values in nonnative forests regardless of lava flow age was apparent in map units 55, 3, 79, and 60 (Figs. 3 and 4), which were 170, 200–400, 400–750, and 750–1500 yr BP and averaged 120, 110, 161, 238 Mg C/ha, respectively (Appendix E). As such, ACD of native forest stands was much less than that of nonnative forest stands during the early stages of primary succession (i.e., 0 to 400 yr BP), but increased with primary succession to effective equivalence with nonnative forest C mass by the 400–750 and 750–1500 yr BP age classes.

ACD of native-dominated forest stands was substantially higher, on average, for ʻaʻā lava flows compared to pāhoehoe lava flows during the early stages of primary succession (i.e., lava flows up to 200–400 yr BP). Map units 22 and 31 illustrate this (Fig. 2; Appendix E): ACD on ʻaʻā lava was more than double that of pāhoehoe lava of the same age (i.e., 220 yr BP). Average ACD of the two lava flow types converged at 400–750 yr BP, and were lower for ʻaʻā compared to pāhoehoe lava flows for 750–1500 yr BP flows (Fig. 6). Nonnative-dominated forest stands exhibited a pattern opposite to that of native-dominated forests; ACD values were on average greater for pāhoehoe lava flows than ʻaʻā lava flows (Fig. 7).

The presence of nonnative N_2-fixing trees such as *F. moluccana* and *C. equisetifolia* manifested in substantially higher ACD relative to their native forest counterparts on young lava flows. Map units 28, 31, and 32 demonstrate this effect; forests dominated by *F. moluccana* (map unit 28) and *C. equisetifolia* (map unit 32) supported ACD values that were two and three times the value of native-dominated forests (map unit 31) growing on the same lava flow (Fig. 2, Appendix E). Similarly, *C. equisetifolia*-dominated forest stands occurring on 170 YPB pāhoehoe lava (i.e., map unit 55, Fig. 3) averaged 120 Mg C/ha (Appendix E), a value

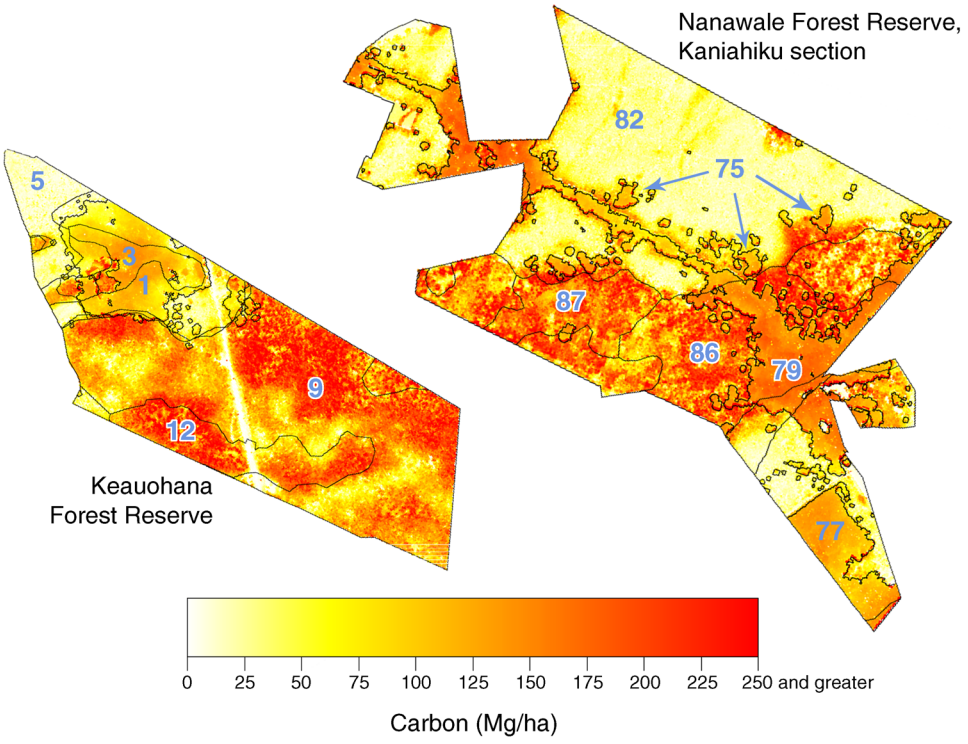

FIG. 4. Aboveground carbon density across the Kanaihiku section of Nanawale forest reserve and Keauohana Forest Reserve in the Puna District of Hawaii Island. Black boundaries delineate lava flows defined by lava age and type. Specific numbers in blue correspond to lava flows and/or dominant vegetation types on lava flows (Appendix E).

