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*Review*

# The allocation of ecosystem net primary productivity in tropical forests

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The allocation of the net primary productivity (NPP) of an ecosystem between canopy, woody tissue and fine roots is an important descriptor of the functioning of that ecosystem, and an important feature to correctly represent in terrestrial ecosystem models. Here, we collate and analyse a global dataset of NPP allocation in tropical forests, and compare this with the representation of NPP allocation in 13 terrestrial ecosystem models. On average, the data suggest an equal partitioning of allocation between all three main components (mean $34 \pm 6\%$ canopy, $39 \pm 10\%$ wood, $27 \pm 11\%$ fine roots), but there is substantial site-to-site variation in allocation to woody tissue versus allocation to fine roots. Allocation to canopy (leaves, flowers and fruit) shows much less variance. The mean allocation of the ecosystem models is close to the mean of the data, but the spread is much greater, with several models reporting allocation partitioning outside of the spread of the data. Where all main components of NPP cannot be measured, litterfall is a good predictor of overall NPP ($r^2 = 0.83$ for linear fit forced through origin), stem growth is a moderate predictor and fine root production a poor predictor. Across sites the major component of variation of allocation is a shifting allocation between wood and fine roots, with allocation to the canopy being a relatively invariant component of total NPP. This suggests the dominant allocation trade-off is a 'fine root versus wood' trade-off, as opposed to the expected 'root–shoot' trade-off; such a trade-off has recently been posited on theoretical grounds for old-growth forest stands. We conclude by discussing the systematic biases in estimates of allocation introduced by missing NPP components, including herbivory, large leaf litter and root exudates production. These biases have a moderate effect on overall carbon allocation estimates, but are smaller than the observed range in allocation values across sites.

**Keywords:** carbon cycle; root–shoot ratio; Amazonia; Andes; Asia; Hawaii

## 1. INTRODUCTION

Tropical forests are among the most productive ecosystems on the Earth, estimated to account for about one-third of global net primary productivity (NPP) [1,2], but have been relatively under-sampled compared with their importance.

The NPP of an ecosystem is one of the fundamental parameters describing its functioning. It is the rate of formation of biomass that is used to create organic structures in plants, including woody, leaf and root tissues, but also root exudates and volatile organic carbon compounds (VOCs) [1]. As such, NPP is an important determinant of the amount of the organic material available to higher trophic levels. It also can indicate the magnitude and turnover of the carbon and nutrient cycles of that ecosystem, and potential response times to disturbance. The allocation of NPP between different tissues and products is also an important descriptor of forest ecosystem ecology. The fraction allocated to woody tissue is a strong control on the overall live biomass, the recalcitrant soil carbon stocks and the

long-term carbon stores in a system. The fraction allocated to leaves influences canopy leaf area, leaf life time, photosynthetic capacity, flower and fruit production and consumption, litterfall rates, decomposition and consumption by soil fauna. The fraction allocated to fine roots and exudates influences water uptake, nutrient acquisition and the soil faunal communities [3]. NPP can be estimated from a number of field measurements, each with methodological challenges [4–6], and in recent decades a dataset of tropical NPP measurement has been building up (e.g. [4,5,7,8]).

At the same time, a major development in Earth System science over the past few decades has been the development of terrestrial ecosystem models, often nested within or interacting with global climate models, aiming to represent the physical (especially energy, water and momentum transfer) and biogeochemical (especially carbon) interactions of the terrestrial biosphere with the atmosphere. In their most advanced form the biosphere in these models is fully coupled with the climate, so that changes in the biosphere (such as dieback of forests) affect climate, which in turn affects the biosphere [9–11]. The response of the biosphere to climate is a major source of uncertainty in predictions of climate change, potentially as large a source of uncertainty as the range of anthropogenic greenhouse gas
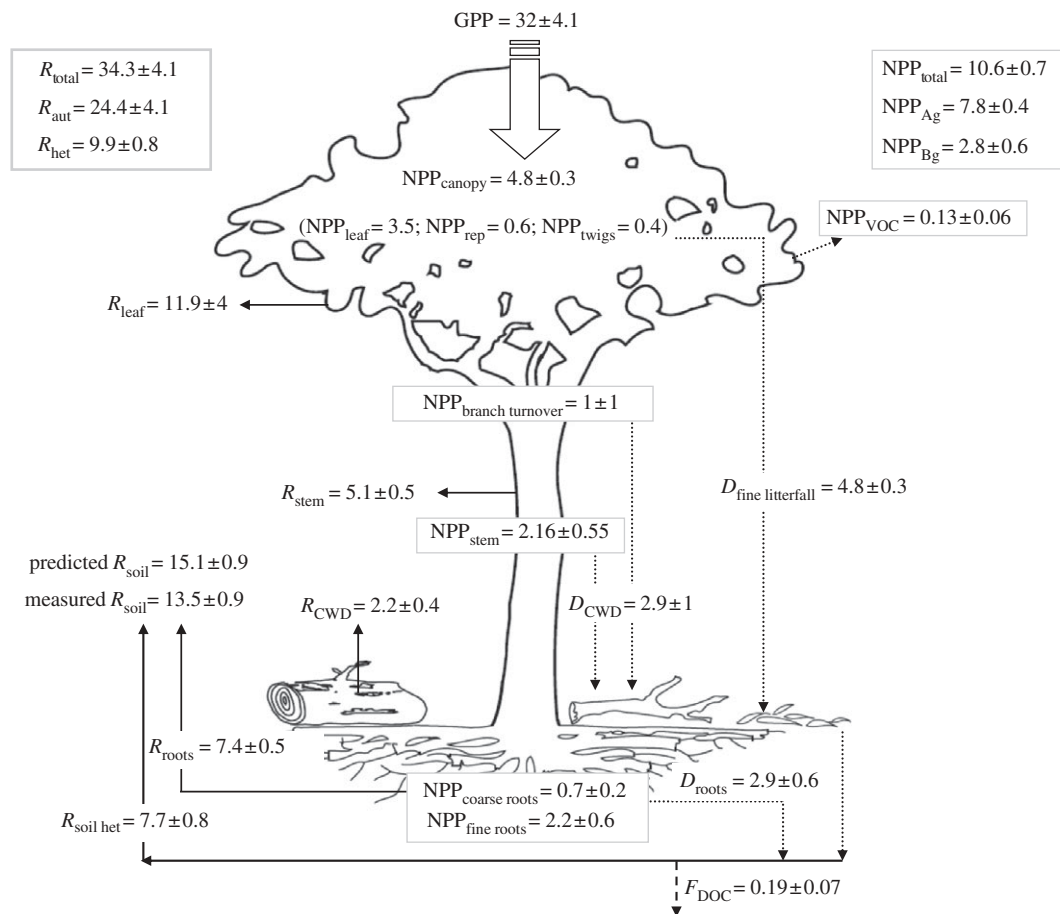
Figure 1. An example of the full carbon cycle for a mature tropical forest in Amazonia (Caxiuanã, Brazil). Based on data from Malhi *et al.* [6] with updated values of canopy and branchfall NPP (A. C. L. Costa, L. E. O. Aragão & Y. Malhi 2011, unpublished data). GPP, gross primary productivity; $R_{total}$, total ecosystem respiration; $R_{aut}$, autotrophic respiration; $R_{het}$, heterotrophic respiration; $NPP_{total}$, total net primary productivity (NPP); $NPP_{Ag}$, above-ground NPP; $NPP_{Bg}$, below-ground NPP; $NPP_{canopy}$, canopy NPP; $NPP_{leaf}$, leaf NPP; $NPP_{rep}$, reproductive NPP; $NPP_{twigs}$, twig NPP; $NPP_{VOC}$, volatile organic compound NPP; $NPP_{branch\ turnover}$, branch turnover NPP; $NPP_{stem}$, above-ground stem wood NPP; $NPP_{coarse\ roots}$, coarse root NPP; $NPP_{fine\ roots}$, fine root NPP; $D_{fine\ litterfall}$, canopy litterfall; $D_{CWD}$, woody mortality; $D_{roots}$, fine root detritus; $F_{DOC}$, outflow of dissolved organic carbon; $R_{soil\ het}$, soil heterotrophic respiration; $R_{roots}$, root respiration, $R_{CWD}$, coarse woody debris respiration; $R_{soil}$, soil respiration; $R_{stem}$, above-ground woody respiration; $R_{leaf}$, leaf dark respiration. All units are Mg C ha$^{-1}$ yr$^{-1}$.

emissions pathways projected for the twenty-first century [12,13]. The response of tropical forest carbon stocks to future climate change is a particularly striking source of uncertainty, with predictions of across-terrestrial ecosystem models varying widely, even when forced with the same amount of climate change [14,15].

The carbon cycle of tropical forests has only been comprehensively described for a handful of sites [4,6,7,16,17]. Figure 1 gives an example (a primary forest site in Caxiuanã, in Brazilian Amazonia, derived from the study of Malhi *et al.* [6]). The gross primary productivity (GPP) is total ecosystem photosynthesis and has been found to be approximately 30 Mg C ha$^{-1}$ yr$^{-1}$ [4,6] for many tropical forests. A large fraction of this GPP is used for the plants' own metabolic needs, resulting in the release of $CO_2$ to the atmosphere through the autotrophic respiration of canopy, woody and fine root tissues. The remainder is available for the construction of organic material (NPP). The ratio of NPP to GPP is often termed the carbon use efficiency (CUE), which averages approximately 30 per cent for the few mature Amazonian tropical forests where it has been measured, but may vary with

disturbance and fertility [4]. Hence around 70 per cent of carbon assimilated by tropical forest photosynthesis is rapidly returned to the atmosphere through autotrophic respiration [6,18]. The NPP is then allocated to leaf, wood and fine root tissue, with smaller fractions to exudates and VOCs. The CUE is likely to be underestimated to some extent because of missing components of NPP, in particular the poorly quantified transfer through root exudates, and transfer to myccorhizal symbionts.

The production of coarse woody biomass is a major control on biosphere carbon stocks. The NPP is the product of two quantities, the GPP and the CUE (figure 2). The woody NPP is dependent on the fraction of NPP allocated to wood, and the woody biomass carbon stock is the product of the woody NPP and the woody biomass residence time (figure 2). Within vegetation model frameworks, much attention has been focused on the correct representation and estimation of photosynthesis or GPP: a function of light, nutrient status, canopy leaf area, water supply and temperature. Much less attention has been focused on other, equally important components of the chain described in
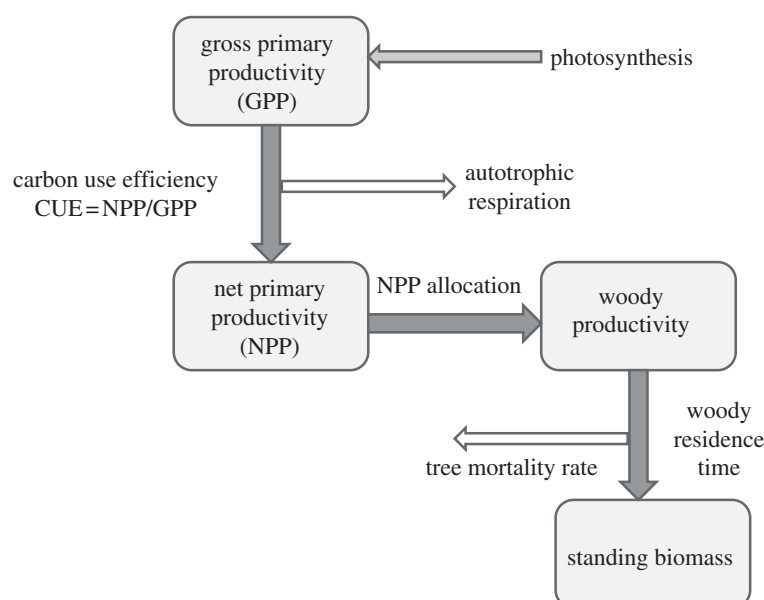
Figure 2. Pathway showing the key processes linking photosynthesis and the (woody) biomass of a forest. Much effort in terrestrial ecosystem models has gone into accurate representation of the first process in this pathway (photosynthesis) but three other processes can be equally important: autotrophic respiration (or CUE), allocation of NPP, and mortality (or woody biomass residence time). This paper focuses on the third process in the pathway, the allocation of NPP.

figure 2, namely CUE, allocation of NPP and biomass residence time. In this paper, we explore one aspect of the chain, the allocation of NPP in tropical forests. Other aspects of the chain (CUE and woody biomass residence time) will be explored in future papers.

