

Ecosystem carbon storage does not vary with mean annual temperature in Hawaiian tropical montane wet forests

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Abstract

Theory and experiment agree that climate warming will increase carbon fluxes between terrestrial ecosystems and the atmosphere. The effect of this increased exchange on terrestrial carbon storage is less predictable, with important implications for potential feedbacks to the climate system. We quantified how increased mean annual temperature (MAT) affects ecosystem carbon storage in above- and belowground live biomass and detritus across a well-constrained 5.2 °C MAT gradient in tropical montane wet forests on the Island of Hawaii. This gradient does not systematically vary in biotic or abiotic factors other than MAT (i.e. dominant vegetation, substrate type and age, soil water balance, and disturbance history), allowing us to isolate the impact of MAT on ecosystem carbon storage. Live biomass carbon did not vary predictably as a function of MAT, while detrital carbon declined by ~14 Mg of carbon ha⁻¹ for each 1 °C rise in temperature – a trend driven entirely by coarse woody debris and litter. The largest detrital pool, soil organic carbon, was the most stable with MAT and averaged 48% of total ecosystem carbon across the MAT gradient. Total ecosystem carbon did not vary significantly with MAT, and the distribution of ecosystem carbon between live biomass and detritus remained relatively constant across the MAT gradient at ~44% and ~56%, respectively. These findings suggest that in the absence of alterations to precipitation or disturbance regimes, the size and distribution of carbon pools in tropical montane wet forests will be less sensitive to rising MAT than predicted by ecosystem models. This article also provides needed detail on how individual carbon pools and ecosystem-level carbon storage will respond to future warming.

Keywords: carbon balance, carbon stocks, climate change, elevation gradient, Hawaii, tropical wet forest

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Introduction

Forest ecosystems are Earth's largest terrestrial carbon sink, with tropical forests storing more carbon than all other forest types combined (Bonan, 2008; Pan *et al.*, 2011). However, the sensitivity of ecosystem carbon stocks to rising temperature remains among the most significant uncertainties constraining coupled biosphere-atmosphere models (Booth *et al.*, 2012; Cox *et al.*, 2013; Huntingford *et al.*, 2013; Wang *et al.*, 2013). This uncertainty limits the ability of ecosystem models to accurately predict how the large amount of carbon stored in tropical wet forests will respond, and potentially feedback, to future climate warming (Wood *et al.*, 2012). Improving model projections of how future climate warming will affect tropical forest carbon storage requires more direct estimates of the long-term,

integrated response of tropical forest carbon pools to the isolated effect of temperature (Luo *et al.*, 2011; Wang *et al.*, 2013).

The two most common approaches to directly estimate ecosystem-level responses to rising temperature are *in situ* artificial warming experiments and cross-site observational studies that substitute space for time, each with their own advantages and disadvantages. Warming experiments conducted *in situ* with appropriate control treatments have the advantage of isolating the effect of increased temperature on ecosystem carbon storage. Results from such experiments in temperate biomes indicate an overall increase in plant biomass carbon and a slight decline in soil carbon with increasing temperature (Dieleman *et al.*, 2012; Lu *et al.*, 2013). However, *in situ* warming experiments are necessarily short term and therefore may not account for long-term acclimation responses of carbon cycling (Smith & Dukes, 2012; Wythers *et al.*, 2013). Moreover, warming experiments in forests have thus far only

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heated certain components of the ecosystem, most often soils (Melillo *et al.*, 2011), and so do not represent an integrated, whole-ecosystem response to warming. While experiments evaluating the warming effects on individual ecosystem components may still be valuable for predicting forest responses to increased temperature, there are currently no published data from such experiments in tropical forest ecosystems (Wood *et al.*, 2012).

Observational, cross-site analyses substitute space for time by comparing carbon pools in forests across a range of temperature environments typically along elevation or latitudinal gradients, and so have the advantage of representing the long term, whole-ecosystem response of forests to changing mean annual temperature (MAT). There are several published studies examining how ecosystem carbon pools in tropical forests vary with MAT across sites (Raich *et al.*, 2006; Stegen *et al.*, 2011), or along elevation gradients (Kitayama & Aiba, 2002; Girardin *et al.*, 2010; Moser *et al.*, 2011). The most comprehensive of these studies indicates climate warming in tropical wet forests will lead to an increase in live biomass carbon, a decline in detrital carbon, and no net change in total ecosystem carbon storage (Raich *et al.*, 2006). In contrast to *in situ* artificial warming experiments, the major limitation of cross-site comparisons of ecosystem carbon storage is variation in factors other than temperature that influence carbon processes, including plant species composition, plant available water, geologic substrate, soil properties, and disturbance. These potentially confounding factors complicate interpretation of cross-site variation in the size of individual ecosystem carbon stocks or their distribution within forest ecosystems (Wood *et al.*, 2012). Because of high levels of local diversity, variation in species composition is especially problematic in comparisons of tropical wet forests across sites or along elevation gradients (Raich *et al.*, 2006; Rapp *et al.*, 2012).

Here, we present results of a comprehensive assessment of ecosystem carbon pools across a 5.2 °C MAT gradient spanning 800 m elevation in native-dominated tropical montane wet forests on Hawaii Island. Because of its geographic isolation and shield volcano topography and origin, Hawaii supports steep environmental gradients that span short distances where species composition, substrate type, and substrate age can be held constant (Vitousek, 2004, 2006). Previous work along the MAT gradient described in this study revealed a near doubling of soil CO₂ efflux with a 5.2 °C increase in MAT (Litton *et al.*, 2011), suggesting this is an ideal model ecosystem to test hypotheses about the response of ecosystem carbon storage to climate warming.

