

## REVIEW AND SYNTHESIS

# Temperature and rainfall interact to control carbon cycling in tropical forests

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### Abstract

Tropical forests dominate global terrestrial carbon (C) exchange, and recent droughts in the Amazon Basin have contributed to short-term declines in terrestrial carbon dioxide uptake and storage. However, the effects of longer-term climate variability on tropical forest carbon dynamics are still not well understood. We synthesised field data from more than 150 tropical forest sites to explore how climate regulates tropical forest aboveground net primary productivity (ANPP) and organic matter decomposition, and combined those data with two existing databases to explore climate – C relationships globally. While previous analyses have focused on the effects of either temperature or rainfall on ANPP, our results highlight the importance of interactions between temperature and rainfall on the C cycle. **In cool forests (< 20 °C), high rainfall slowed rates of C cycling, but in warm tropical forests (> 20 °C) it consistently enhanced both ANPP and decomposition.** At the global scale, our analysis showed an increase in ANPP with rainfall in relatively warm sites, inconsistent with declines in ANPP with rainfall reported previously. Overall, our results alter our understanding of climate – C cycle relationships, with high precipitation accelerating rates of C exchange with the atmosphere in the most productive biome on earth.

### Keywords

Carbon cycle, climate change, decomposition, net primary production, nutrient cycling, precipitation, temperature, tropical forest.

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## INTRODUCTION

Climate strongly regulates the terrestrial carbon (C) cycle. Relatively warm temperatures and high rainfall in equatorial regions sustain tropical forests that store and process large amounts of carbon dioxide (CO<sub>2</sub>) via plant productivity and ecosystem respiration. In doing so, tropical forests play a disproportionate role in terrestrial CO<sub>2</sub> exchange with the atmosphere, underscoring the importance of understanding how climatic variation governs rates of forest C cycling. For example, recent research has shown that the tropical forest C cycle is highly responsive to temporal variations in temperature and rainfall, and severe droughts in the Amazon Basin have been linked to increasing plant mortality and large, episodic C losses from tropical forests (Malhi *et al.* 2008; Lewis *et al.* 2011; Cleveland *et al.* 2015). Similarly, a recent study across 321 Amazonian forest plots showed a decline in C accumulation rates by *c.* 30% over the past decade compared to the 1990s, potentially due to increased average temperature across

the Amazon basin (Brienen *et al.* 2015). But while understanding these short-term (i.e. inter-annual to decadal) responses to climate variation is unquestionably important (Phillips *et al.* 2009; Lewis *et al.* 2011; Doughty *et al.* 2015; Rowland *et al.* 2015), longer-term increases in temperature and changes in precipitation are predicted to continue and perhaps accelerate in the coming century (Malhi *et al.* 2004; Wohl *et al.* 2012).

Understanding the response of tropical forest ecosystems to these longer-term changes – that is, timescales over which ecosystems will reorganise and quasi-equilibrate to a shifting climate – is critical to understanding global carbon and climate dynamics through the next century and beyond (Schimel *et al.* 1997; Cleveland *et al.* 2015). Past studies using a space-for-time substitution approach have clearly shown that both C inputs (via net primary production; NPP) and losses (via decomposition and soil respiration) increase with temperature and rainfall (Lieth 1975; Raich & Schlesinger 1992; Chapin *et al.* 2011). More recent efforts using newer tropical forest

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NPP data suggest that tropical forest aboveground NPP (ANPP) increases with mean annual precipitation (MAP) up to *c.* 3000 mm year<sup>-1</sup>, but declines with higher rainfall (Schuur 2003; Del Grosso *et al.* 2008). That decline was proposed to occur because of lower rates of nutrient cycling under progressively anoxic conditions (Schuur 2001; Schuur & Matson 2001; Schuur 2003), implying that plant – soil nutrient responses to long-term climate conditions may regulate rates of C cycling (e.g. Hobbie 2015). Relationships depicting a decline in ANPP with precipitation in very wet ecosystems (> 3000 mm year<sup>-1</sup>) have now been described and/or reproduced in multiple textbooks (e.g. Chapin *et al.* 2011; Smith & Smith 2012; Cain *et al.* 2013; Schlesinger & Bernhardt 2013), and imply that future increases in rainfall in forests that receive > 3000 mm year<sup>-1</sup> will drive long-term declines in tropical ANPP, and potentially alter the long-term tropical and global C balance (Phillips *et al.* 2009; Anderegg *et al.* 2013, 2015).

A historical paucity of information for wet, lowland tropical forest may have biased prior synthesis efforts (e.g. Schuur 2003). In the past two decades, however, there has been an increase in ecosystem research in lowland tropical regions, including the Center for Tropical Forest Science (CTFS) (Anderson-Teixeira *et al.* 2015), the Large Scale Biosphere-Atmosphere Experiment in Amazonia (LBA) (Avissar *et al.* 2002), the Amazon Forest Inventory Network (RAINFOR) (Malhi *et al.* 2002; Phillips *et al.* 2009), the Andes Biodiversity and Ecosystem Research Group (ABERG) (Malhi 2010), and the Global Ecosystem Monitoring Network (GEM). These and other efforts have led to a substantial increase in data from lowland tropical forests, providing a new opportunity to formally synthesise and re-examine C-climate relationships across the tropical biome, and globally.