## 2. AIMS
In this paper, we will explore the allocation of NPP in the context of tropical forests. We will:

— review the theoretical model descriptions and parameter settings employed by a wide range of vegetation models, with a particular focus on tropical forest vegetation functional types;
— collate a global dataset on the allocation of NPP in tropical forests, with discussion of uncertainties in field measurements; and
— analyse this dataset to explore mean values and generalities in the data, and test the frameworks and parameter settings of NPP allocation employed in models.

We focus our analysis on three components of NPP that are most frequently measured: above-ground woody biomass production, canopy production and fine root production, because the full suite of components of NPP is rarely measured in forest ecosystems [6]. In sites in Amazonia, these typically account for 93 per cent of total estimated NPP (figure 1). However, most ecosystem models do not distinguish between above-ground and below-ground woody biomass, and for model-data comparison purposes it would be helpful to estimate total woody production from the data, which we do by applying a simple multiplier assumed to be uniform across forest sites. We account for 99 per cent of total estimated NPP (figure 1) when we include woody root production. However, total estimated NPP does not account for poorly quantified missing

components such as herbivory, root exudate production and carbon transfer to myccorhizal symbionts, which we discuss in §5*e*.

In our analysis, we ask the following specific questions:

— Are there any general rules or fixed values in the allocation of NPP between canopy and woody biomass?
— How is NPP allocated between canopy, woody biomass and fine roots, and how much variance is there around the mean value? Are there biogeographic differences in allocation?
— Is measurement of a single component of NPP a useful predictor of total NPP?
— How well do terrestrial ecosystem models capture observed patterns of allocation in tropical forests?
— How sensitive are our estimates of allocation to poorly measured components of NPP, such as loss to herbivory and root exudate production?

## 3. GENERAL FRAMEWORKS FOR MODELLING NET PRIMARY PRODUCTIVITY ALLOCATION IN TERRESTRIAL ECOSYSTEM MODELS
'Bottom-up' field estimates of ecosystem carbon budgets (e.g. [6,17]) identify a number of compartments to which NPP is allocated, including leaves, stems, branches, fine roots, coarse roots, reproductive structures, VOCs and dissolved organic carbon. Usually, terrestrial ecosystem models allocate NPP to three pools: leaves, wood and fine roots. A small number of models allocate a fraction of their NPP to reproductive structures (e.g. LPJ and ORCHIDEE), while an equally small number of models take coarse roots into consideration by assuming that they account for a fixed fraction of total woody biomass (e.g. ORCHIDEE [19] and the ecosystem demography (ED) group of models [20,21]). Ecosystem models

allocate NPP to different carbon pools either in a fixed or dynamic fashion. Fixed allocation schemes assume that the fractions of NPP allocated into foliage, wood and fine roots are constant while dynamic schemes allow these fractions to vary in accordance with allometric constraints or resource availability. Table 1 provides the values of the allocation coefficients used for a typical tropical tree plant functional type (PFT) in a number of models that assume fixed allocation of NPP and also for some models with dynamic allocation schemes. For the latter, we assume no water stress or nutrient stress and assume a leaf area index (LAI) of 5.0 when this is required to calculate allocation to different carbon pools. This value of LAI is a typical value for tropical rainforests [34].

### (a) Approach 1: fixed allocation coefficients
Fixed allocation schemes represent the simplest approach to modelling NPP allocation and assume that NPP is partitioned among individual pools according to invariant allocation coefficients. These allocation coefficients often differ between PFTs. Models that currently use fixed allocation coefficients include BIOME-BGC [23], DALEC [35], Hyland [29] and IBIS [30]. Many of the earlier terrestrial ecosystem models such as CASA [25], CARAIB [36] and DEMETER [37] also adopted fixed schemes.

### (b) Approach 2: dynamic allocation driven by allometric constraints
In a number of models, NPP allocation must satisfy allometric relationships that exist between the different carbon pools. West *et al.* [38] proposed a general law for the origin of allometric scaling relationships in biology, driven by the existence of hierarchical, fractal-like vascular networks that minimize hydrodynamic resistance while maximizing the scaling of surfaces where resources are exchanged with the environment. This model was found to successfully predict tree architecture and many of the scaling laws that exist between and within individual plants [39] and has been specifically applied to biomass partitioning in plants [40,41]. The allometric biomass partitioning model predicts that leaf mass should scale to the three-fourth power of stem and root mass and that stem mass should scale isometrically (i.e. the exponent is 1.0) with root mass:

$$M_{\mathrm{L}} = \left(\frac{1}{\beta_{13}}\right) M_{\mathrm{R}}^{3/4}, \tag{3.1}$$

$$M_{\mathrm{L}} = \left(\frac{1}{\beta_{11}}\right) M_{\mathrm{S}}^{3/4} \tag{3.2}$$

$$\text{and} \quad M_{\mathrm{S}} = \left(\frac{\beta_{12}}{\beta_{13}}\right) M_{\mathrm{R}}, \tag{3.3}$$

where $M_{\mathrm{L}}$, $M_{\mathrm{S}}$ and $M_{\mathrm{R}}$ are the biomass of leaves, stems and roots, respectively, and the $\beta$ terms are coefficients that vary across species or different environments [42]. Allometric scaling principles have informed the representation of biomass allocation in the TRIFFID model [32] where the stem biomass is taken to scale allometrically with the LAI as:

$$M_{\mathrm{S}} = \alpha \cdot \mathrm{LAI}^{5/3} \tag{3.4}$$

where $\alpha$ is an allometric constant that varies according to PFTs (analogous to the $\beta$ terms in equations (3.1)–(3.3)). TRIFFID assumes that the biomass of leaves and fine roots are equivalent, as do ED 1.0 [20] and Hybrid v. 3.0 [43].

A number of ecosystem models use the pipe model idea proposed by Shinozaki *et al.* [44], which states that there is a direct proportionality between the sapwood area at a given height and the leaf biomass or area above it:

$$M_{\mathrm{L}} = K_{\mathrm{L:S}} \cdot S, \tag{3.5}$$

where $M_{\mathrm{L}}$ is the leaf biomass, $S$ is the cross-sectional sapwood area and $k_{\mathrm{L:S}}$ is the proportionality constant linking leaf biomass and sapwood area. Models that employ the pipe model theory in their allocation schemes include Hybrid v. 3.0 [43], LPJ [45], the ED models [20,21] and SEIB [46]. A limitation of this approach, especially in the context of tropical ecosystems, is the scarcity of data on $k_{\mathrm{L:S}}$, which also varies according to tree height [47].

Carbon allocation in models that simulate individual trees (either of different age and size classes or 'average individuals') is often constrained by empirical relationships between the diameter at breast height (d.b.h.) of an individual tree and other attributes, such as height (LPJ, ED, SEIB) or leaf biomass (ED). In LPJ, a further 'packing' constraint is introduced through an assumed relationship between tree diameter and average crown size [45].

### (c) Approach 3: dynamic allocation driven by resource availability
The optimal partitioning theory suggests that plants should allocate biomass according to the most limiting resource [48]. Indeed, a number of studies have shown that plants allocate relatively more carbon to roots when water or nutrients are limiting and to shoots when light is limiting [49,50]. Friedlingstein *et al.* [26] incorporated these ideas into a global modelling framework, considering three limiting resources: light, water and nitrogen. Light limitation favours stem allocation of carbon, whereas water limitation and nitrogen limitation favour the allocation of carbon to roots. In our literature review, most models that explicitly considered the influence of light limitation on carbon allocation used the approach of Friedlingstein *et al.* [26], simulating a light availability factor, $f(L)$ as follows:

$$f(L) = \exp(-k \cdot \mathrm{LAI}), \tag{3.6}$$

where LAI is the leaf area index and $k$ is the light extinction coefficient and is usually set to 0.5. Models that simulate light limitation of carbon allocation include CTEM [28] and ORCHIDEE [19]. Similarly, a water availability factor, $f(W)$ is often used to adjust allocation to roots. A common formulation for this water availability factor is that used in the CTEM model:

$$f(W) = \max\left[0, \min\left(1, \frac{\theta - \theta_{\mathrm{wilt}}}{\theta_{\mathrm{fc}} - \theta_{\mathrm{wilt}}}\right)\right], \tag{3.7}$$

where $\theta$ is the actual soil moisture content, $\theta_{\mathrm{fc}}$ is the soil moisture content at field capacity and $\theta_{\mathrm{wilt}}$ is the soil moisture at wilting point. Only two of the models

Table 1. Allocation fractions for the dominant tropical plant functional types in a number of ecosystem models.

| model | allocation scheme | dominant tropical rainforest PFT | fraction of NPP allocated to canopy | fraction of NPP allocated to wood | fraction of NPP allocated to fine roots | model references |
|---|---|---|---|---|---|---|
| aDGVM[a] | dynamic | tropical tree | 0.45 | 0.16 | 0.39 | Scheiter & Higgins [22] |
| BIOME-BGC | fixed | evergreen broadleaf forest | 0.30 | 0.30 | 0.39 | White et al. [23], Ise et al. [24] |
| CASA (original version) | fixed | broadleaf evergreen tree | 0.33 | 0.33 | 0.33 | Potter et al. [25] |
| CASA (Friedlingstein et al. version)[b] | dynamic | tropical rainforest | 0.19 | 0.77 | 0.04 | Friedlingstein et al. [26] |
| CCM3 (LSM)[c] | dynamic | evergreen broadleaf forest tree | 0.29 | 0.39 | 0.32 | Dickinson et al. [27] |
| CTEM[d] | dynamic | broadleaf evergreen tree | 0.20 | 0.45 | 0.35 | Arora & Boer [28] |
| ED 1.0[e] | dynamic | tropical evergreen tree | 0.26 | 0.48 | 0.26 | Moorcroft et al. [20] |
| Hyland | fixed | broadleaf tree (not different to temperate broadleaf trees) | 0.1 | 0.7 | 0.2 | Levy et al. [29] |
| IBIS | fixed | tropical broadleaf evergreen tree | 0.3 | 0.5 | 0.2 | Foley et al. [30], Kucharik et al. [31] |
| JULES/TRIFFID[f] | dynamic | broadleaf tree (no different from temperate trees) | 0.33 | 0.33 | 0.33 | Cox [32] |
| ORCHIDEE[g] | dynamic | tropical broadleaf evergreen | 0.28 | 0.675 | 0.045 | Krinner et al. [19] |
| Post and co-workers' model | fixed | tropical evergreen rainforest | 0.3 | 0.5 | 0.2 | Post et al. [33] |
| VISIT[h] | fixed | tropical forest | 0.19 | 0.42 | 0.39 | Ise et al. [24] |