We examined the temperature sensitivity of tropical montane wet forest carbon pools along a highly con-

strained 13.0–18.2 °C MAT gradient in Hawaii where dominant canopy species, disturbance history, soil water availability, geological substrate, and soil type are largely held constant (Litton *et al.*, 2011; Iwashita *et al.*, 2013). We tested two hypotheses based on results from the Raich *et al.* (2006) synthesis of how temperature influences carbon storage and distribution in evergreen broad-leaved tropical wet forests: (i) live biomass carbon increases and detrital carbon decreases with rising MAT, such that ecosystem carbon is dominated by detrital pools in cooler forests and by live biomass pools in warmer forests; and (ii) the temperature-induced increase in live biomass carbon and decrease in detrital carbon counterbalance each other, resulting in no net change in ecosystem carbon storage with MAT.

Materials and methods

Study site

Above- and belowground live biomass and detrital carbon pools were estimated in nine 20 × 20 m plots in native-dominated tropical montane wet forest arrayed across an 800 m elevation gradient on the northeastern slope of Mauna Kea volcano on the Island of Hawaii (Litton *et al.*, 2011). The two highest elevation sites are located in the Hakalau Forest National Wildlife Refuge (HFNWR) and the seven lower elevation sites in the Hawaii Experimental Tropical Forest (HETF). The nine sites range from 800 to 1600 m elevation, corresponding to a MAT range of 18.2 °C at the lowest elevation site to 13.0 °C at the highest site (Table 1). Mean annual temperature for each site was estimated using a long-term (1961–1990) climate record at nearby Hilo International Airport (8 m elevation) and the environmental lapse rate of 6.49 °C 1000 m⁻¹ (Litton *et al.*, 2011). Mean annual rainfall is not constant across MAT plots (Table 1). However, both rainfall and potential evapotranspiration (Table 1) are positively correlated with MAT (Pearson's $r = 0.59$ and 0.84 , respectively). As a result, all nine MAT plots are characterized by nearly identical mean monthly soil water content (0.52 ± 0.02 m³ m⁻³, CV = 10.5%; Table 1) because declining rainfall is balanced by a reduction in evapotranspiration driven by lower air temperatures as elevation increases (Table 1). While we acknowledge that real-world warming will likely reduce soil moisture in the absence of changes to rainfall, our goal was to isolate the effects of temperature as cleanly as possible within a space-for-time substitution design. All plots are below the average base height of the trade wind inversion (2225 m; Cao *et al.*, 2007) and receive similar amounts of solar radiation (Table 1). All nine plots are classified as tropical montane wet forest dominated by *Metrosideros polymorpha* in the upper canopy and a mixture of *Cheirodendron trigynum* and three tree fern species (*Cibotium* spp.) in the mid-canopy. Geologic substrate underlying all nine MAT sites is classified as a single geological unit consisting of a Pleistocene-age Mauna Kea lava flow dominated by hawaiiite and mugearite

Table 1 Environmental characteristics of the nine permanent plots along a 5.2 °C mean annual temperature gradient in tropical montane wet forests on the Island of Hawaii, where VWC is volumetric water content and PET is potential evapotranspiration. Data are from Litton *et al.* (2011) unless otherwise indicated

Latitude (°N)	Longitude (°W)	Elevation (m)	Mean annual temperature (°C)	Mean annual rainfall (mm y ⁻¹)*	Mean annual soil VWC (m ³ m ⁻³)	Mean annual PET (mm y ⁻¹)†	Mean annual solar radiation (W m ⁻² y ⁻¹)†
19.945	155.262	800	18.2	4570	0.55	2298	201.10
19.938	155.267	934	17.3	4292	0.55	2232	200.86
19.933	155.274	1024	16.7	3975	0.57	2214	202.42
19.929	155.279	1116	16.1	3734	0.48	2127	204.89
19.939	155.294	1116	16.1	3433	0.51	2137	210.06
19.935	155.301	1204	15.5	3181	0.40	2211	214.45
19.931	155.304	1274	15.1	3101	0.51	2234	216.16
19.846	155.277	1468	13.8	4119	0.55	1888	202.63
19.842	155.293	1600	13.0	3282	0.57	1961	213.14

*Mean annual rainfall estimates from the Rainfall Atlas of Hawaii (Giambelluca *et al.*, 2013).

†Mean annual potential evapotranspiration and solar radiation estimates from Giambelluca *et al.* (2014).

(Wolfe & Morris, 1996). Soils along the MAT gradient are derived from volcanic tephra deposited on top of this lava flow ~20 000 years BP based on ¹⁴C dating of deep soil layers (C.P. Giardina, unpublished results). Soils at all nine sites are well-drained Acrudoxic Hydudands with similar surface soil pH (3.9 ± 0.2), cation exchange capacity (11.87 ± 0.92 cmol kg⁻¹), and bulk density (0.21 ± 0.03 g cm⁻³; Litton *et al.*, 2011). We did not measure exact soil depth at each MAT plot, but the volcanic tephra layer from which soils in all MAT plots were derived is up to 20 m deep at sites near our study area (Wolfe & Morris, 1996) and none of the 91.5 cm soil cores taken for this study reached bedrock.

