



## Variation in above-ground forest biomass across broad climatic gradients

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### ABSTRACT

**Aim** An understanding of the relationship between forest biomass and climate is needed to predict the impacts of climate change on carbon stores. Biomass patterns have been characterized at geographically or climatically restricted scales, making it unclear if biomass is limited by climate in any general way at continental to global scales. Using a dataset spanning multiple climatic regions we evaluate the generality of published biomass–climate correlations. We also combine metabolic theory and hydraulic limits to plant growth to first derive and then test predictions for how forest biomass should vary with maximum individual tree biomass and the ecosystem water deficit.

**Location** Temperate forests and dry, moist and wet tropical forests across North, Central and South America.

**Methods** A forest biomass model was derived from allometric functions and power-law size distributions. Biomass and climate were correlated using extensive forest plot (276 0.1-ha plots), wood density and climate datasets. Climate variables included mean annual temperature, annual precipitation, their ratio, precipitation of the driest quarter, potential and actual evapotranspiration, and the ecosystem water deficit. The water deficit uniquely summarizes water balance by integrating water inputs from precipitation with water losses due to solar energy.

**Results** Climate generally explained little variation in forest biomass, and mixed support was found for published biomass–climate relationships. Our theory indicated that maximum individual biomass governs forest biomass and is constrained by water deficit. Indeed, forest biomass was tightly coupled to maximum individual biomass and the upper bound of maximum individual biomass declined steeply with water deficit. Water deficit similarly constrained the upper bound of forest biomass, with most forests below the constraint.

**Main conclusions** The results suggest that: (1) biomass–climate models developed at restricted geographic/climatic scales may not hold at broader scales; (2) maximum individual biomass is strongly related to forest biomass, suggesting that process-based models should focus on maximum individual biomass; (3) the ecosystem water deficit constrains biomass, but realized biomass often falls below the constraint; such that (4) biomass is not strongly limited by climate in most forests so that forest biomass may not predictably respond to changes in mean climate.

### Keywords

Climate change, embolism, evapotranspiration, forest carbon storage, SALVIAS, tree height, tropical/temperate forests, water deficit, wood density.

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## INTRODUCTION

Change in forest biomass in response to global change, including changes in climate, land use and atmospheric composition, is expected to have a strong influence on the future course of climate change (Laurance *et al.*, 1997; Hurtt *et al.*, 1998; Phillips *et al.*, 1998; Clark *et al.*, 2003; Baker *et al.*, 2004a; Malhi & Phillips, 2004; Meiri *et al.*, 2006). However, we still know relatively little about how the abiotic environment influences variation in the biomass of forested ecosystems. Before we can develop more detailed predictions of how terrestrial carbon stores could be altered under future global change, it is thus necessary to improve our understanding of how abiotic factors influence current stocks of forest biomass.

A growing number of studies have proposed factors that govern forest biomass. These studies have highlighted several climatic variables including mean annual temperature (Raich *et al.*, 2006), annual precipitation (Sankaran *et al.*, 2005), the ratio of mean annual temperature to annual precipitation (Brown & Lugo, 1982), the combination of mean annual temperature and annual precipitation (Keith *et al.*, 2009), and precipitation of the driest quarter (Saatchi *et al.*, 2007). Non-climatic factors such as disturbance (Chave *et al.*, 2001), nutrient availability (van Groenigen *et al.*, 2006) and productivity (Whittaker & Likens, 1973; Kerkhoff & Enquist, 2006; Keeling & Phillips, 2007) also appear to be important in some systems. If at least some of these factors are causal and influence forest biomass in a consistent manner across broad geographic scales and climatic gradients (e.g. Keith *et al.*, 2009), they could be used to predict the influence of global change on standing biomass. Such predictions will be essential for understanding feedbacks between climate change and plant community carbon storage (Cox *et al.*, 2000).

Many forest biomass studies are based on empirical correlations restricted to a single forest type, and have relatively few samples or are limited in their geographic extent (but see Keith *et al.*, 2009). For example, Raich *et al.* (2006) sampled 22 plots within moist tropical forests, while Brown & Lugo (1982) sampled across tropical forest types, but with only 31 sites. Although patterns described in these studies are certainly relevant to the scale at which they were characterized, it is unclear if patterns found in previous studies should be extrapolated to a larger geographic scale and climatic scope. To understand potential feedbacks between global change and carbon stored in standing biomass, however, predictions are needed at the global scale.

To determine if robust global-scale predictions can be made, we pursue three primary goals, one theoretical and two empirical. On the theory side we place forest biomass in a theoretical framework by recognizing that biomass reflects the combination of the distribution of individual tree masses and the number of trees in a community. We show that combining the individual size distribution with abundance predicts that biomass should be strongly correlated with the biomass of the largest tree. This suggests that if climate does influence forest biomass it is fundamentally through an influence on maximum individual tree

biomass such that models for forest biomass could be built by considering the limitations to maximum individual biomass. Along these lines, we develop a conceptual model linking climate to maximum individual biomass and forest biomass. Subsequent to developing theory related to forest biomass in the following two subsections, we characterize forest biomass–climate relationships and compare these empirical patterns with our theoretical predictions.