more than double that of native-dominated forest on the same lava flow (map unit 63, Fig. 3; Appendix E). On ʻaʻā lava aged 55 yr BP, *F. moluccana*-dominated stands (map unit 1, Fig. 4) were four times greater than native-dominated stands (map unit 5, Fig. 4; Appendix E). As primary succession progressed, however, differences diminished between native- and nonnative stands. For example, map units 86 and 79 consisted of native-

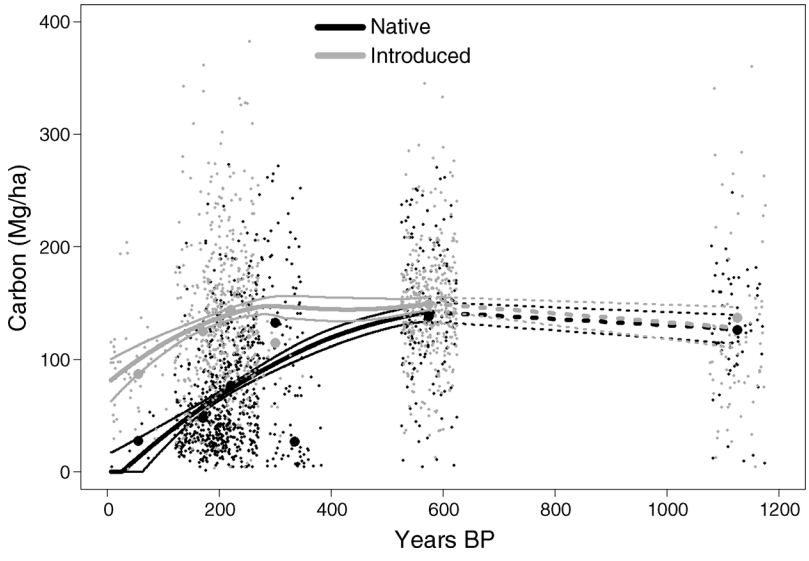

FIG. 5. Aboveground carbon density (ACD) of individual 25-m^2 pixels arrayed across both ʻaʻā and pāhoehoe lava flows in forest reserves of the Puna District of Hawaii Island. ACD values are categorized by dominant vegetation (i.e., native or nonnative) and distributed along a horizontal axis defined by lava flow age (i.e., years before present, or yr BP). Trend lines are indicated as thick lines; narrower lines denote a 95%-confidence interval around each trend line. Dashed lines beyond 650 yr BP indicate increased uncertainty of the trend line due to lack of data points.