[a] Assumes no water or light limitation and a value of $C_i$ of 0.43 in eqns 2–4 in Scheiter & Higgins [22].
[b] Assumes no water or nitrogen limitation and LAI of 5.0.
[c] Assumes LAI of 5.0 and an equilibrium ratio between woody biomass and root biomass.
[d] Assumes no water limitation and LAI of 5.0.
[e] Assumes canopy height of 30 m.
[f] In JULES/TRIFFID, not all of the NPP is available for growth, with some of it being available for 'spreading' of PFT area. Here we scale the NPP estimates for each component pool so that they add to 1 and thus disregard the 'spreading' fraction. The relative allocation in JULES also depends upon the amount of carbon available for growth. The numbers shown here are for a forest at equilibrium (i.e. NPP = turnover).
[g] Assumes no water limitation, no nitrogen limitation and an LAI of 5.0. ORCHIDEE assumes that 10% of NPP is allocated to reproductive structures. In this analysis, this fraction is included in the canopy NPP fraction.
[h] The allocation fractions for VISIT refer to allocated 'EPP' rather than NPP. EPP is defined as the carbon available for growth [24] but differs from NPP in that it also includes carbon that is available for growth respiration.
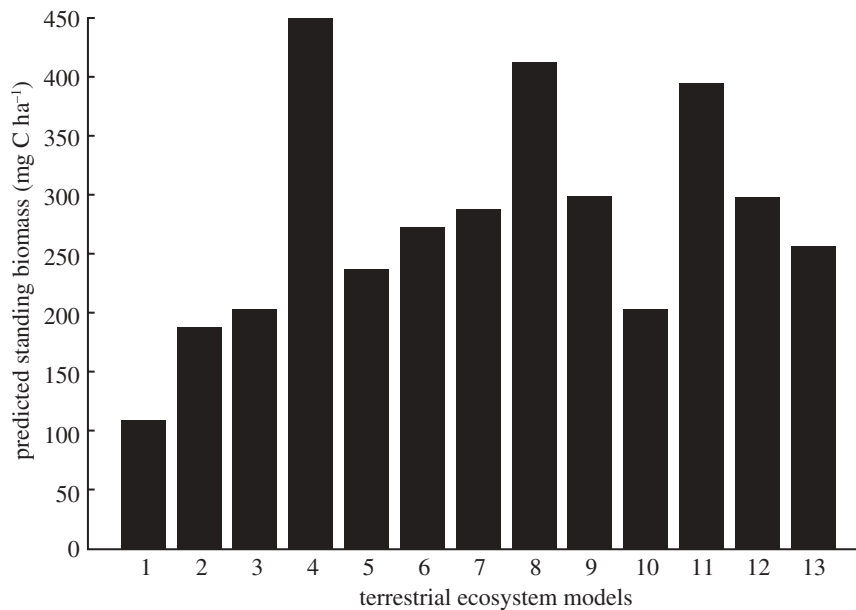
Figure 3. Impact of allocation scheme of eleven terrestrial ecosystem models on the standing biomass of a typical tropical rainforest site (model 1, aDGVM; model 2, BIOME-BGC; model 3, CASA (original); model 4, CASA (Friedlingstein *et al.* 1999); model 5, CCM3; model 6, CTEM; model 7, ED1; model 8, Hyland; model 9, IBIS; model 10, JULES/TRIFFID; model 11, ORCHIDEE; model 12, Post *et al.*; model 13, VISIT). We assume a total annual NPP of 11.6 Mg C ha$^{-1}$ yr$^{-1}$ [4], a fine root turnover time of 0.45 years (based on data from Jimenez *et al.* [52]), a leaf turnover time of 1 year (from Chave *et al.* 2009 [54]) and a woody biomass turnover time of 50 years (based on data from Malhi *et al.* [53]).

reviewed (the Friedlingstein *et al.* [26] version of CASA and ORCHIDEE) explicitly considered nitrogen limitation. In both of these models, these limitations were simulated indirectly, through impacts of soil moisture and temperature on nitrogen availability. Tropical forests, however, are believed to be more limited by phosphorus than by nitrogen [51], although phosphorus was not considered to affect allocation patterns in any of the ecosystem models evaluated.

### (d) Sensitivity analysis of the influence of allocation coefficients on standing biomass

One of the main reasons that correct representation of allocation is important is because allocation to woody NPP can have a strong effect on biomass and soil carbon stocks. To demonstrate this, we performed a simple sensitivity analysis to explore the impact of the allocation coefficients used in terrestrial ecosystem models (table 1) on predictions of standing biomass. The standing biomass of each carbon compartment ($M_i$) is calculated as:

$$M_i = \frac{NPP_i}{\tau_i}, \tag{3.8}$$

where $NPP_i$ is the above-ground NPP (Mg C ha$^{-1}$ yr$^{-1}$) of an individual carbon pool and $\tau_i$ is the annual turnover rate ($=1$/residence time) of the pool. Thus, leaf biomass ($M_L$), woody biomass ($M_W$) and fine root biomass ($M_R$) can be calculated as:

$$M_L = \frac{NPP_L}{\tau_L}, \tag{3.9}$$

$$M_W = \frac{NPP_W}{\tau_W} \tag{3.10}$$

and $$M_R = \frac{NPP_R}{\tau_R}. \tag{3.11}$$

The total standing biomass is the sum of these three compartments:

$$M_{tot} = M_L + M_W + M_R. \tag{3.12}$$

We assume values of $\tau_L$, $\tau_W$ and $\tau_R$ that appear typical of tropical forests. $\tau_R$ was taken to be 0.45 yr$^{-1}$, the median value reported across 15 mature rainforest plots in South America by Jimenez *et al.* [52], $\tau_w$ was taken to be 0.02 yr$^{-1}$ based on a median residence time of woody biomass of 50 years across 93 plots reported in Malhi *et al.* [53] and $\tau_L$ was taken to be 1.0 yr$^{-1}$ following Chave *et al.* [54]. We assume an annual total NPP of 11.6 Mg C ha$^{-1}$ yr$^{-1}$, the median value of 10 Amazonian sites reported by Aragão *et al.* [4]. This analysis assumes that the turnover times of individual pools are fixed. In reality, turnover rates in mature tropical forests appear to increase as NPP increases [53], but this observation is not generally incorporated in terrestrial ecosystem models (but see Delbart *et al.* [55] for an implementation of a scheme with time-varying turnover times). We ran the simple model described above with the allocation coefficients in table 1 as the inputs to the model. Mean total standing biomass predicted across all terrestrial ecosystem models considered was 278 $\pm$ 53 Mg C ha$^{-1}$. However, our results show that the standing biomass values predicted by the models are very sensitive to the choice of allocation coefficients used as the total standing biomass of a typical tropical rainforest was found to range from 108 to 450 Mg C ha$^{-1}$ (figure 3). Malhi *et al.* [56] reported a mean above-ground biomass of 143 $\pm$ 10 Mg C ha$^{-1}$ across 227 old-growth forests in Amazonia, corresponding to a mean total biomass of 173 $\pm$ 12 Mg C ha$^{-1}$ (assuming total biomass = above-ground biomass $\times$ 1.21) with a total range of 54–270 Mg C ha$^{-1}$.

## 4. METHODS: NET PRIMARY PRODUCTIVITY DATA COMPILATION AND ANALYSIS

For the next stage of the paper, we collate a global dataset of tropical forest NPP. The core of our analysis is a compilation of data from sites where the three largest components of NPP (canopy, wood and fine root NPP) have been measured. We also include a larger dataset where the above-ground components (canopy and wood) have been measured.

Canopy NPP is estimated from a fairly simple measurement: frequent litterfall collection from a number of litterfall traps distributed around the sample plot, with litter samples collected at around two to four week intervals, over at least one full annual cycle. Canopy NPP differs from other components of NPP in that it measures outputs (litterfall) from canopy biomass rather than direct inputs. These are broadly similar over long periods in steady-state systems. There exist a number of systematic biases causing canopy NPP to be underestimated, including: partial decomposition of the material prior to collection [3], loss of canopy NPP to vertebrate and invertebrate herbivory, decomposition *in situ* before abscission, interception of canopy material as it falls through the canopy, difficulty of capture of large elements such as palm leaves and lack of capture of ground flora. All these suggest that measured canopy NPP underestimates true canopy NPP, but the extent of this underestimate is poorly known. In our discussion, we explore the implications of these underestimated components on estimations of NPP allocation.

Most field estimates do not distinguish between leaves and reproductive tissue (flowers, fruit). Where they do, reproductive NPP has typically been 5–15% of canopy NPP (six sites in lowland Amazonia average 15%, Y. Malhi & D. B. Metcalfe 2011, unpublished data; sites in lowland Borneo average 5% [5]).

Woody NPP is estimated from recensus of sample plots. For these estimates, stem diameter is generally measured annually at 1.3 m. The largest source of uncertainty in woody NPP comes from the allometric equation used to estimate biomass from stem diameter, though uncertainty is greatly reduced if height data are also included. Allometric equations that are frequently employed include those of Brown [57], Baker *et al.* [58] for Amazonian forests and Chave *et al.* [59] based on a pan-tropical synthesis.

A rarely measured component of woody NPP is the below-ground component, including both coarse root production and the growth of the below-ground stem and any tap root. Coarse root production can in principle be measured by coring of soils, but this misses the important high mass component immediately below the stem. A third component of woody NPP, also rarely measured, is turnover of branches and other large pieces of litter, which are too large and sparsely distributed to be adequately captured by litter traps. This can be surveyed by regular transects and ranges from 0 to $2 \, \text{Mg C ha}^{-1} \text{yr}^{-1}$. A survey of branch turnover across nine sites in Amazonia and the Andes suggests that on average branchfall is an additional 36 per cent ($\pm 19\%$ standard deviation) of above-ground stem production (D. B. Metcalfe 2011, unpublished data). An additional source of underestimation of

woody NPP is the usual neglect of small trees and lianas, typically those below 10 cm diameter.

Fine root NPP is especially difficult to measure owing to the disturbance caused by root observation systems. The most common methods, such as ingrowth cores or sequential coring [60], involve the extraction and weighing of fine roots. Alternatively, roots can be observed with rhizotrons [61], which are typically regions of soil covered by clear plastic or glass in which new root growth can be measured at regular intervals. These techniques may underestimate fine root NPP owing to fine root herbivory or turnover of roots faster than the interval at which they are measured, or through soil disturbance effects if the measurement results in changes in the soil environment that inhibit fine root growth.

Possibly the largest unknown term in NPP is the transfer of material out of fine roots, either through production of root exudates directly into the soil or as a carbon supply for mycorrhizae [62]. Mycorrhizal respiration rates can be an indicator of exudate production (this assumes that all carbon respired by mycorrhizae is supplied by plant roots), and data from Amazonian tropical forests suggest that this can be about 10 per cent of NPP [17] (D. B. Metcalfe 2011, unpublished data). The production and emission of VOCs from the canopy is another component of NPP. Although it is important for atmospheric chemistry, it has been found to be only a small component of NPP, with estimates from the Amazon lowlands suggesting it is 1 per cent of NPP (e.g. figure 1, [6]).