Each of the nine MAT plots were selected to represent the maximum aboveground biomass present at a given elevation while keeping dominant overstory plant species composition, disturbance history, underlying geology, soil type, and soil water balance constant (see Litton *et al.*, 2011). We chose to use sites representing the maximum aboveground biomass at each elevation to minimize disturbance history effects, avoid bias in plot selection, and to minimize variation in factors other than MAT across the gradient (e.g. soil drainage or nutrient availability). Briefly, airborne light detection and ranging (LiDAR) measurements of forest structure were used to select sites within the HETF that were within 10% of the maximum aboveground biomass at a given elevation (Asner *et al.*, 2009, 2012; Litton *et al.*, 2011). Because LiDAR data were not available for the HFNWR, we selected the two highest elevation sites using intensive ground-based survey techniques using the same criteria as the remote-sensing approach employed for the HETF (Litton *et al.*, 2011). Disturbance history was analyzed by repeat LiDAR measurements of forest structure (Kellner & Asner, 2009), which confirmed that the seven stands are all mature, moderately aggrading forests.

Live biomass carbon

Live biomass in stems, branches, foliage, aboveground prop roots and belowground coarse and fine roots was estimated in each of the nine plots along the MAT gradient. Aboveground

biomass of woody trees was estimated with allometry after identifying to species and measuring diameter at breast height (DBH; 1.3 m height) of all woody stems ≥ 1 cm DBH in each MAT plot between April and May of 2009. Aboveground biomass of tree ferns was also estimated by allometry after identifying to species and measuring stem diameter and stem height of all tree ferns (*Cibotium* spp.) ≥ 50 cm in height. We used species-specific allometric equations to estimate aboveground biomass of *M. polymorpha* individuals ≤ 33 cm DBH and *A. koa* individuals ≤ 30 cm DBH and a generalized wet tropical forest allometric equation that incorporates wood specific gravity, tree height and DBH for larger individuals of these two species and all other woody species (Chave *et al.*, 2005; see Table S1). Aboveground biomass of *Cibotium* spp. was estimated using a genus-specific allometric equation based on specific gravity of stem tissue, stem height and stem diameter (Table S1). Aboveground prop root biomass was estimated within each plot using the point-intercept method along the same transects used to estimate coarse woody debris (CWD) biomass, and equations for Decay Class 1 CWD (see below and Iwashita *et al.*, 2013).

Our plot size (20 × 20 m) is small compared to those in other tropical forest studies. To confirm that any trend in aboveground biomass carbon along the MAT gradient was not a function of plot size, we compared our DBH-based estimates of aboveground biomass carbon to LiDAR-based estimates of aboveground biomass carbon in the 60 × 60 m area surrounding the center of each of the seven lower elevation MAT plots for which LiDAR data were available as described in Asner *et al.* (2009). Briefly, LiDAR-estimates of mean canopy profile height (MCH) were derived at 30 m resolution using the Carnegie Airborne Observatory LiDAR sensor (Asner, 2007). The LiDAR MCH maps were then combined with plot-aggregate estimates of wood density and tree diameter-to-height relationships in allometric equations derived for Hawaiian forests to estimate aboveground biomass carbon on a 30 m resolution basis (Asner *et al.*, 2009). Statistics were then generated for each 60 × 60 m area centered on the MAT field plots described earlier.

A global synthesis points to a relatively narrow range of biome-specific above- to belowground biomass ratios (Mokany *et al.*, 2006). We estimated belowground coarse plus fine root biomass across all sites both as a fixed proportion of aboveground biomass and as a power function of aboveground biomass (Mokany *et al.*, 2006). The fixed proportion approach is the best biome-specific predictor of total root biomass, while the power function approach incorporates the widely observed decrease in root-to-shoot ratio (R/S) with increasing aboveground biomass (Mokany *et al.*, 2006). For the fixed proportion estimate of belowground live biomass, we assumed total root biomass was 0.235 of aboveground biomass, which is the median value for tropical wet forests with aboveground biomass >125 Mg ha⁻¹ based on a critical analysis of published R/S estimates (Mokany *et al.*, 2006). For the power function estimate of belowground live biomass we used Eqn (1), an allometric equation based on R/S estimates of 207 forests and woodlands worldwide (Mokany *et al.*, 2006):

$$y = 0.489x^{0.890} \quad (1)$$

where, y is total root biomass and x is total aboveground biomass. For all estimates of live biomass, we assumed a carbon content of 48%.

Detrital carbon

Standing and down coarse woody debris (CWD), litter, and soil organic carbon (SOC) were quantified in all nine plots across the MAT gradient. We define CWD as standing or fallen dead wood >2 cm in diameter. Estimates of standing and down CWD carbon are from Iwashita *et al.* (2013). Briefly, CWD volume was estimated using the point-intercept method along thirteen 20 m transects in each 20 × 20 m MAT plot, and CWD carbon was quantified using custom decay classes, decay class wood density, and decay class carbon content. Iwashita *et al.* (2013) showed that plot-level estimates of CWD from this sampling protocol match well with estimates from longer transects (>100 m) recommended for tropical forests. We define litter as partially decomposed nonliving plant biomass <2 cm in diameter lying above the soil surface (Kiermann *et al.*, 2008), which is consistent with definitions used by the United Nations Food and Agriculture Organization (UN-FAO) Forestry Department and the United Nations program on Reducing Emissions from Deforestation and forest Degradation (UN-REDD). Litter mass was estimated by collecting litter from the forest floor in eight replicate 0.174 m² quadrats within each of the nine 20 × 20 m MAT plots. Soil organic carbon was estimated by collecting three to five soil cores (5.75 cm diameter) down to a depth of 91.5 cm within each of the 20 × 20 m MAT plots. To ensure representative sampling, we collected a minimum of three soil cores per MAT plot. If the coefficient of variation (CV) within a plot was >25%, we collected two additional soil cores.