Our first empirical approach examines forest biomass directly by regressing forest biomass against a suite of climate variables. The empirical data vary across a broad range of climate regimes that include temperate, dry tropical, moist tropical and wet tropical forests distributed across North, Central and South America. The climatic variables used in these analyses include mean annual temperature, annual precipitation, the ratio of mean annual temperature to annual precipitation, and the precipitation of the driest quarter. These variables were chosen because previous studies have related them to forest biomass. We are therefore able to evaluate the generality of previously documented biomass–climate relationships within the ecosystems for which they were originally developed.

Our second empirical approach primarily examines forest biomass indirectly by evaluating the key components of forest biomass, and works towards a more mechanistic understanding of how climate influences forest biomass. As shown in our theoretical derivations, when community abundance varies with mean individual tree biomass as a power function, maximum individual biomass is expected to strongly govern total forest biomass. As such, we examine the relationship between abundance and mean tree size, which is found to be well approximated as a power function. Subsequently, we characterize the relationship between maximum individual biomass and forest biomass, which supports the prediction that maximum individual biomass governs forest biomass. In turn, we test our conceptual expectation that maximum individual biomass and forest biomass are related to the ecosystem water deficit in the form of constraint functions. Upon finding support for this prediction, we evaluate how the components of the water deficit, potential and actual evapotranspiration, relate to maximum individual biomass and forest biomass.

## METHODS

### Modelling forest biomass: partitioning the components of community biomass

We start by developing an analytical model for variation in forest biomass. Our model recognizes the fact that the total biomass of a forest ( $M_{\text{tot}}$ ) is equal to the product of the number of individuals ( $N$ ) and the mean tree biomass ( $\bar{M}$ ) in a community such that  $M_{\text{tot}} = N\bar{M}$ . As an alternative to modelling biomass directly, these two components are considered separately. If  $N$  and  $\bar{M}$  vary independently then theoretical developments of forest biomass would require two models, one for  $N$  and another for  $\bar{M}$ . However,  $N$  and  $\bar{M}$  often covary, typically as a power function of the form  $N = a\bar{M}^{-b}$  (Li, 2002; White *et al.*,

2007), where  $a$  is a normalization constant independent of tree mass. Therefore,  $M_{\text{tot}}$  can be described as

$$M_{\text{tot}} = a\bar{M}^{-b}\bar{M} = a\bar{M}^{1-b}. \quad (1)$$

Any residual variation in  $N$  not explained by  $\bar{M}$ , while potentially important for predicting  $M_{\text{tot}}$ , will not affect the general form of this relationship.

To model  $\bar{M}$  we consider that tree community size distributions have been hypothesized to be described by power functions (Enquist & Niklas, 2001; White *et al.*, 2007, 2008; Stegen & White, 2008; Enquist *et al.*, 2009; West *et al.*, 2009), such that the individual size distribution can be approximately characterized by  $f(M) = cM^\alpha$ , where  $M$  is tree mass ( $c$  is defined below). We begin by assuming  $\alpha = -11/8$  as this value of  $\alpha$  is expected for an idealized (i.e. space filling) forest in resource and demographic steady state and has empirical support (Stegen & White, 2008; Enquist *et al.*, 2009; West *et al.*, 2009; but see Muller-Landau *et al.*, 2006). These simplifying assumptions, while certainly not upheld across all forests, allow us to estimate the factors governing forest biomass. So that  $f(M)$  is a valid probability density function, in the form of the truncated Pareto (Page, 1968; Aban *et al.*, 2006), the coefficient,  $c$ , is defined as  $(\alpha + 1)(M_{\text{max}}^{\alpha+1} - M_{\text{min}}^{\alpha+1})^{-1}$  (see White *et al.*, 2008). Here,  $M_{\text{min}}$  and  $M_{\text{max}}$  are the sizes (biomass) of the smallest and largest trees in a community. Integrating  $f(M)M \, dM$  from observed  $M_{\text{min}}$  to observed  $M_{\text{max}}$  (which may be smaller than the biomass of the largest tree that could grow in a location) gives average individual mass as

$$\bar{M} = \frac{-0.6(M_{\text{max}}^{5/8} - M_{\text{min}}^{5/8})}{(M_{\text{max}}^{-3/8} - M_{\text{min}}^{-3/8})}. \quad (2)$$

Equation 2 shows that average individual mass is governed primarily by  $M_{\text{max}}$ , and to a lesser extent by  $M_{\text{min}}$ . Substituting equation 2 into equation 1 shows that  $M_{\text{tot}}$  is at least indirectly determined by  $M_{\text{max}}$ , but also by the observed values of  $a$  and  $b$  in  $N = aM^{-b}$ :

$$M_{\text{tot}} = a \left[ \frac{-0.6(M_{\text{max}}^{5/8} - M_{\text{min}}^{5/8})}{(M_{\text{max}}^{-3/8} - M_{\text{min}}^{-3/8})} \right]^{1-b}. \quad (3)$$

Furthermore,  $M_{\text{min}}$  should be less variable across forests than  $M_{\text{max}}$  such that variation in  $M_{\text{max}}$  will be responsible for the majority of variation in  $M_{\text{tot}}$ . One caveat is that this prediction assumes that the individual size distribution can be approximated by  $f(M) = cM^\alpha$ . Strong departures from this assumption, in heavily disturbed or even-aged stands for example, will lead to different relationships among mean, maximum and minimum tree size. While there are certainly important departures (e.g. Muller-Landau *et al.*, 2006), the individual size distributions of many forests are at least roughly characterized by a power function such that equation 3 is broadly relevant.