Here, we gathered published data from individual field sites and a number of regional, plot-based monitoring networks located across the tropics to rigorously address the question: How do broad scale climate drivers [i.e. mean annual temperature (MAT) and mean annual precipitation (MAP)] regulate the tropical forest C cycle over the long term? We explored whether previously observed declines in C cycling with high rainfall persist given the substantial increase in available data from very wet lowland tropical forests. In addition, unlike past studies that examined the roles of temperature and precipitation independently, we explicitly investigated their potential interactive effects on tropical forest ANPP and decomposition rates. Finally, we combined our new dataset with previously existing datasets in an effort to increase our understanding of the effects of climate on the global C cycle.

To do so, we assembled published estimates of ANPP (the net C gained via plant growth on an annual basis, and the dominant C input vector in terrestrial forested ecosystems) and organic matter decomposition (*k*; reflecting rates of C loss as organic matter decays, and the primary C loss vector and nutrient recycling process in terrestrial ecosystems). Overall, we show that the magnitude and direction of ANPP and decomposition response to rainfall is highly dependent on mean annual temperature (and vice versa). Our results alter our understanding of the effects of rainfall on the ANPP and decomposition both in tropical forests and globally, and

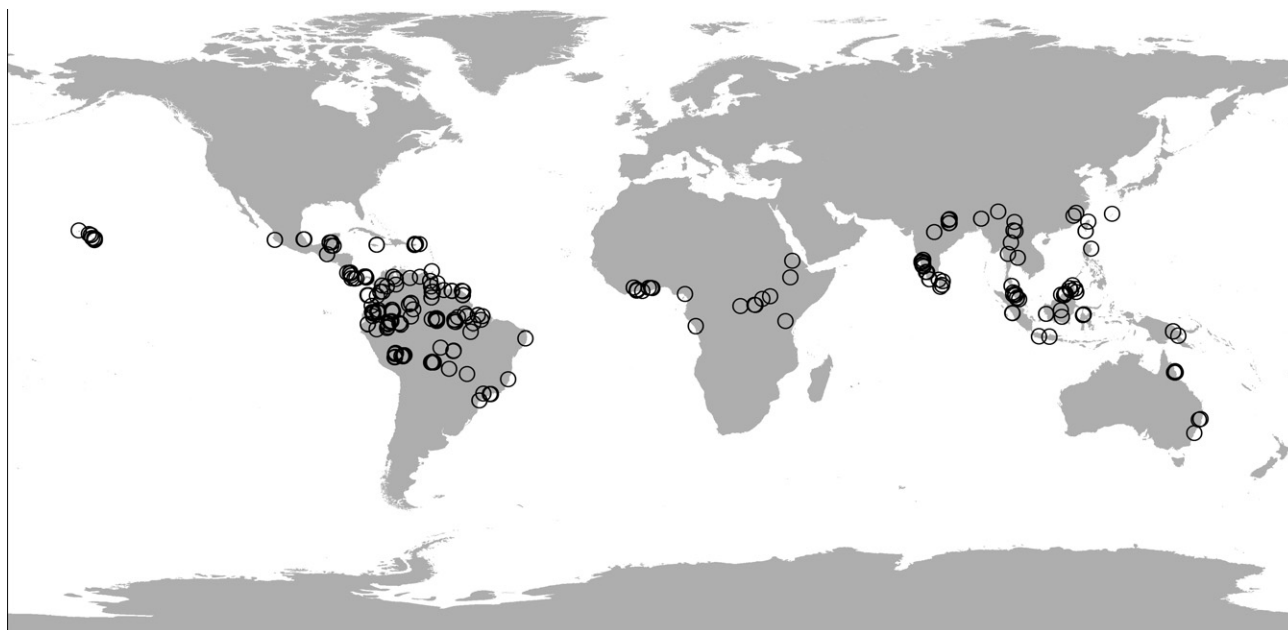
provide a new framework to understand and validate projections of ecosystem-scale C cycle responses to climate change (Randerson *et al.* 2009; Houghton *et al.* 2015; Negrón-Juárez *et al.* 2015; Smith *et al.* 2015).

## METHODS

We gathered and synthesised data from the peer-reviewed literature and explored relationships between climate and C cycling in tropical forest ecosystems. We conducted an extensive, web-based search for field measurements of ANPP (leaf production, approximated by fine litterfall; stem growth, approximated by diameter increase) and decomposition from forest sites located within tropical latitudes (i.e.  $\pm 23.5^\circ$  N and S). The resulting TROPICS database includes data from a broad range of primary and undisturbed tropical forests. Data from mangroves, secondary forests or heavily disturbed forests were excluded from the analysis. The final version of the TROPICS database contained plot measurements from more than 43 countries (Fig. 1), and included 145 measurements of total ANPP, 428 measurements of litterfall, 244 measurements of woody growth, and 138 measurements of litter decomposition. To explore the relationship between climate and ANPP globally, we combined the TROPICS data with two previously published databases (Schuur 2003; Del Grosso *et al.* 2008).