In this study, we take a pragmatic approach based on available data. For canopy NPP, we include leaf, flower and fruit production, but do not attempt to account for losses owing to herbivory, interception and decomposition biases as these are poorly quantified. For woody NPP, we include above-ground wood production, but also assume that branch turnover is an additional $36 \pm 19\%$ of above-ground woody NPP, and estimate an additional $21 \pm 4\%$ of woody production below-ground (based on a compilation of global below-ground biomass inventories, as outlined in Aragao *et al.* [4]), combining to a multiplier of 60.8 per cent. For fine root production, we consider only reported values, and do not attempt to include exudate production, carbon transfer to mycorrhizae or unmeasured losses to root herbivory. Uncertainties introduced by these assumptions are discussed later.

## 5. RESULTS

### (a) *The allocation of above-ground net primary productivity between stems and canopy*

We turn our attention first to the partitioning of above-ground NPP between two components—canopy production (measured through litterfall) and above-ground woody NPP (measured through forest censuses). This is the focus of a separate analysis as a much larger dataset is available (table 2; $n = 71$), as both litterfall and woody NPP are frequently reported for many tropical forest sites. For this first analysis, we do not correct the woody NPP for branchfall and below-ground production, as our focus is on constancy

Table 2. Canopy NPP, stem NPP, woody NPP (which includes an estimate of branch and coarse root NPP based on stem NPP) ($n = 71$) plus yearly averaged site rainfall, temperature, latitude, longitude and elevation.

| reference | field site | canopy NPP (Mg C ha⁻¹ yr⁻¹) | stem NPP (Mg C ha⁻¹ yr⁻¹) | woody NPP (Mg C ha⁻¹ yr⁻¹) | rainfall (mm yr⁻¹) | temperature (°C) | latitude | longitude | elevation (m) |
|---|---|---|---|---|---|---|---|---|---|
| Schuur & Matson [63] | Maui, Hawaii | 4.25 | 0.375 | 0.62 | 2200 | 16 | 20.9 | −156.4 | 1370 |
| | Maui, Hawaii | 5.0 | 0.125 | 0.21 | 2450 | 16 | 20.9 | −156.4 | 1370 |
| | Maui, Hawaii | 4.25 | 0.625 | 1.03 | 2750 | 16 | 20.9 | −156.4 | 1370 |
| | Maui, Hawaii | 4.5 | 0.125 | 0.21 | 3350 | 16 | 20.9 | −156.4 | 1320 |
| | Maui, Hawaii | 3.0 | 0.75 | 1.24 | 4050 | 16 | 20.9 | −156.4 | 1300 |
| | Maui, Hawaii | 2.0 | 0.05 | 0.08 | 5050 | 16 | 20.9 | −156.4 | 1270 |
| Kitayama & Aiba [64] | Mt. Kinabulu, Borneo | 5.55 | 4.015 | 6.64 | 2200 | 24 | 6.08 | 116.55 | 650 |
| | Mt. Kinabulu, Borneo | 3.995 | 2.115 | 3.50 | 2250 | 18 | 6.08 | 116.55 | 1560 |
| | Mt. Kinabulu, Borneo | 2.66 | 1.24 | 2.05 | 2150 | 12 | 6.08 | 116.55 | 2590 |
| | Mt. Kinabulu, Borneo | 3.155 | 0.925 | 1.53 | 2100 | 9 | 6.08 | 116.55 | 3080 |
| | Mt. Kinabulu, Borneo | 5.565 | 3.01 | 4.98 | 2200 | 24 | 6.08 | 116.55 | 700 |
| | Mt. Kinabulu, Borneo | 3.14 | 0.925 | 1.53 | 2250 | 18 | 6.08 | 116.55 | 1860 |
| | Mt. Kinabulu, Borneo | 2.97 | 0.655 | 1.08 | 2150 | 12 | 6.08 | 116.55 | 2700 |
| | Mt. Kinabulu, Borneo | 0.82 | 0.175 | 0.29 | 2100 | 9 | 6.08 | 116.55 | 3050 |
| Takyu et al. [65] | Mt. Kinabulu, Borneo Q ridge | 2.7 | 0.3 | 0.50 | 2380 | 18.3 | 6.08 | 116.55 | 1860 |
| | Mt. Kinabulu, Borneo T ridge | 3.95 | 0.7 | 1.16 | 2380 | 18.3 | 6.08 | 116.55 | 1560 |
| | Mt. Kinabulu, Borneo U ridge | 2.1 | 0.35 | 0.58 | 2380 | 18.3 | 6.08 | 116.55 | 1860 |
| | Mt. Kinabulu, Borneo U lower | 3.3 | 0.95 | 1.57 | 2380 | 18.3 | 6.08 | 116.55 | 1860 |
| Paoli & Curran [8] | West Kalimantan, Indonesia | 3.85 ± 0.2 | 6 ± 1 | 9.9 | 4125 | | −1.0 | 109.0 | 190 |
| Foster [66], cited in Malhi et al. [53] | BCI Plateau, Panamá | 6.07 | 3.62 | 5.99 | 2912 | 26.11 | −79.85 | 9.17 | 137 |
| Jordan et al. [67] | San Carlos terra firme | 2.93 | 1.76 | 2.91 | 3093 | 25.98 | −67.05 | 1.93 | 122 |
| Cuevas & Medina [68] | San Carlos caatinga | 2.81 | 1.53 | 2.53 | 3093 | 25.88 | −67.05 | 1.75 | 117–122 |
| Luizao [69] cited in Clark et al. [70] | Bionte, Brazil | 3.7 | 2.6 | 4.30 | 2272 | 27.08 | −60.17 | −2.63 | 73 |
| | BDFFP Fazenda Dimona | 4.2 | 2.2 | 3.97 | 2167 | 26.88 | −60.17 | −2.63 | 100 |
| Nepstad et al. [71] cited in Malhi et al. [53] | Tapajós, Brazil | 3.93 | 2.6 | 4.30 | 1988 | 26.13 | −55 | −2.75 | 100 |
| | Mocambo, Brazil | 4.95 | 2.53 | 4.18 | 2933 | 26.63 | −48.45 | −1.45 | 24 |

(Continued.)

Table 2. (*Continued.*)

| reference | field site | canopy NPP (Mg C ha⁻¹ yr⁻¹) | stem NPP (Mg C ha⁻¹ yr⁻¹) | woody NPP (Mg C ha⁻¹ yr⁻¹) | rainfall (mm yr⁻¹) | temperature (°C) | latitude | longitude | elevation (m) |
|---|---|---|---|---|---|---|---|---|---|
| Kira *et al.* [72] | Pasoh, Malaysia | 5.3 | 2.7 | 4.47 | 1807 | 25 | 2.98 | 102.3 | 100 |
| Herbert & Fownes [73] | Puu Kolekole, Hawaii | 4.4 | 2.6 | 4.30 | 2500 | 16 | 25.15 | −156.8 | 1200 |
| Trumbore *et al.* [74] | Paragominas, Brazil | 4.6 | 1.3 | 2.15 | 1750 | | 2.98 | −47.52 | 0 |
| Herbert & Fownes [73] | Laupahoehoe, Hawaii | 2.7 | 2.1 | 3.47 | 2500 | 16 | 19.95 | −155.3 | 1170 |
| | Kohala, Hawaii | 3.2 | 1.4 | 2.32 | 2500 | 16 | 20.05 | −155.9 | 1122 |
| | Kokee, Hawaii | 2.1 | 1.9 | 3.14 | 2500 | 16 | 22.05 | −159.5 | 1134 |
| Raich *et al.* [75] | Hawaii 6 | 1.1 | 0.5 | 0.83 | 2600 | 13 | 19.75 | −155.25 | 1660 |
| | Hawaii 5 | 0.9 | 0.3 | 0.50 | 5800 | 19.3 | 19.75 | −155.25 | 700 |
| Sierra *et al.* [76] | Porce, Colombia | 4.72 | 4.44 | 8.06 | 2078 | 23 | 6.75 | −75.1 | 900 |
| Martinez-Yrizar *et al.* [77] | Upper Chamela, Mexico | 1.65 | 1.0 | 1.65 | 707 | 24.9 | 19.5 | −105.05 | 150 |
| | Middle Chamela, Mexico | 1.6 | 1.14 | 1.89 | 707 | 24.9 | 19.5 | −105.05 | 130–150 |
| | Lower Chamela, Mexico | 2.11 | 1.45 | 2.40 | 707 | 24.9 | 19.5 | −105.05 | 70–150 |
| Adamek *et al.* [78] | Fortuna, Panama | 4.41 | 2.03 | 3.36 | 5545 | 20 | 8.75 | −82.25 | 1200 |
| Chave *et al.* [79] | Nouragues, French Guiana | 4.97 | 4.33 | 7.16 | 2960 | 27 | 4.08 | −52.67 | 100 |
| | Nouragues, French Guiana | 4.13 | 4.02 | 6.65 | 2960 | 27 | 4.08 | −52.67 | 100 |
| Yang *et al.* [80] | Xiaohu NF, China | 4.45 ± 0.51 | 2.076 ± 0.495 | 3.43 | 1749 | 19.1 | 26.18 | 117.43 | 100 |
| Swamy *et al.* [81] | Western Ghats, India | 2.55 | 3.5 | 5.79 | 2800 | 26.6 | 12.42 | 75.42 | 1000 |
| | Western Ghats, India | 3.7 | 3.7 | 6.12 | 3200 | 24.6 | 12.42 | 75.42 | 1500 |
| | Western Ghats, India | 2.65 | 2.4 | 3.97 | 2800 | 26.6 | 12.42 | 75.42 | 1100 |
| | Western Ghats, India | 3.05 | 3.8 | 6.29 | 3000 | 25.6 | 12.42 | 75.42 | 1300 |
| Malhi *et al.* [6] | Manaus, Brazil | 3.57 ± 0.75 | 2.58 | 3.61 | 2349 | 27.6 | −2.60 | −60.20 | 90 |
| | Tapajós, Brazil | 6.53 ± 0.71 | 3.75 ± 0.075 | 6.20 | 1920 | 27.2 | −2.81 | −54.95 | 200 |
| Aragao *et al.* [4] | Caxiuanã, Brazil | 4.77 ± 0.32 | 2.18 ± 0.16 | 3.61 | 2299 | 27.6 | −1.72 | −51.45 | 15 |
| | Caxiuanã, Brazil | 4.2 ± 0.087 | 2 ± 0.1 | 3.31 | 2299 | 27.6 | −1.72 | −51.45 | 15 |
| | Caxiuanã, Brazil | 5.6 | 2.48 ± 0.257 | 4.10 | 2299 | 27.6 | −1.72 | −51.45 | 15 |
| | Tambopata, Peru | 5.53 ± 0.42 | 2.80 ± 0.24 | 4.63 | 2730 | 26.4 | −12.8 | −69.8 | 207 |
| | Tambopata, Peru | 4.83 ± 0.24 | 2.637 ± 1 | 4.36 | 2730 | 26.4 | −12.8 | −69.8 | 207 |
| | Agua Pudre, Colombia | 3.87 ± 0.2 | 3.35 ± 0.3 | 5.54 | 2562 | 25.8 | −3.72 | −70.3 | 105 |
| | Agua Pudre, Colombia | 3.65 ± 0.2 | 3.84 ± 0.3 | 6.35 | 2562 | 25.8 | −3.72 | −70.3 | 110 |
| | Zafire, Colombia | 2.67 ± 0.1 | 1.32 ± 0.3 | 2.18 | 2552 | 26.1 | −4.0 | −69.9 | 130 |

