Carbon dynamics, net primary productivity (NPP) and human appropriated NPP (HANPP) across a forest-cocoa farm landscape in West Africa

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Running Title

Carbon, NPP and HANPP in Cocoa and Forest

Authors

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Abstract

Terrestrial net primary productivity (NPP) is an important metric of ecosystem functioning; however, there is little empirical data on the NPP of human-modified ecosystems, particularly smallholder, perennial crops like cocoa (*Theobroma cacao*), which are extensive across the tropics. Human appropriated NPP (HANPP) is a measure of the proportion of a natural system's NPP that has either been reduced through land-use change or harvested directly and, previously, has been calculated to estimate the scale of the human impact on the biosphere. Additionally, human-modification can create shifts in NPP allocation and decomposition, with concomitant impacts on the carbon cycle. This study presents the results of three years of intensive monitoring of forest and smallholder cocoa farms across disturbance, management intensity, distance from forest and farm age gradients. We measured among the highest reported NPP values in tropical forest, 17.57 ± 2.1 and 17.7 ± 1.6 Mg C ha^{-1} yr^{-1} for intact and logged forest respectively; however, the average NPP of cocoa farms was still higher, 18.8 ± 2.5 Mg C ha^{-1} yr^{-1}, which we found was driven by cocoa pod production. We found a dramatic shift in litterfall residence times, where cocoa leaves decomposed more slowly than forest leaves and shade tree litterfall decomposed considerably faster, indicating significant changes in rates of nutrient cycling. The average HANPP value for all cocoa farms was 2.1 ± 1.1 Mg C ha^{-1} yr^{-1}; however, depending on the density of shade trees it ranged from -4.6 to 5.2 Mg C ha^{-1} yr^{-1}. Therefore, rather than being related to cocoa yield, HANPP was reduced by maintaining higher shade levels. Across our monitored farms 18.9% of farm NPP was harvested (i.e. whole cocoa pods) and only 1.1% (i.e. cocoa beans) was removed from the system; suggesting that the scale of HANPP in smallholder cocoa agroforestry systems is relatively small.

Keywords: Theobroma cacao, Smallholder, Ghana, HANPP, Net Primary Productivity, Carbon Cycling

Article type: Primary Research Article

Introduction

Net primary productivity (NPP) describes the rate at which carbon is assimilated from the atmosphere and fixed as plant biomass. Its dynamics can relate to carbon and nutrient cycling and recovery following disturbance (Malhi et al., 2011). Carbon captured through global photosynthesis is considered to be the annualised biotic consumption potential of the earth and, therefore, the NPP of natural and managed systems represents the captured solar energy available for consumption by higher trophic levels. Changes to this distribution of energy across species, particularly its domination by only one species, is assumed to have negative implications for the biosphere's ability to support high biodiversity levels (Haberl, 1997; Haberl et al., 2004; Miko and Storch, 2015; Vitousek et al., 1986; Wright, 1990). Allocation of NPP, particularly into woody tissue instead of short-lived leaf or fine root tissue, is a direct control on an ecosystem's ability to store carbon over the long-term. However, the biotic and abiotic drivers of these dynamics are still not fully understood, particularly in managed forest systems.

Some satellite-based estimates of global land surface NPP have estimated a relatively stable value of 53.6 Pg C yr^{-1} for the last three decades, with inter-annual variation of less than 2% (Running, 2012), whereas satellite-informed process-based models have estimated a similar terrestrial NPP of ~54.6 Pg C yr^{-1} but a much higher inter-annual variability of 12% (Field et al., 1998; Goetz et al., 2000). A low level of NPP variability would suggest a physical ceiling on ecosystem productivity and, by extension, energy available to meet the consumption demand of the biosphere (Running, 2012). In contrast, Defries (2002) argued that in a high variability context, the impact of human influence would need to be larger than the level of variability to be discernible, particularly if relying on estimates derived from satellite imagery. Efforts to improve global-scale estimates of NPP through upscaling from ground-based measurements are ongoing, particularly incorporating data from land covers other than mature, undisturbed forest (Anderson-Teixeira et al., 2016).

Twenty percent of global NPP is estimated to be found on the continent of Africa (Williams et al., 2007), but there remain large uncertainties around the carbon budget of the continent due to a dearth of field studies and CO_2 flux data (Ardö, 2015; Ciais et al., 2011; Valentini et al., 2014). Broadly, the evergreen forests of Africa are considered to be a carbon sink while the fire dynamics in savannahs and drylands and the uncertainty in domestic wood harvesting contribute significantly to the inter-annual variability in the observed African carbon cycle. The continent as a whole is estimated to contribute 25% of the variability in the global carbon budget (Valentini et al., 2014).

The proportion of global NPP that is either directly consumed by humans or has been reduced due to alterations to vegetation cover has been given the term human appropriation of NPP (HANPP). HANPP was first suggested by Vitousek et al (1997) as a way to document the global scale of human influence on the biosphere and has been proposed to be a conceptually robust and quantifiable planetary boundary (Running, 2012). There are a number of ways to define HANPP (e.g. embedded versus area-based), which may or may not include land-use change and backflows to nature components. These decisions may be influenced by a study's focus on the carbon storage potential of human modified systems versus a measure of the human "domination" of an ecosystem (Haberl et al., 2014). Proportional estimates of HANPP have been calculated using total photosynthesis of the biosphere (Imhoff et al., 2004; Rojstaczer et al., 2001; Vitousek et al., 1986) or with potential NPP prior to human modification in the denominator (Haberl et al., 2007; Wright, 1990).

Global estimates of HANPP, calculated over the last several decades, seem to have settled on human society appropriating between 20 and 30% of global NPP (Haberl et al., 2007; Imhoff et al., 2004; Rojstaczer et al., 2001; Wright, 1990), with the most recent calculation reporting a global HANPP of 25% (Krausmann et al., 2013). However, these global estimates are largely derived from satellite data and dynamic vegetation models (e.g. the Lund–Potsdam–Jena (LPJ) DGVM), with few field-based studies that test and evaluate these HANPP estimates (Haberl et al., 2014, 2007). This is particularly true in tropical systems. Considering Africa, methods to estimate HANPP have previously relied on extrapolated literature values (Fetzel et al., 2016), medium-resolution imagery (Abdi et al., 2016, 2014; Imhoff et al., 2004) and household surveys paired with community-scale, one-off ecological measurements (Pritchard et al., 2018). However, there remains a dearth of studies providing measures of *in situ* NPP in contiguous forest and managed landscapes and, therefore, empirically calculated HANPP (Haberl et al., 2014).

The agricultural sector dominates global HANPP estimates, consisting of 84-86% of global NPP appropriated, 42-46% due to conversion to cropland and 29-33% to grazing (Krausmann et al., 2013). Spatially explicit landscape analyses of recent HANPP values have shown that crops replacing non-forested natural systems come close to replicating previously available NPP (Krausmann et al., 2013), whereas only particularly intensive agricultural systems in temperate regions were found to be able to produce NPP levels similar to or greater than replaced forested systems (DeFries, 2002; Plutzar et al., 2016). Perennial crops, such as coffee, cocoa or palm oil, have been estimated to cover 1.8 million km^2 or 13% of the global cultivated area in 2000 and are recognised to have a different impact on carbon sequestration and NPP potentials than annual crops (Monfreda et al., 2008). Cocoa, a tree crop, is currently the fastest expanding perennial commodity in Sub-Saharan Africa, but the tree canopies and fine spatial scales of smallholder cocoa farming make it very difficult to differentiate from forest using remote sensing techniques (Ordway et al., 2017). Therefore, estimates of the impact of cocoa on regional and planetary NPP do not exist.

West Africa has shown the largest increase in total agricultural area of the continent's regions, increasing 120% since 1980 (Fetzel et al., 2016). According to FAOSTAT (2016), planted area of cocoa has increased by 92% over the same time period and consists of ~6% of total agricultural area in the region. Cocoa-dominated landscapes with extensive shade tree cover have been cited as potentially important reserves for tree diversity and significant carbon storage, resulting in a win-win in terms of biodiversity conservation and economic development (Tscharntke et al., 2005). However, with the increase in hybrid cocoa planting, younger cocoa farms consist of fewer shade trees and lower diversity of tree species (Anglaaere et al., 2011). Therefore, there remains uncertainty in the current state of and potential for carbon storage under different land uses, particularly in these tropical settings (Erb et al., 2017). Shifts from forest to cocoa agroforestry can also impact decomposition rates of litterfall, which is an important mechanism for recycling nutrients (i.e. nitrogen and phosphorus) in a forest ecosystem (Vitousek, 1984). In the case of cocoa in Ghana, fertilisation rates are often low. Results reported by Morel et al (in review) found an average fertiliser application of 1.1 ± 0.3 times per year, with 20% of surveyed farmers reporting zero fertiliser applications over the previous five years. As a result, nutrient returned through decomposing litter is an important maintainer of soil fertility; however, it has been shown that litterfall decomposition rates were slower in cocoa farms than in secondary forest, potentially suppressing the return of nutrients to the soil (Dawoe et al., 2010).

The objectives of this study were to directly measure annual NPP in intact forest, logged forest and smallholder cocoa agroforest farms to provide empirical estimates of HANPP. These data represent one of the first directly comparable NPP measures in both natural and human modified systems, particularly in a tropical smallholder landscape. Intensive cocoa monitoring plots were established across gradients of farm age, distance from forest and management intensity. We were interested to assess how consistent or variable NPP was across these gradients, what were the strongest drivers of this pattern and whether forest conversion to cocoa had a discernible impact on carbon cycling. The data collected allowed us to answer the following questions: 1) to what extent does total NPP in cocoa farms differ in magnitude and allocation from forest and how much is that driven by the productivity of cocoa trees; 2) are there differences in the rates of biomass turnover and litter recycling between cocoa farms and forest; 3) what is the average HANPP of a cocoa farm and can it be predicted by farm attributes; 4) how do our measurements of NPP and HANPP compare with published measures from other continents and, finally, 5) how meaningful is the HANPP metric in this context?

Materials and Methods

Sampling design

We established ten 0.36 ha (60 m x 60 m) plots across a forest to cocoa-dominated landscape gradient surrounding the Kakum Conservation Area (5°26′53″, N1°20′42″W) comprising the Kakum National Park and the adjacent Assin-Attandanso Resource Reserve in Ghana's Central Region. The area is characterized by moist evergreen forest with an annual precipitation of 1500 mm and average temperatures of 24-27°C. The soils are predominantly weathered oxisols with high sand content. One forest plot was located within the Assin-Attandanso Resource Reserve approximately 800 metres in from the forest edge, which we considered to be representative of "intact forest"; although there had been light logging in this area prior to establishment of the conservation area in 1992. The second forest plot was established within the Ajueso shelter belt, which is currently undergoing extensive selective logging both legal and illegal, which we labelled "logged forest". Within the surrounding cocoa landscape, three contrasting-aged plots (e.g. young, medium and old) were established in cocoa farms located within 100 metres and 500 metres of the forest edge. Two older cocoa farms were monitored at 1 km and 5 km from the forest edge (see Table 1 for details). The cocoa farm at 5 km is a particularly old cocoa farm with several mature timber trees maintained above the cocoa canopy. This cocoa farm seemed to be managed more as a timber plantation than a farm intended to maximize cocoa production; therefore, in subsequent tables this plot was reported separately as "Timber/Cocoa" rather than averaged with the other cocoa farms monitored.

The plots were monitored continuously from October 2014 to October 2017. Each plot consisted of nine sub-plots of 20 m x 20 m. Canopy gap over cocoa trees was calculated by averaging leaf area index (LAI) derived from hemispherical photos taken at 4.5 m above the ground (i.e. above the cocoa trees) for all nine sub-plots. Management practices, including reported fertiliser application rates, were collected from a household survey of the eight cocoa farmers as part of a larger study (Morel et al., in review). Other aspects of the social context of these study sites are reported in Hirons et al (2018a, 2018b). Soil samples were collected from all plots for the top 30 cm to assess bulk density and carbon content following ClimAfrica protocols (http://www.climafrica.net). We limited analysis to the top 30 cm, where the most readily labile carbon is found. Below 30 cm, carbon stores are likely to be less labile (Malhi et al., 2009).