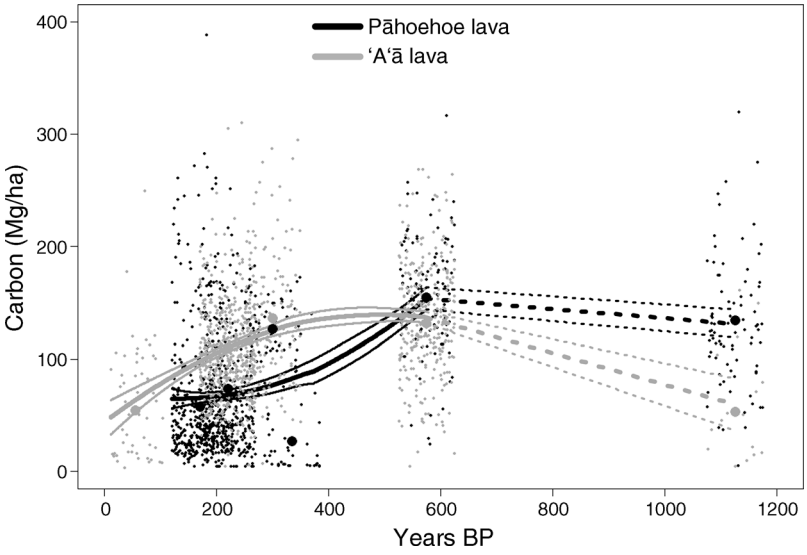

FIG. 6. Aboveground carbon density (ACD) of native-dominated forest stands within individual 25-m^2 pixels arrayed across forest reserves of the Puna District of Hawaii Island. ACD values are categorized by lava flow type and distributed along a horizontal axis defined by lava flow age (i.e., years before present, or yr BP). Trend lines are indicated as thick lines, with narrower lines denoting a 95%-confidence interval around each trend line. Dashed lines beyond 650 yr BP indicate increased uncertainty of the trend line due to lack of data points.

dominated and *F. moluccana*-dominated stands on the same lava flow (i.e., pāhoehoe, 400–750 yr BP), and they exhibited virtually identical average ACD values (i.e., 166 and 161 Mg C/ha, respectively).

With only one exception, map units supporting exceedingly high ACD values occurred on 400–750 yr BP lava flows, whether on ʻaʻā or pāhoehoe lava, and whether nonnative or native dominated. Forest stands dominated by *C. equisetifolia* were among the most massive within this lava flow age range, exhibiting average ACD values of 193 and 238 Mg C/ha for map units 42 and 60, respectively (Figs. 2 and 3; Appendix E). *Mangifera indica*-dominated stands averaged 164 Mg C/ha (Map unit 46, Fig. 3), and an *F. moluccana*-dominated stand averaged 161 Mg C/ha (Map unit 79, Fig. 4). Map units 51, 86, and 87 (Figs. 3 and 4)

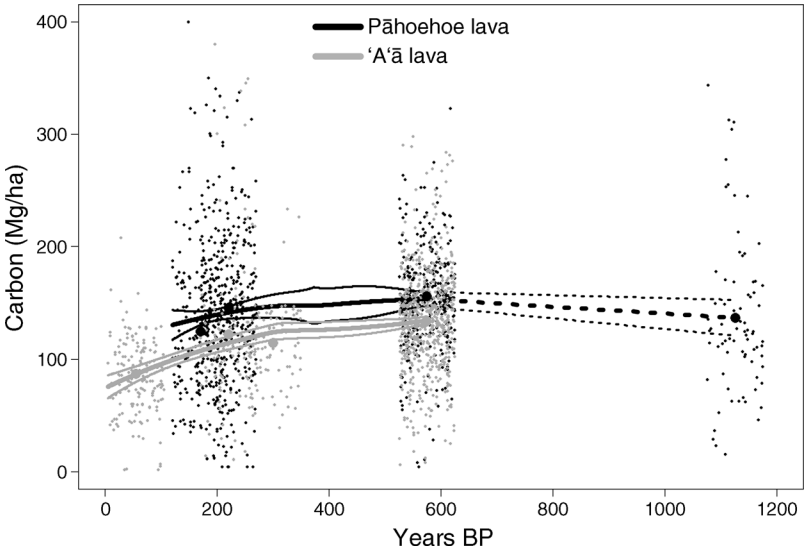

FIG. 7. Aboveground carbon density (ACD) of nonnative-dominated forest stands within individual 25-m^2 pixels arrayed across forest reserves of the Puna District of Hawaii Island. ACD values are categorized by lava flow type and distributed along a horizontal axis defined by lava flow age (i.e., years before present, or yr BP). Trend lines are indicated as thick lines; narrower lines denote a 95% confidence interval around each trend line. Dashed lines beyond 650 yr BP indicate increased uncertainty of the trend line due to lack of data points.

consisted of native-dominated forests exhibiting high average ACD as well (i.e., 173, 166, and 162 Mg/ha, respectively; Appendix E). Map unit 32 was exceptional in that it was dominated by *C. equisetifolia*, occurred on a relatively young 220 yr BP lava flow, and averaged 160 Mg/ha (Fig. 2; Appendix E).