(*Continued.*)

Table 2. (*Continued.*)

| reference | field site | canopy NPP (Mg C ha⁻¹ yr⁻¹) | stem NPP (Mg C ha⁻¹ yr⁻¹) | woody NPP (Mg C ha⁻¹ yr⁻¹) | rainfall (mm yr⁻¹) | temperature (°C) | latitude | longitude | elevation (m) |
|---|---|---|---|---|---|---|---|---|---|
| Girardin et al. [7] | Wayquecha, Peru | $1.92 \pm 0.1$ | $1.2 \pm 0.12$ | 1.98 | 1706 | 12.5 | −13.18 | −71.58 | 3025 |
| | Trocha Union, Peru | $1.19 \pm 0.05$ | $1 \pm 0.1$ | 1.65 | 1776 | 11.8 | −13.1 | −71.58 | 3020 |
| | Trocha Union, Peru | $1.83 \pm 0.06$ | $1.57 \pm 0.16$ | 2.60 | 2318 | 13.5 | −13.1 | −71.58 | 2720 |
| | Trocha Union, Peru | $1.44 \pm 0.06$ | $0.79 \pm 0.08$ | 1.31 | 1827 | 17.4 | −13.06 | −71.55 | 2020 |
| | Trocha Union, Peru | $1.44 \pm 0.08$ | $0.79 \pm 0.08$ | 1.31 | 2472 | 18 | −13.06 | −71.55 | 1855 |
| | San Pedro, Peru | $2.76 \pm 0.13$ | $1.62 \pm 0.16$ | 2.68 | 2631 | 18.8 | −13.03 | −71.53 | 1500 |
| | Tono, Peru | $2.49 \pm 0.22$ | $1.34 \pm 0.13$ | 2.22 | 3087 | 20.7 | −12.95 | −71.55 | 1000 |
| Hertel et al. [82] | Sulawesi, Indonesia | $3.11 \pm 0.55$ | $2.65 \pm 0.13$ | 4.38 | 3534 | 20.8 | −1.48 | 120.05 | 1050 |
| Russell et al. [83] | La Selva, Costa Rica, *Hieronyma alchorneoides* | $5.49 \pm 0.13$ | $2.71 \pm 0.46$ | 4.48 | 3960 | 25.8 | 10.43 | −83.98 | 44–89 |
| | La Selva, Costa Rica, *Pentaclethra macroloba* | $5.09 \pm 0.32$ | $3.05 \pm 0.87$ | 5.04 | 3960 | 25.8 | 10.43 | −83.98 | 44–89 |
| | La Selva, Costa Rica, *Pinus patula* | $4.76 \pm 0.31$ | $6.53 \pm 3.2$ | 10.80 | 3960 | 25.8 | 10.43 | −83.98 | 44–89 |
| | La Selva, Costa Rica, *Virola koschnyi* | $3.56 \pm 0.31$ | $1.99 \pm 0.44$ | 3.29 | 3960 | 25.8 | 10.43 | −83.98 | 44–89 |
| | La Selva, Costa Rica, *Vochysia guatemalensis* | $4.26 \pm 0.13$ | $3.97 \pm 0.15$ | 6.57 | 3960 | 25.8 | 10.43 | −83.98 | 44–89 |
| Tan et al. [84] | Menglun, China | 4.16 | 3.38 | 5.59 | 1487 | 21.7 | 21.92 | 101.25 | 750 |
| Lugo et al. [85] | Luquillo, Puerto Rico | 4.1 | 1.4 | 2.32 | 1650 | 25.6 | 18.32 | −65.82 | 200–400 |

Figure 4. Canopy NPP (Mg C ha$^{-1}$ yr$^{-1}$) versus stem NPP (Mg C ha$^{-1}$ yr$^{-1}$) for the Americas (row 1) ($n = 33$), Asia (row 2) ($n = 21$) and Hawaii (row 3) ($n = 12$), and for lowlands (column 1; less than 1000 m elevation), highlands (column 2; greater than 1000 m elevation), and lowlands and uplands combined (column 3). We plot linear regressions (dashed line) forced through the origin and a reference line of $y = 1.75x$ (solid line) to facilitate comparison across graphs. (*a*) Americas lowlands: slope = 1.50 $\pm$ 0.10; (*b*) Americas highlands: slope = 1.73 $\pm$ 0.14; (*c*) Americas total: slope = 1.51 $\pm$ 0.08; (*d*) Asia lowlands; (*e*) Asia highlands; (*f*) Asia total; (*g*) Hawaii highlands and (*h*) Hawaii total. Regression lines are plotted and equations given only when significant ($p < 0.05$).

of partition (which is unaffected by multiplier corrections) rather than actual proportions of partition. Similarly, for litterfall, we do not attempt to correct for herbivory, *in situ* decomposition and missing litterfall (e.g. large palm leaves). In reality, the magnitude of these multiplier corrections may vary across the landscape and introduce undetected regional biases, e.g. losses to herbivory may be higher in forests on fertile soils.

Despite the much larger dataset of sites with litterfall and wood production, there are still large geographical gaps. The only lowland region that is relatively well-reported is lowland Amazonia (25 sites), followed by six sites from lowland Asia. We have no sites from tropical Africa, the second biggest tropical forest region after Amazonia. Upland sites ($> 1000$ m) are relatively well-represented given their small geographical area, with particular representation from Hawaii (11 sites), followed by South East Asia (15 sites) and the Andes (eight sites). Based on data from 19 sites in the lowland Neotropics, Malhi *et al.* [53] suggested that there may be a tendency for relatively fixed allocation between canopy and woody NPP, a finding that has been further supported by more recent datasets from Amazonia [4] and the Andes [7]; more recently, in a global analysis, Shoo & VanDerWal [86] suggested that there was no simple pan-tropical relationship. Here, we explore this question further, while also updating the evidence base with more recently published datasets.

Figure 4 plots various subsets of NPP$_{canopy}$ versus above-ground NPP$_{wood}$, divided in rows by three geographical regions (Americas, Asia and Hawaii) and in

columns as lowlands ($\leq 1000$ m), upland ($\geq 1000$ m) and all data. Turning to the best-studied category, the lowland Neotropics ($n = 25$ sites; figure 4*a*), there is a significant linear relationship between NPP$_{canopy}$ and NPP$_{wood}$ (least-squares regression, slope = 0.76 $\pm$ 0.2, $r^2 = 0.39$, $p < 0.001$; slope = 1.50 $\pm$ 0.10 when forced through the origin). There are a few deviations from this relationship, notably Agua Pudre in Colombia over a waterlogged Endostagnic Plinthosol soil, and two plots at Nouragues in French Guiana (which both deviate to the right: having higher NPP$_{wood}$/ lower NPP$_{canopy}$ than predicted) and Paragominas, Brazil (which deviates to the left). When we consider upland sites (all but one site are from a transect in southeast Peru), a very similar relationship appears (for all data, slope = 2.11 $\pm$ 0.47, $r^2 = 0.77$, $p < 0.001$; slope = 1.73 $\pm$ 0.14, $r^2 = 0.75$ when forced through the origin).

Turning attention to the Asian lowland datasets ($n = 6$), we do not see a similar pattern. Three sites have allocation similar to that reported in the Neotropics (Pasoh, Malaysia; Mt. Kinabalu, Borneo; Xiaohu, China) but some other sites deviate to the right of the Neotropical relationship; in particular, sites in West Kalimantan are the most extreme deviations to the right. Paoli & Curran [8] suggest there is a saturating function of NPP$_{canopy}$ versus NPP$_{wood}$ at very high NPP sites. Another feature to note is that these Western Kalimantan data were collected over 1998–2001, immediately after a severe El Niño event. It is possible that there was a major shift in allocation after the El

Niño, either because of drought disturbance, or else after extensive masting (= allocation to canopy) by the dominant diptercarp trees during the El Niño. Examining Asian highland plots, sites deviate both to the left and to the right of the Neotropical reference relationship. Most sites (dominated by studies in Mt. Kinabalu, Malaysia) tend to have higher allocation to the canopy. Combining all Asian sites, there is almost no relationship, with $NPP_{canopy}$ ranging between 2 and $4\,Mg\,C\,ha^{-1}\,yr^{-1}$ independent of the values of $NPP_{wood}$ (which ranges from 0 to $6\,Mg\,C\,ha^{-1}\,yr^{-1}$). Finally, we turn to the Hawaii datasets, all but one in the uplands. The plots cover a range of substrates and elevations, and there is no obvious and consistent relationship.

An alternative interpretation of the lowland dataset (figure 4; Americas lowlands and Asia lowlands) is that the linearity between $NPP_{canopy}$ and $NPP_{wood}$ holds only for low NPP sites ($NPP_{canopy}$ approx. less than $3.8\,Mg\,C\,ha^{-1}$). Above this value there is no consistent relationship between canopy and wood productivity. All the Asian sites fall above this threshold and hence do not show any relation between the two terms.

In summary, there is clear substantial variation in above-ground allocation, with no single ratio of litterfall to woody production for all tropical forest sites. On the other hand, there is strong evidence of fairly fixed allocation for the majority of lowland Neotropical forests (and fairly strong evidence for montane Neotropical forests) with deviations where they occur tending to favour woody production. There is a suggestion of a very different relationship for Asian lowland forests (which tend to be dominated by dipterocarp trees) though the dataset for the lowlands is rather small. If the different relationship for Asian forests is genuine, perhaps such historical biogeographic 'accidents' as dipterocarp dominance [87] result in very different allocation relationships across continents. Collection of more data points in Asia and particularly Africa would greatly inform the generality of the observed Neotropical relationship.

### (b) *The allocation of net primary productivity between canopy, woody tissue and fine roots*

Next, we explore the relative allocation between the three major components of NPP, for a dataset of sites where all three components are measured (table 3; $n = 35$). The dataset consists of 22 sites in the Neotropics (10 in lowland Amazonia, eight in the Andes and four in Central/North America), eight sites in Asia and five in Hawaii. For this analysis, $NPP_{wood}$ is corrected for woody root production and branchfall as outlined above; the other two components are not corrected. We plot the three components on a ternary diagram (figure 5).

Overall, the data points cluster in the centre of the diagram, with the mean ($NPP_{canopy} = 3.32\,Mg\,C\,ha^{-1}\,yr^{-1}$, $NPP_{wood} = 3.80\,Mg\,C\,ha^{-1}\,yr^{-1}$, $NPP_{fineroot} = 2.72\,Mg\,C\,ha^{-1}\,yr^{-1}$, or in fractions, $NPP_{canopy} = 34\%$; $NPP_{wood} = 39\%$; $NPP_{fineroot} = 27\%$) suggesting almost equal partitioning between the three components (or more accurately, a partitioning of $6:7:5$

(canopy : wood : fine roots). Overall, the data cluster fairly close to the mean. A noteworthy feature of the spread of data points is that there is relatively little variance in $NPP_{canopy}$, with much of the inter-site variation caused by shifting allocation between fine roots and woody NPP, i.e. the sites always tend to allocate about 25–45% of NPP to the canopy; what varies most between sites is how the remaining NPP is allocated between woody growth and fine root production. The relatively low variance in $NPP_{canopy}$ may also be partially explained by the higher precision of $NPP_{canopy}$ measurements.