To assess how representative these plots were, we compare them to 36 plots we established and monitored for a larger study on the ecological drivers of cocoa yields outlined in Morel et al (in review). Comparing characteristics of all monitored plots with Tables

Table ***1***, we find the median cocoa farm age was 29.5 ± 3.9 years compared to 25 ± 4.9 years in this study, median cocoa density was 528 ± 65.7 trees ha^{-1} compared to 410 ± 89.0 trees ha^{-1} in this study, median canopy gap was 59.9 ± 4.6 % compared to 47.4 ± 4.4 % in this study and median shade tree density was 24.0 ± 8.4 trees ha^{-1} compared to 34.9 ± 12.3 trees ha^{-1} in this study. All values reported include 95% confidence intervals. These values suggest that our monitored plots were somewhat higher in shade, with lower cocoa density and younger than our larger sample dataset; therefore our averaged results may be somewhat overestimating NPP and underestimating HANPP. Regarding our intact forest and logged forest plots, we wanted to compare direct measurements of remnant forest in close vicinity to actively managed cocoa farms; however, as we only monitored one of each we augmented our analysis with NPP measurements in moist semi-deciduous forest published by Moore et al (2017).

[insert Table 1]

NPP Estimates

Field measurements followed the protocols of the Global Ecosystems Monitoring network (gem.tropicalforests.ox.ac.uk; Marthews et al., 2012), with minor modifications. Due to the number of replications undertaken for this study, and the low tree species diversity and spatial homogeneity of the cocoa farms, plots consisted of only nine 20 m x 20 m sub-plots rather than the twenty-five subplots required to monitor a full hectare of forest. Three components of NPP were estimated for forest/shade trees, namely canopy NPP (leaves, twigs, flowers, seeds and other material), woody NPP (stems, coarse roots and branches) and fine root NPP. For cocoa farms an additional important NPP component, cocoa pod production, was estimated. Annual NPP values were calculated by summing monthly and seasonal measures of individual components. Standard errors were computed for each component at each time step and propagated through quadrature for every calculation (as in Malhi et al., 2015).

Canopy NPP

To estimate canopy production (NPP_{canopy}), litterfall was collected every two weeks in 0.5 m by 0.5 m litter traps, one metre above the ground. Samples were oven-dried at 70°C to a consistent weight, sorted into leaves, twigs, branches ≤ 2 cm diameter, flowers, seeds and undefined debris and each category was weighed separately. For cocoa farms, leaves were additionally sorted into cocoa and shade tree categories to estimate canopy productivity for each. For estimating the decomposition rate of litterfall, quarterly measures of ground litter were collected from a marked 0.5 m by 0.5 m area on the forest/farm floor per subplot and processed in the same way as the litterfall trap samples. The first collection of ground litter was a stock estimate and all subsequent collections were cumulative measures. Carbon content was assumed to be 47.4% (Malhi et al., 2009).

Woody NPP

The woody component of NPP (NPP_{woody}) was estimated by summing coarse root, stem growth and branch turnover. For stem growth, all trees >10 cm DBH were tagged and measured annually to the nearest mm. In five sub-plots, all trees 2-10 cm DBH were tagged and measured annually. Stem height was measured for all trees in the forest plots and for all shade trees in cocoa farms using a laser hypsometer during the first census. Sixty cocoa tree heights across all plots were measured. Subsequent height growth was considered to be too small to be measured reliably; therefore, separate equations for predicting height from DBH measurements were developed for forest species and cocoa trees. Aboveground biomass was estimated using allometric equations from Chave et al (2014) with measured DBH, estimated height and species specific wood density taken from a global wood density database (Chave et al., 2009; Zanne et al., 2009). Coarse root stock was not directly measured but estimated for each census using the equation from (Cairns et al., 1997):

$$BGB = e^{(-1.0587+0.8836*\ln(AGB))} \quad (1)$$

where BGB is belowground biomass and AGB is estimated aboveground biomass from the census and extrapolated to one hectare. Annual NPP for aboveground and belowground components were calculated by taking the difference between consecutive census estimates of surviving trees and then averaged over total years of monitoring for forest/shade and cocoa trees separately. New recruits were included in subsequent census NPP estimates when their incremental growth between censuses could be calculated and mortality events were treated as a loss of incremental growth and total stored carbon moved to the dead biomass pool. Branch turnover was estimated from quarterly measurements of four 1 m x 60 m coarse woody debris transects, located along the boundaries of each plot. All fallen branches >2 cm DBH that were not associated with tree mortality were categorised by diameter size, decay class (Harmon et al., 1995) and weighed in the field. A representative sample of diameter and decay class samples were taken from the field to calculate average dry matter and wood density values for each diameter and decay class combination. Branch turnover was apportioned between shade and cocoa trees based on proportion of litterfall estimated for each category. The first survey measured total coarse woody debris stock with subsequent surveys monitoring additional branchfall by removing all samples from transects after weighing.

Root NPP

Fine root production ($NPP_{fine\ root}$) was estimated from quarterly measures of four 12 cm diameter by 30 cm deep ingrowth cores made from wire mesh in each plot. When cores were installed, soil with fine roots was extracted for measuring total fine root stocks and the wire mesh was filled with root-free soil for subsequent measures of fine root productivity. In order to standardise extraction effort, field team members searched for fine roots during four separate 10 minute periods following Metcalfe et al (2007). Total root mass was estimated after generating a cumulative sum curve for root mass and extrapolating to 120 minutes of search effort. Fine root NPP was apportioned between shade and cocoa tree pools based on the proportion of stem growth for each category. Root biomass was converted to carbon assuming a carbon content of 47.4% (Malhi et al., 2009).

Cocoa Pod NPP

In the eight plots located in cocoa farms, cocoa pod productivity ($NPP_{cocoa\,pod}$) was estimated using data from a monthly disease survey of 18 trees, distributed as two trees per sub-plot. Pod counts were categorised by size class (i.e., small, medium and large) and differences in monthly measures were apportioned between pods maturing to larger size classes, harvested or removed due to fungal, insect and mammal attack. Total pod production included estimates for all removal categories. Shells from harvested pods are left in the field and considered to be the "unused" component for subsequent HANPP calculations, while the beans are removed for subsequent drying and sale. Field-measured total pod, fresh beans and shell weights were made across plots and averaged for each size class. Dry weights were estimated using literature values of 60% for beans (ICCO, 2018) and 14.1 % for shells (Daud et al., 2013). Calculated carbon values assumed a carbon content of 47.4%.

Therefore, total NPP was calculated using the equation:

$$NPP_{Total} = NPP_{woody} + NPP_{canopy} + NPP_{fine\,root} + NPP_{cocoa\,pod} \qquad (2)$$

Where all values were reported in Mg C ha^{-1} yr^{-1}.

NPP Allocation and Residence Times

The proportion of total NPP allocated into each component (*x*) was calculated using the equation:

$$Allocation_x = {}^{NPP_x}\!/_{NPP_{Total}} \tag{3}$$

Biomass residence time (τ_x) was estimated for each component by dividing total biomass by productivity (Galbraith et al., 2013):

$$\tau_x = {}^{biomass_x}\!/_{NPP_x} \tag{4}$$

For the plots outside of the intact forest, biomass residence times were not calculated for the woody component as they were assumed to not be in equilibrium. Calculations of litterfall residence time required additional steps, which are outlined in supplemental materials.

Comparative studies

To augment our study sample we compared our findings with several forest and cocoa NPP measurements from the literature. To compare our intact forest plot measurements with other semi-deciduous forest in Ghana, we added the total and allocation patterns of forest NPP from Moore et al (2017). This study followed the same GEM protocol (Marthews et al., 2012) and monitored two semi-deciduous, one-hectare forest plots located within 5 km of each other within the Bobiri Forest Reserve. Continuous NPP measurements were collected from 2012-2015. Data on total NPP and allocation patterns for comparative forest plots from Southeast Asia were taken from Riutta et al (2018) and the Amazon from Malhi et al (2015). Riutta et al (2018) collected continuous NPP measurements following the GEM protocol (Marthews et al., 2012) in six old-growth and five logged one-hectare forest plots over different 24 month periods between 2011-2016. The study by Malhi et al (2015) summarises the dynamics of continuous NPP measures collected across ten plots in the Amazon during the years 2005-2011 also following the GEM protocol (Marthews et al., 2012). We averaged the NPP measures and allocation patterns for three one-hectare plots in old-growth forest of Western Amazonia (Allpahuayo and Tampobata) and two one-hectare plots in old-growth forest of Eastern Amazonia (Kenia).

For comparative cocoa NPP data we identified a recent study by Abou Rajab et al (2016). This study was conducted in Sulawesi, Indonesia and established three

20 m by 20 m plots across three cultivation methods, namely: 1) cocoa monoculture, 2) cocoa planted beneath leguminous shade trees (e.g. *Gliricidia sepium*) and 3) cocoa planted beneath diverse shade tree species. To collect NPP data the authors manually harvested cocoa pods from 10-20 cocoa trees per plot over a 12-month period and measured wet weight in the field. Dry weights were derived from a subset of pods across size classes taken to a laboratory. Woody increment was measured from dendrometers of 20 trees per plot, litterfall was collected in 10 litterfall traps collected monthly and root productivity was estimated using 10 ingrowth cores per plot and collected after 10 months. All measures were extrapolated to 12 months. They estimated below ground productivity from above ground woody biomass.

For cocoa productivity in the Americas, we identified a study by Beer et al (1990) where plots with mono-specific timber tree species (e.g. *Cordia alliodora*) and plots with mono-specific leguminous trees (e.g. *Erythrina poeppigiana*) were planted with cocoa. These treatments were established on 18 m by 18 m plots with four replicates of each. Standing biomass was measured when the farms were 5 years old and 10 years old, through a combination of non-destructive and destructive sampling methods that provided estimates of stem, leaf and branch biomass. Pod production was calculated from bi-monthly harvesting of mature pods from 1979 to 1987 and dry weights for beans and husks calculated from oven drying. Increment growth was estimated from DBH and height measurements taken once or twice a year. Litterfall was derived from six litterfall traps randomly placed across the plots; therefore, there were not replicate samples within plots. Pruning residues were measured during the standing biomass inventories. Sampling of roots was described by Alpízar et al (1986), whereby a ring of 27.4 cm diameter and 15 cm in height sampled soils at three depths (0-15, 15-30 and 30-45 cm). The roots were dried and then weighed and extrapolated to one ha using 16 repetitions. Root turnover was estimated for time periods 0-5 years and 5-10 years.

HANPP calculations

HANPP has both a land-use change ($HANPP_{LUC}$) and a harvested ($HANPP_{HARV}$) component (see Figure S1). The land-use change component represents how much productivity declines in the shift from a purely natural ecosystem to a human-modified one; it can be negative in cases where human-modification has boosted ecosystem NPP, as in irrigated or some heavily fertilised agricultural systems. The harvested HANPP represents how much biomass is actually harvested, and can be partitioned into how much is left as slash to decompose in the ecosystem ($HANPP_{\text{UNUSED}}$) and how much is removed from the system ($HANPP_{\text{USED}}$). In both cases, total NPP measured in our intact forest plot was considered to be the baseline level of productivity for comparison.

$$HANPP_{LUCi} = NPP_{POT} - NPP_{ACTi} \qquad (6)$$

Where HANPP from $HANPP_{LUCi}$, in Mg C ha^{-1} yr^{-1}, for plot *i* is the difference between potential total NPP measured in the intact forest (NPP_{POT}) and actual total NPP measured in that plot (NPP_{ACTi}).