We calculated ANPP as the sum of litterfall and stem growth, the two most common measures of ANPP. Litterfall data were obtained from studies that included measurements made using common methods (Clark *et al.* 2001) for at least 12 months. In the majority of cases, litter collections occurred at *c.* 2 week intervals, but in some cases (e.g. in some tropical dry forest sites), litterfall was collected less frequently reflecting reduced risk of *in situ* litter decomposition during the dry season. When data on fruits, flowers, twigs (< than 2 mm diameter) and other miscellaneous material that accumulated in litterfall traps were reported, they were classified as fine litterfall (Clark *et al.* 2001). Aboveground NPP also includes C losses via herbivory, leaching, volatile organic compound emissions and *in situ* decomposition (Clark *et al.* 2001). However, since they are rarely measured and are not thought to account for a large proportion of ANPP (Greenberg *et al.* 2004; Kuhn *et al.* 2007), we did not attempt to estimate these fluxes.

Stem growth is typically estimated from repeated measurements of tree biomass in forest field plots. In most cases, measurements are collected on stems > 10 cm diameter at breast height (dbh; 1.3 m) that typically account for > 90% of the standing biomass in a field plot (Aiba & Kitayama 1999). Wood biomass is then estimated by applying allometric scaling equations to census data, which includes information on dbh and less frequently wood density and tree height (Chave *et al.* 2005; Feldpausch *et al.* 2010). As in other recent syntheses (Malhi *et al.* 2011; Hofhansl *et al.* 2015), we did not standardise allometric models for estimating woody growth due to the impracticality of coalescing raw plot data. Branch fall is a poorly understood component of woody growth (Malhi *et al.* 2011) that we did not correct for in ANPP calculations.



**Figure 1** Map illustrating the locations of the tropical forest sites used in the synthesis.

In most cases, litter decomposition values reported in the literature were generated using the litterbag method (e.g. Cleveland *et al.* 2006), but some were generated using mass balance estimates (e.g. Hobbie *et al.* 2006). The litterbag method measures the rate of mass loss of undecomposed litter placed in the field and sampled over a defined time period. The decomposition constant ( $k$ ) is estimated by fitting an exponential decay model to leaf litter mass loss curves: higher decomposition rates equate to higher  $k$  values (Robertson & Paul 2000). In some studies,  $k$  was assessed using a mass balance approach (the quotient of litterfall and litter standing crop). However, for sites where both types of measurements were used to generate  $k$ , the two methods produced very similar results ( $r = 0.94$ ,  $P < 0.001$ ; See Figure S1).

### Statistical analyses

We used regression modeling to explore the empirical relationship between our response variables (ANPP,  $k$ , litterfall, and stem growth) and predictor variables (MAT and MAP) in both the tropical and global datasets. We did not presume an *a-priori* model for the association between response and predictors but instead allowed the data to inform this relationship. We initially fit regression models using generalised additive modeling (GAM) which allowed us to visually examine the shape of response functions in a flexible and data-defined manner. We then used this information to structure a model selection procedure based on generalised linear modeling (GLM). Both ANPP and  $k$  showed evidence of being right-skewed with non-constant variance over the range of predictors. Consequently, we fit GLM models for these responses with a gamma error distribution and a square root link function. Additionally, MAP was right-skewed, so we transformed those data using a natural-log transformation.

Given the results from the GAM analysis, we began model selection using a base model that included a linear term for MAT and a second degree orthogonal polynomial term for ln (MAP). We used orthogonal polynomials for model selection because interpretation of regression terms is often hindered when individual monomials are highly correlated. We examined simplifications of the base model (i.e. a linear term for MAP) and whether the inclusion of an interaction term between MAT and MAP was justified using the Akaike Information Criterion (AIC) and adjusted proportion of deviance explained ( $D^2$ ) (Guisan & Zimmermann 2000). In all cases, the interaction between the climate covariates was supported (See Table S1). In order to provide an equation for each model surface, we refit final models using standard polynomial regression and present model coefficients (See Table S2).