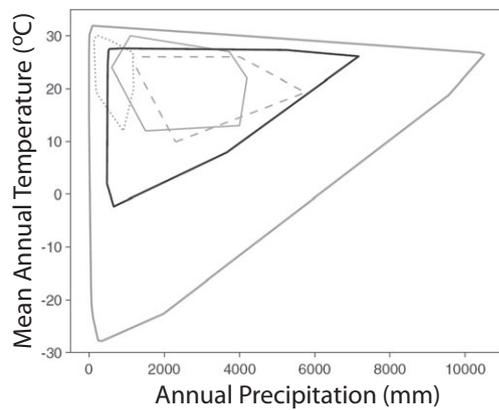
## Modelling forest biomass: what determines the biomass of the largest tree?

Equations 2 & 3 show that the biomass of the largest tree should have an important influence on stand biomass, and it is therefore important to determine the factors that limit maximum individual biomass. It has been hypothesized that maximum tree height is limited by stress on the water column (the hydraulic limitation hypothesis; Ryan and Yoder, 1997), and this hypothesis has received some empirical support (Midgley, 2003; Koch *et al.*, 2004; Ryan *et al.*, 2006). The basic tenet of the hydraulic limitation hypothesis is that taller trees exhibit increased stomatal closure due to an increase in hydraulic resistance with tree height combined with the need to maintain a minimum leaf water potential to avoid catastrophic embolism (Ryan *et al.*, 2006). For water to move vertically, the leaf water potential must decline with increasing tree height (Koch *et al.*, 2004). Furthermore, to extract water from the soil a tree's root water potential must be lower than that of the soil. The  $y$ -intercept of the function relating leaf water potential to height should therefore decline as the soil water potential becomes more negative. As water becomes less available to plants (i.e. the water potential of the soil decreases) hydraulic limitation will occur at increasingly smaller sizes. That is, at lower soil water potential, a tree's minimum water potential will be reached at a shorter height and therefore at lower mass. Other aspects of tree morphology such as basal area, crown area, leaf number and total leaf mass should also decrease towards lower soil water potentials. At broad geographic scales, the soil water potential is negatively related to the ecosystem water deficit, approximated as the difference between potential and actual evapotranspiration (Stephenson, 1990, 1998). The largest possible biomass, as set by the water deficit, is not likely to be realized across all forests, so we hypothesize that the upper bound on maximum individual biomass will decline with the water deficit. Given equation 3, forest biomass should increase strongly with maximum individual biomass and, in turn, we expect forest biomass to also be constrained by the water deficit.

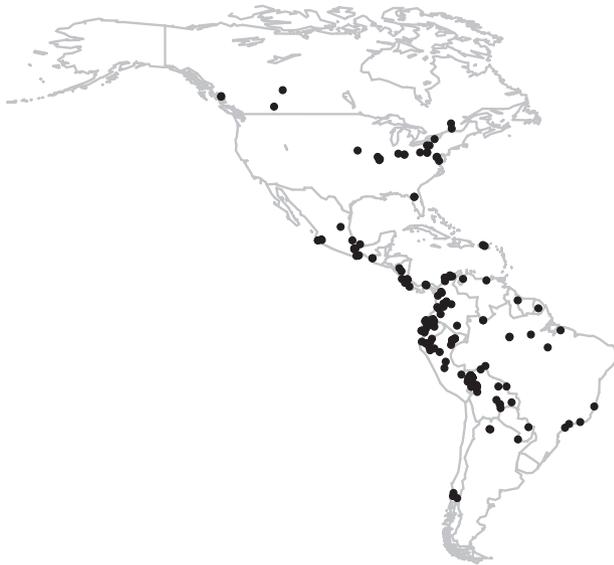
## Datasets and statistical analyses

The current study makes use of a consistent sampling regime based on 0.1-ha forest inventory plots (based on the methods of Alwyn Gentry; see Phillips & Miller, 2002) that sample a broad region of global climatic space (Fig. 1). We analysed 267 plots distributed across the Americas from 40.7° S to 54.6° N latitude (SALVIAS, 2002 and onward) (Fig. 2). Plots known to be in early successional forests were excluded from the dataset. Within each plot, consisting of 10 transects with dimensions 2 m × 50 m, all woody stems greater than or equal to 2.5 cm diameter at breast height (including lianas) were measured and identified to species or morphospecies.

We estimated the biomass of each plot using equations specific to tropical forest type, liana and temperate angiosperm and gymnosperm (Appendix S1). These equations are the best available for estimating biomass across a diverse assemblage of



**Figure 1** Convex hulls showing the distribution of climate data based on mean annual temperature (°C) and annual precipitation (mm). Distributions are presented for global lands (thick grey) and the climate space encompassed by this study (black), Brown & Lugo (1982) (thin grey), Sankaran *et al.* (2005) (dotted grey) and Raich *et al.* (2006) (dashed grey).