The harvested component of HANPP is estimated as the sum of the agricultural yield removed from the field and the agricultural yield left in the field, which in this study were the estimates for annual production of cocoa beans ($HANPP_{\text{USED}}$) and cocoa pod shells ($HANPP_{\text{UNUSED}}$), respectively.

$$HANPP_{HARV} = HANPP_{USED} + HANPP_{UNUSED} \qquad (7)$$

Total HANPP ($HANPP_{TOT}$) is the sum of $HANPP_{LUC}$ and $HANPP_{HARV}$.

$$HANPP_{TOT} = HANPP_{HARV} + HANPP_{LUC} \qquad (8)$$

We report HANPP values in Mg C ha^{-1} yr^{-1}, which is equivalent to 100 g C m^{-2} yr^{-1}. HANPP can also be presented as a percentage of baseline NPP, in this case NPP_{POT}, with negative values indicating a net productivity increase compared with native forest.

HANPP efficiency ($HANPP_E$) has been defined as the ratio harvested biomass ($HANPP_{HARV}$) over total HANPP ($HANPP_{TOT}$) (Haberl et al., 2014); however, for studying a perennial crop like cocoa, we found ratios between $HANPP_{HARV}$ and NPP_{ACTi} and $HANPP_{USED}$ and $NPP_{ACTi}$to be more meaningful, which we defined as HANPP efficiency ($HANPP_E$) and HANPP use efficiency ($HANPP_{UE}$) and calculated using the following equations:

$$HANPP_E = {}^{HANPP_{HARV}}/_{NPP_{ACTi}} \tag{9}$$

$$HANPP_{UE} = {}^{HANPP_{USED}}/_{NPP_{ACTi}} \tag{10}$$

These metrics are different from their original purpose in Haberl et al (2014), which was to contrast the influence of $HANPP_{LUC}$ versus $HANPP_{HARV}$ on $HANPP_{TOT}$. However, as the majority of our results showed a negative or small $HANPP_{TOT}$, we found it difficult to interpret negative or extremely large efficiencies and, therefore, focused on the proportion of NPP_{ACT} that was being harvested and/or removed from the system.

Statistical Analysis

For assessing the drivers of carbon storage, NPP and HANPP, ANOVA and linear models were run in R (R Development Core Team, 2014). Compositional analysis of NPP allocation patterns across plots were run using the R package compositions (Tolosana-Delgado and van den Boogaart, 2011; van den Boogaart et al., 2014; van den Boogaart and Tolosana-Delgado, 2008). Due to the unique management of the cocoa farm at 5 km from the forest, this farm was treated as a separate land cover during statistical analysis to differentiate total NPP and NPP allocation between forest and cocoa and across cocoa farms, and is subsequently referred to as “Timber/Cocoa”. For allocation patterns of the components for total NPP, cocoa pods were combined with canopy measures. Fertiliser application rates were changed to a binary variable (0 indicating none applied and 1 indicating some applied).

Results

Above and Belowground Carbon

The average biomass carbon stock across all cocoa farms was 69.9 ± 2.2 Mg C ha^{-1}, ranging from 21.6 ± 2.3 Mg C ha^{-1} to 194.1 ± 3.8 Mg C ha^{-1}. The highest carbon values overall were found in the Timber/Cocoa farm. This farm stores 48% more biomass carbon than the intact forest plot (131.9 ± 2.3 Mg C ha^{-1}) and 111% more carbon than the logged forest plot (93.1 ± 2.7 Mg C ha^{-1}) (Figure 1). Across cocoa farms, above and belowground biomass carbon values did not differ by distance from forest or farm age. Soil carbon did not differ significantly between forest and cocoa farms nor over distance from forest and age gradients in cocoa farms. The highest soil carbon content was measured in the old cocoa farm 100 metres from the forest (39.7 Mg C ha^{-1}) and the lowest in the logged forest plot (13.2 Mg C ha^{-1}). Soil carbon ranged from being 12.0% to 53.6% of total plot carbon and, on average, was 24.8 Mg C ha^{-1} in cocoa farms. Fine root stocks did not differ by land cover, distance from forest or age of cocoa farm.

[insert Figure 1]

Total NPP and NPP allocation

Mean total NPP measured in the intact (17.6 ± 2.1 Mg C ha^{-1} yr^{-1}) and logged (17.7 ± 1.6 Mg C ha^{-1} yr^{-1}) forest plots were among the highest values reported for tropical forest, though similarly high values were reported by Moore et al (2017) for a different semi-deciduous forest site in Ghana (Table S1). Remarkably, the NPP of the cocoa farms was similar to that of intact forest, and in many cases was higher, with an average across our monitored farms of 18.8 ± 2.5 Mg C ha^{-1} yr^{-1}. Mean total NPP was highest in the young cocoa farm at 100 m from the forest edge (24.3 ± 2.2 Mg C ha^{-1} yr^{-1}), closely followed by the Timber/Cocoa farm (23.9 ± 1.9 Mg C ha^{-1} yr^{-1}) and the old farm at 500 m (24.0 ± 3.7 Mg C ha^{-1} yr^{-1}) (Table 2). Only three cocoa farms were less productive than the intact forest plot (Figure 2). Total mean NPP of cocoa farms did not vary by distance from forest, age of cocoa farm or application of fertiliser. The strongest predictors for total NPP were above ground carbon and canopy gap between shade trees ($R^2 = 0.93$, $p<.001$, Figure S2).

[insert Figure 2]

[insert Table 2]

In terms of NPP components, total canopy NPP was a strong predictor of total plot NPP (Figure 3); although, it is important to keep in mind the x- and y- axes are not independent. When considering total NPP for cocoa and shade trees separately woody NPP of cocoa trees was the only component that was *not* a reliable predictor (Figure S3). Across all monitored plots, NPP of shade trees was significantly different from cocoa trees ($F_{1,14}$= 18.06, p<.001), averaging 8.2 ± 1.3 Mg C ha^{-1} yr^{-1} and 10.5 ± 2.2 Mg C ha^{-1} yr^{-1}, respectively. The strongest predictor of total cocoa NPP was canopy NPP of cocoa trees (R^2 = 0.935, p<.001) and woody NPP of shade trees was the strongest predictor for total shade tree NPP (R^2 = 0.883, p<.001).

[insert Figure 3]

When including allocation data of forest plots from Moore et al (2017) and cocoa plots from Abou Rajab et al (2016) and Beer et al. (1990), allocation patterns of total NPP were not significantly different between forest and cocoa farms; however allocation patterns of cocoa farms did differ across studies by continent (p<.05), which is visibly due to very little allocation of NPP to roots (Figure 3). This phenomenon is consistent with reported allocation patterns of forests in Southeast Asia (Riutta et al., 2018); although, due to the small number of studies we are comparing to we cannot make continent-wide generalisations. Within study cocoa plots, pod production dominated NPP, which, on average, consisted of 40% (ranging 9-59%) of total cocoa NPP or 22% (ranging 5-34%) of total farm NPP (Table 2). Allocation patterns were not related to age of cocoa farm, distance from forest or fertiliser application, either for cocoa pods included with canopy production or as a fourth component. The two farms with lower overall NPP than our forest plots, allocated only 16 and 9% of cocoa NPP to pod production and when pod and canopy production were combined, were the only two farms with less than 50% of total farm NPP allocated to litterfall/pod production. Compared to cocoa trees, shade trees disproportionately invested in woody growth, especially in the Timber/Cocoa farm; although NPP allocation patterns of shade trees did not vary significantly between forest and cocoa farms. This may be due to the large variation in allocation patterns reported in monitored forests (Table S1). The shade trees on an average cocoa farm allocated 32% (14%), 29% (13%) and 39% (17%) of shade tree NPP (total farm NPP) to canopy, woody growth and fine roots respectively.

[insert Figure 4]

Biomass Residence Times

The average farm, has a litterfall layer similar in mass to intact and logged forest, but the proportion of litterfall due to cocoa leaves varied widely across our monitored cocoa farms (7.1-66.7%, average of 27.1%). The average across cocoa farms had similar residence times for cocoa and shade leaves, 0.5 ± 0.3 and 0.5 ± 0.2 years, respectively. However, the range in residence times varied widely across farms, particularly for cocoa leaves (0.1 to 1.6 years) and somewhat for shade leaves (0.3 to 0.7 years). Forest leaves had a much higher mean residence time of 1.0 ± 0.2 and 0.9 ± 0.2 years in intact and logged forest, respectively. Total biomass residence in cocoa farms was not significantly different than forest, however, shade leaves did have a significantly shorter residence time in cocoa farms ($F_{2,7} = 8.368$, $p < .05$) (Table 3). Residence times of shade leaves were positively correlated with basal area of leguminous trees present in the plot ($R^2 = 0.695$, $p<.01$), although the effect becomes negative when considering the interaction of higher basal area of leguminous shade trees and canopy gap ($F_{3,4} = 14.77$, $p < .05$). Across cocoa plots, biomass residence time of cocoa leaves was higher for farms applying fertilisers ($F_{1,6} = 7.841$, $p <.05$), but was not significantly related to farm age, distance from forest, canopy cover or shade density. Residence time and biomass of roots (τ_{roots}) were similar in both forest and cocoa plots, and did not vary by age of cocoa farm, distance from forest or fertiliser application within cocoa plots.

[insert Table 3]

HANPP

Total human appropriated NPP ($\mathrm{HANPP_{TOT}}$) values and both HANPP use efficiency ($\mathrm{HANPP_{E}}$ and $\mathrm{HANPP_{UE}}$) metrics are presented in Table 2, in Mg C ha^{-1} yr^{-1} and percentages, respectively. These measures varied widely across our monitored cocoa plots (Figure S4). All but three of the cocoa farms exhibited negative $\mathrm{HANPP_{LUC}}$ values, which was largely driven by cocoa pod NPP. Once taking into account the portion of HANPP that was harvested, $\mathrm{HANPP_{TOT}}$ values were only negative for the particularly productive, young cocoa farm at 100 m and the Timber/Cocoa farm. $HANPP_{TOT}$ was best predicted by the density of shade and cocoa trees ($R^2 = 0.859$, p <.01, Figure S2). The average $HANPP_{TOT}$ value across farms was 2.1 ± 1.1 Mg C ha^{-1} yr^{-1} (210 ± 110 g C m^{-2} yr^{-1}), with an average $HANPP_E$ of 18.9% and $HANPP_{UE}$ of 1.1%.

Discussion

Difference in magnitude and allocation of NPP between cocoa farms and forests

We found NPP allocated to litterfall to be the most reliable predictor of the combined total farm NPP for both shade and cocoa trees, consistent with previous studies in mature forest (Malhi et al., 2015, 2011; Moore et al., 2017). The hypothesis for these systems is that individual trees are driven by resource competition with immediate neighbors to trade-off between investing in wood and root tissue and, therefore, assuming overall NPP stays relatively constant, allocation of NPP to litterfall would be expected to be more consistent interannually (Malhi et al., 2011). On the other hand, when considering shade trees and planted cocoa trees as separate systems, that model applied across our cocoa management gradient would suggest that competition for light between shade trees should be minimal compared to competition for water and nutrients. Therefore, as we would surmise, we found that woody NPP was the most reliable predictor for shade tree NPP, while cocoa NPP was largely predicted by canopy production (e.g. litterfall and pod production). These findings offer a practical shortcut for estimating NPP in cocoa farms in future.