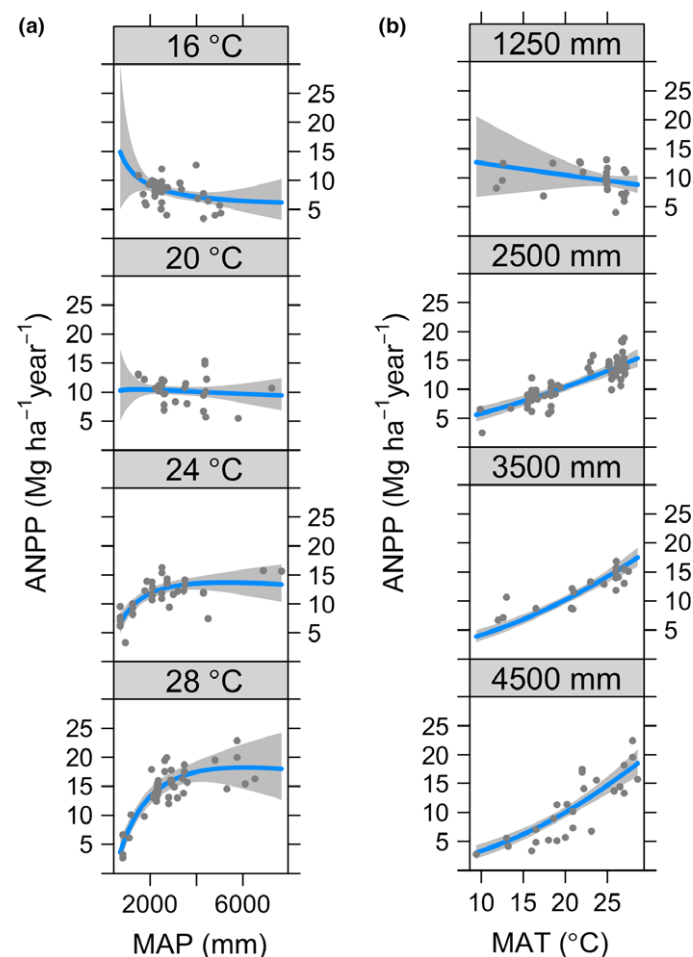
To visualise non-linear and interactive effects in our models, we used surface and cross-sectional plots. Surface plots provide a three-dimensional representation of the model response surface but do not readily portray model uncertainty and the distribution of partial residuals. Cross-sectional plots describe the relationship between the response and a predictor for a subset of values of a grouping variable (Breheny & Burchett 2013). Here we define the cross sections based on a single value of a grouping climate variable (MAT or MAP) such that partial residuals appear only once in the panel in which they are closest to. All data analysis was conducted using R (R Core Team 2015).

### RESULTS

Overall, our results highlight the importance of interactions between temperature and rainfall on the C cycle both in tropical and global forests. Among the sites in the TROPICS database for which litterfall and stem growth measurements were

both available, the effects of rainfall on total ANPP were highly temperature dependent (Fig. 2a). For example, at relatively low temperature sites ( $16^{\circ}\text{C}$ ), increasing rainfall had negative effects on ANPP (Fig. 2a). For sites nearest to  $20^{\circ}\text{C}$  MAT, there was little effect of increasing rainfall on ANPP. By contrast, in relatively warm sites (i.e.  $> 24^{\circ}\text{C}$ ), ANPP asymptotically increased and plateaued around precipitation values of  $4000\text{ mm year}^{-1}$ , but there was no evidence of negative effects of high rainfall on ANPP. Similarly, the effects of increasing temperature on ANPP increased with precipitation. At low rainfall, increases in temperature had negative effects on ANPP (Fig. 2b), but as rainfall increased from  $2500$  to  $4500\text{ mm year}^{-1}$ , there were positive, and increasing effects of temperature on ANPP (Fig. 2b).

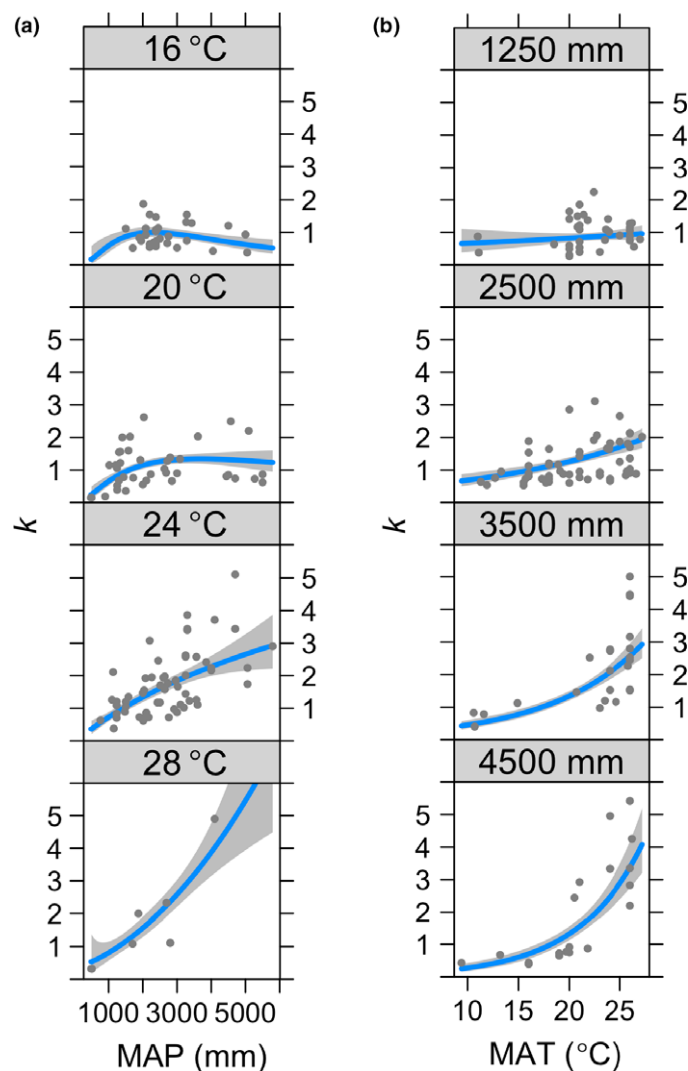
The effects of climate on the individual components of ANPP showed similar patterns and further underscore the importance of interactions between rainfall and temperature (See Figure S2). At relatively low temperature sites, litterfall decreased with increasing rainfall, but at warmer sites litterfall