**Figure 2** Spatial distribution of forest plots (black dots) used in the current study.

forests, but they are general so that their use will add some error to biomass estimates. However, there is no reason to believe that their use will result in any systematic bias. Each plot in our dataset was designated as dry tropical, moist tropical, wet tropical or temperate. All plots greater than 23° from the equator were considered temperate, and all other plots were considered tropical. Within the tropical zone we divided plots using the Holdridge life-zone designation system (Holdridge, 1947), with the subcategories lumped into dry, moist and wet. We also incorporated differences in wood density between species to improve biomass estimates (Fearnside, 1997; Chave *et al.*, 2003, 2004; Baker *et al.*, 2004b). Wood density data were obtained from the literature and pre-existing databases (Swenson & Enquist, 2007).

For individuals within each 0.1-ha plot, wood density was taken as the mean species value, or if the species was not represented in our database, wood density was estimated as the genus average. In cases where the individual was not identified to genus or wood density data was lacking for a given genus the average wood density of the other individuals in the plot was used. Average plot-level wood density was used in this case because most variation in wood density exists among genera and average plot wood density shows spatial gradients (Baker *et al.*, 2004b; Swenson & Enquist, 2007). Mean wood density, total forest biomass and the fractions of species with species-level, genus-level or plot-level wood density values are reported for each forest plot in Appendix S2. The wood density correction is inherent in the equations from Chave *et al.* (2005) that were used in our study. For all other equations, biomass was corrected for wood density by multiplying the basic biomass equation by an individual's wood density divided by the mean wood density for that individual's taxonomic group (angiosperm, gymnosperm or liana). Forest-type-specific mean forest biomass, maximum individual biomass, annual precipitation and mean annual temperature are given in Appendix S3.

Data on mean annual temperature, annual precipitation, precipitation of the driest quarter and monthly mean temperature and precipitation were taken from the WorldClim database (Hijmans *et al.*, 2005) at a resolution of 2.5 arcmin (c. 5 km at the equator). While some error in these data is expected, there is no systematic bias so that observed biomass–climate correlations should be robust. Mean monthly values for temperature and precipitation were used to calculate monthly potential and actual evapotranspiration following Dingman (2001). More specifically, potential evapotranspiration is derived solely from energy inputs into the system, whereas actual evapotranspiration is a combination of energy inputs and precipitation. These monthly values were summed to give annual potential and actual evapotranspiration. Water deficit was defined as potential minus actual evapotranspiration (Stephenson, 1990; Dingman, 2001) such that the water deficit cannot be negative (see Dingman, 2001 for further details).

Using the biomass and climate data, patterns in our dataset were compared with those already published. Analyses were first conducted with the subset of data most closely matching the range of conditions evaluated in previous studies, allowing for an evaluation of the generality of previously observed patterns. To evaluate biomass–climate relationships across all forest types, forest biomass values from our entire dataset were regressed against mean annual temperature, annual precipitation, the ratio of mean annual temperature to annual precipitation, precipitation of the driest quarter, the ecosystem water deficit and potential and actual evapotranspiration.

For all relationships with  $R^2 \geq 0.1$  we have provided model II regression lines in the figures presented. Poor fits were generally observed when model II functions were determined for relationships with  $R^2 < 0.1$  (O'Connor *et al.*, 2007). Ordinary least-square functions for these regressions are provided for presentation purposes only.

Some analyses required log transformation. Specifically, log transformation was used to control for residual heteroscedasticity in the regression of forest biomass against precipitation of the driest quarter within dry tropical forests. In addition, forest biomass is predicted to vary as an approximate power function of maximum individual biomass (equation 3), so both variables were log transformed prior to regressing forest biomass against maximum individual biomass. Lastly, an exponential function provided the best-fit model relating the constraint boundaries of maximum individual biomass and forest biomass to the water deficit. As such, for visualization purposes both biomass variables were natural log transformed prior to regression against the water deficit.