It was interesting that so many cocoa farms had higher total NPP than both forest plots, which was largely driven by high cocoa pod production (Figure 1

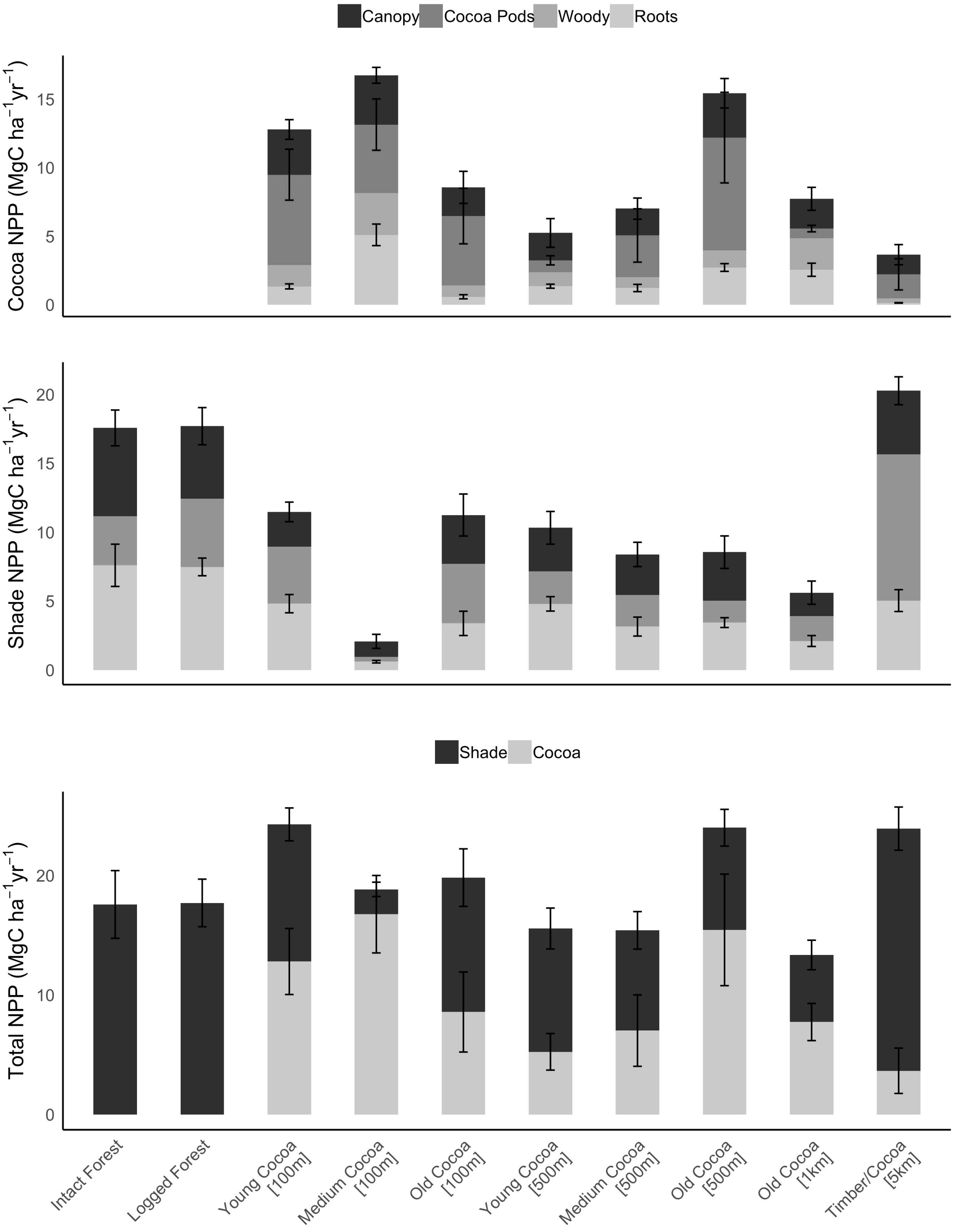

Figure 1), except in one specific farm, Cocoa/Timber, where shade trees were being managed for timber production. This farm had both high total carbon and annual NPP; although, that is without considering a rotational harvest as it is not currently legal for farmers to harvest and sell trees growing on their land due to national land and tree tenure laws (Fenske, 2011; Hirons et al., 2018a). It is well established in the literature that the rate of carbon sequestration in trees is much slower than the rate of release

once felled (Körner, 2003); therefore, these carbon storage estimates would be rapidly reduced once a harvesting regime were initiated. Nevertheless, this study does provide empirical data to address some of the uncertainty around the potential carbon storage managed forest areas in the tropics could provide for meeting the commitments of the Paris Climate Change Agreement (Erb et al., 2017). It has been proposed that African agroforestry systems could be designed for greater carbon sequestration (Kongsager et al., 2012), which for cocoa agroforestry would be accomplished primarily through enhanced shade management (Norgrove and Hauser, 2013).

Impacts of human modification on biomass turnover

Residence time of litterfall components did vary significantly between forest and cocoa farms, although it is difficult to discern the main drivers due to the high variability in this measure across our farms. It has been hypothesized that due to the uneven canopy cover in cocoa farms, forest dependent decomposer communities would be absent or diminished; however, we did not see a correlation to biomass residence time with canopy cover or distance from forest. By using the mass balance approach to estimate decomposition, we are assuming this detrital mass to be in equilibrium; however, it has been reported that cocoa farmers may spread cocoa leaf litter around the farm to suppress weeds (R. Ashley Asare, *personal communication*). This may partially explain why our estimates for cocoa leaf residence times are so varied. Previous studies using litter bags in cocoa farms and secondary forest have found significantly higher resident times for cocoa leaves, and that these rates vary between wet and dry seasons (Dawoe et al., 2010).

Increased residence time of cocoa leaves with fertilization across cocoa farms, could be revealing a changing microbial dynamic as described by Bhatnagar et al (2018); although our observations suggest an opposite effect to what they found. Bhatnagar et al (2018) found that by manipulating their litter experiments with N-fertiliser, they found both fungal and bacterial community compositions changed and that the fungal community was dominated by cellulose preferring guilds relative to the wild community. We did not see the same effect on shade tree leaf or total litterfall residence times, so perhaps a more complex dynamic is occurring. We also found that residence times for shade and cocoa leaves increased with basal area of nitrogen fixing shade trees, although considering residence times are higher in forest plots where canopies are more closed, we explored the trade-off between more nutrient rich leaf material and open canopies. We found the interaction between these two factors to have an overall negative effect on shade, but not cocoa, leaf residence times. With so many nutrients stored in leaf material and a documented dynamic of soil nutrient mining (Morel et al., in review), it will be valuable to better understand the decomposition dynamics and their drivers in this smallholder agroforestry system.

HANPP estimates and farm attributes

For this study we focused on the cocoa-related aspects of farm-level NPP that could be measured using the same methods for the intact and logged forest plots. As a result, we did not collect data on other elements of farm-level productivity that farmers may have consumed (e.g. fruit production from other tree crops, harvested wood, or intercropped subsistence crops). Also, our HANPP estimates are based on the NPP measures of only one intact forest plot that was measured in close proximity. To assess the effect of this assumption, we compared our forest measures with a similar study (Moore et al., 2017) and found our estimates to be within 5%. Therefore, we feel our forest NPP values to be within a reasonable range for calculating locally relevant HANPP measures.

We found a wide variety of $HANPP_{TOT}$ values ranging from -4.6 to 5.2 Mg C ha^{-1} yr^{-1}, which were largely driven by the density of shade trees and to a lesser extent planted cocoa trees. By choosing to calculate modified ratios of HANPP efficiency, we avoided the confusion of trying to interpret negative, or in some cases very large negative, percentages. We also did not use NPP of the intact forest in the denominator, which would have provided an informative metric of the intensity of human use relative to potential productivity and would have been a closer approximation to the efficiency measure proposed by Haberl et al (2014). Instead, by considering the actual NPP of the farm in the denominator, we were focusing efficiency measures on the proportion of farm productivity that was being harvested and eventually removed from the system. In a perennial system, a higher proportion of NPP being removed for human consumption would suggest greater pressure on the system and, likely, lower overall productivity of the farm, which would also relate to the size of $HANPP_{LUC}$. We found that the proportion of total farm NPP dedicated to producing cocoa pods ($HANPP_{E}$) varied between 5.3 and 34.3% and, if only considering the proportion of farm NPP being removed for human consumption ($HANPP_{UE}$) never went above 2%. As the harvested portion of cocoa yield was such a small component of cocoa farm NPP, the predominant driver of HANPP in this landscape is land-use change, particularly, shade management.

Comparison of NPP and HANPP measures with the literature

Moore et al (2017) reported similarly high NPP values for semi-deciduous forest plots in Ghana, which were among the most productive reported for the tropics. However, we did not see the same high proportion of total NPP allocated to litterfall production. Instead we found a pattern of more equal allocation between NPP components as reported pan-tropically by Malhi et al (2011). Riutta et al (2018) found a shift in carbon allocation to greater woody growth in logged forest compared to undisturbed plots, unfortunately we were not able to confirm this statistically due to our small number of forest plot replicates; however, it does appear our single logged plot is investing a higher proportion of NPP to woody growth.

Our total measured cocoa NPP values were similar to those reported in previous published studies performed in Southeast Asia and the Americas (Table 4) and mixed shade tree farms had significantly higher NPP than cocoa monoculture. We also found a significant difference in allocation patterns between studies, particularly related to investment in roots; although, methods to collect root productivity did vary across cocoa studies (see Materials and Methods). Our study shows that it is feasible to have a diverse and carbon rich shade cover while maintaining reasonable cocoa production, consistent with results from Indonesia (Abou Rajab et al., 2016). Nevertheless, all of our measured farm plots had NPP values higher than calculated NPP values using yield estimates from FAOSTAT and equations from Monfreda et al (2008) for Sub-Saharan Africa, which averaged around 12 Mg C ha^{-1} yr^{-1} for the years 2000-2016. This value seems to be more similar to monoculture cocoa reported by Abou Rajab et al (2016).

[insert Table 4]

Figure 5 shows a comparison of this study's average cocoa farm, by NPP component, and total NPP of intact forest as well as comparisons of reported humid forest NPP and cocoa farm NPP for the Americas and Southeast Asia, with the caveat that neither forest or cocoa farm NPP were measured in close proximity and this figure is not meant to assume generalised NPP measures for each continent. Dashed lines in this figure indicates the proportion of total cocoa NPP that would be considered "background" compared to a "baseline" forest, for possible calculation of comparable HANPP values. Only the cocoa NPP values for the Americas are less than the "baseline" forest, though the cited study was monitoring the first 12 years of an established cocoa farm, which may be underestimating the NPP of a mature cocoa farm. This figure suggests that our estimates of cocoa NPP and HANPP would be similar across continents and, potentially, higher than most measured forest NPP.

[insert Figure 5]

This study is unique in having collected empirical NPP data of a perennial crop system with analogous intact and disturbed forest plots, allowing for the direct calculation of HANPP values. Our study found an average HANPP value of 2.1 ± 1.1 Mg C ha^{-1} yr^{-1} (210 ± 110 g C m^{-2} yr^{-1}), which compares reasonably well to the continent-wide average of 1.59 Mg C ha^{-1} yr^{-1} (159 g C m^{-2} yr^{-1}) for 2005 reported in Fetzel et al (2016). This study was one of many that calculated global HANPP using model-derived NPP (Fetzel et al., 2016; Haberl et al., 2007; Krausmann et al., 2013). To more directly compare their estimates over our study landscape, we extracted HANPP estimates from their published maps and found an average HANPP of 2.7 Mg C ha^{-1} yr^{-1}. We were surprised at how similar our results were considering the coarse resolution and broad-scale model of these studies. However, even though our average HANPP values were consistent with this estimate, we also found high variability in measured HANPP across our farms and, therefore, when considering the relative representation of each land cover, average landscape values may differ. Using HANPP estimates from spatial datasets derived from drone imagery, we found values closer to 6.0 Mg C ha^{-1} yr^{-1} across our study landscape, which included fallow lands and subsistence crop production (Moore et al., in review). Assuming similar dynamics across other heterogenous landscapes dominated by smallholder agriculture, we suggest caution in relying on globally-derived estimates of HANPP.

Applicability of the HANPP metric

HANPP provides a quantifiable measure of human influence on the biosphere and at a global-scale has been suggested as a meaningful planetary boundary (Running, 2012). By empirically calculating HANPP across a management and distance from forest gradient, we were interested to explore how well this metric was able to capture the variability within a smallholder perennial system and what a large or small HANPP value might mean for the sustainability of cocoa cultivation. Our results suggest that a large negative HANPP value could be driven by either high cocoa pod productivity or high shade tree density. While large positive HANPP values could either refer to low producing farms or farms with low shade density. HANPP efficiency formulae from the literature do not help parse that apart, because the proportion of farm-level NPP being removed from the system was consistently low (~2%) in either case. For instance, if shade cover were to be removed, as reported in Abou Rajab et al. (2016), $\text{HANPP}_{\text{LUC}}$ would be larger and NPP litterfall would increase without significant changes in cocoa pod production, resulting in low HANPP use efficiency. Therefore, we would argue that the logic of the HANPP metric is more relevant to annual crop cultivation. Otherwise, the considerable carbon investment of the farm into cocoa litterfall and shade tree woody growth, which has ecological benefits for the sustainability of the agroforestry system, is presented as being inefficient because it does not scale with agricultural productivity.