For estimates of detrital carbon content, representative samples of each CWD decay class (Iwashita *et al.*, 2013), litter and soil samples were oven dried at 70 °C and finely ground using a ball mill. These samples were analyzed directly for percentage

carbon using a Costech 4010 Elemental Combustion system (Valencia, CA, USA) at the University of Hawaii at Hilo Analytical Lab.

Statistical analyses

We used ordinary least-squares linear regression to determine whether total ecosystem, live biomass, and detrital carbon pools varied significantly as a function of MAT. We confirmed that the assumptions of normality and homoskedasticity were met for all linear regression analyses. All statistical analyses were performed in R version 3.0.1 (R Core Team, 2013) using an α -level of 0.10 for all tests due to small sample sizes ($n = 9$).

Results

Soil organic carbon ranged from 194 to 288 Mg of carbon ha⁻¹ and was the single largest pool of carbon at eight of the nine plots along the MAT gradient, accounting for an average of 47% (±2.5%) of total ecosystem carbon (Table 2). Aboveground live biomass was the second largest pool of carbon for eight of the nine plots across the MAT gradient and averaged 36% (±2.5%) of total ecosystem carbon across the MAT gradient (range = 94–417 Mg of carbon ha⁻¹; Table 2). The vast majority of aboveground biomass across the MAT gradient was accounted for by a single species, *M. polymorpha* (average = 86 ± 2.1%). The other two most prevalent taxa, *C. trigynum* and *Cibotium* spp., together averaged 8% (±1.8%) of aboveground biomass across the MAT gradient (range = 2.1–18.3%).

LiDAR-based estimates of aboveground biomass carbon in the 60 × 60 m area surrounding the center of each of the seven lower elevation MAT plots were positively correlated with DBH-based estimates of aboveground biomass carbon within the 20 × 20 m plots (Pearson's $r = 0.73$). Although the trend in aboveground biomass carbon with increasing MAT remains the same whether assessed on a 20 × 20 m or 60 × 60 m basis (Figure S1), LiDAR-based 60 × 60 m estimates were lower than DBH-based 20 × 20 m estimates for some high biomass MAT plots. This discrepancy is likely the result of careful plot selection; the high biomass 20 × 20 m plots are carbon-dense 'hot-spots' with portions of the surrounding 60 × 60 m area consisting of forests of somewhat lower biomass (Figure S2).

The two approaches used to estimate total root biomass from aboveground biomass yielded very similar results (Table 2) and were highly correlated (Pearson's $r = 0.99$). Across all sites, R/S estimates via the power function approach [Eqn (1)] averaged 0.252 ± 0.004 across sites (range = 0.232–0.271) and were an average

Table 2 The carbon content of above- and belowground live biomass and detritus pools in nine permanent plots located along a 5.2 °C mean annual temperature gradient in tropical montane wet forests on the Island of Hawaii. All data are rounded to three significant digits

MAT (°C)	Live biomass carbon (Mg ha ⁻¹)			Detrital carbon (Mg ha ⁻¹)		
	Aboveground	Belowground*	Belowground†	Soil	Coarse woody debris	Litter
18.2	97.0	26.3	22.8	194	21.9	2.68
17.3	248	60.7	58.3	279	21.9	3.82
16.7	139	35.7	32.7	270	28.8	3.66
16.1	417	96.8	98.1	254	11.8	4.06
16.1	244	59.0	57.3	288	33.3	4.28
15.5	164	42.3	38.6	285	14.4	4.29
15.1	177	45.0	41.7	250	96.6	3.77
13.8	158	40.7	37.0	220	78.1	3.23
13.0	203	51.1	47.7	253	66.8	4.98

*Belowground coarse and fine root biomass estimated as a power function [Eqn (1)] of aboveground biomass at each site.

†Belowground coarse and fine root biomass estimated as a fixed proportion (0.235) of aboveground biomass at each site.

of 7.1% ($\pm 1.6\%$) higher than estimates using the fixed proportion of 0.235. Both approaches to estimating R/S yielded results well within the overall range of 0.220–0.327 reported for tropical wet forests with aboveground biomass >125 Mg ha⁻¹ (Mokany *et al.*, 2006). For our calculations of total ecosystem carbon, we chose to use estimates of belowground root biomass derived from the power function approach [Eqn (1)] because these estimates were very similar to those from the fixed proportion approach yet incorporated the widely observed phenomenon of decreasing R/S with increasing aboveground biomass (Mokany *et al.*, 2006). Importantly, both approaches to estimating belowground biomass yielded identical patterns and conclusions about relationships between temperature and the size and distribution of ecosystem carbon pools.

Live biomass carbon did not vary predictably with MAT (Fig. 1a). In contrast, detrital carbon (the sum of carbon in SOC, CWD, and litter) declined by ~ 14 Mg of carbon ha⁻¹ for each 1 °C increase in MAT (Fig. 1b). Total ecosystem carbon storage did not vary as a function of MAT, averaging 556 ± 42 Mg C ha⁻¹ across the MAT gradient (Fig. 2a). The proportional amounts of carbon present in live biomass and detritus also remained relatively stable across the MAT gradient, averaging $\sim 45\%$ in live biomass and 55% in detritus (Fig. 2b).

Soil organic carbon made up 71–94% of detrital carbon at each site but did not vary significantly with MAT (Fig. 3a). In contrast, the sum of carbon in CWD and litter declined linearly with increasing MAT (Fig. 3b). This trend was driven primarily by CWD (Iwashita *et al.*, 2013), but also in part by a statistically nonsignificant decline in litter carbon ($R^2 = 0.31$, $P = 0.12$). As a result of these detrital carbon patterns,

the fraction of detrital carbon stored as SOC increased with rising MAT (Fig. 4a). However, the fraction of total ecosystem carbon stored as SOC did not vary significantly with MAT, averaging 47% ($\pm 3\%$) across the gradient (Fig. 4b).

