



## RESEARCH ARTICLE

# Global Patterns in the Allocation of Forest Net Primary Production

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**Received:** 19 December 2023 | **Revised:** 28 October 2024 | **Accepted:** 9 January 2025

**Funding:** This work was supported by National Taiwan University, National Science and Technology Council, Ministry of Education Republic of China (Taiwan).

**Keywords:** bioclimate | carbon allocation | fine root | litterfall | machine learning | random forests | remote sensing

## ABSTRACT

**Aim:** Environmental factors that govern the allocation of net primary production (NPP) between long-lived components (wood) and short-lived components (leaves, fine roots) are poorly understood yet essential when relating NPP to carbon stocks, especially among different plant functional types. We conducted a spatially synoptic analysis to investigate the relationships between NPP allocation and climate at the global scale. We ask a fundamental question in forest ecology and terrestrial carbon science: What environmental drivers influence NPP allocation?

**Location:** Global forests (64.21 N–41.53 S).

**Taxon:** Trees.

**Methods:** We investigated the relationships between field forest NPP data ( $n = 131$ ) and 31 bioclimatic, meteorological, geographical, topographic and vegetation variables using machine learning.

**Results:** These environmental variables accounted for 94%, 93% and 85% of the variation in canopy, woody and fine-root NPP fractions, respectively. Most of the important predictors were temperature-related. Allocation to the canopy was facilitated by warm and stable climates. In contrast, woody and fine-root carbon growth could endure cold and extreme temperatures.

**Main Conclusions:** Our analysis suggested that the most important drivers were annual mean (e.g. high canopy and fine-root NPP ratios in favourable climates), variation and extreme (e.g. significant woody and fine-root NPP ratios where light- and nutrient-limited) of temperatures. Overall, most carbon was stored in woody tissue and in a constant proportion to the canopy, which could be explained by allometric scaling and resource availability. Our results pointed to a ‘root-wood’ trade-off rather than the previously prevailing ‘root-leaf’ trade-off, but may vary regionally. For example, regarding particular plant functional types, ‘wood-leaf’ and ‘root-leaf’ were only evident in broadleaved and coniferous forests, respectively, to adapt to climates and compete for resources. Knowing the relationships between NPP allocation and the environment, we could assess forest carbon cycle dynamics in the face of climate change.

## 1 | Introduction

Net primary productivity (NPP), defined as the amount of new plant tissue produced over a period of time (Šimová and

Storch 2017), is one of the most commonly used metrics to quantify carbon flux among sinks in the biosphere, and is sensitive to environmental change (Field et al. 1998; Nemani et al. 2003; Zhao and Running 2010). NPP can be generally allocated as

the growth of leaf (canopy NPP [ $NPP_{\text{canopy}}$ ]), woody ( $NPP_{\text{woody}}$ ) and fine-root ( $NPP_{\text{root}}$ ) tissues (del Aguila-Pasquel et al. 2014; Malhi 2012; Malhi, Doughty, and Galbraith 2011).  $NPP_{\text{canopy}}$  primarily controls carbon turnover,  $NPP_{\text{woody}}$  is the main contributor to terrestrial vegetation structure and carbon storage, and  $NPP_{\text{root}}$  dictates water and nutrient uptake (Malhi, Doughty, and Galbraith 2011; McCormack et al. 2013). The allocations (or ratios, both terms used interchangeably hereafter) of labile and recalcitrant tissues, as well as respiration, determine the residence time of carbon in terrestrial ecosystems (Dufresne et al. 2002; Ise et al. 2010). Hence, where the sequestered carbon dioxide goes is pivotal for understanding the terrestrial carbon cycle (Chen, Yang, and Robinson 2013). However, due to the difficulty of field NPP data collection, especially for the belowground component (Clark et al. 2001; Johnson et al. 2001; Nadelhoffer and Raich 1992), investigating NPP allocation poses a significant challenge (Aragão et al. 2009; Clark et al. 2001; Malhi et al. 2009).