Map units exhibiting exceedingly low ACD occurred in native-dominated vegetation on either very young or very old lava flows or in vegetation dominated by the native fern *Dicranopterus linearis*. Map units 4 and 5 consisted of ʻaʻā lavas aged 55 yr BP that supported native vegetation averaging 20 to 38 Mg C/ha (Fig. 4; Appendix E); pāhoehoe lava aged 750–1500 yr BP supported native-dominated vegetation averaging 28 Mg C/ha (Map Unit 71, Fig. 3; Appendix E). Pāhoehoe lavas aged 335 yr BP and dominated by *D. linearis* averaged 18 to 29 Mg C/ha (Map Units 66 and 67, Fig. 3; Appendix E).

Discussion

Results indicate that Hawaiian lowland wet forests contain substantial amounts of aboveground carbon. ACD values (i.e., 93 Mg/ha overall, and 128 to 142 Mg/ha on the majority of lava flows >300 yr BP) were similar to those of intact tropical forests elsewhere. Chave et al. (2003) reported ACD values of 130 Mg C/ha for old-growth forests of Panama. Asner et al. (2012*a*, *b*) reported average ACD values of 100 and 130 Mg C/ha for humid forests of Madagascar and the Columbian Amazon, respectively. Forests of the Peruvian Amazon exhibited ACD values ranging from 65 to 125 Mg C/ha (Asner et al. 2010*a*), and ACD in old-growth forests from across the Amazon Basin ranged between 100 to 175 Mg/ha (Malhi et al. 2006). Plot-based ACD values of intact tropical forests of Africa ranged from 76 to 398 Mg C/ha (Lewis et al. 2009). These Hawaiian forests were also comparable to average ACD values (i.e., 150 Mg C/ha) developed and used by the IPCC for Tier 1 carbon assessments (IPCC 2006). Within Hawaii Island, lowland wet forest ACD values were generally comparable to those of a variety of montane moist forest types inventoried on the slopes of Mauna Kea volcano (Asner et al. 2009) and agreed with plot-scale measures of ACD in native and nonnative forests of Hawaii's wet lowlands reported by Mascaro et al. (2012*b*).

Mature native forest stands (i.e., >300 yr BP) exhibited relatively high ACD values primarily because *M. polymorpha* is their main constituent. Although individual *M. polymorpha* trees do not often reach remarkably large diameters, this species exhibits high wood density values (i.e., 0.7 g/cm^3 [Asner et al. 2011]). In addition, stand-level densities in large, mature *M. polymorpha* forests tend to be high compared to other tropical forests (i.e., ~260 stems >20 cm dbh/ha [Zimmerman et al. 2008, Asner et al. 2012*a*]). As such, where this tree species is abundant, high ACD values are expected. The same factors apply with regard to high ACD values of forest stands dominated by the nonnative tree *C. equisetifolia*; it exhibits dense wood (i.e., 0.8 g/cm^3 [Asner et al. 2011]) and high stand-level stem densities (Mascaro et al. 2012*b*). In contrast, wood density of *F. moluccana* is comparatively low (i.e., 0.4 g/cm^3), and densities of mature stands are quite low as well, due to pronounced self-thinning (Hughes and Denslow 2005). Where *F. moluccana* exhibited high ACD values, it was the result of widely spaced, remarkably large individuals.

Results revealed clear landscape-scale controls of lava age, lava type, and native vs. nonnative tree dominance on ACD accumulation during primary succession. Increases in ACD of native-dominated ecosystems with increasing lava age have been demonstrated in Hawaii at both field-plot scales (Aplet and Vitousek 1994, Kitayama et al. 1995, Raich et al. 1997, Mascaro et al. 2012*b*) and at the landscape level (Asner et al. 2009, 2011). Gradual C accumulation tightly constrained by N limitation is a salient feature of primary succession on Hawaii's lava flows (Vitousek et al. 1993, Crews et al. 2001). Because Hawaii's lowland wet forests lack native N_2-fixing plants at early stages of primary succession, forest productivity and C mass accumulation are constrained (Harrington et al. 2001, Hughes and Denslow 2005) well below levels expected when N_2-fixing plants are present during primary succession (Bormann and Sidle 1990, Kamijo et al. 2002).