Discussion

Quantifying how the size and distribution of forest carbon pools respond to rising temperature is critical to understanding the impacts of climate change on terrestrial carbon balance and the likelihood of positive feedbacks to future warming. We conducted a comprehensive survey of ecosystem carbon pools along a highly controlled MAT gradient in Hawaiian tropical montane wet forests to test two hypotheses based on results from a prior cross-site synthesis (Raich *et al.*, 2006). First, we hypothesized that live biomass carbon would increase and detrital carbon would decrease with rising MAT, leading to a shift in the distribution of ecosystem carbon from detrital-dominated cooler forests to live biomass-dominated warmer forests. Second, we hypothesized that increases in live biomass carbon with rising temperature would be largely offset by declines in detrital carbon storage, resulting in no net change in total ecosystem carbon storage with rising MAT. Results from our study provided only mixed support for these hypotheses. We found that both total ecosystem carbon storage and the relative distribution of carbon in Hawaiian tropical montane wet forests are less sensitive to rising MAT than would be predicted from both warming experiments in temperate biomes (Dieleman *et al.*, 2012; Lu *et al.*, 2013) and observational studies across sites and along elevation gradients in the tropics (Kitayama & Aiba, 2002; Raich *et al.*, 2006;

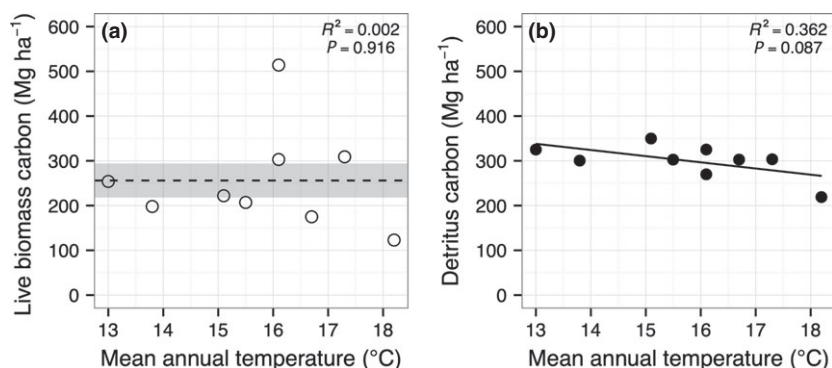


Fig. 1 Total live biomass carbon (a) and detrital carbon (b) across a 5.2 °C mean annual temperature gradient in Hawaiian tropical montane wet forests. Live biomass includes aboveground stems, branches and leaves, aboveground prop roots, and belowground coarse and fine roots. Detrital carbon includes litter (i.e. forest floor), standing and fallen coarse woody debris, and soil organic carbon to a depth of 91.5 cm. Dashed line and gray shaded area (a) represent the overall mean and ± 1 SE, respectively. Solid line (b) represents the fitted regression line.

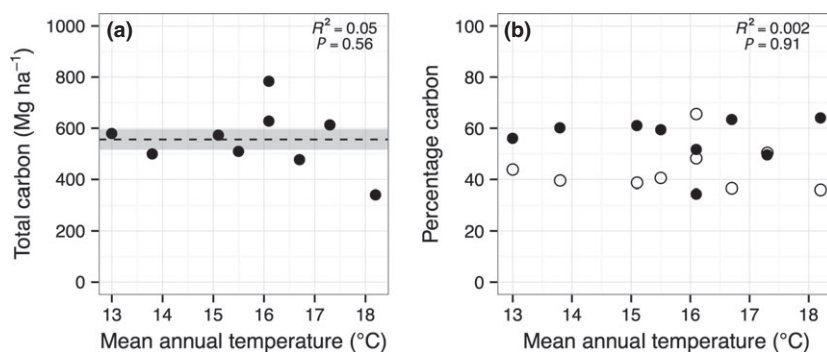


Fig. 2 Total ecosystem carbon (a) and the relative amounts of live biomass carbon and detrital carbon (b) across a 5.2 °C mean annual temperature gradient in Hawaiian tropical montane wet forests. Dashed line and gray shaded area (a) represent the overall mean and ± 1 SE, respectively. Filled circles represent detrital carbon and open circles represent live biomass carbon (b). Regression coefficient and p-value in Fig. 2b are identical for both data series.

Girardin *et al.*, 2010; Moser *et al.*, 2011; Dieleman *et al.*, 2013). We suspect the contrast across studies relates to the highly constrained nature of our gradient that allowed us to isolate the impacts of MAT on ecosystem carbon storage.

Live biomass carbon

Our estimates of carbon stored in aboveground live biomass (97–417 Mg C ha⁻¹ across the MAT gradient) are at the high end of the range reported for moist and wet tropical forests globally (Raich *et al.*, 2006; 46–418 Mg C ha⁻¹; Chave *et al.*, 2008; Keith *et al.*, 2009; Lewis *et al.*, 2009), which is at least partially a result of our plot selection method. Across the MAT gradient, aboveground live biomass carbon was greatest (244–417 Mg C ha⁻¹) in plots with MAT from 16.1 to 17.3 °C, a temperature range that tightly brackets the model-predicted MAT (16.5 °C) at which forest aboveground biomass is maximized globally in the absence of either

water limitation or seasonal and diurnal temperature fluctuation (Larjavaara & Muller-Landau, 2012). This finding is also in line with an earlier LiDAR-based analysis of the Laupahoehoe unit of the Hawaii Experimental Tropical Forest showing a peak in aboveground live biomass in this same MAT range (Asner *et al.*, 2009). However, these findings do not support our first hypothesis that live biomass carbon would increase with rising MAT. Raich *et al.* (2006) found that live biomass carbon in 22 moist tropical forests increased by 5.2 Mg C ha⁻¹ for each 1 °C increase in MAT, with MAT explaining ~23% of the variation in live biomass carbon. A more comprehensive survey of forest biomass-climate relationships in the Americas also found a weak positive relationship between MAT and aboveground biomass in moist tropical forests (Stegen *et al.*, 2011). However, this trend was reversed for wet tropical forests, and MAT explained less than 15% of the variation in aboveground live biomass of both moist and wet tropical forests (Stegen *et al.*,