Human-induced perturbations such as land use and land cover change in concert with elevated temperatures may have altered regional precipitation patterns, resulting in extreme meteorological events such as prolonged droughts (Overpeck and Udall 2010) or intensified rainfall (Myhre et al. 2019). Doughty et al. (2015) found that climatic variation (dry vs. wet seasons) in the Amazon Basin might have more influences on the ratios of NPP than on total NPP. This is due to temporal decoupling between total photosynthesis and carbon usage, which suggests the existence of nonstructural carbohydrates that could enable growth and the allocation of carbon at times that are ecologically advantageous rather than when environmental conditions permit. Plant responses to global changes in altered resource availability are critical to future atmospheric  $CO_2$  concentrations and hydrology (Clark et al. 2001; Dewar et al. 2009). However, the degree to which environmental factors govern the ratios of NPP remains unclear. Bioclimatic attributes, mainly temperature and precipitation, affect how forests allocate carbon to above- (branches, leaves and stems) and belowground (fine and coarse roots) biomass. Higher temperatures generally enhance plant metabolism and increase aboveground carbon accumulation (Ma et al. 2021; Zhou et al. 2022). In some regions (e.g. tropical montane forests), increasing elevation (cooler temperatures) results in more carbon distributed to the root system. Low temperatures often coincide with less nutrient availability, resulting in more carbon investment in roots to facilitate nutrient uptake (Cornejo et al. 2021). Water availability may also be crucial for tree growth, such as apportioning more carbon to the root system to improve water absorption. This adaptive strategy helps plants cope with water stress, but the impacts on woody plants were relatively moderate compared to herbaceous species (Xia et al. 2023). Overall, since water availability is directly related to the presence of forests, temperature factors may play a more critical role in forest ecosystems.

Previous literature regarding the relationships between NPP ratios and climate mainly consisted of local field studies focusing on the tropics. For example, Hofhansl et al. (2015) synthesised pantropical old-growth rainforest data to investigate environmental controls on the allocating of aboveground NPP; they found that temperature and soil phosphorus availability

indirectly affected wood production by enhancing productivity, while precipitation and dry season length directly increased wood production to maximise plant hydraulic safety with increasing drought frequency and intensity. Although literature (e.g. Luyssaert et al. 2007) and established databases such as ForC (Anderson-Teixeira et al. 2018) are available on the forest carbon budget at the global scale, few studies have discussed the environmental drivers and spatial patterns of NPP allocation. Furthermore, mechanisms driving the photosynthesis product allocations are fundamental in developing mechanistic models of allocation in a single tree, a stand and an ecosystem (Fyllas et al. 2017; Wolf, Field, and Berry 2011) in terms of optimal responses in finding the strategy of maximal fitness (Dewar et al. 2009; Franklin et al. 2012). Empirical and allometric methods are explicit but lack the power to explain the multifaceted effects of environmental variability (Franklin et al. 2012). Such knowledge is, therefore, of paramount importance in developing and parameterizing global vegetation models for predicting future responses of terrestrial carbon sequestration and allocation to global changes (Chen, Yang, and Robinson 2013; Hofhansl et al. 2015; Litton, Raich, and Ryan 2007; McMurtrie and Dewar 2013).

In this study, we conducted a spatially synoptic analysis to investigate the relationships between forest NPP allocation and physical geography by collating and analysing previously reported global field NPP data and spatiotemporally corresponding environmental attributes. We ask a fundamental question in forest ecology and terrestrial carbon science: What are the main environmental drivers influencing the allocation of forest NPP? We hypothesize that: Forests are present in regions receiving a certain amount of precipitation by nature. Therefore, temperature attributes (particularly related to seasonality [e.g. growing season]) would be more sensitive to forest NPP ratios than other variables.

## 2 | Methods

### 2.1 | Field NPP Data Compilation

The study region was global forests. We conducted a literature review using Google Scholar (<https://scholar.google.com/>) to search through previously compiled annual NPP datasets from data syntheses (Anderson-Teixeira et al. 2018; Campioli et al. 2016; Luyssaert et al. 2007; Malhi et al. 2009, 2021; Malhi, Doughty, and Galbraith 2011; Michaletz et al. 2014) or site studies (Araujo-Murakami et al. 2013; Girardin et al. 2010; Kho, Malhi, and Tan 2013; Malhi et al. 2013; Swamy et al. 2010) (Table S1). We selected only directly collected  $NPP_{\text{canopy}}$ ,  $NPP_{\text{woody}}$  and  $NPP_{\text{root}}$ . Additionally, we added three datasets of subtropical montane forests in Taiwan: A humid evergreen conifer forest plot in Chilan Mountain (Hu and Huang 2019) and two broadleaf forest plots with different annual precipitation in the Fushan (Chang et al. 2020) and Lienhuachi (Chung and Huang 2020) Experimental Stations.