Temperature also influences ACD values during succession, and native-dominated forests of Hawaii's warm, wet lowlands exhibited higher ACD values than cooler wet montane environments. ACD values of wet lowland forests (i.e., <250 m above sea level) on 140-year-old lavas were ~50 Mg C/ha compared to values of 10 and 8 Mg C/ha for native forests growing on similarly aged flows located at 914 m and 1219 m above sea level, respectively (Aplet and Vitousek 1994). Raich et al. (1997) documented ACD values of 15 to 3 Mg C/ha for native forests growing on pāhoehoe lavas aged 110 to 136 yr BP located at 290 to 1600 m elevations. The low values documented by Raich et al. (1997) may also be a function of lava type, given that those sites occurred on pāhoehoe lavas. Our results documented a clear difference in ACD with lava type; at any given age up to 550 yr BP, ACD of native-dominated forest stands was greater on ʻaʻā lava compared to pāhoehoe lava. Raich et al. (1996) found growth of *M. polymorpha* individuals to be >50% greater on ʻaʻā compared to pāhoehoe lava in a plot-scale study of controls on native forest primary succession. Aplet et al. (1998) also documented greater plant biomass on ʻaʻā lava flows compared with similarly aged pāhoehoe flows on the low, wet flank of Mauna Loa volcano. They attributed this pattern to a greater surface area of ʻaʻā lava resulting in increased rates of rock weathering and increased nutrient availability. Kitayama et al. (1995) and Drake (1992) noted that *M. polymorpha* recruitment and growth appeared constrained only by availability of

appropriate sites for germination. Such sites are not limited on ʻaʻā lava flows where numerous pockets with fine mineral particles occur, but are very much limited to cracks in the planes or sheets of pāhoehoe lava (Aplet et al. 1998). These geomorphic controls and resulting vegetation patterns were writ large in our study. Interestingly, we saw a slightly opposing pattern for stands dominated by introduced trees; ACD values were somewhat greater, on average, and for any given lava flow age up to 550 YPB, for forest stands occurring on ʻaʻā compared to pāhoehoe substrates. We do not know why this pattern occurred, but wonder if it might be driven by an as yet unexplained affinity by introduced N-fixing trees for pāhoehoe lavas over ʻaʻā.

Whether forests were dominated by native or introduced trees made a substantial difference for ACD values on lavas aged <400 yr BP, but was not important on lavas aged >500 yr BP. We attribute this to several factors. First, during the initial centuries of primary succession, native forests accumulate C mass gradually as they develop from initial pioneer cohort stands of *M. polymorpha*, to more compositionally and structurally complex forests as new species establish. This process accounts for the nearly linear trend of increasing native forest ACD with increasing lava age, and the absence of native N_2-fixing plants constrains the rate at which this process unfolds (Hughes and Denslow 2005, Mascaro et al. 2012*b*). In contrast, ACD values for forests dominated by introduced trees were quite large, even at the earliest phases of primary succession. This was almost entirely due to the presence of two prevalent nonnative N_2-fixing trees, *F. moluccana* and *C. equisetifolia*, whose stands accounted for the majority of nonnative-dominated vegetation on young lavas. Mascaro et al. (2012*b*) found that on lava flows aged 300 yr BP and younger, both *F. moluccana*- and *C. equisetifolia*-dominated forests exhibited rates of litterfall, aboveground growth increment, and aboveground net primary production that were >200%-higher than rates for native forest stands dominated by *M. polymorpha* on similarly aged lava flows. While these authors did not find significant differences in ACD between native- and nonnative-dominated stands, ACD estimates of forest plots in *C. equisetifolia* and *F. moluccana* stands averaged 134 and 90 Mg C/ha, respectively (Mascaro et al. 2012*b*). These values rest well within patterns of high ACD for nonnative-dominated forests revealed in this study; such high values are even more notable given that the earliest plantings of *F. moluccana* and *C. equisetifolia* in these forest reserves occurred only 85 and 75 years ago, respectively. The mechanism for such high rates of C accumulation and storage is clear; newly formed lava substrates lack plant-available N (Vitousek et al. 1993), and inputs from sources other than higher plants (e.g., precipitation and dryfall, free-living cyanobacteria, heterotrophic bacteria) are low (Hughes and Denslow 2005). *F. moluccana* and *C. equisetifolia* have the capacity to fix N, thus freeing them from N limitation and allowing for large increases in primary productivity, and increased nutrient acquisition (Binkley et al. 2004, Mascaro et al. 2012*b*). In contrast, *M. polymorpha*, virtually the sole woody plant component of native-dominated primary succession on these lava flows, lacks the capacity to symbiotically fix N, and its productivity is highly constrained by N limitation (Hughes and Denslow 2005, Mascaro et al. 2012*b*).