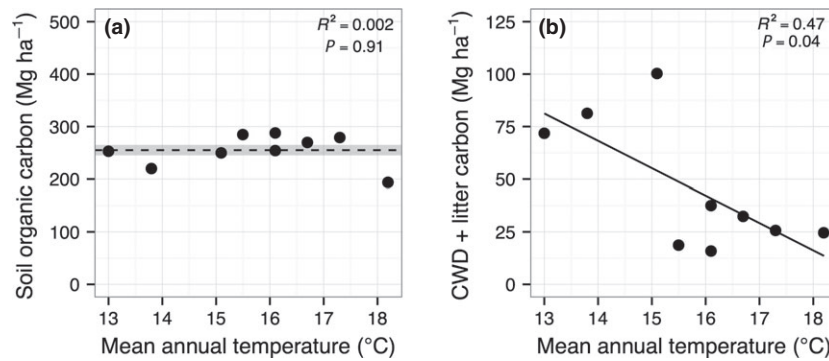


Fig. 3 Soil organic carbon (a) and the sum of carbon in coarse woody debris and litter (b) across a 5.2 °C mean annual temperature gradient in Hawaiian montane wet tropical forests. Dashed line and gray shaded area (a) represent the overall mean and ± 1 SE, respectively. Solid line (b) represents the fitted regression line.

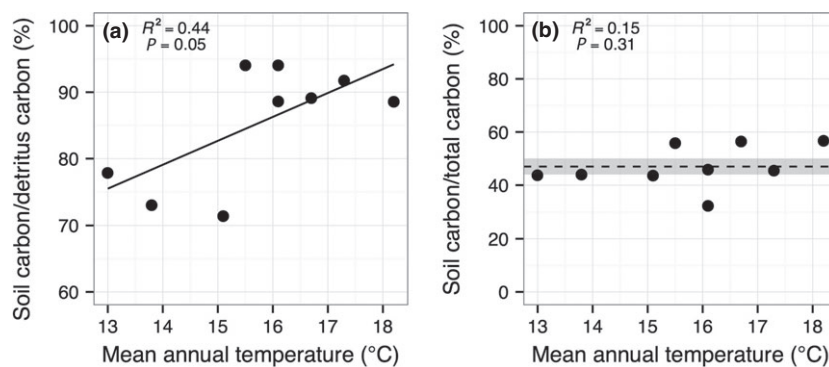


Fig. 4 Soil organic carbon as a fraction of detrital carbon (a) and as a fraction of total ecosystem carbon (b) across a 5.2 °C mean annual temperature gradient in Hawaiian tropical montane wet forests. Solid line (a) represents the fitted regression line. Dashed line and gray shaded area (b) represent the overall mean and ± 1 SE, respectively.

2011). Results from elevation gradient studies in the tropics are likewise inconsistent, where relationships between MAT and aboveground live biomass can be positive (Kitayama & Aiba, 2002; Girardin *et al.*, 2010; Moser *et al.*, 2011), negative (Alves *et al.*, 2010), or invariant (Culmsee *et al.*, 2010; Unger *et al.*, 2012). Taken together, results from previous studies along latitudinal and elevational gradients, along with data presented here, suggest that MAT is a poor predictor of aboveground biomass carbon in tropical wet forest ecosystems.

Much of the variability in the response of tropical forest live biomass to increasing temperature, both across broad latitudinal gradients and along more local elevation gradients, can be attributed to the confounding effects of variation in other environmental factors such as species composition, water availability, and soil physical and chemical properties. We acknowledge that climate warming is predicted to cause shifts in precipitation regimes and plant community

composition, and so tropical elevation gradients incorporating these variations (Culmsee *et al.*, 2010; Girardin *et al.*, 2010; Leuschner *et al.*, 2013) yield valuable insights into the response of aboveground biomass to this suite of factors, especially where these factors covary as predicted by coupled climate-dynamic vegetation models. However, covariation of temperature, species composition, water availability, and soil physical and chemical properties across elevation gradients greatly complicates efforts to separate the effects of individual factors. Sites along our MAT gradient were carefully selected to isolate the effect of temperature by minimizing variation in each of these other potentially confounding variables (Litton *et al.*, 2011), and we used remote-sensing (LiDAR) to select plots to minimize the effect of disturbance history. This level of constraint gives us a high degree of confidence that MAT does not have a consistent positive effect on live biomass carbon storage in the tropical montane wet forests that make up this gradient.