Comparing extrapolated estimates of HANPP from the regional to continental level, we further discuss the caveats of generalising this metric at a large-scale. Fetzel et al (2016) report $\text{HANPP}_{\text{TOT}}$ values of 33% for West Africa and 35% across Africa. They concede that these are relatively low compared to parts of Europe and Asia, but highlight declining to stagnating trends in efficiency of HANPP as worrying and unique to this continent. A remote sensing-based study by Abdi et al (2016) found that $\text{HANPP}_{\text{TOT}}$ in the drylands of Africa can vary by 80% and be heavily impacted by climatological phenomena such as El Niño and La Niña. They found a 7.2% increase in demand for NPP relative to supply; although the mean trends they identified varied from -0.25 Mg C ha^{-1} yr^{-1} (southern Africa) to 0.02 Mg C ha^{-1} yr^{-1} (Western Sahel) to 0.3 Mg C ha^{-1} yr^{-1} (central Africa). These values are much lower than the NPP we measured and would indicate that dryland trends are significantly more marginal than what we are observing in this highly productive region of West Africa. This would suggest that averaging NPP and HANPP measures over the entire continent would be obscuring very different patterns in human appropriation. Krausmann et al (2013) reported trends of population growth and HANPP for Africa, whereby $\mathrm{HANPP}_{\mathrm{TOT}}$ has increased dramatically, largely driven by "inefficiencies" in $\mathrm{HANPP}_{\mathrm{LUC}}$, while per capita HANPP has reduced considerably. At the landscape scale, studies have shown that $\mathrm{HANPP}_{\mathrm{TOT}}$ tends to increase with development and affluence, with wealthier households appropriating larger proportions of NPP (Haberl et al., 2014; Pritchard et al., 2018), a phenomenon we did not explore for this study. However, as stated, our results suggest this fixation on "efficiency" may not be as meaningful in more heterogenous, smallholder dominated landscapes, which current satellite remote sensing methods do not discern particularly well (Curtis et al., 2018; Ordway et al., 2017) and that will require higher resolution imagery and improved classification algorithms to adequately capture (Moore et al., in preparation). If we contrast these studies with results reported for industrialised countries, which have shown decreasing trends in HANPP and a supposed disconnection of HANPP with population growth and GDP (Haberl et al., 2014), it seems that HANPP is more a metric of the dependence of a society on natural systems, particularly agricultural, rather than being related to the level of a society's consumption. As a result, we would caution against implementing this metric at a broad-scale. Averaging these values in our study landscape obscured non-trivial dynamics that could have very different implications for the long-term sustainability of smallholder agriculture and, therefore, does not appear to us to be a helpful metric for informing a planetary boundary.

Conclusion

This study presents intensive, empirical data on carbon cycling and allocation across a forest to cocoa farm management gradient. For our study system and comparable shaded cocoa agroforestry systems globally, we found the average smallholder cocoa farm to be more productive than baseline forest with a low HANPP efficiency of 18.9%. Therefore, to improve satellite derived NPP and HANPP estimates it will be important to be able to differentiate shade tree density above smallholder cocoa farms. We measured higher total biomass carbon values in a high shade cocoa farm than both intact and logged forest plots. These results are not meant to suggest that shaded cocoa farms are as valuable as intact or logged forest areas, as we are only comparing carbon productivity and storage and are not considering nutrients, biodiversity, micro-climate or other ecosystem services. They do, however, quantify how shaded cocoa farms can yield ecosystem benefits and lower environmental footprints compared to intensive, monoculture cocoa farms.

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References

Abdi, A.M., Seaquist, J., Tenenbaum, D.E., Eklundh, L., Ardö, J., 2014. The supply and demand of net primary production in the Sahel. Environ. Res. Lett. 9, 094003.

Abdi, A.M., Vrieling, A., Yengoh, G.T., Anyamba, A., Seaquist, J.W., Ummenhofer, C.C., Ardö, J., 2016. The El Niño – La Niña cycle and recent trends in supply and demand of net primary productivity in African drylands. Clim. Change 138, 111–125.

Abou Rajab, Y., Leuschner, C., Barus, H., Tjoa, A., Hertel, D., 2016. Cacao Cultivation under Diverse Shade Tree Cover Allows High Carbon Storage and Sequestration without Yield Losses. PLoS One 11, e0149949. https://doi.org/10.1371/journal.pone.0149949

Alpízar, L., Fassbender, H.W., Heuveldop, J., Fölster, H., Enríquez, G., 1986. Modelling agroforestry systems of cacao (Theobroma cacao) with laurel (Cordia alliodora) and poro (Erythrina poeppigiana) in Costa Rica. Agrofor. Syst. 4, 175–189. https://doi.org/10.1007/BF02028353

Anderson-Teixeira, K.J., Wang, M.M.H., McGarvey, J.C., LeBauer, D.S., 2016. Carbon dynamics of mature and regrowth tropical forests derived from a pantropical database (TropForC-db). Glob. Change Biol. 22, 1690–1709. https://doi.org/doi:10.1111/gcb.13226

Anglaaere, L.C.N., Cobbina, J., Sinclair, F.L., McDonald, M.A., 2011. The effect of land use systems on tree diversity: farmer preference and species composition of cocoa-based agroecosystems in Ghana. Agrofor. Syst. 81, 249–265. https://doi.org/10.1007/s10457-010-9366-z

Ardö, J., 2015. Comparison between remote sensing and a dynamic vegetation model for estimating terrestrial primary production of Africa. Carbon Balance Manag. 10, 8. https://doi.org/10.1186/s13021-015-0018-5

Beer, J., Bonnemann, A., Chavez, W., Fassbender, H.W., Imbach, A.C., Martel, I., 1990. Modelling agroforestry systems of cacao (Theobroma cacao) with laurel (Cordia alliodora) or poro (Erythrina poeppigiana) in Costa Rica. Agrofor. Syst. 12, 229–249. https://doi.org/10.1007/bf00137286

Bhatnagar, J.M., Peay, K.G., Treseder, K.K., 2018. Litter chemistry influences decomposition through activity of specific microbial functional guilds. Ecol. Monogr. 88, 429–444. https://doi.org/doi:10.1002/ecm.1303

Cairns, M.A., Brown, S., Helmer, E.H., Baumgardner, G.A., 1997. Root biomass allocation in the world's upland forests. Oecologia 111, 1–11. https://doi.org/10.1007/s004420050201

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12, 351–366. https://doi.org/doi:10.1111/j.1461-0248.2009.01285.x

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrízar, A., Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A., Nogueira, E.M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C.M., Saldarriaga, J.G., Vieilledent, G., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Glob. Change Biol. 20, 3177–3190. https://doi.org/doi:10.1111/gcb.12629

Ciais, P., Bombelli, A., Williams, M., Piao, S.L., Chave, J., Ryan, C.M., Henry, M., Brender, P., Valentini, R., 2011. The carbon balance of Africa: synthesis of recent research studies. Philos. Trans. R. Soc. Math. Phys. Eng. Sci. 369, 2038–2057. https://doi.org/10.1098/rsta.2010.0328

Curtis, P.G., Slay, C.M., Harris, N.L., Tyukavina, A., Hansen, M.C., 2018. Classifying drivers of global forest loss. Science 361, 1108. https://doi.org/10.1126/science.aau3445

Daud, Z., Kassim, A.S.M., Aripin, A.M., Awang, H., Hatta, M.Z.M., 2013. Chemical Composition and Morphological of Cocoa Pod Husks and Cassava Peels for Pulp and Paper Production. Aust. J. Basic Appl. Sci. 7, 406–411.

Dawoe, E.K., Isaac, M.E., Quashie-Sam, J., 2010. Litterfall and litter nutrient dynamics under cocoa ecosystems in lowland humid Ghana. Plant Soil 330, 55–64. https://doi.org/10.1007/s11104-009-0173-0

DeFries, R., 2002. Past and future sensitivity of primary production to human modification of the landscape. Geophys. Res. Lett. 29, 36-1-36–4. https://doi.org/10.1029/2001GL013620

Erb, K.-H., Kastner, T., Plutzar, C., Bais, A.L.S., Carvalhais, N., Fetzel, T., Gingrich, S., Haberl, H., Lauk, C., Niedertscheider, M., Pongratz, J., Thurner, M., Luyssaert, S., 2017. Unexpectedly large impact of forest management and grazing on global vegetation biomass. Nature 553, 73. https://doi.org/10.1038/nature25138

Fassbender, H.W., 1998. Longterm studies of soil fertility in cacao-shade trees-agroforestry systems: Results of 15 years of organic matter and nutrients research in Costa Rica, in: Schulte, A., Ruhiyat, D. (Eds.), Soils of Tropical Forest Ecosystems. Springer, Berlin, Heidelberg.

Fenske, J., 2011. Land tenure and investment incentives: Evidence from West Africa. J. Dev. Econ. 95, 137–156. https://doi.org/10.1016/j.jdeveco.2010.05.001

Fetzel, T., Niedertscheider, M., Haberl, H., Krausmann, F., Erb, K.-H., 2016. Patterns and changes of land use and land-use efficiency in Africa 1980–2005: an analysis based on the human appropriation of net primary production framework. Reg. Environ. Change 16, 1507–1520.

Field, C.B., Behrenfeld, M.J., Randerson, J.T., Falkowski, P., 1998. Primary Production of the Biosphere: Integrating Terrestrial and Oceanic Components. Science 281, 237–240. https://doi.org/10.1126/science.281.5374.237

Food and Agriculture Organization of the United Nations (FAO), 2016. FAOSTAT Statistics Database [WWW Document].

Goetz, S.J., Prince, S.D., Small, J., Gleason, A.C.R., 2000. Interannual variability of global terrestrial primary production: Results of a model driven with satellite observations. J. Geophys. Res. Atmospheres 105, 20077–20091. https://doi.org/doi:10.1029/2000JD900274

Haberl, H., 1997. Human Appropriation of Net Primary Production as an Environmental Indicator: Implications for Sustainable Development. Ambio 26, 143–146.

Haberl, H., Erb, K.-H., Krausmann, F., 2014. Human Appropriation of Net Primary Production: Patterns, Trends, and Planetary Boundaries. Annu. Rev. Environ. Resour. 39, 363–391.

Haberl, H., Erb, K.H., Krausmann, F., Gaube, V., Bondeau, A., Plutzar, C., Gingrich, S., Lucht, W., Fischer-Kowalski, M., 2007. Quantifying and mapping the human appropriation of net primary production in earth’s terrestrial ecosystems. Proc. Natl. Acad. Sci. 104, 12942–12947. https://doi.org/10.1073/pnas.0704243104

Haberl, H., Schulz, N.B., Plutzar, C., Erb, K.H., Krausmann, F., Loibl, W., Moser, D., Sauberer, N., Weisz, H., Zechmeister, H.G., Zulka, P., 2004. Human appropriation of net primary production and species diversity in agricultural landscapes. Agric. Ecosyst. Environ. 102, 213–218. https://doi.org/10.1016/j.agee.2003.07.004

Harmon, M.E., Whigham, D.F., Sexton, J., Olmsted, I., 1995. Decomposition and Mass of Woody Detritus in the Dry Tropical Forests of the Northeastern Yucatan Peninsula, Mexico. Biotropica 27, 305–316. https://doi.org/10.2307/2388916

Hirons, M., McDermott, C., Asare, R., Morel, A., Robinson, E., Mason, J., Boyd, E., Malhi, Y., Norris, K., 2018a. Illegality and inequity in Ghana's cocoa-forest landscape: How formalization can undermine farmers control and benefits from trees on their farms. Land Use Policy 76, 405–413. https://doi.org/10.1016/j.landusepol.2018.02.014

Hirons, M., Robinson, E., McDermott, C., Morel, A., Asare, R., Boyd, E., Gonfa, T., Gole, T.W., Malhi, Y., Mason, J., Norris, K., 2018b. Understanding poverty in agro-forestry cash-crop systems: evidence from Ghana and Ethiopia. Ecol. Econ. 154, 31–41.