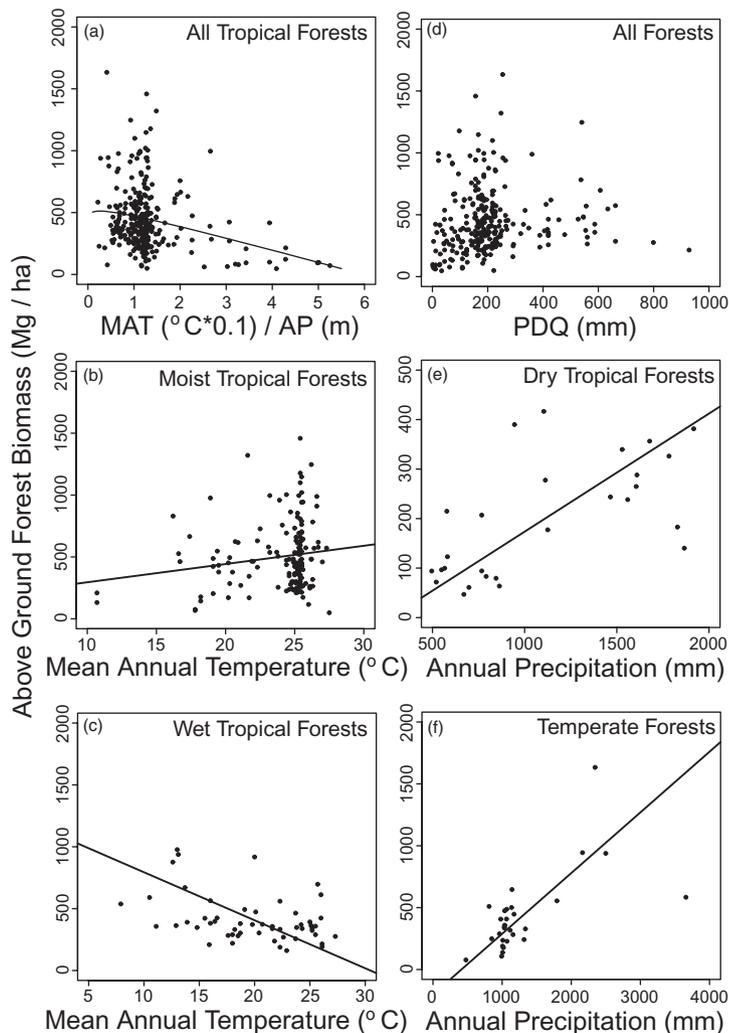
## RESULTS

### Modelling community biomass directly

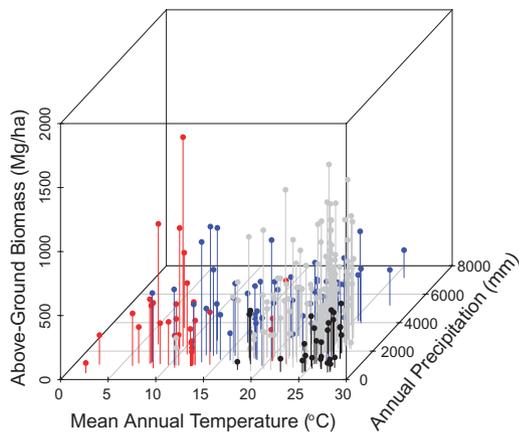
In this section, to test the generality of previously characterized forest biomass–climate relationships, forest biomass is regressed against mean annual temperature, annual precipitation, the

ratio of mean annual temperature to annual precipitation, and the precipitation of the driest quarter. Across tropical forests the relationship between forest biomass and the ratio of mean annual temperature to annual precipitation was poorly described by the functional form given in Brown & Lugo (1982) (Fig. 3a). We also found no relationship between forest biomass and mean annual temperature across all forest types ( $P = 0.9$ ). Raich *et al.* (2006) found forest biomass to increase with mean annual temperature in moist tropical forests, and while this relationship is significant in our dataset ( $P = 0.047$ ), mean annual temperature explained little variation in forest biomass ( $R^2 = 0.02$ ) (Fig. 3b). Similarly, forest biomass in temperate ( $P = 0.8$ ) and dry tropical ( $P = 0.3$ ) forests showed no trend with mean annual temperature. However, forest biomass declined with mean annual temperature in wet tropical forests ( $R^2 = 0.13$ ,  $P = 0.004$ ) (Fig. 3c).

In terms of precipitation there was a significant, but weakly positive, relationship between forest biomass and annual precipitation ( $R^2 = 0.03$ ,  $P = 0.005$ ) across all forests. In contrast, forest biomass increased strongly with annual precipitation in dry tropical ( $R^2 = 0.37$ ,  $P = 0.0004$ ) and temperate forests ( $R^2 =$



**Figure 3** (a) Total above-ground community biomass in tropical forests plotted against the ratio of mean annual temperature (MAT) to annual precipitation (AP). The solid line is the best fit to the function described in Brown & Lugo (1982),  $M_{tot} = 576.3 + 62.5 \log_{10} (MAT/AP) - 104.6 (MAT/AP)$ . (b), (c) Biomass plotted against temperature in moist and wet tropical forests, respectively. (d) Biomass plotted against precipitation of the driest quarter (PDQ). (e), (f) Biomass plotted against annual precipitation in dry tropical and temperate forests, respectively. In (b) biomass is weakly related to temperature, in terms of explained variance, so that the ordinary least squares regression model is presented. Model II regressions are shown in (c), (e) and (f).



**Figure 4** Total community biomass plotted simultaneously against mean annual temperature and annual precipitation. Different forest types are indicated: temperate (red), tropical dry (black), tropical moist (grey) and tropical wet (blue).

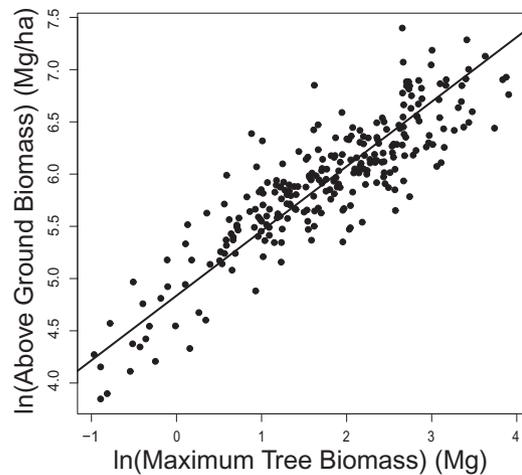
0.39,  $P = 0.0002$ ) (Fig. 3e, f). In moist ( $P = 0.15$ ) and wet tropical ( $P = 0.11$ ) forests, forest biomass showed no trend with annual precipitation.