Although MAT most likely has a strong influence on maximum attainable forest biomass in the absence of water limitation and disturbance (Larjavaara & Muller-Landau, 2012), realized biomass most often falls below this 'carrying capacity' (Stegen *et al.*, 2011). We suggest that gap-phase dynamics, weather-related events, or other localized disturbance events may be more important drivers of realized forest biomass (Kellner & Asner, 2009; Stegen *et al.*, 2011; Silva *et al.*, 2013). Although forest productivity often varies positively with MAT, net primary productivity is a poor predictor of aboveground biomass, especially in tropical forest ecosystems (Keeling & Phillips, 2007). Moreover, increasing temperature will not elicit a predictable response in the standing aboveground biomass of forest ecosystems when gap-phase dynamics or weather events are not accounted for (Kellner & Asner, 2009; Stegen *et al.*, 2011).

Our estimates of belowground root biomass at each site are based on aboveground biomass estimates, so we cannot test for a direct effect of rising temperature on belowground root biomass or a shift in root-to-shoot biomass carbon distribution with rising temperature. However, there is no relationship between forest R/S and MAT on a global scale – in contrast to moisture and nutrient responses, where R/S tends to increase with declining water availability and, to a lesser extent, declining nutrient availability (Cairns *et al.*, 1997; Mokany *et al.*, 2006). Long-term water limitation to plant productivity is unlikely across our MAT gradient because all plots receive greater than 3000 mm of annual rainfall, which appears to be a zone of maximum productivity (Schoor, 2003; Luyssaert *et al.*, 2007). In addition, soil volumetric water content is high and invariant year round (Litton *et al.*, 2011), and mean annual PET is well below mean annual rainfall (Table 1). Although we did not measure nutrient availability in this study, evidence from other studies suggests a decline in nutrient availability with rising MAT is also unlikely, given that rates of forest nutrient cycling tend to increase with warming (Melillo *et al.*, 2011; Dieleman *et al.*, 2012). Finally, the majority of belowground biomass is made up of coarse roots providing structural support rather than nutrient acquisition functions. Although coarse root biomass is sensitive to variation in slope inclination and maximum wind velocities, it is relatively insensitive to either positive or negative changes in nutrient availability driven by rising MAT.

Detrital carbon

We defined detrital carbon as comprised of three pools: litter, CWD, and SOC. Litter carbon along the MAT gra-

dient (2.68–4.98 Mg C ha⁻¹ across the MAT gradient) is largely within the average range of litter carbon values (2.67–3.2 Mg C ha⁻¹) reported for tropical forests in Africa, South Asia, and the Americas (Pan *et al.*, 2011), and at the high end of the range reported by Raich *et al.* (2006) for 22 tropical moist forests. Similarly, our estimates of CWD along the MAT gradient (Iwashita *et al.*, 2013) are mostly within the range reported for other tropical wet forest ecosystems (10–88 Mg C ha⁻¹), but are at the high end or exceed the maximum reported value at cooler sites (Pregitzer & Euskirchen, 2004). In contrast, our estimates of SOC along the MAT gradient are much higher than those reported for tropical moist and wet forests globally (Jobbágy & Jackson, 2000; Amundson, 2001), which is likely a result of the high carbon storage capacity of Andisols in warm, wet climates (Kramer *et al.*, 2012). When considered alongside our estimates of live biomass carbon storage, the large amount of detrital carbon in these Hawaiian tropical montane wet forests place them among the most carbon-dense forests in the world. Again, this may reflect our effort to select the highest biomass plots at each elevation.

Consistent with our second hypothesis, detrital carbon storage declined with increasing MAT in these tropical montane wet forests, a pattern driven entirely by declines in CWD and litter carbon. Soil organic carbon, the largest component of detrital carbon across the gradient, remained stable with MAT. As discussed in Iwashita *et al.* (2013), the significant decline in CWD with increasing MAT is driven by the large amount of CWD at the three coolest MAT plots. This trend is consistent with evidence of higher accumulation of CWD at lower MAT in both tropical and temperate forested biomes (Raich *et al.*, 2006; Woodall & Liknes, 2008). The apparent threshold response of CWD to MAT may result from a combination of both increased rates of decomposition and a decline in tree mortality in warmer MAT plots, a phenomenon reported in other tropical forest ecosystems (Lewis *et al.*, 2006). We carefully selected plots along this MAT gradient to minimize variation in disturbance history, so it is unlikely the trend in CWD is driven by a shift in forest dynamics unrelated to temperature.

The apparent insensitivity of the SOC pool to rising MAT is an important result of this study given the uncertainty surrounding model projections of how soil carbon will respond to climate change (Conant *et al.*, 2011; Schmidt *et al.*, 2011). Although we sampled SOC only in the top 91.5 cm, this depth likely includes the most temperature-sensitive portion of the soil profile given resistance to heat flux in soil from the surface below ~50 cm (Perry *et al.*, 2008). We suggest two potential mechanisms to explain why SOC is less tem-

perature sensitive than litter or CWD carbon in these forests. First, physico-chemical interactions with soil minerals are a major driver of SOC stability (Conant *et al.*, 2011; Schmidt *et al.*, 2011), but play little to no role in protecting litter or CWD carbon from degradation by microbial enzymes. As such, temperature-induced increases in extracellular hydrolytic enzyme activity should lead to greater carbon losses from CWD and litter than from soil, where substrate availability due to mineral protection is a more limiting factor (Giardina & Ryan, 2000; Schmidt *et al.*, 2011). Second, soils across this MAT gradient may be saturated with respect to carbon input (Stewart *et al.*, 2007), resulting in limited capacity to protect and store additional organic carbon despite a warming-induced increase in soil respiration of ~50% across the MAT gradient (Litton *et al.*, 2011). These two proposed mechanisms are complementary to one another, and could greatly inform future modeling efforts of how SOC and less protected detrital carbon stocks like CWD and litter will respond to warming temperatures.