**Figure 2** Cross-sectional plots showing the relationships between ANPP (dry weight), MAP (a), and MAT (b) for tropical forest sites as derived from a generalised linear model (Table S1). Cross-sectional plots depict the relationship between ANPP and MAP or MAT for a subset of values within the other grouping climate variable. Cross sections are defined by values of the grouping variable such that partial residuals appear only once in the grouping panel they are closest to. Gray bands depict 95% confidence intervals.

increased to an asymptote of  $c. 11\text{ Mg ha}^{-1}\text{ year}^{-1}$  at very high rainfall (See Figure S2). Similarly, stem growth decreased or showed little change with rainfall at low temperature sites but increased with rainfall in sites with MAT  $> 24^{\circ}\text{C}$ , with an obvious steepening of the relationship as rainfall increased (See Figure S3).

Decomposition dynamics among sites in the TROPICS database also reflected the effects of strong interaction between temperature and rainfall on  $k$  values (Fig. 3). At low temperature sites ( $16^{\circ}\text{C}$ ), rainfall in excess of  $c. 2000\text{ mm year}^{-1}$  had negative effects on decomposition (Fig. 3a). At  $20^{\circ}\text{C}$ , decomposition increased with rainfall to  $c. 2000\text{ mm year}^{-1}$ , but further increases in rainfall had neutral to slightly negative effects on  $k$ . At warm sites ( $> 24^{\circ}\text{C}$ ),



**Figure 3** Cross-sectional plots showing the relationships between decomposition ( $k$ ), MAP (a), and MAT (b) for tropical forest sites as derived from a generalised linear model (Table S1). Cross-sectional plots depict the relationship between  $k$  and MAP or MAT for a subset of values within the other grouping climate variable. Cross sections are defined by values of the grouping variable such that partial residuals appear only once in the grouping panel they are closest to. Gray bands depict 95% confidence intervals.



increasing rainfall had strong positive effects on decomposition. All of the highest decomposition rates in the database were from warm, wet sites, with evidence that rates increased exponentially with rainfall and temperature (Fig. 3b) at the warmest and wettest tropical sites (Fig. 3b).

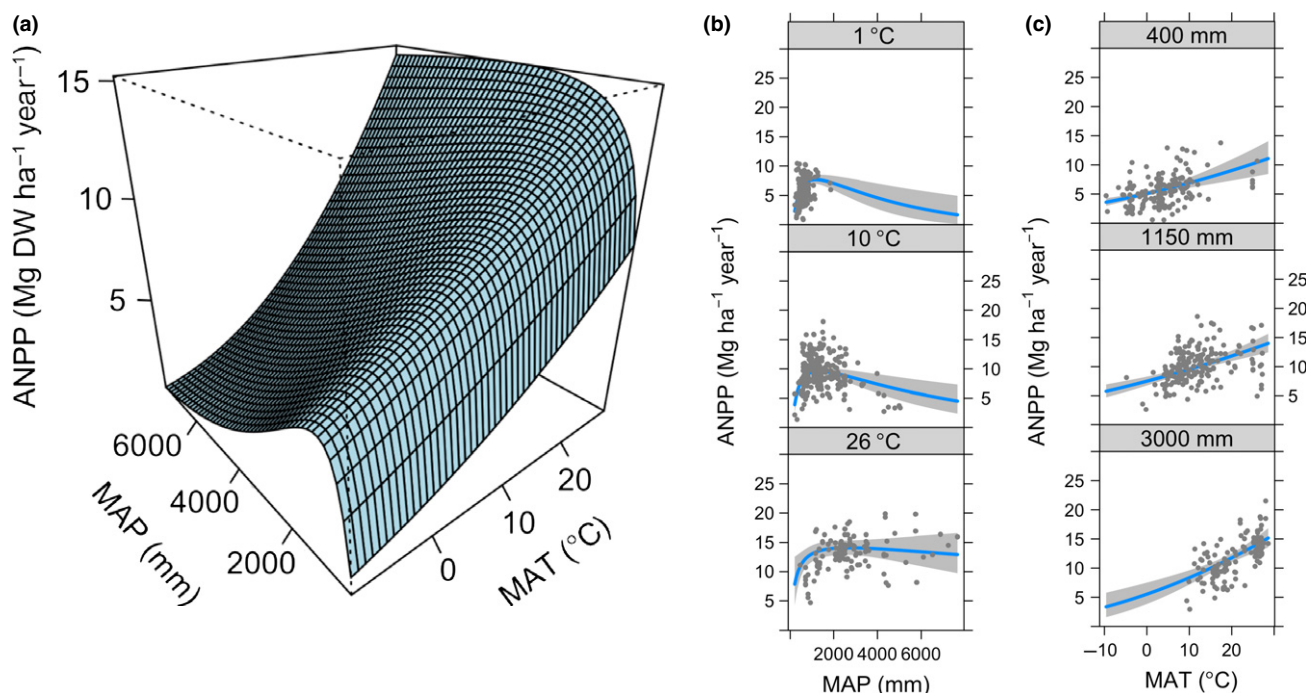
When we combined the TROPICS data with the existing global datasets, the importance of the interaction between rainfall and temperature on ANPP in the tropical database was also obvious (Fig. 4a). At sites with low MAT (1 and 10 °C cross sectional plots; Fig. 4b), ANPP increased with rainfall up to *c.* 2000 mm year<sup>-1</sup>, but further increases in rainfall had negative effects on ANPP. In contrast, in warm sites (26 °C), ANPP increased with rainfall to *c.* 2000 mm year<sup>-1</sup>, but further increases in rainfall had neutral to perhaps slightly negative effects on ANPP. Similarly, rates of ANPP increased most rapidly with temperature at wet sites (Fig. 4c).