We also evaluated forest biomass as a function of precipitation of the driest quarter. Correlations between forest biomass and precipitation of the driest quarter were non-significant across all forest types ( $R^2 = 0.007$ ,  $P = 0.09$ ) (Fig. 3d), across tropical forests ( $P = 0.18$ ), within moist tropical forests ( $P = 0.3$ ) and within wet tropical forests ( $R^2 = 0.05$ ,  $P = 0.07$ ). As with annual precipitation, forest biomass did increase with precipitation of the driest quarter in temperate ( $R^2 = 0.2$ ,  $P = 0.009$ ) and dry tropical forests ( $R^2 = 0.33$ ,  $P = 0.001$ ).

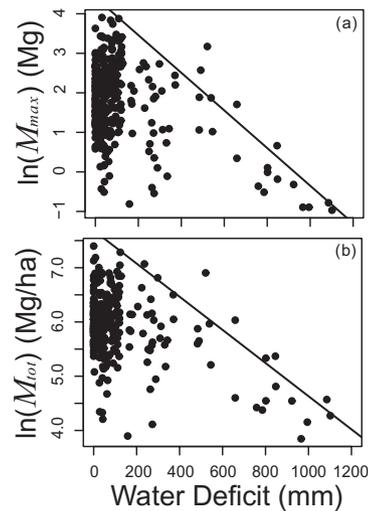
Simultaneously relating forest biomass to mean annual temperature and annual precipitation showed that temperate forests had the highest biomass per area, and that forest biomass peaks in two distinct regions of the mean annual temperature–annual precipitation climate space (Fig. 4). Specifically, there is a forest biomass peak in relatively cool, wet areas corresponding to temperate forests and a second peak in similarly wet, but much warmer, forests corresponding to moist tropical forests, which also had the highest mean forest biomass (Appendix S3). Moving away from these peaks through the mean annual temperature–annual precipitation climate space in any direction, including towards higher annual precipitation, leads to lower forest biomass.

**Modelling the components of community biomass**

Climate variables, including mean annual temperature, annual precipitation, potential evapotranspiration, actual evapotranspiration and water deficit explained little variation in  $N$  ( $R^2 < 0.06$  for all). In contrast,  $N$  did decrease with  $\bar{M}$  as a power function ( $N = 970.47\bar{M}^{-0.53}$ ;  $R^2 = 0.37$ ,  $P < 0.00001$ ). The decline in  $N$  with  $\bar{M}$  is consistent with our derivation of equation 3, which implies that forest biomass may be determined by maximum individual biomass. Indeed, maximum individual



**Figure 5** Relationship between natural log-transformed total above-ground community biomass ( $M_{max}$ ) and maximum individual biomass ( $M_{tot}$ ). The solid line represents the model II regression function (see text for parameter estimates and statistics).



**Figure 6** Natural log-transformed (a) maximum individual biomass ( $M_{max}$ ) within each forest plot and (b) total above-ground community biomass ( $M_{tot}$ ) plotted against ecosystem water deficit. In each panel the solid line represents the exponential function fit to the maximum values within each 100-mm water-deficit bin (see text for parameter estimates and statistics).

biomass explains a great deal of variation in forest biomass and the observed relationship was well described as a power law such that  $M_{tot} = 126M_{max}^{0.62}$  ( $R^2 = 0.76$ ,  $P < 0.00001$ ) (Fig. 5), and the 95% confidence interval for the exponent was 0.58–0.66.

As expected, the water deficit appears to impart an upper bound on maximum individual biomass and forest biomass (Fig. 6). The constraint boundaries were well described by exponential functions, where  $W$  is the water deficit:  $M_{max} = 82.4e^{-0.0048W}$  ( $R^2 = 0.87$ ;  $P < 0.00001$ ) and  $M_{tot} = 2180e^{-0.0031W}$  ( $R^2 = 0.84$ ;  $P < 0.0001$ ). These functions were evaluated by

regressing maximum values of maximum individual biomass or forest biomass within 100-mm bins along the water deficit axis against the midpoint of the water deficit bins. We took this approach because the distribution of maximum individual biomass and forest biomass was such that quantile regression failed to yield valid characterizations of the data.

Water deficit is defined as the difference between potential and actual evapotranspiration. To determine if either variable alone can account for the constraint placed on maximum individual biomass and forest biomass by the water deficit we fit exponential functions to the regression between both biomass metrics and maximum potential and actual evapotranspiration values within 100-mm bins along the potential and actual evapotranspiration axes. None of these four regressions were significant ( $P > 0.1$  for all).

## DISCUSSION

In order to predict the effects of global change on forested ecosystems it is necessary to work towards a better understanding of the processes which currently limit standing forest biomass. Our approach to this problem falls into two broad categories. First, as with previous studies, we have modelled forest biomass directly, but at a much larger climatic and/or geographic scale than most previous work (but see Keith *et al.*, 2009). Second, we approached forest biomass indirectly by modelling its components.

We found mixed support for previously documented forest biomass–climate models. For example, Raich *et al.* (2006) found forest biomass to increase with mean annual temperature in moist tropical forests, but we found a very weak relationship in which mean annual temperature explained only 2% of the variation in forest biomass (Fig. 3b). We sampled 156 moist tropical plots distributed across the landscape while Raich *et al.* (2006) sampled 22 plots along elevation transects. The pattern observed by Raich *et al.* (2006) may therefore have resulted from sampling within montane environments suggesting that it may not be general. Furthermore, we note that forest biomass is uncorrelated with mean annual temperature in dry tropical and temperate forests, but declines with mean annual temperature in wet tropical forests (Fig. 3c) possibly due to water limitation resulting from consistently high humidity. These varied patterns suggest that the role of temperature is not consistent across forest types. As a result, it will be difficult to make general predictions concerning changes in biomass in response to changes in mean annual temperature. Forests are therefore not likely to compensate for anthropogenic sources of carbon via a strong positive biomass response to increasing temperature (see also Raich *et al.*, 2006).