Our results regarding whether nonnative trees increased ACD beyond corresponding native-dominated communities were clearly time dependent; nonnative forests on younger lavas (i.e., <300 yr BP) dominated by *F. moluccana* and *C. equisetifolia* exhibited substantially greater ACD than corresponding native-dominated forest stands, but native and nonnative forests did not differ in ACD on lavas aged 600 yr BP and older. This was due to both the plateauing of nonnative forest ACD at ~130 Mg C/ha on lavas aged 200 yr BP and beyond, as well the attainment, by 550 yr BP, of native forest ACD values that were roughly equivalent to those of nonnative forest values. As such, we document no difference between native and nonnative forest stands after 550 years of primary succession despite the exceedingly rapid accumulation of ACD by nonnative forest stands and correspondingly slow accumulations in forests dominated by native Hawaiian species. In study plots located across the same lowland wet forest landscape of Puna, Hawaii, Mascaro et al. (2012*b*) also found values of native- and nonnative-dominated forest for a number of important ecosystem parameters (i.e., litterfall biomass and N mass, aboveground increment, aboveground NPP, and nitrogen use efficiency) converged by ca. 550 yr BP. However, it is important to keep in mind that while patterns of ACD among native forest stands were strongly controlled by lava substrate age and developed within century-scale time frames, patterns of ACD accumulation among nonnative forest stands were decoupled from substrate age and developed within decadal time frames. Indeed, all nonforest stands inventoried in this study were established during the 1900s, and their ACD values were the result of no more than 90 years of succession. This attests to their capacity for comparatively rapid rates of ACD accumulation, particularly where such stands were dominated by tree species capable of symbiotic N-fixation.

Of special note were low ACD values of native-dominated forest on lavas aged 335 yr BP. These values diverged substantially from the trend of steady, gradual C accumulation by native-dominated vegetation. This anomaly most likely resulted from the prevalence of the mat-forming fern *Dicranopteris linearis* (Hawaiian common name, Uluhe) across those particular pāhoehoe lava flows. Native to Hawaii, *D. linearis* is a common component of primary and secondary succession on young and old basaltic substrates (Russell et al. 1998, Vitousek et al. 2009). It is capable of slowing or arresting native forest succession in Hawaii and elsewhere by constraining light and nutrient availability (Russell et al.

1998, Walker et al. 2010). These same traits and effects serve to inhibit colonization and spread of many nonnative plant species considered invasive pests in Hawaii (Russell et al. 1998), and may, by creating C-rich and N-poor soil organic matter (Russell and Vitousek 1997), promote the long-term persistence of native species, particularly *M. polymorpha*, over nonnative species. *D. linearis* was quite widespread across the younger pāhoehoe lava substrates of the forest reserves sampled here, often in association with scattered populations of *M. polymorpha*, and appeared to simultaneously slow native forest succession and constrain invasion by nonnative species, particularly shade-intolerant species such as *F. moluccana* (Soerianegara and Lemmens 1994).