There is some evidence of geographical variation in allocation patterns (figure 5). Sites from the Neotropics tend to lie below and right of the mean (lower wood allocation, slightly higher canopy allocation), sites from Asia above and right of the mean (high wood allocation, low fine root allocation), the four Hawaiian sites to the left of the mean (low canopy allocation). However, with a low number of sites in most regions, it is premature to generalize to regional patterns. Fine root productivity is challenging to measure, and is measured using a variety of approaches. We explore whether methodological approach affects the fine root fraction (figure 5). There appears to be no clustering or systematic bias associated with measurement approach.

### (c) *Is measurement of a single component of net primary productivity (e.g. above-ground biomass production or litterfall) a good predictor of overall net primary productivity?*

Measuring all three major components of NPP can be a challenge, and it would be practically useful if a single component of NPP were a good indicator of total NPP. We now explore the relationships between $NPP_{total}$ (here defined as $NPP_{wood} + NPP_{canopy} + NPP_{fineroots}$) and each component (figure 5). $NPP_{canopy}$ shows a very significant linear relationship with $NPP_{total}$ with high explained variance (figures 5 and 6a; linear fit not forced through origin, slope $= 1.87 \pm 0.18$, $r^2 = 0.88$, $p < 0.0001$; linear fit forced through origin, slope $= 2.27 \pm 0.086$, $r^2 = 0.83$). $NPP_{wood}$ also shows a very significant linear relationship with $NPP_{total}$ but with greater unexplained variance (figure 6b, linear fit not forced through origin, slope $= 2.45 \pm 0.57$, $r^2 = 0.55$, $p < 0.001$; linear fit forced through origin, slope $= 3.61 \pm 0.27$, $r^2 = 0.40$). $NPP_{root}$ also shows a significant linear relationship with $NPP_{total}$ but with very low explained variance (linear fit not forced through origin, slope $= 1.60 \pm 0.42$, $r^2 = 0.49$, $p < 0.01$; linear fit forced through origin, slope $= 2.8 \pm 0.26$, $r^2 = 0.13$). As the two axes are not independent in figure 6a–c ($NPP_{canopy}$ is a component of both axes), the coefficients of determination ($r^2$) are indicative rather than robust. In all three cases, the curvilinearity (tested with an $F$-test on a quadratic fit) was not significant.

The analysis suggests that measurement of litterfall is a reasonably good indicator of $NPP_{total}$, as originally suggested by Bray & Gorham's [89] global model, and confirmed by Aragão *et al.* [4] and Girardin *et al.* [7] for lowland and montane Neotropical sites. Our analysis suggests that this holds for a larger pan-tropical

Table 3. Canopy NPP, stem NPP, woody NPP, fine root NPP and total NPP ($n = 40$) with yearly averaged site rainfall, temperature, latitude, longitude, and soil type for each site. Soil types are either US soil taxonomy or FAO taxonomy depending on study.

| reference | code | site | method | canopy NPP (Mg C ha$^{-1}$ yr$^{-1}$) | stem NPP (Mg C ha$^{-1}$ yr$^{-1}$) | woody NPP (Mg C ha$^{-1}$ yr$^{-1}$) | fine root NPP (Mg C ha$^{-1}$ yr$^{-1}$) | total NPP (Mg C ha$^{-1}$ yr$^{-1}$) | latitude | longitude | rainfall (mm yr$^{-1}$) | temperature (°C) | soil type |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Malhi et al.[6] | TAP-04 | Tapajós, Brazil | c | 6.53 ± 0.71 | 3.75 ± 0.075 | 6.29 | 2.01 ± 0.34 | 14.8 | −2.81 | −54.95 | 1920 | 27.2 | Geric Ferralsol |
| Aragão et al. [4] | CAX-06 | Caxiuanã, Brazil | i | 4.77 ± 0.32 | 2.18 ± 0.16 | 3.61 | 3.52 ± 0.36 | 11.9 | −1.72 | −51.45 | 2299 | 27.6 | Geric Acric Ferralsol |
| Aragão et al. [4] | CAX-03 | Caxiuanã, Brazil | i | 4.2 ± 0.087 | 2.0 ± 0.1 | 3.31 | 1.7 ± 0.3 | 9.2 | −1.72 | −51.45 | 2299 | 27.6 | Vetic Acrisol |
| Aragão et al. [4] | CAX-08 | Caxiuanã, Brazil | i | 5.6 | 2.48 ± 0.257 | 4.10 | 6.78 ± 0.82 | 16.5 | −1.72 | −51.45 | 2299 | 27.6 | Hortic Archeo-Anthrosol |
| Aragão et al. [4] | TAM-05 | Tambopata, Peru | i | 5.53 ± 0.42 | 2.80 ± 0.24 | 4.63 | 4.03 ± 0.90 | 14.2 | −12.8 | −69.8 | 2730 | 26.4 | Haplic Camisol |
| Aragão et al. [4] | TAM-06 | Tambopata, Peru | i | 4.83 ± 0.24 | 2.64 ± 1 | 4.36 | 2.34 ± 0.61 | 11.5 | −12.8 | −69.8 | 2730 | 26.4 | Haplic Alisol |
| Aragão et al. [4] | AGP-01 | Agua Pudre, Colombia | i | 3.87 ± 0.2 | 3.35 ± 0.3 | 5.54 | 2.2 ± 0.4 | 11.6 | −3.72 | −70.3 | 2562 | 25.8 | Endostagnic Plinthosol |
| Aragão et al. [4] | AGP-02 | Agua Pudre, Colombia | i | 3.65 ± 0.2 | 3.84 ± 0.3 | 6.35 | 2.2 ± 0.4 | 12.2 | −3.72 | −70.3 | 2562 | 25.8 | Endostagnic Plinthosol |
| Aragão et al. [4] | ZAR-01 | Zafire, Colombia | i | 2.67 ± 0.1 | 1.32 ± 0.3 | 2.18 | 3.9 ± 0.68 | 8.8 | −4.0 | −69.9 | 2552 | 26.1 | Orteinic Podzol |
| Girardin et al. [7] | WAY | Wayquecha, Peru | r + i | 1.92 ± 0.1 | 1.2 ± 0.12 | 1.98 | 1.23 | 5.1 | −13.18 | −71.58 | 1706 | 12.5 | Histic Lithosol |
| Girardin et al. [7] | TU3 | Trocha Union, Peru | r + i | 1.19 ± 0.05 | 1.00 ± 0.10 | 1.65 | 1.31 ± 0.23 | 4.2 | −13.1 | −71.58 | 1776 | 11.8 | Histic Lithosol |
| Girardin et al. [7] | TU4 | Trocha Union, Peru | r + i | 1.83 ± 0.06 | 1.57 ± 0.16 | 2.60 | 1.63 ± 0.34 | 6.1 | −13.1 | −71.58 | 2318 | 13.5 | Histic Lithosol |
| Girardin et al. [7] | TU7 | Trocha Union, Peru | r + i | 1.44 ± 0.06 | 0.79 ± 0.08 | 1.31 | 1.8 ± 0.18 | 4.6 | −13.06 | −71.55 | 1827 | 17.4 | Histic Lithosol |
| Girardin et al. [7] | TU8 | Trocha Union, Peru | r + i | 1.44 ± 0.08 | 0.79 ± 0.08 | 1.31 | 3.26 ± 0.73 | 6.0 | −13.06 | −71.55 | 2472 | 18 | Umbric Gleysol |
| Girardin et al. [7] | SPD | San Pedro, Peru | r + i | 2.76 ± 0.13 | 1.62 ± 0.16 | 2.68 | 1.7 ± 0.4 | 7.1 | −13.03 | −71.53 | 2631 | 18.8 | Umbric Gleysol |
| Girardin et al. [7] | TON | Tono, Peru | r + i | 2.49 ± 0.22 | 1.34 ± 0.13 | 2.22 | 2.42 ± 0.81 | 7.1 | −12.95 | −71.55 | 3087 | 20.7 | Fluvic Gleysol |
| Hertel et al. [82] | Ind | Sulawesi, Indonesia | i | 3.11 ± 0.55 | 2.65 ± 0.13 | 4.38 | 0.9 ± 0.09 | 8.4 | −1.48 | 120.05 | 3534 | 20.8 | Ferralsol soils |
| Yang et al. [81] | ch1 | Xiaohu NF, China | c | 4.45 ± 0.51 | 2.08 ± 0.50 | 3.43 | 4.32 ± 0.69 | 12.2 | 26.18 | 117.43 | 1694 | 18.5 | Humic Planosols |
| Sierra et al. [76] | col | Porce, Colombia | i | 4.72 | 4.44 | 8.06 | 1.7 | 14.5 | 6.75 | −75.1 | 2078 | 23 | Entisols and Ultisols |
| Martinez-Yrizar et al. [77] | me1 | Upper Chamela, Mexico | c | 1.65 | 1 | 1.65 | 2.12 | 5.4 | 19.5 | −105.05 | 707 | 24.9 | Entisols |
| Martinez-Yrizar et al. [77] | me2 | Middle Chamela, Mexico | c | 1.6 | 1.14 | 1.89 | 2.12 | 5.6 | 19.5 | −105.05 | 707 | 24.9 | Entisols |
| Martinez-Yrizar et al. [77] | me3 | Lower Chamela, Mexico | c | 2.11 | 1.45 | 2.40 | 2.12 | 6.6 | 19.5 | −105.05 | 707 | 24.9 | Entisols |

(*Continued.*)

Table 3. (*Continued.*)