ICCO, 2018.

Imhoff, M.L., Bounoua, L., Ricketts, T., Loucks, C., Harriss, R., Lawrence, W.T., 2004. Global patterns in human consumption of net primary production. Nature 429, 870. https://doi.org/10.1038/nature02619

Kongsager, R., Napier, J., Mertz, O., 2012. The carbon sequestration potential of tree crop plantations. Mitig. Adapt. Strateg. Glob. Change 18, 1197–1213.

Körner, C., 2003. Slow in, Rapid out--Carbon Flux Studies and Kyoto Targets. Science 300, 1242. https://doi.org/10.1126/science.1084460

Krausmann, F., Erb, K.-H., Gingrich, S., Haberl, H., Bondeau, A., Gaube, V., Lauk, C., Plutzar, C., Searchinger, T.D., 2013. Global human appropriation of net primary production doubled in the 20th century. Proc. Natl. Acad. Sci. 110, 10324–10329. https://doi.org/10.1073/pnas.1211349110

Malhi, Y., Aragão, L.E.O.C., Metcalfe, D.B., Paiva, R., Quesada, C.A., Almeida, S., Anderson, L., Brando, P., Chambers, J.Q., Da Costa, A.C.L., Hutyra, L.R., Oliveira, P., Patiño, S., Pyle, E.H., Robertson, A.L., Teixeira, L.M., 2009. Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. Glob. Change Biol. 15, 1255–1274. https://doi.org/doi:10.1111/j.1365-2486.2008.01780.x

Malhi, Y., Doughty, C., Galbraith, D., 2011. The allocation of ecosystem net primary productivity in tropical forests. Philos. Trans. R. Soc. B Biol. Sci. 366, 3225–3245. https://doi.org/10.1098/rstb.2011.0062

Malhi, Y., Doughty, C.E., Goldsmith, G.R., Metcalfe, D.B., Girardin, C.A.J., Marthews, T.R., Aguila-Pasquel, J., Aragão, L.E.O.C., Araujo-Murakami, A., Brando, P., Costa, A.C.L., Silva-Espejo, J.E., Farfán Amézquita, F., Galbraith, D.R., Quesada, C.A., Rocha, W., Salinas-Revilla, N., Silvério, D., Meir, P., Phillips, O.L., 2015. The linkages between photosynthesis, productivity, growth and biomass in lowland Amazonian forests. Glob. Change Biol. 21, 2283–2295. https://doi.org/doi:10.1111/gcb.12859

Marthews, T.R., Metcalfe, D., Malhi, Y., Phillips, O., Huaraca Huasco, W., Riutta, T., Ruiz Jaén, M., Girardin, C., Urrutia, R., Butt, N., Cain, R., Oliveras Menor, I., and colleagues from the RAINFOR and GEM networks, 2012. Measuring Tropical Forest Carbon Allocation and Cycling: A RAINFOR-GEM Field

Manual for Intensive Census Plots (v2.2)., Manual. Global Ecosystems Monitoring network.

Metcalfe, D.B., Williams, M., Aragão, L.E.O.C., Da Costa, A.C.L., De Almeida, S.S., Braga, A.P., Gonçalves, P.H.L., De Athaydes, J., Junior, S., Malhi, Y., Meir, P., 2007. A method for extracting plant roots from soil which facilitates rapid sample processing without compromising measurement accuracy. New Phytol. 174, 697–703. https://doi.org/doi:10.1111/j.1469-8137.2007.02032.x

Miko, L., Storch, D., 2015. Biodiversity conservation under energy limitation: Possible consequences of human productivity appropriation for species richness, ecosystem functioning, and food production. Ecosyst. Serv. 16, 146–149. https://doi.org/10.1016/j.ecoser.2015.05.003

Monfreda, C., Ramankutty, N., Foley, J.A., 2008. Farming the planet: 2. Geographic distribution of crop areas, yields, physiological types, and net primary production in the year 2000. Glob. Biogeochem. Cycles 22. https://doi.org/doi:10.1029/2007GB002947

Moore, C., Kruitwagen, L., Ramirez Mendiola, J.L., Morel, A.C., Malhi, Y., in preparation. Classifying Land Use in Complex Mosaic Landscapes using Drone Imagery and Machine Learning.

Moore, C., Morel, A., Asare, R.A., Adu Sasu, M., Adu-Bredu, S., Aronson, J., Malhi, Y., in review. Human Appropriated Net Primary Productivity of Complex Mosaic Landscapes.

Moore, S., Adu-Bredu, S., Duah-Gyamfi, A., Addo-Danso, S.D., Ibrahim, F., Mbou, A.T., de Grandcourt, A., Valentini, R., Nicolini, G., Djagbletey, G., Owusu-Afriyie, K., Gvozdevaite, A., Oliveras, I., Ruiz-Jaen, M.C., Malhi, Y., 2017. Forest biomass, productivity and carbon cycling along a rainfall gradient in West Africa. Glob. Change Biol. 22, 1690. https://doi.org/10.1111/gcb.13907

Morel, A.C., Hirons, M., Adu Sasu, M., Quaye, M., Ashley Asare, Mason, J., Adu-Bredu, S., Boyd, E., McDermott, C.L., Robinson, E.J.Z., Straser, R., Malhi, Y., Norris, K., in review. The Ecological Limits Acting on Cocoa Smallholders and the Implications for Poverty Alleviation in an African Forest-Agriculture Landscape.

Norgrove, L., Hauser, S., 2013. Carbon stocks in shade *Theobroma cacao* farms and adjacent secondary forests of similar age in Cameroon. Trop. Ecol. 54, 15–22.

Ordway, E.M., Asner, G.P., Lambin, E.F., 2017. Deforestation risk due to commodity crop expansion in sub-Saharan Africa. Environ. Res. Lett. 12.

Plutzar, C., Kroisleitner, C., Haberl, H., Fetzel, T., Bulgheroni, C., Beringer, T., Hostert, P., Kastner, T., Kuemmerle, T., Lauk, C., Levers, C., Lindner, M., Moser, D., Müller, D., Niedertscheider, M., Paracchini, M.L., Schaphoff, S., Verburg, P.H., Verkerk, P.J., Erb, K.-H., 2016. Changes in the spatial patterns of human appropriation of net primary production (HANPP) in Europe 1990–2006. Reg. Environ. Change 16, 1225–1238. https://doi.org/10.1007/s10113-015-0820-3

Pritchard, R., Ryan, C.M., Grundy, I., van der Horst, D., 2018. Human Appropriation of Net Primary Productivity and Rural Livelihoods: Findings From Six Villages in Zimbabwe. Ecol. Econ. 146, 115–124. https://doi.org/10.1016/j.ecolecon.2017.10.003

R Development Core Team, 2014. R: A language and environment for statistical computing. R Found. Stat. Comput.

Riutta, T., Malhi, Y., Kho Lip, K., Marthews, T.R., Huaraca Huasco, W., Khoo, M., Tan, S., Turner, E., Reynolds, G., Both, S., Burslem, D.F.R.P., Teh, Y.A., Vairappan, C.S., Majalap, N., Ewers, R.M., 2018. Logging disturbance shifts net primary productivity and its allocation in Bornean tropical forests. Glob. Change Biol. 24, 2913–2928. https://doi.org/doi:10.1111/gcb.14068

Rojstaczer, S., Sterling, S.M., Moore, N.J., 2001. Human Appropriation of Photosynthesis Products. Science 294, 2549–2552. https://doi.org/10.1126/science.1064375

Running, S.W., 2012. A Measurable Planetary Boundary for the Biosphere. Science 337, 1458–1459. https://doi.org/10.1126/science.1227620

Tolosana-Delgado, R., van den Boogaart, K.G., 2011. Linear models with compositions in R, in: Pawlowsky-Glahn, V., Buccianti, A. (Eds.), Compositional Data Analysis: Theory and Applications. John Wiley & Sons, Ltd, Chichester, pp. 356–371.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecol. Lett. 8, 857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x

Valentini, R., Arneth, A., Bombelli, A., Castaldi, S., Cazzolla Gatti, R., Chevallier, F., Ciais, P., Grieco, E., Hartmann, J., Henry, M., Houghton, R.A., Jung, M., Kutsch, W.L., Malhi, Y., Mayorga, E., Merbold, L., Murray-Tortarolo, G., Papale, D., Peylin, P., Poulter, B., Raymond, P.A., Santini, M., Sitch, S., Vaglio Laurin, G., van der Werf, G.R., Williams, C.A., Scholes, R.J., 2014. A full greenhouse gases budget of Africa: synthesis, uncertainties, and vulnerabilities. Biogeosciences 11, 381–407. https://doi.org/10.5194/bg-11-381-2014

van den Boogaart, K.G., Tolosana, R., Bren, M., 2014. Compositions: Compositional data analysis, R package version 1.40-2. https://CRAN.R-project.org/package=compositions.

van den Boogaart, K.G., Tolosana-Delgado, R., 2008. “compositions”: A unified R package to analyze compositional data. Comput. Geosci. 34, 320–338. https://doi.org/10.1016/j.cageo.2006.11.017

Vitousek, P.M., 1984. Litterfall, Nutrient Cycling, and Nutrient Limitation in Tropical Forests. Ecology 65, 285–298. https://doi.org/10.2307/1939481

Vitousek, P.M., Ehrlich, P.R., Ehrlich, A.H., Matson, P.A., 1986. Human Appropriation of the Products of Photosynthesis. Bioscience 36, 368–373.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human Domination of Earth’s Ecosystems. Science 277, 494–499. https://doi.org/10.1126/science.277.5325.494

Williams, C.A., Hanan, N.P., Neff, J.C., Scholes, R.J., Berry, J.A., Denning, A.S., Baker, D.F., 2007. Africa and the global carbon cycle. Carbon Balance Manag. 2, 3. https://doi.org/10.1186/1750-0680-2-3

Wright, D.H., 1990. Human Impacts on Energy Flow through Natural Ecosystems, and Implications for Species Endangerment. Ambio 19, 189–194.

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C., Chave, J., 2009. Data from: Towards a worldwide wood economics spectrum. Dryad Data Repository.

Tables

Table 1 Plot names and characteristics for eight monitored cocoa farms. Age of farm was based on reports from farmers, distance from forest was measured by GPS and confirmed from satellite imagery, canopy openness was measured from hemispherical photos taken at 4.5 metres (above the cocoa canopy) during the wet (July) and dry season (January), cocoa density, shade tree density and shade tree basal area were estimated from a small and large tree census and species of shade tree are ordered by basal area dominance and represent 80% of plot-level basal area, excluding *Theobroma cacao*.