## DISCUSSION

Some previous syntheses have focused on the effect of either temperature or precipitation on NPP (Lieth 1975; Schuur 2003; Del Grosso *et al.* 2008; Knapp *et al.* 2016; Chu *et al.* 2016), but our analysis clearly demonstrates that interaction between temperature and rainfall are essential to understanding climate controls over both plant productivity and decomposition. The influence of rainfall on ANPP and *k* varies with temperature (Fig. 2; Fig. 3). In cooler tropical forests (*c.* 20 °C and below), rainfall in excess of *c.* 3000 mm year<sup>-1</sup> reduces both ANPP and *k*, consistent with past global

syntheses (Schuur 2003; Del Grosso *et al.* 2008). In warmer sites, however, increasing rainfall enhances both ANPP and *k*, which is inconsistent with previous understanding of climate – forest C cycling relationships. We argue that focusing on a single-factor climate control (i.e. regressing ANPP or *k* as a function of either MAP or MAT) precludes the ability to detect the temperature dependency of rainfall effects on forest C cycling, and belies the demonstrated importance of such interactions on vegetation productivity and plant distributions via the climatic water balance (Stephenson 1990; Schimel *et al.* 1997; Dobrowski *et al.* 2012; Restaino *et al.* 2016). As well, the prior scarcity of data from very warm forests with high rainfall unquestionably limited our ability to detect the differential effects of rainfall on C cycling in cool vs. warm tropical forests (Figs 2 and 3).

What mechanisms could lead to the variable effects of rainfall with temperature? The parallel responses of both ANPP and *k* across all tropical forests ecosystems (Figs 2 and 3) suggest the importance of plant – soil nutrient feedbacks in driving climatic responses. Generally, ANPP increases with greater rainfall because water is a limiting resource for plant growth, up to a point (e.g. Sala *et al.* 1988; Chu *et al.* 2016; Knapp *et al.* 2016). However, once precipitation exceeds plant demand (i.e. when precipitation exceeds hydrologic losses via evapotranspiration and runoff), the influence of further increases in rainfall on ANPP is likely indirect. The vast majority of forests with MAT < 20 °C in the tropical biome are montane ecosystems, where very high rainfall can saturate soils, promote soil anoxia (e.g. Silver *et al.* 1999; Schuur & Matson 2001), and reduce soil decomposition rates by



**Figure 4** Surface (a) and cross-sectional plots (b, c) showing the relationships between ANPP (dry weight), mean annual temperature (MAT), and MAP for global forest sites as derived from a generalised linear model (Table S1). Cross-sectional plots depict the relationship between ANPP and MAP (b) or MAT (c) for a subset of values within the other grouping climate variable. Cross sections are defined by values of the grouping variable such that partial residuals appear only once in the grouping panel they are closest to. Gray bands depict 95% confidence intervals.

restricting microbial and root metabolism (Liptzin & Silver 2015). In these cool, wet ecosystems, slower litter decay ( $k > 1$ ) can also enhance soil organic matter accumulation, reduce nutrient recycling rates, and limit nutrient availability for plant growth (Gonçalves & Carlyle 1994; Tanner *et al.* 1998; Rustad *et al.* 2001; Fahey *et al.* 2016). These more organic-rich surface soils can absorb water and retain nutrients bound within organic matter (Grieve *et al.* 1990), thereby reinforcing a slow nutrient feedback between plant and soil systems that may negatively affect plant growth. In fact, cool, montane tropical forest ecosystems often exhibit low soil nutrient availability and conservative nutrient cycling (but see Brookshire *et al.* 2012a,b), evidenced by positive effects of nitrogen and phosphorus fertilizer applications on productivity (e.g. Homeier *et al.* 2012; Fisher *et al.* 2013; Fahey *et al.* 2016) soil nutrient cycling (e.g. Baldos *et al.* 2015; Nottingham *et al.* 2015) and plant biogeochemistry (e.g. Martinelli *et al.* 1999; Asner & Martin 2016).