| reference | code | site | method | canopy NPP (Mg C ha$^{-1}$ yr$^{-1}$) | stem NPP (Mg C ha$^{-1}$ yr$^{-1}$) | woody NPP (Mg C ha$^{-1}$ yr$^{-1}$) | fine root NPP (Mg C ha$^{-1}$ yr$^{-1}$) | total NPP (Mg C ha$^{-1}$ yr$^{-1}$) | latitude | longitude | rainfall (mm yr$^{-1}$) | temperature (°C) | soil type |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ostertag [88] | Hw1 | Hawaii, USA | c | 2.74 | 2.53 | 4.15 | 2.62 | 9.5 | 19.83 | −155.11 | 2500 | 16 | volcanic tephra (300 ybp) |
| Ostertag [88] | Hw2 | Hawaii, USA | c | 2.74 | 2.11 | 3.46 | 3.17 | 9.4 | 19.83 | −155.11 | 2500 | 16 | volcanic tephra (20 000 ybp) |
| Ostertag [88] | Hw3 | Hawaii, USA | c | 2.06 | 1.95 | 3.22 | 3.57 | 8.9 | 19.83 | −155.11 | 2500 | 16 | volcanic tephra (4.1×10$^6$ ybp) |
| Lugo et al. [85] | PR | Luquillo, Puerto Rico | c | 4.1 | 1.4 | 2.32 | 4.23 | 10.7 | 18.32 | −65.82 | 1650 | 25.6 | clayey Oxidic Isohyperthermic Tropeptic Haplorthox |
| Kira et al. [72] | Mal | Pasoh, Malaysia | c | 5.3 | 2.7 | 4.47 | 2.3 | 12.1 | 2.98 | 102.31 | 2054 | 26.3 | |
| Jordan et al. [67] | Ve1 | San Carlos, Venezuela | c | 2.93 | 1.76 | 2.91 | 5.59 | 11.4 | 1.93 | −67.05 | 3565 | 26.3 | Oxisol |
| Swamy et al. [81] | In1 | Western Ghats, India | e | 2.55 | 3.5 | 5.79 | 1.35 | 9.7 | 12.42 | 75.42 | 2800 | 26.6 | Oxisol |
| Swamy et al. [81] | In2 | Western Ghats, India | e | 3.7 | 3.7 | 6.12 | 1.8 | 11.6 | 12.42 | 75.42 | 3200 | 24.6 | Oxisol |
| Swamy et al. [81] | In3 | Western Ghats, India | e | 2.65 | 2.4 | 3.97 | 1.1 | 7.7 | 12.42 | 75.42 | 2800 | 26.6 | Oxisol |
| Swamy et al [81] | In4 | Western Ghats, India | e | 3.05 | 3.8 | 6.29 | 1.55 | 10.9 | 12.42 | 75.42 | 3000 | 25.6 | Oxisol |
| Tan et al. [84] | Xis | Menglun, China | e | 4.16 | 3.38 | 5.59 | 5.46 | 15.2 | 21.92 | 101.25 | 1487 | 21.7 | Lateritic |
| Herbert & Fownes [73] | Hw3 | Hawaii, USA | e | 3.2 | 1.4 | 2.32 | 4.31 | 9.8 | 19.83 | −155.11 | 2500 | 16 | volcanic tephra (1.5×10$^5$ ybp) |
| Herbert & Fownes [73] | Hw4 | Hawaii, USA | e | 4.4 | 2.6 | 4.3 | 2.81 | 11.5 | 19.83 | −155.11 | 2500 | 16 | volcanic tephra (1.4×10$^6$ ybp) |
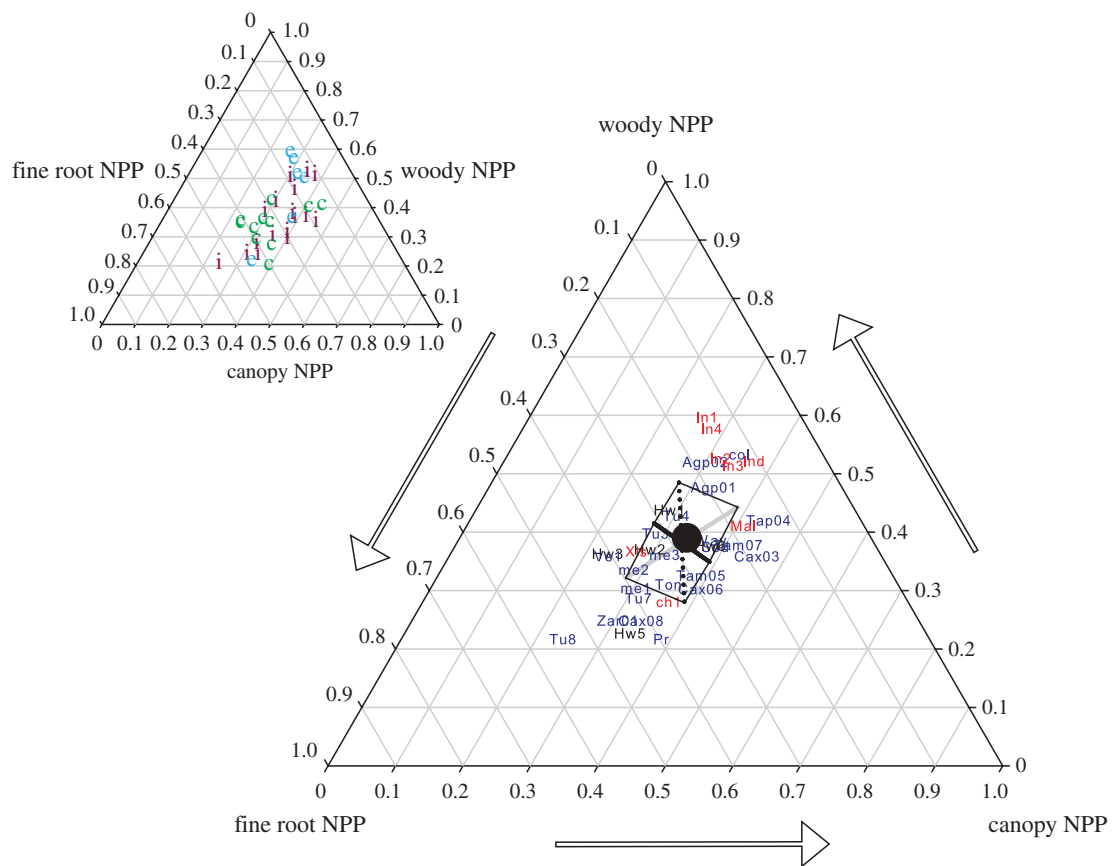
Figure 5. Ternary diagram (main figure) for woody NPP (includes branch and coarse root NPP), leaf litter NPP (includes reproductive NPP) and fine root NPP for 35 individual field sites and average among all sites (solid circle) surrounded by standard deviation (grey line is s.d. for fine root NPP, black line is s.d. for canopy NPP, dotted line is s.d. for woody NPP). The colour indicates geographical region, with blue for the Americas, red for Asia and black for Hawaii. (inset) Ternary diagram for the same dataset with labels describing methodology for fine root NPP (i, ingrowth core or rhizotron method (purple); e, estimated with litterfall and soil respiration (cyan); and c, sequential coring (green)).

dataset. Eighty-eight per cent of the variance in the dataset is explained by a simple linear relationship of $NPP_{total}$ with litterfall. This observation is consistent with the observation in the ternary diagrams (figure 5) of relatively little variance in allocation to canopy, despite much larger variation in allocation to wood and fine roots. Figure 5 also suggests that the greater variance in canopy versus wood allocation (figure 4) is mainly driven by shifting allocation between wood and fine roots, with little variation in canopy allocation. Hence, while there is only moderate evidence of constancy of allocation between wood and canopy (figure 4), once fine roots are taken into account a pattern does seem to emerge of relatively constant allocation to canopy, and shifting allocation between woody growth and fine root productivity.

As $NPP_{canopy}$ is a large component of total NPP, the two axes of figure 6a are not independent. Hence, it is unsurprising that there is a relationship between $NPP_{canopy}$ and total NPP, although the observed relationship is valuable as a practical tool for estimation of $NPP_{total}$ from litterfall data. To test the independent value of this relationship in more depth, we plot $(NPP_{fineroot} + NPP_{wood})$ against $NPP_{canopy}$ (figure 6d). As expected, there is a strong relationship between these terms (linear fit not forced through origin: slope $= 0.87 \pm 0.18$, $r^2 = 61$, $p < 0.001$; linear fit forced through origin: slope $= 1.27 \pm 0.09$, $r^2 = 0.47$).

### (d) Model predictions of net primary productivity allocation

Figure 7 shows the predicted allocation of NPP in the models listed in table 1. The allocation in many models is close to the overall mean of the data but inclined to higher wood allocation, but there is much greater spread in allocation across models. Of the outlying models, three models (Hyland, ORCHIDEE and the Friedlingstein *et al.* version of CASA) have very high allocation to wood and low allocation to fine roots and canopy, and one model (aDGVM) has relatively low allocation to wood and high allocation to fine roots. Allocation in Hyland is fixed with a very high fraction (70%) of the NPP going into the woody pool. The allocation schemes in ORCHIDEE and the Friedlingstein *et al.* version of CASA are both based on optimal partitioning theory where the fraction of NPP allocated to wood increases with increasing LAI, getting close to or exceeding 70 per cent when LAI is 5.0 (the value assumed in this study). The models closest in allocation to the mean of the data in our analysis are the original version of CASA, CCM3-LSM and JULES/TRIFFID. Both the former models assume fixed allocation schemes, while the allocation in JULES/TRIFFID is driven by allometric relationships among the different pools. However, it is important to note that the allocation coefficients in JULES/TRIFFID have been re-scaled
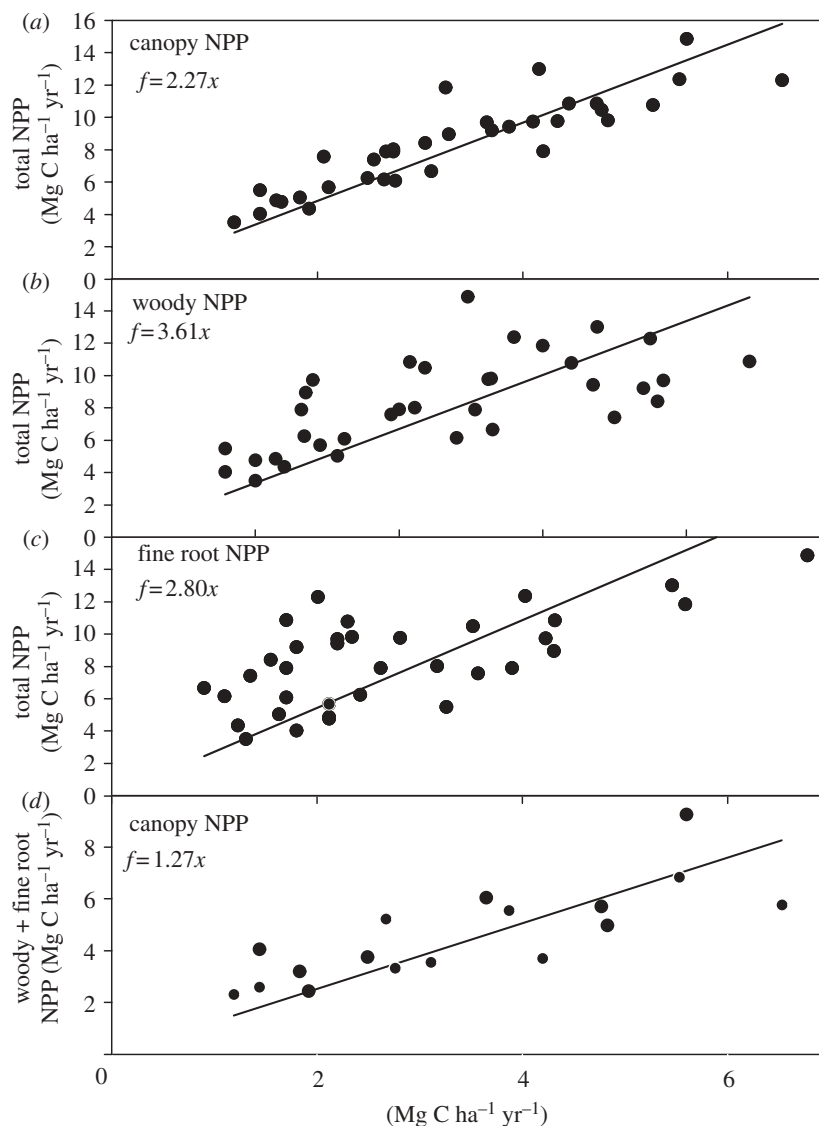
Figure 6. Total NPP (y axis) versus (*a*) canopy NPP, (*b*) woody NPP and (*c*) fine root NPP ($n = 35$) for all sites worldwide; (*d*) woody and fine root NPP versus canopy NPP. A linear function is a sufficient model to predict total NPP based on canopy NPP (linear fit not forced through origin, slope = $1.87 \pm 0.18$, $r^2 = 0.88$, $p < 0.0001$; linear fit forced through origin, slope = $2.27 \pm 0.086$, $r^2 = 0.83$), woody NPP (linear fit not forced through origin, slope = $2.45 \pm 0.57$, $r^2 = 0.55$, $p < 0.001$; linear fit forced through origin, slope = $3.61 \pm 0.27$, $r^2 = 0.40$) and fine root NPP (linear fit not forced through origin, slope = $1.60 \pm 0.42$, $r^2 = 0.49$, $p < 0.01$; linear fit forced through origin, slope = $2.80 \pm 0.26$, $r^2 = 0.13$). We also regress canopy NPP against woody and fine root NPP (linear fit not forced through origin, slope = $0.87 \pm 0.18$, $r^2 = 0.61$, $p < 0.001$; linear fit forced through origin, slope = $1.27 \pm 0.086$, $r^2 = 0.47$).

so that the fine root, wood and foliage components add up to 1. In reality, a considerable proportion of the NPP in a typical tropical forest in the model is allocated to a 'spreading' term that is difficult to relate to field measurements.