Plot	**Age of Farm [yr]**	**Canopy Gap [%]**	**Cocoa Density [trees ha^{-1}]**	**Shade Tree Density [trees ha^{-1}]**	**Shade Tree Basal Area [m^2 ha^{-1}]**	**Dominant Shade Tree Species**
Young Cocoa [100 m]	8	36.9-39.7	709	55	6.4	*Terminalia ivorensis* *Ceiba pentandra* *Entandrophragma angolense* *Milicia regia* *Bombax buonopozense* *Petersianthus macrocarpus* *Triplochiton scleroxylon*
Medium Cocoa [100 m]	18	58.3-74.5	784	8	0.71	*Triplochiton scleroxylon* *Terminalia ivorensis*
Old Cocoa [100 m]	30	43.4-45.5	414	52	12.2	*Discoglypremna caloneura* *Hannoa klaineana* *Afzelia bella* *Parkia bicolor* *Bombax buonopozense* *Erythrina vogelii*
Young Cocoa [500 m]	9	48.0-49.4	337	72	11.4	*Ricinodendron heudelotii* *Sterculia tragacantha* *Cola nitida* *Antiaris toxicaria* *Lannea welwitschii* *Amphimas pterocarpoides* *Entandrophragma angolense* *Daniellia ogea* *Citrus sinensis* *Morinda lucida*
Medium Cocoa [500 m]	15	60.4-63.4	406	52	7.4	*Ficus sur* *Morinda lucida* *Petersianthus macrocarpus* *Celtis zenkeri* *Ficus exasperate* *Citrus sinensis* *Irvingia gabonensis* *Celtis mildbraedii*
Old Cocoa [500 m]	40	38.7-44.3	738	36	7.8	*Hannoa klaineana* *Erythrina vogelii* *Nesogordonia papaverifera* *Sterculia tragacantha* *Discoglypremna caloneura* *Ficus sur*
Old Cocoa [1 km]	30	60.1-60.8	117	61	2.5	*Ficus sur* *Nesogordonia papaverifera* *Albizia zygia* *Voacanga Africana* *Pycnanthus angolensis* *Milicia excelsa* *Morinda lucida*

Cocoa/Timber [5 km]	50	20.0-29.3	478	119	34.7	*Petersianthus macrocarpus* *Lannea welwitschii* *Bridelia atroviridis* *Zanthoxylum zanthoxyloides* *Spathodea campanulata* *Antiaris toxicaria* *Discoglypremna caloneura*

Table 2 Total NPP measured separately for shade trees and cocoa trees for each cocoa plot, including proportion of productivity for each NPP component (e.g. canopy, woody, roots and cocoa pods), total HANPP calculated as the sum of land use change (LUC) and harvested NPP (HANPP$_{TOT}$), HANPP efficiency (HANPP$_{E}$) calculated as HANPP$_{HARV}$ over total NPP and HANPP use efficiency (HANPP$_{UE}$) calculated as HANPP$_{USED}$ over total NPP. Negative values indicate NPP production greater than levels measured in intact forest.

Plot	Tree Category	Total NPP [Mg C ha^{-1} yr^{-1}]	Allocation of Productivity:				HANPP$_{TOT}$ [Mg C ha^{-1} yr^{-1}]	HANPP$_{E}$ [%]	HANPP$_{UE}$ [%]
			Canopy	Woody	Roots	Pods			
Young Cocoa [100 m]	Cocoa	12.8 ± 2.0	0.26	0.12	0.10	0.52	-0.1	27.2	1.0
	Shade	11.5 ± 1.0	0.22	0.36	0.42				
	All*	24.3 ± 2.2	0.51	0.23	0.25				
Medium Cocoa [100 m]	Cocoa	16.8 ± 2.1	0.22	0.18	0.30	0.30	3.7	26.5	1.3
	Shade	2.1 ± 0.5	0.55	0.16	0.29				
	All*	18.8 ± 2.2	0.52	0.18	0.30				
Old Cocoa [100 m]	Cocoa	8.6 ± 2.4	0.24	0.10	0.07	0.59	2.8	25.5	1.4
	Shade	11.3 ± 1.8	0.31	0.39	0.30				
	All*	19.8 ± 2.9	0.54	0.26	0.20				
Young Cocoa [500 m]	Cocoa	5.2 ± 1.1	0.38	0.20	0.26	0.16	2.9	5.5	0.3
	Shade	10.3 ± 1.3	0.31	0.23	0.46				
	All*	15.6 ± 1.7	0.39	0.22	0.40				
Medium Cocoa [500 m]	Cocoa	7.0 ± 2.1	0.28	0.11	0.17	0.44	5.2	19.8	1.7
	Shade	8.4 ± 1.1	0.35	0.27	0.38				
	All*	15.4 ± 2.4	0.52	0.20	0.28				
Old Cocoa [500 m]	Cocoa	15.4 ± 3.5	0.21	0.08	0.18	0.53	1.8	34.3	1.9
	Shade	8.6 ± 1.2	0.41	0.19	0.40				
	All*	24.0 ± 3.7	0.62	0.12	0.26				
Old Cocoa [1 km]	Cocoa	7.7 ± 1.0	0.28	0.30	0.33	0.09	4.9	5.3	0.2
	Shade	5.6 ± 0.9	0.30	0.32	0.37				
	All*	13.3 ± 1.4	0.34	0.31	0.35				
Timber/ Cocoa [5 km]	Cocoa	3.7 ± 1.4	0.39	0.09	0.04	0.48	-4.6	7.4	0.6
	Shade	20.3 ± 1.3	0.23	0.52	0.25				
	All*	23.9 ± 1.9	0.33	0.46	0.22				
Average Cocoa Farm[†]	Cocoa	10.5 ± 2.2	0.25	0.15	0.20	0.40	3.0	22.5	1.1
	Shade	8.2 ± 1.3	0.32	0.29	0.39				
	All*	18.8 ± 2.5	0.51	0.21	0.28				

*Cocoa pods included in canopy pool.

[†] Not including timber/cocoa plot

Table 3 Comparison of carbon stock and biomass residence times of the three NPP components for intact forest, logged forest, the cocoa farm with high timber tree density and averages across the remaining cocoa plots. Values presented with ± 1 SE. Superscripts indicate groups of land covers that are different ($p < 0.05$) according to Tukey's HSD test.

Plot	**Intact Forest**	**Logged Forest**	**Timber/Cocoa**			**Mean Cocoa**		
			Total	***Shade***	***Cocoa***	***Total***	***Shade***	***Cocoa***
Woody biomass [Mg C ha^{-1}]	131.9 ± 2.3^{a,b}	93.1 ± 2.7^{a,c}	194.1 ± 3.7^{b}	169.0 ± 3.8	25.2 ± 0.2	69.6 ± 9.6^{c}	46.6 ± 7.4	23.4 ± 3.7
Woody residence time [years]	39.9 ± 0.6							
Litter biomass [Mg C ha^{-1}]	4.9 ± 1.4	4.0 ± 1.3	3.4 ± 1.0	3.2 ± 1.1	2.3 ± 1.5	3.8 ± 1.4	1.3 ± 1.0	1.0 ± 0.7
Litter residence time [years]	1.0 ± 0.2	0.9 ± 0.2	0.7 ± 0.1	0.7 ± 0.2	1.6 ± 0.7	0.9 ± 0.2	0.5 ± 0.3	0.5 ± 0.2
Fine root biomass [Mg C ha^{-1}]	2.0 ± 0.2	2.3 ± 0.3	1.9 ± 0.2	1.6 ± 0.2	0.3 ± 0.02	1.9 ± 0.7	1.0 ± 0.1	0.4 ± 0.04
Fine root residence time [months]	3.3 ± 0.4	3.8 ± 0.5		4.4 ± 1.8			4.4 ± 2.2	

Table 4 Comparison of study measurements to cocoa NPP values published in the literature across continents.

Category	Component	NPP [Mg C ha^{-1} yr^{-1}]	Country	Reference
Shade Trees	Litterfall	2.7 ± 1.0	Ghana	This study
		2.1 ± 0.4	Costa Rica	(Beer et al., 1990; Fassbender, 1998)
		3.2 ± 0.3	Indonesia	(Abou Rajab et al., 2016)
	Woody	2.4 ± 0.5	Ghana	This study
		1.8 ± 0.2	Costa Rica	(Beer et al., 1990)
		6.8 ± 0.7†	Indonesia	(Abou Rajab et al., 2016)
	Fine Roots	3.2 ± 0.6‡	Ghana	This study
		1.6 ± 0.6	Costa Rica	(Beer et al., 1990)
		0.2 ± 0.0	Indonesia	(Abou Rajab et al., 2016)
Cocoa Trees	Litterfall	2.6 ± 0.9	Ghana	This study
		1.54 ± 0.65	Costa Rica	(Beer et al., 1990; Fassbender, 1998)
		1.3 ± 0.1	Indonesia	(Abou Rajab et al., 2016)
	Woody	1.6 ± 0.3	Ghana	This study
		0.46 ± 0.05	Costa Rica	(Beer et al., 1990)
		1.6 ± 0.6†	Indonesia	(Abou Rajab et al., 2016)
	Fine Roots	2.1 ± 0.4‡	Ghana	This study
		0.33 ± 0.1	Costa Rica	(Beer et al., 1990)
		0.5 ± 0.1	Indonesia	(Abou Rajab et al., 2016)
	Pods*	3.9 ± 1.8	Ghana	This study
		1.3 ± 0.2	Costa Rica	
		4.2 ± 1.9	Indonesia	(Abou Rajab et al., 2016)
Combined	Total	18.8 ± 2.5	Ghana	This study
		16.4 ± 5.2§	Costa Rica	(Beer et al., 1990)
		17.7 ± 0.6	Indonesia	(Abou Rajab et al., 2016)
		9.1 ± 2.0Ω	Indonesia	(Abou Rajab et al., 2016)

*Beans and shells combined

†Combined above-ground carbon and coarse-root measures.

‡Apportioned between cocoa and shade trees proportionally based on coarse root biomass estimates.

§Includes pruning residues.

ΩEstimate for cocoa monoculture.

Figures

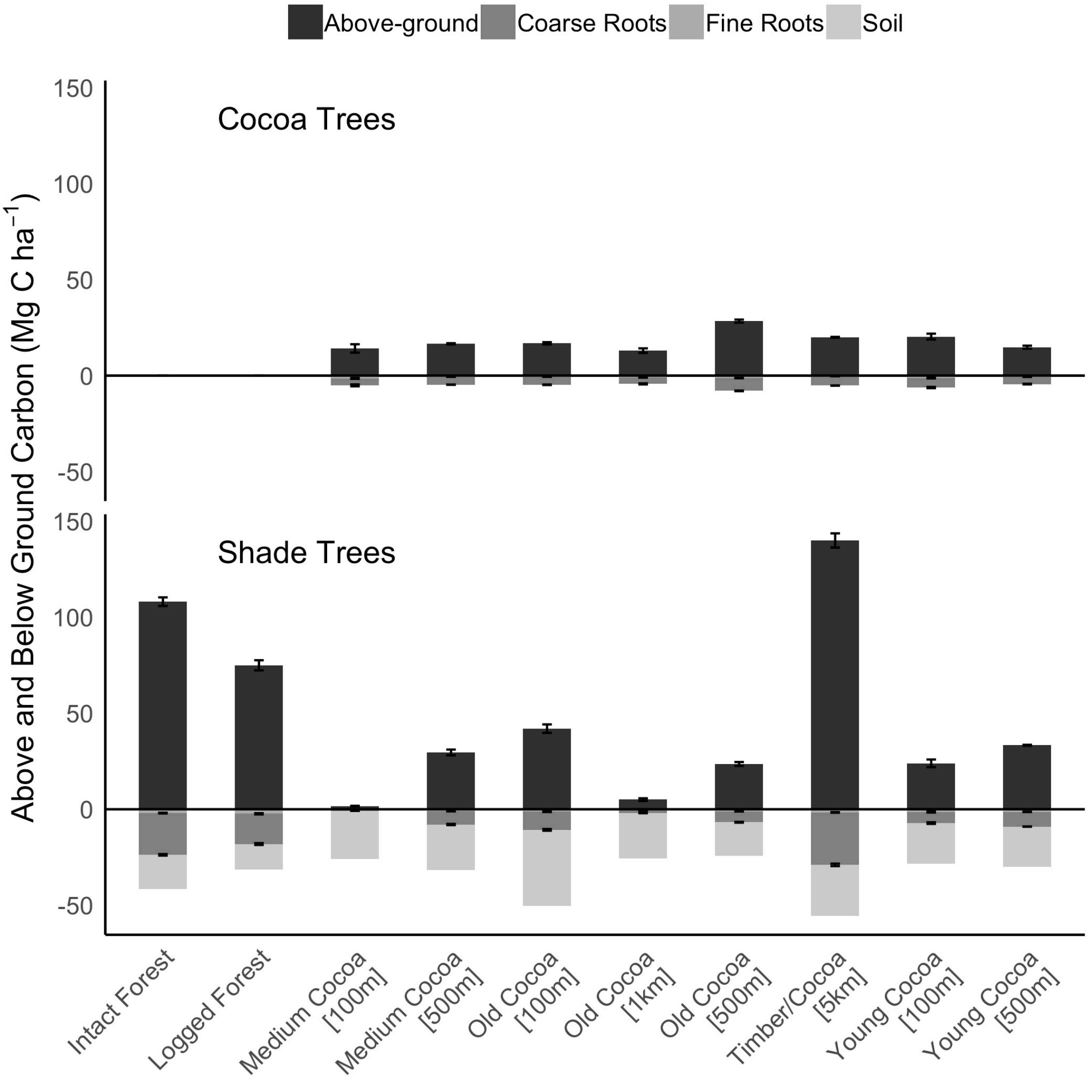

Figure 1 Above and below ground carbon stored in forest and cocoa plots with error bars representing ±1 SE. Carbon stored in cocoa trees represents all trees >2 cm DBH and soil values are for carbon stored in the top 30 cm.