The various responses of CWD, litter and SOC to rising MAT explain why SOC accounts for an increasing fraction of detrital carbon as MAT increases. Because SOC and live biomass carbon are so large relative to the amount of carbon in CWD and litter, SOC was a constant fraction of total ecosystem carbon across the MAT gradient and the decline in litter and CWD detrital carbon stocks had no effect on total ecosystem carbon storage. Taken together, these results suggest that soil carbon stocks in tropical montane wet forests may be less sensitive to rising MAT than indicated by warming experiments in temperate biomes (Dieleman *et al.*, 2012; Lu *et al.*, 2013) or by less well-constrained observational studies across temperature gradients in the tropics (Raich *et al.*, 2006; Dieleman *et al.*, 2013). Moreover, our results indicate that carbon loss from individual detrital pools with rising MAT will impact carbon storage in tropical montane wet forest ecosystems only where these temperature-sensitive detrital pools combine to represent a sizable fraction of total ecosystem carbon.

Total ecosystem carbon storage

Our results demonstrate that total ecosystem carbon storage and the distribution of carbon between live biomass and detritus in these carbon-dense tropical montane wet forests were insensitive to rising MAT. Our finding of no net change in ecosystem carbon storage with rising MAT is consistent with our second hypothesis, but not because declining detrital carbon storage was offset by increasing live biomass carbon storage, as we predicted. Although detrital carbon declined significantly with rising MAT as hypothe-

sized, the decline was small relative to SOC storage, which did not vary with MAT. Further, live biomass carbon did not vary significantly with MAT, but rather peaked at the intermediate MAT sites. Therefore, it was the lack of a consistent MAT effect on the two largest carbon pools, SOC, and live biomass that led to no net change in total ecosystem carbon storage across the MAT gradient.

As would be expected from the individual patterns, the relative distribution of ecosystem carbon between detritus and live biomass was also invariant to rising MAT. However, we note that the three MAT plots with the highest aboveground live biomass between 16.1 and 17.3 °C MAT had near even or the opposite distribution of carbon between detritus and live biomass as the other seven MAT plots. These results bolster recent evidence that forest biomass may be maximized at relatively constant, cool air temperatures (~16.5 °C) in the absence of water limitation (Keith *et al.*, 2009; Larjavaara & Muller-Landau, 2012), but that detrital carbon, especially SOC, may not increase correspondingly with this peak in live biomass. We suggest this differential response of live biomass and detrital carbon to changes in temperature resulted in the observed shift in ecosystem carbon distribution at high biomass plots between 16.1 and 17.3 °C MAT and adds further support for the idea that soils can reach a carbon saturation point (Stewart *et al.*, 2007).

Our comprehensive assessment of live biomass and detrital carbon pools across a well-constrained 5.2 °C MAT gradient in tropical montane wet forests provides unique insight into the long-term, whole-ecosystem response of forest carbon pools to climate warming because other environmental factors that could affect ecosystem carbon storage, such as dominant tree species, soil physical and chemical properties, disturbance history and soil water balance, are held largely constant. Although the range of MAT along this gradient (13–18.2 °C) is below the MAT of many lowland tropical wet forests (~25 °C), our results have several implications for predicting how carbon storage in tropical wet forests in general will respond to climate warming and, importantly, provide testable hypotheses that can be applied to studies in other tropical wet forest ecosystems. First, litter and CWD carbon were the most temperature-sensitive carbon stocks, but their decline with rising MAT had little impact on total ecosystem carbon storage because even when combined, litter, and CWD made up a small proportion of total ecosystem carbon. Nevertheless, our results suggest these two detrital pools should be a focal point of carbon storage accounting and long-term monitoring in undisturbed tropical wet forests. Second, SOC, which is often the largest carbon pool in forest ecosystems (Perry *et al.*, 2008), may

be far less sensitive to climate warming than indicated by current ecosystem modeling efforts (Todd-Brown *et al.*, 2012), warming experiments in temperate biomes (Dieleman *et al.*, 2012; Lu *et al.*, 2013) and cross-site syntheses from the tropics (Raich *et al.*, 2006). Third, live biomass carbon storage in forest ecosystems may be less sensitive to the direct effect of rising MAT than to indirect effects, such as temperature-induced changes in precipitation, vegetation composition, and widespread disturbance (Clark *et al.*, 2010; Silva *et al.*, 2013). Taken together, our results strongly suggest that, within the MAT range studied here and where increasing temperature does not drive large scale increases in disturbance or changes to soil water balance, the direct effect of climate warming on carbon storage in tropical montane wet forests will not result in a positive feedback to climate change.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Aboveground biomass equations, wood or stem tissue specific gravity values, and height equations used to calculate aboveground biomass of woody trees and tree ferns (*Cibotium* spp.) across the nine MAT gradient sites on the Island of Hawaii, where D is diameter in centimeters at breast height (1.3 m), AGB is aboveground biomass in kilograms, ρ is wood or stem tissue specific gravity in grams per cubic centimeter, H is height in meters, π is the ratio of a circle's circumference to its diameter, Dt is top diameter in centimeters and Db is bottom diameter in centimeters.

Figure S1. LiDAR-based estimates of aboveground live biomass carbon (where ACD is aboveground carbon density) for the 60 × 60 m area surrounding plot-centers of the seven lower elevation MAT plots along a 5.2 °C mean annual temperature gradient in Hawaiian tropical montane wet forests.

Figure S2. KML 30 m resolution maps of LiDAR-estimated forest aboveground carbon density along the northeast slope of Mauna Kea volcano on the Island of Hawaii, where darker shading indicates lower carbon density. Red squares indicate the 60 × 60 m area centered on each of the seven lower elevation MAT plots.