Alternatively, factors other than temperature that vary with altitude (e.g. atmospheric pressure, radiation and cloudiness) could also work to reduce ANPP as rainfall increases in these cooler, montane forests (e.g. Bruijnzeel & Veneklas 1998; Hofhansl *et al.* 2015; Fahey *et al.* 2016; Malhi *et al.* 2016). For example, cloud immersion can reduce ANPP by restricting solar radiation and/or evapotranspiration (Girardin *et al.* 2010; Fahey *et al.* 2016), which could indirectly affect C cycling by influencing ecosystem water balance. A recent study (Malhi *et al.* 2016) along a 3000 m tropical elevation gradient found no significant change in carbon use efficiency, but a linear reduction of gross primary production (GPP) at higher elevations. Such a decline in GPP could be due to a nutrient induced reduction in light-saturated leaf photosynthetic capacity, a decline in realised rates of leaf-level photosynthesis such as through increased cloudiness or increased leaf wetness (Goldsmith *et al.* 2013) or through a decline in canopy leaf area. Though the factors that influence plant allocation, productivity and biomass with elevation are still being investigated (Bruijnzeel *et al.* 2010; Fahey *et al.* 2016; Malhi *et al.* 2016), a suite of environmental factors and interactions likely contribute to the decline in ANPP with rainfall in excess of plant demand in cool tropical forests.

In contrast, both ANPP and  $k$  increased with rainfall in relatively warm (mostly lowland) tropical forests (Figs 2 and 3). There, rainfall accelerates plant – soil nutrient feedbacks: high rainfall (Cusack *et al.* 2009) and warm temperatures (Salinas *et al.* 2011) combine to enhance decomposition by maximising decomposer activity and promoting physical leaching of forest floor material (Wieder *et al.* 2009; Cleveland *et al.* 2010). Nutrient mineralisation during litter decomposition provides the bulk of nutrition for new production (Vitousek 1984), thus high rates of decomposition – often much faster than 1 year (Fig. 3) – translate to greater nutrient fluxes needed to fuel high plant growth rates (Cleveland *et al.* 2006; Wieder *et al.* 2009; Corre *et al.* 2010). In addition, with higher rates of rainfall, increasing thermal sensitivity of decomposition suggests that decomposition and ANPP rates would be maximised in the wettest, warmest tropical forests (Figs 2 and 3).

There are several other noteworthy features of the climate – C cycling patterns we observed. First, two recent studies

suggested that 20 °C MAT may represent a temperature ‘threshold’ where patterns in C and nutrient cycling diverge in progressively cooler vs. warmer forests (Cleveland *et al.* 2011; Hofhansl *et al.* 2014). Our analyses support that notion; note, for example, the flat relationships between climate variables and C metrics at 20 °C (Figs 2 and 3). We posit that in forests where MAT > 20 °C and where annual litterfall decays very rapidly (< 1 year), the factors that promote anoxic slow-downs in cooler environments are largely absent. Rather, rapid decomposition of leaf litter prevents the accumulation of true organic horizons that store and retain nutrients. Instead, high rainfall and warm temperatures drive rapid release of nutrients from plant litter (e.g. Wieder *et al.* 2009), creating and reinforcing a positive and tight feedback between plant productivity and growth (e.g. Hobbie 2015). The apparent temperature inflection around 20 °C for both ANPP and  $k$  and its implications are worthy of further investigation.

That said, warm forest ecosystems exhibit a saturating response of ANPP to rainfall (Fig. 2) while rates of decomposition do not (Fig. 3). What potential mechanism(s) could explain this divergence? First, there may be progressive decoupling between soil nutrient supply and plant demand in wet forests, thereby limiting the response of ANPP to greater rainfall. In the wettest, warmest forests, temperature and rainfall accelerate decomposition rates to time periods < 6 months (i.e.  $k > 2$ ; Fig. 3), suggesting that the bulk of nutrient mineralisation may occur too rapidly to sustain sufficient nutrient pools to support optimal plant growth. Such rapid mineralisation rates, coupled with high rates of hydrologic and erosional losses, also constrain overall system fertility in the long term (Hedin *et al.* 2003; Houlton *et al.* 2008; Bai & Houlton 2009; Brookshire *et al.* 2012a,b; Taylor *et al.* 2015), and might also help to explain the progressive shift toward conservative (tight) nutrient cycling observed in some very wet tropical forests (Posada & Schuur 2011; Wieder *et al.* 2011; Craine *et al.* 2015; Taylor *et al.* 2015). Alternatively, forests with very high rainfall may also experience lower solar radiation due to increased cloudiness, potentially limiting photosynthetic rates (Graham *et al.* 2003), but the relationship between precipitation and solar radiation is often not straightforward (Banin *et al.* 2012). Finally, the saturating relationship may reflect upper limits on ANPP that are governed by factors operating at other ecological scales, from community dynamics to evolutionary history. The mechanisms that govern how rainfall affects ANPP and decomposition in lowland tropical ecosystems are less clear than montane ecosystems, but warrant further study.