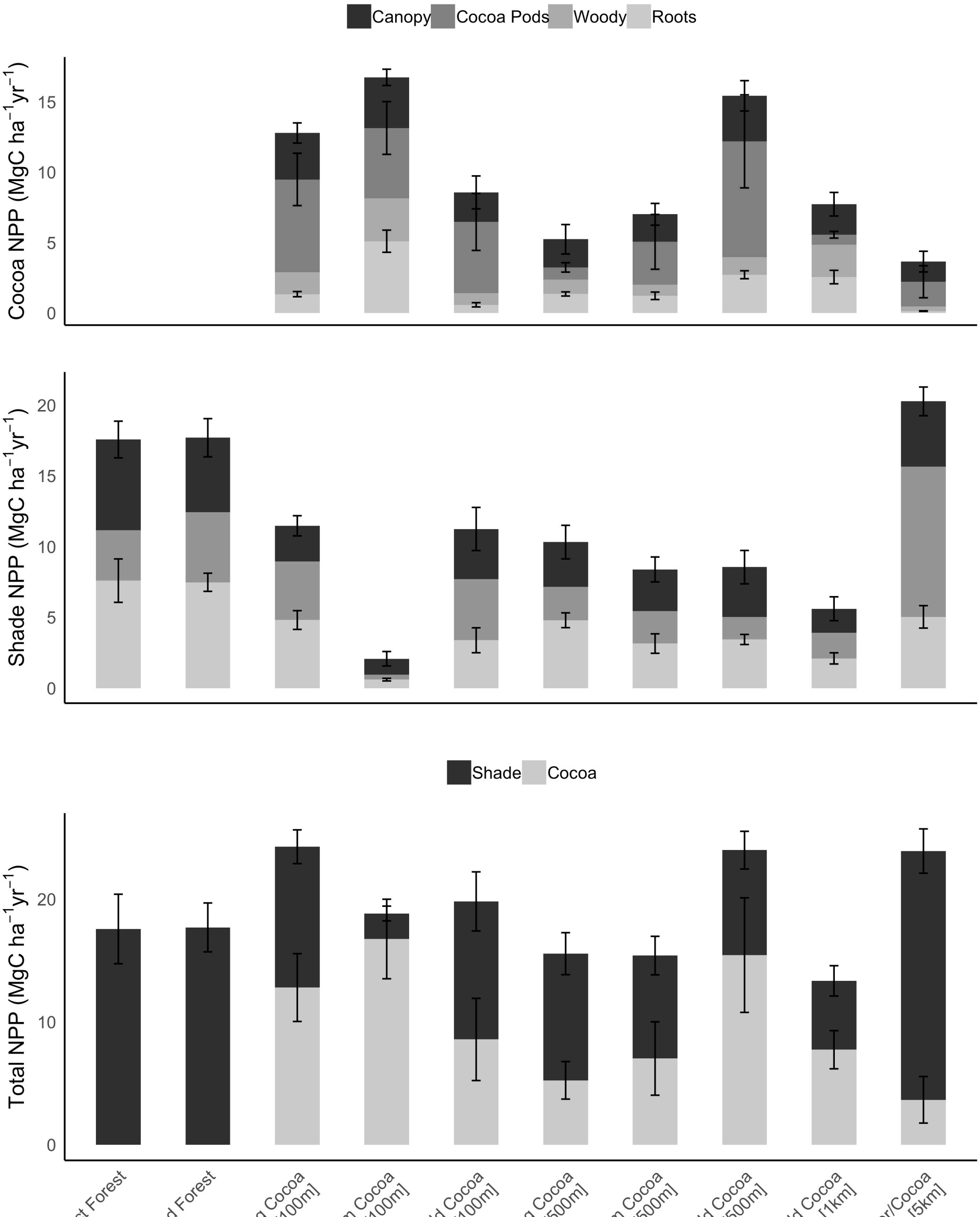

Figure 1 Total net primary productivity for cocoa trees (top), forest and shade trees (middle) and combined (bottom), shaded to indicate contributions from different components of NPP (e.g. woody, canopy, root and cocoa pods). Error bars represent ±1 SE.

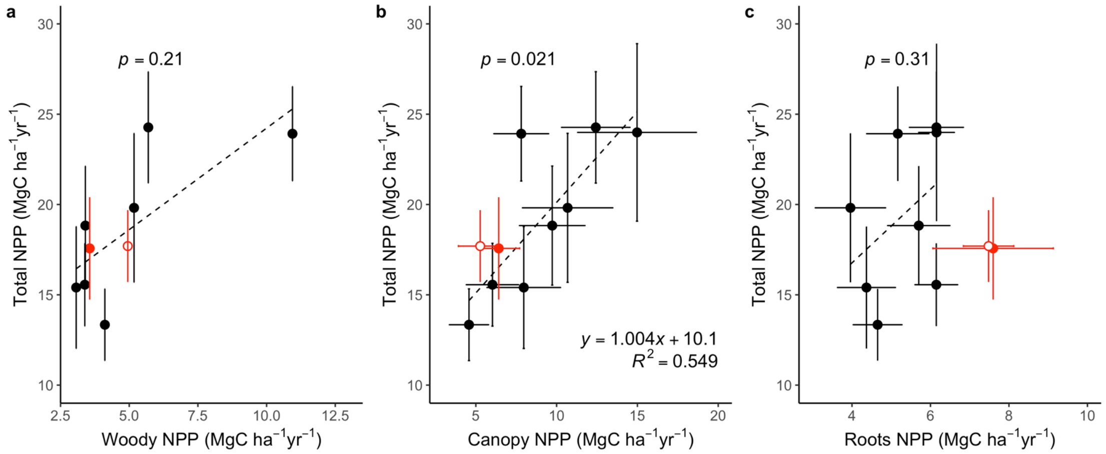

Figure 2 Total NPP as a function of NPP components: (a) above- and below ground coarse woody NPP, (b) canopy NPP and (c) fine root NPP, across monitored cocoa plots. Error bars signify ± 1 SE. Values for forest plots are plotted in red, intact (solid) and logged forest (hollow).

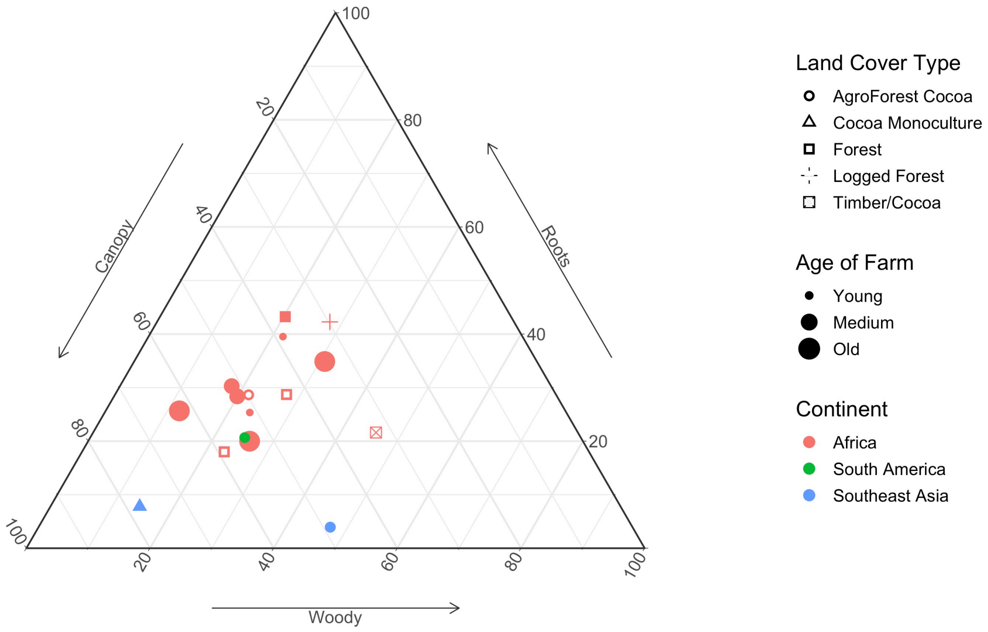

Figure 3 Ternary diagram of NPP allocation patterns across forest and cocoa plots. Size of symbol indicates age of shaded cocoa farms measured for this study including the average (hollow circle). Symbol shape indicates land cover type, including agroforest cocoa, monoculture cocoa, forest, logged forest and cocoa farm managed for timber. Forest plots from Moore et al (2017) are included (hollow squares) as well as cocoa measures from Abou Rajab et al (2016) and Beer et al (1990), coloured by continent.

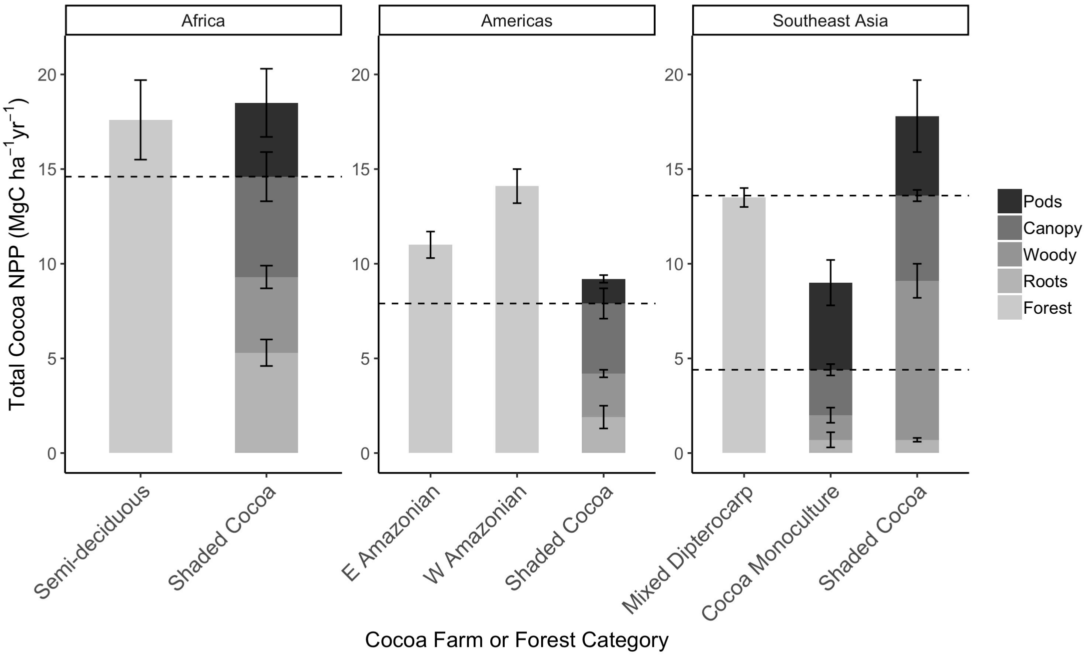

Figure 4 Comparison of average lowland tropical forest NPP and cocoa farm NPP published in the literature and this study by continent, reported in Table S1 and Table 4 respectively. Dashed lines indicate NPP for each cocoa farm type after harvest of pods and error bars are ± 1 SE.