Though not purposefully planted within the forest reserves during the 1900s, and not common in undisturbed native forest stands as recently as 1970 (Atkinson 1970), the invasive understory tree *Psidium cattleianum* exhibited high densities across many areas inventoried in this study. This species was particularly abundant on lava substrates aged 300 yr BP and older (Zimmerman et al. 2009) and on younger lavas where nonnative, N-fixing trees such as *F. moluccana* and *C. equisetifolia* have facilitated its proliferation (Hughes and Denslow 2005). *P. cattleianum* has the potential to constrain native plant recruitment and thus alter future successional patterns in this region (Zimmerman et al. 2008). Ramifications of *P. cattleianum* proliferation for ACD of lowland wet forests are apparent from previous studies. Asner et al. (2008*a*) documented distinct shifts in the structure of forests formerly dominated by *M. polymorpha* but now heavily invaded by *P. cattleianum*, where *P. cattleianum* formed a dense midcanopy layer ~10 m in height, often engulfing much taller, mature *M. polymorpha* trees. Such changes tripled the volume of the midcanopy but reduced the volume of the *M. polymorpha*-dominated overstory by 60%, reducing understory light levels to 5% of ambient levels, and thereby constraining subsequent native seedling recruitment. While *P. cattleianum* is found at high densities throughout the forest reserves inventoried in this study, it most often occurred in association with mature *M. polymorpha* stands, and thus its contribution to total stand basal area, often an accurate proxy for relative ACD values, was typically dwarfed by much larger, though more scattered, *M. polymorpha* trees (Hughes and Denslow 2005, Zimmerman et al. 2009). Although many forests inventoried in this study contained a mixture of large *M. polymorpha* stems and more numerous but much smaller *P. cattleianum* stems, we characterized them as native dominated with respect to relative contribution to total ACD, and these characterizations were confirmed where possible by results of previous studies (Hughes and Denslow 2005, Carlson et al. 2007, Zimmerman et al. 2008, Mascaro et al. 2012*a*). However, when these larger, native trees senesce in the future, we expect ecosystem retrogression to short-stature, monotypic stands of *P. cattleianum* exhibiting both low ACD values and little hope for native regeneration in the absence of effective integrated management of this pest plant.

There is a world-wide interest to protect and even increase C storage in ecosystems in order to mitigate climate change (IPCC 2006), and we did find that the invasion of native forests by nonnative N_2-fixing trees increased ACD on young lava flows of Hawaii's wet lowlands, though this was not the case on older lavas with more developed native forest. Indeed, given the relatively large areas of early-successional *M. polymorpha*-dominated forest on young lava flows studied, further proliferation of *F. moluccana* and *C. equisetifolia* populations would likely increase ACD stocks. Yet this would be in the near term only, would effectively preempt the eventual, though more gradual, accretion of native-dominated forest ACD to similar levels seen in nonnative forest, and, perhaps most importantly, would lead to further facilitation of nonnative species and further extirpation and exclusion of native species (Hughes and Denslow 2005). As such, it is difficult to invoke a positive benefit in terms of ecosystem services (i.e., increased C sequestration) for these Hawaiian forests, particularly when Hawaii's citizens increasingly view nonnative trees such as *F. moluccana* as financial burdens at best and threats to life and property at worst (Hughes et al. 2013).

Consequently, the intrinsic value of native forests for the biodiversity they represent and support outweigh any short-term shortcoming in C sequestration potential. The Hawaiian archipelago as a whole has been identified as a key contributor to the world's biodiversity hotspots (Myers et al. 2000), and Hawaii is a prime example of how islands contain disproportionately high levels of earth's biodiversity (Caujape-Castells et al. 2010). In particular, native-dominated lowland wet forests studied here and previously (Carlson et al. 2007, Zimmerman et al. 2008, Cordell et al. 2009) are a unique and increasingly rare reservoir of native biodiversity. In addition to the endemic plant species that currently comprise these communities, native-dominated lowland wet forests provide important potential habitat for threatened and endangered plant species (Price et al. 2012) and food resources and habitat for many of Hawaii's endemic fauna, including several of the native honeycreeper species observed with increasing frequency in lowland wet forests (Ostertag et al. 2009). As such, while our results indicate that continued transformation of native forests to nonnative forests in the wet lowlands of Hawaii may increase forest ACD at the landscape scale, such transformations would further indelibly compromise the contributions of Hawaii's native ecosystems to global biodiversity.

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Supplemental Material

Appendix A

Recorded plantings of the Hawaii Division of Forestry from 1910 to 1960 on the forest reserves of the lower Puna District, Hawaii Island (*Ecological Archives* A024-042-A1).

Appendix B

Diameter-to-biomass models used to estimate aboveground biomass (AGB) of Hawaii's forests (*Ecological Archives* A024-042-A2).

Appendix C

Species-specific and general diameter-to-height models used to estimate height of common native and nonnative trees in Hawaii (*Ecological Archives* A024-042-A3).

Appendix D

Estimates of wood density of common native and nonnative trees of Hawaii (*Ecological Archives* A024-042-A4).

Appendix E

The number of pixels and average aboveground C of individual lava flows across the various Forest Reserves of the Puna District of Hawaii Island (*Ecological Archives* A024-042-A5).