### (e) Sensitivity of data on allocation to missing net primary productivity terms

Field measurements tend to underestimate actual NPP, because of missing aspects of the main components of NPP, or because there are missing components. For our final analysis, we explore the potential effects of missing and poorly estimated NPP terms on the estimated allocation patterns. These poorly estimated terms have rarely been measured, and there exist very few data to draw general correction factors or relationships as to their significance. We consider $NPP_{canopy}$

first. For the sensitivity analysis, we assign a value of $0.4 \, \text{Mg C ha}^{-1} \, \text{yr}^{-1}$ for canopy herbivory ($0.25 \, \text{Mg C}$ insects; $0.15 \, \text{Mg C}$ vertebrates) based on a study in BCI, Panama summarized by Chave *et al.* [90]. *In situ* decomposition of leaves in the canopy (either prior to abscission or after interception of falling litter in the canopy) may be a major cause of underestimation of litterfall but has rarely been reported, with the only two reported sites being a palm rich forest and a montane forest, both atypical of the majority of lowland forests. Litter may also decompose partially in the litter traps prior to collection and drying. For the sensitivity analysis, we apply a 30 per cent correction to the litterfall because of *in situ* decomposition. As a correction for $NPP_{fineroot}$ we apply a root exudates and transfer to myccorhizae correction of $1.35 \, \text{Mg C ha}^{-1} \, \text{yr}^{-1}$ (50% of the mean fine root production), a value similar to
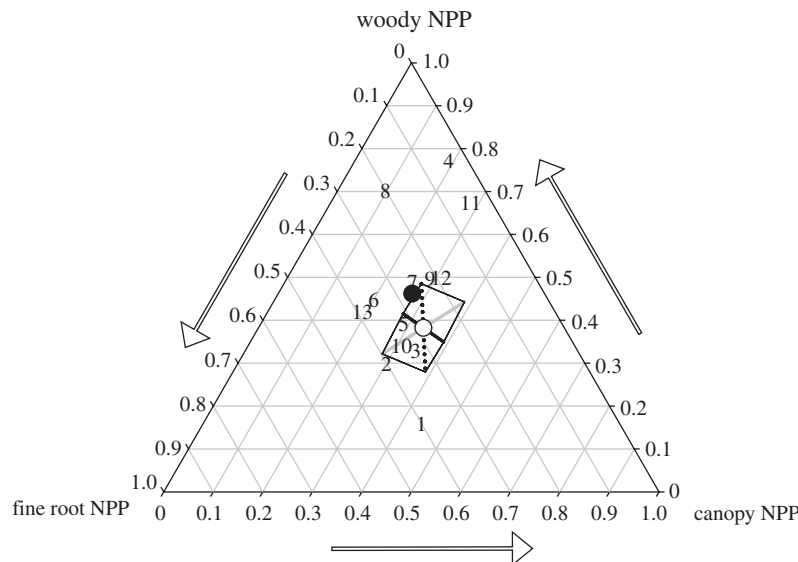
Figure 7. Ternary diagram for allocation patterns of woody NPP (includes branch and coarse root NPP), canopy NPP (includes reproductive NPP), and fine root NPP according to 13 individual models and average among all models (black circle). The average of the data is shown as an open circle surrounded by standard deviation (solid line polygon). The lines within the polygon indicate the standard deviations of woody NPP allocation (dotted line), canopy NPP allocation (solid black line) and fine root NPP allocation (solid grey line). Numbers refer to models as listed in table 1 and figure 3.

the estimates of myccorhizal respiration reported for several Amazonian lowland sites (D. B. Metcalfe 2011, unpublished data) and at a tropical forest in Panama [91]. For $NPP_{wood}$, we add a correction of 10 per cent for small trees ($<10\%$ d.b.h.) and lianas, based on an estimate of their contribution to standing biomass [92]. The range of these corrections is shown in figure 8, and is an indicator of the overall uncertainty around any one data point introduced by missing NPP terms. The actual correction for any one site will probably vary from site to site.

If all three corrections (to wood, leaves and roots) apply, the corrections partially offset each other and the overall effect of these corrections on allocation is modest (figure 7), shifting the allocation even closer to equal partitioning by reducing relative wood allocation, but with the litter and root corrections offsetting each other and not substantially shifting canopy : root partitioning. Overall, the analysis gives an indication of the systematic uncertainties associated with the dataset, in addition to the geographical and stochastic uncertainties captured in figure 4. The systematic uncertainties appear smaller than the spread of data values, but do have the potential to be larger than the stochastic random error of the dataset. In combination, the potential corrections to $NPP_{canopy}$ and $NPP_{root}$ tend to push the data mean away from the allocation patterns in the majority of models (compare figure 8 with figure 7). The discrepancies between models and the mean of the data are unlikely to be explained by missing NPP terms. Moreover, the uncertainty introduced by missing NPP terms (figure 7) is smaller than the spread in field observations (figure 5) and much smaller than the spread in model simulations (figure 7). Hence, it is very unlikely that the overall spread of field data can be explained by missing NPP terms, or that the outlying models can be accommodated by taking missing NPP terms into account.

## 6. CONCLUSION

In this study, we have compiled and analysed a global dataset on the allocation of NPP in tropical forests. We find evidence of substantial variation in NPP allocation across sites, but also some consistent patterns. Relative allocation to canopy production appears less variable than allocation to wood and fine roots, a feature that enables litterfall collection to provide reasonable estimates of total NPP. The relationship between canopy and wood allocation appears relatively fixed in lowland Neotropical sites, and possibly also in highland Neotropical sites. There is much less evidence of fixed allometric partitioning in Asian lowland forests; if verified with a larger dataset, it suggests that biogeographic differences cause differences in allometric partitioning between major tropical forest regions. Highland regions (in Asia and Hawaii) appear to have much more variable allometric partitioning, perhaps not surprising given the highly variable resource and structural demands imposed by slope, aspect, soils and landslide disturbance in montane environments. This dataset provides a benchmark dataset with which to evaluate NPP partitioning in terrestrial ecosystem models. The data suggest something close to equal partitioning of NPP between canopy, wood and fine roots. Most terrestrial ecosystem models come fairly close to the data mean, but there are a number of outlying models.

The relatively low variance in allocation to canopy NPP indicates that shifting allocation between wood and fine roots is the dominant cause of variation in NPP allocation. This existence of a 'wood–fine root' trade-off, as opposed to a 'root–shoot' trade-off, has recently been posited by Dybzinski *et al.* [93] in a theoretical framework for old-growth stands. Their framework predicts the most competitive allocation of NPP in invading trees as they compete with established trees, in old-growth stands where the stand is
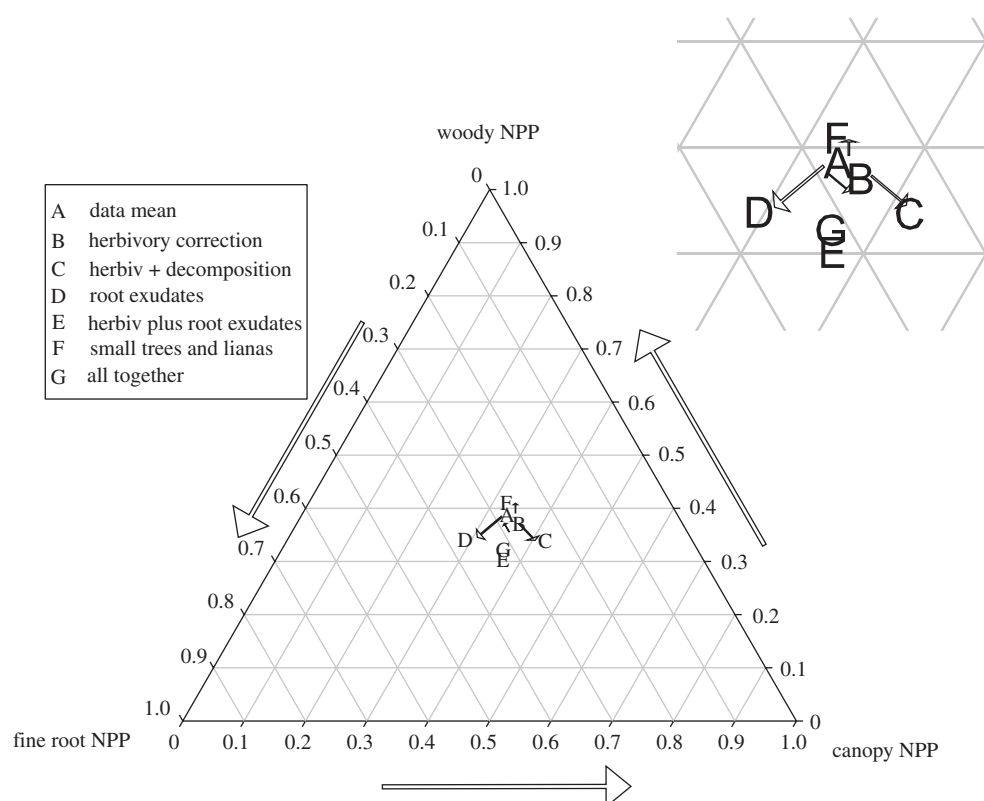
Figure 8. The sensitivity of allocation patterns to inclusion of the potential missing terms herbivory, decomposition and root exudates (see main text for details). Total canopy NPP correction is A–C; total fine root NPP correction is A–D and woody production correction is A–F. If corrections are applied to all three terms the net correction is A–G.

dual-limited by light and nutrients. Self-shading ultimately limits returns on foliage investment, whereas competitive considerations dominate investment in fine roots versus wood. Our observations of NPP allocation in old-growth tropical forest are consistent with this posited trade-off. This trade-off also explains why litterfall is a better indicator of total NPP than stem growth or fine root productivity.

The sensitivity analysis highlights that there is still room for improvement in field estimation of NPP and its allocation. The degree to which litterfall collection underestimates NPP$_{canopy}$ (by not accounting for herbivory, *in situ* decay and large litter) is the greatest major source of uncertainty, together with missing below-ground NPP terms such as provision of root exudates and carbohydrate transfer to myccorhizae. There are very few data to consistently apply corrections for these missing terms. Both these corrections would tend to move the mean downwards in the ternary diagrams (i.e. less wood allocation), although the overall shift in allocation is still relatively modest. In addition to the methodological gaps, the other major gap is geographical. The complete lack of data from Africa, which accounts for a quarter of the world's tropical forests, is particularly apparent, but all regions could benefit from extended data collection of a range of ecological and physical conditions. Both improving understanding of missing NPP terms at a variety of tropical sites, and extending data collection, particularly so in Africa, should be a priority for future NPP data collection in tropical forests.

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