The importance of other drivers on C cycling can be seen in the relationships presented here. While unquestionably important, climate only explains 44 and 53% of the total model deviance in tropical forest ANPP and  $k$ , respectively (See Table S1). Unmeasured climatic effects, such as dry season length and cloudiness, also likely play a role (Hofhansl *et al.* 2014), as well as variation in other state factor controls. Soil fertility, forest composition, topography and disturbance history can also strongly influence forest C cycling (e.g. Raich *et al.* 1997; Aiba & Kitayama 1999; Paoli *et al.* 2008; Cleveland *et al.* 2011; Moser *et al.* 2011; Quesada *et al.* 2012; Asner *et al.* 2015; Girardin *et al.* 2010). Resolving other controls on

rates of ecosystem C exchange will require more holistic biogeochemical research alongside field inventories of forest C budgets.

Belowground NPP also likely plays a substantial role in forest C productivity (Malhi *et al.* 2011, 2015), but is rarely measured. A recent study found that ANPP may be a good predictor of total NPP (above- and belowground components), and therefore the climate response of ANPP might be a proxy for total NPP response (Malhi *et al.* 2011). Yet, plant allocation into above- vs. belowground productivity is quite variable and may be differentially responsive to climate conditions. For example, following a major Amazonian drought, six one-hectare forests plots showed no net change in total NPP (Doughty *et al.* 2015). Another Amazonian study found a decrease in gross primary production from 25 to 40 Mg C ha<sup>-1</sup> year<sup>-1</sup> from the wettest plots to the driest plots, but that changes in total NPP were difficult to explain because moisture stress caused large changes in C use efficiency (Malhi *et al.* 2015). Finally, studies along elevation transects that include full ecosystem carbon accounting show that trees tend to allocate proportionally more NPP belowground at higher, colder altitudes (Leuschner *et al.* 2007; Girardin *et al.* 2010; Homeier *et al.* 2012), potentially masking the apparent effect of temperature observed on ANPP (see Fig. 2). Ultimately, the climate sensitivity of ecosystem productivity and C allocation are still unclear, and will be important to resolve to understand the impact of long-term climate conditions on whole-ecosystem C dynamics (e.g. Hofhansl *et al.* 2014, 2015).

At the global scale, our work reveals forest C – climate relationships that are very different from previous global analyses (Schoor 2003; Del Grosso *et al.* 2008) (Fig. 4a). Namely, with ANPP from many more locations than were previously available, our analysis revealed strong interaction between MAT and MAP, and suggests an increase – not a decline – in ANPP with rainfall at warm sites (Fig. 4). Thus, we argue that while previously documented rainfall – C cycling models (e.g. Schoor 2003; Del Grosso *et al.* 2008) may be broadly relevant to forests with MAT < 20 °C, they do not adequately capture the effects of climate on C cycling in the overwhelming majority of warm subtropical and tropical forests – forests that disproportionately regulate terrestrial CO<sub>2</sub> exchange (Fig. 4a). While the patterns revealed here do not speak to how rapid climatic change may influence forest C cycling on time-scales shorter than ecosystem equilibration to long-term climatic conditions, our findings revise expectations for how forest regions may respond to projected long-term changes in warming and rainfall (e.g. Cox *et al.* 2004; Neelin *et al.* 2006; England *et al.* 2015).

Finally, our findings also raise important questions for policy and conservation strategies that seek to protect valuable ecosystem services in tropical regions. For example, wet tropical forests have among the highest rates of aboveground forest productivity in our analyses (Fig. 4), are often among the most species rich forests of the tropics, and are thought to represent a large C sink (Stephens *et al.* 2007; Pan *et al.* 2011; Phillips & Lewis 2014; Houghton *et al.* 2015). Our analyses suggest that current efforts to develop and refine tropical forest representations in Earth system models should incorporate the temperature-dependency of rainfall- forest C cycling

relationships shown here. In addition, more experimental studies are needed to resolve the effects of climate on the edaphic and biogeochemical factors that likely underpin the varied C cycle responses to climate that we observed.

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## AUTHORSHIP

PT, CC, WW and AT designed the study. PT assembled the database, PT, WW, BS, and SD analysed the data, PT and CC wrote the paper, and all authors edited drafts and contributed to the revisions.

## DATA ACCESSIBILITY

Data used in this analysis are available at the public repository at NCEAS (<https://data.nceas.ucsb.edu/#view/knb.1274.1>), doi:10.5063/F19021QT.

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