Similarly, forest biomass was not consistently related to precipitation of the driest quarter or annual precipitation across forest types. In dry tropical and temperate forests, forest biomass increased with precipitation of the driest quarter and annual precipitation (Fig. 3d–f), but was not correlated with precipitation of the driest quarter or annual precipitation in moist and wet tropical forests. When data from all forest types were con-

sidered together, forest biomass was not correlated with precipitation of the driest quarter or annual precipitation. Dry tropical and temperate forests are drier than moist and wet tropical forests (Appendix S3), suggesting that precipitation is limiting only for relatively dry systems. Sankaran *et al.* (2005) have also provided support for the limiting role of precipitation in arid and semi-arid systems. That precipitation limits biomass in dry ecosystems is not surprising, but may prove important for understanding forest biomass dynamics in the context of changing precipitation regimes (e.g. Goswami *et al.*, 2006).

How moist and wet tropical forest biomass will respond to changes in precipitation regimes is less clear. Saatchi *et al.* (2007), using over 500 plots, have suggested that biomass increases with precipitation of the driest quarter in moist and wet tropical forests of the Amazon Basin. Our results do not support this pattern, and this discrepancy is probably due to the much larger spatial extent sampled by our dataset. Specifically, Saatchi *et al.* (2007) sampled only the Amazon Basin whereas our dataset spans much of the New World tropics (Fig. 2). Regional-scale correlations between biomass and precipitation of the driest quarter in moist and wet tropical forests are therefore not consistently realized at larger scales. In turn, feedbacks between climate change and climatically driven changes in biomass and stored carbon may not be consistent across moist and wet tropical forests.

Lack of consistent feedback is also supported by using a more integrative measure of climate, the ratio of mean annual temperature to annual precipitation. Brown & Lugo (1982) found that for tropical forests, forest biomass was well described as a unimodal function of the ratio of mean annual temperature to annual precipitation. Fitting the same function to our tropical forest biomass data showed that this function poorly explained forest biomass. Our sampling of the tropics is much more intensive ( $n = 236$ ) than that of Brown & Lugo ( $n = 31$ ), and this increased sampling makes it clear that the distribution of forest biomass is less regular than previously suggested (Fig. 3a).

Relative to other previous work, Keith *et al.* (2009) sampled a broader range of forest types and evaluated forest biomass as a function of both mean annual temperature and annual precipitation. These authors found that per-area forest biomass peaks in relatively cool, wet regions of the temperate zone. Consistent with these results, the highest per-area forest biomass in our dataset was observed in the temperate zone (Fig. 4). However, across the climate space defined by mean annual temperature and annual precipitation, we observed two peaks in forest biomass. As in Keith *et al.* (2009) there was a peak in wet, cool regions, but another peak in similarly wet, but much warmer environments corresponding to moist tropical forests. This bi-modal pattern suggests that climate change may have region-specific and nonlinear influences on forest biomass. For example, declining precipitation in moist tropical forests or very wet tropical forests could lead to declining or increasing forest biomass, respectively. Realized changes in stored carbon will depend critically on context-specific changes in forest biomass and the relative contribution of each forest type to total terrestrial carbon stores.

Our analyses have so far failed to identify any climatic variables that are consistently correlated with forest biomass. In an attempt to work towards a better understanding of how climate influences biomass we modelled forest biomass using an alternative approach. We modelled the constituents of forest biomass instead of modelling forest biomass directly, and showed theoretically (equation 3) and empirically (Fig. 5) that forest biomass is determined by maximum individual biomass. The link between forest biomass and maximum individual biomass suggests that understanding patterns of forest biomass may rely on more a mechanistic understanding of patterns of maximum individual biomass. We have proposed that the maximum biomass of a tree is determined in part by the water deficit. Our model posits that maximum individual biomass should be limited by the water deficit due to a loss of hydraulic conductivity as the water deficit increases. Loss of conductivity is ultimately linked to an increased risk of embolism as leaf water potential declines (Tyree & Sperry, 1989) with height (Koch *et al.*, 2004) and water deficit, and maximum individual biomass should therefore decline with the ecosystem water deficit. In support of this hypothesis, across all forest types the water deficit sets an upper bound on maximum individual biomass and, in turn, on total forest biomass (Fig. 6).

It may not be surprising that the water deficit more consistently limits forest biomass than the other climate variables analysed here. The annual water deficit provides a much more detailed characterization of the abiotic environment than, for example, mean annual temperature or annual precipitation by incorporating seasonal (monthly) changes in climate. Water deficit also integrates temperature and precipitation by taking account of both potential and actual evapotranspiration. However, potential and actual evapotranspiration did not constrain forest biomass in a manner similar to the water deficit. These patterns point to the water deficit as an integrative environmental variable that consistently constrains forest biomass across a broad range of forest types.

Although a consistent upper bound on maximum individual biomass and forest biomass appears to be set by the water deficit, Fig. 6 clearly demonstrates that these maxima are not realized in the majority of forest plots. Most forests are therefore not in equilibrium with limits set by the long-term mean water deficit. Recent work conducted at local scales shows that forest biomass is often limited by disturbance (Chave *et al.*, 2001; Lawes *et al.*, 2006) or nutrients (van Groenigen *et al.*, 2006; Reich *et al.*, 2006) rather than climate directly, and our results suggest that these local-scale patterns may apply at broad geographic scales. In turn, changes in the long-term average water deficit may not cause substantial changes in maximum individual biomass or forest biomass across the majority of forests, but climate may still be important if the frequency of extreme droughts increases. In this case both maximum individual biomass and forest biomass may decline across many forests due to increased tree mortality in the largest size classes, as has been observed recently (Nepstad *et al.*, 2007; Brando *et al.*, 2008; Phillips *et al.*, 2009, 2010). Furthermore, increases in the long-term average water deficit due to declining precipitation and/or increasing

temperatures may cause declines in forest biomass in the forests that currently store the largest quantities of carbon (i.e. those forests currently at the upper bound set by the water deficit).

It is important to consider the limitations of our data and analyses. First, our use of 0.1-ha forest plots to estimate biomass represents a compromise between accuracy of biomass estimation, in an absolute sense, and broad geographic/climatic sampling with consistent sampling protocols. While the absolute magnitude of our biomass estimates may be skewed towards lower biomass per unit area than is representative of an entire forest (Chave *et al.*, 2004), all data will be equally affected (Chave *et al.*, 2003) such that the patterns we have reported are robust. While 0.1-ha plots should be used with caution, the standardized methodology is an improvement over previous work that has sampled from plots of inconsistent size or type (Howard *et al.*, 2004; Sankaran *et al.*, 2005), which may cause systematic biases in biomass estimates (see Chave *et al.*, 2004). Moreover, stems under 10 cm d.b.h. and lianas can represent over 10% of a forest's biomass and should thus be included for accurate biomass estimates (Gerwing & Farias, 2000; Haripriya, 2002; Chave *et al.*, 2003). Hence, this sampling regime is distinct from studies that estimate biomass by excluding lianas and only sampling stems greater than 10 cm d.b.h. (e.g. Brown & Lugo, 1984; Malhi *et al.*, 2006). In addition, using 0.1-ha plots has allowed us to sample from a much broader geographic range and from a greater portion of the global climate space than many previous studies (Fig. 1).

The second limitation to consider is that the biomass–water deficit constraint functions are approximate. Although quantile regression can be used to estimate a constraint function (Cade & Noon, 2003), small sample sizes in the upper quantiles along both axes limited our ability to use this methodology. Instead we extracted the maximum biomass values within bins along the water deficit axis, which provides a first approximation of the constraint function (Currie, 1993; Gaston & Blackburn, 2000). In addition, Chave *et al.* (2004) have shown that within a forest, 0.1-ha plot biomass is drawn from a positively skewed distribution. By chance this can result in some plots overestimating regional biomass, but there is an equal probability of overestimating biomass within a forest across the entire water deficit range. In our dataset, sample size generally decreased towards high water deficit. In turn there is a greater chance that we have overestimated biomass in at least one forest at low as compared to high water deficit. As a result the actual slope and intercept of the constraint boundaries may be lower than those reported. These caveats do not diminish the presence of the constraint boundary, and only suggest that the quantitative form of the boundary may deviate from that described.

We conclude that previously documented forest biomass–climate relationships do not hold at large geographic scales or across independent datasets that encompass a broad climatic range. This is surprising, because climate would be expected to have its greatest influence at these broad spatial scales. In addition, by focusing on the components of forest biomass we have provided evidence consistent with a causal link between the ecosystem water deficit and above-ground

biomass. Specifically, the long-term average water deficit appears to constrain community biomass by imposing a limit on the biomass of individual trees via its effect on embolism and hydraulic conductance. It is important to recognize that this hypothesized effect of the water deficit is only one factor among many that influence realized biomass. Indeed, the vast majority of forests fall well below the water-deficit-imposed constraint boundary, which is probably due to local-scale factors such as disturbance and extreme droughts causing punctuated increases in the water deficit and thus mortality in the largest size classes. Additional studies that evaluate the influence of rare droughts on maximum individual biomass and forest biomass will be critical for understanding how changes in the frequency of extreme climatic events will alter future terrestrial carbon stores.

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## SUPPORTING INFORMATION

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

**Appendix S1** Equations used in this study to calculate above-ground biomass from diameter at breast height and wood density.

**Appendix S2** Species richness, mean wood density, total biomass and fraction of species with species-level, genus-level and plot-level wood density data for each forest plot.

**Appendix S3** Forest-type-specific sample size, above-ground biomass, maximum individual biomass, annual precipitation and mean annual temperature.

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## BIOSKETCH

**James C. Stegen** is a National Science Foundation post-doctoral fellow in bioinformatics residing in the Department of Biology at the University of North Carolina at Chapel Hill. His research interests include understanding the processes regulating patterns of biological diversity, the structure of ecological communities and terrestrial carbon stores, especially in the context of the influence of metabolism over feedbacks among organismal ecology, community structure, evolution and ecosystem processes.

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