Field NPP data collection generally followed (Clark et al. 2001; Malhi et al. 2021). Canopy productivity ( $NPP_{\text{canopy}}$ ) was mostly forest leaf and branch litterfall collected using litterfall traps; a few studies also considered the dynamics of canopy closure (see

Doughty and Goulden 2008 for details).  $NPP_{\text{woody}}$  referred to increments in standing-wood biomass, including stem, branch and coarse-root production, estimated by site-specific or general tree allometries;  $NPP_{\text{root}}$  was measured from ingrowth cores or minirhizotron. We note that the losses of NPP due to herbivory and debris heterotrophic respiration were usually not measured or mentioned in the literature. In addition, a small and poorly quantified fraction of the overall NPP of components, including NPP to non-structural carbohydrate reserves, reproductive materials (e.g. seeds, fruits and inflorescences), herbivores, root exudation, volatile organic compounds and symbionts (e.g. mycorrhizae and epiphytes) (Malhi, Doughty, and Galbraith 2011), were omitted from the data analysis. They occupied about 20% of forest NPP in the tropics (Doughty et al. 2015) but may vary across regions.

## 2.2 | Field Site Biome, Leaf, and Soil Properties

Biotic and climatic factors influencing NPP ratios comprised leaf characteristics, biome type and soil fertility. Leaf characteristics included leaf habit (deciduous, evergreen and mixed) and type (broad-leaved, coniferous and mixed). Biome types were tropical, temperate or boreal biomes, depending on the climate zone. Attributes for each field site were assigned by referring to Anderson-Teixeira et al. (2018), Olson et al. (2001) and Wei et al. (2014). We extracted soil fertility information for each site from the Harmonised World Soil Database v. 1.2 (Fischer et al. 2008) and regrouped it into high (fertile), medium (moderately fertile) or low (infertile) classes by referring to soil total exchangeable bases (Michaletz et al. 2014). We used a one-way analysis of variance (ANOVA) to determine the significance of the effects of leaf, biome and soil features on NPP allocation. Furthermore, we applied the Tukey–Kramer multiple comparison tests on NPP components re-grouped by leaf, biome and soil properties.

## 2.3 | Global NPP Ratio Predictors

We acquired 31 global-scale bioclimatic, geographical, topographic and vegetation attributes, which could potentially (directly or indirectly) influence plant growth (Table S2). We obtained 24 geographically corresponding bioclimatic features for the NPP sites from the 30-s ( $\sim 1 \text{ km}^2$ ) spatial resolution WorldClim2 (Fick and Hijmans 2017) from 1970 to 2000 using R v. 3.5.1 (<https://www.r-project.org/>) and RStudio v. 1.4 (<https://www.rstudio.com/>). The bioclimatic attributes were aggregated monthly data on different temporal scales (month, quarter and year) and averaged to the mean or sum annual values. These include 13 temperature ( $^{\circ}\text{C}$ )- and eight precipitation (mm)-related variables (for details, see Table S2), solar radiation ( $\text{kJ m}^{-2} \text{ day}^{-1}$ ), wind speed ( $\text{m s}^{-1}$ ) and water vapour pressure (kPa). The geographical factors were longitude (ocean current-influenced climates) and absolute latitude; those for topography were elevation (m) (related to temperature), slope ( $^{\circ}$ ) (soil stability) and aspect ( $^{\circ}$ ) (solar radiation and soil humidity) from the Global Multi-resolution Terrain Elevation Data (GMTED2010) (Danielson and Gesch 2011). Aspect cannot be directly utilised for the analysis since this metric is not incremental (e.g. north-facing aspects of  $0^{\circ}$  and  $359^{\circ}$  were akin but in contrast to the

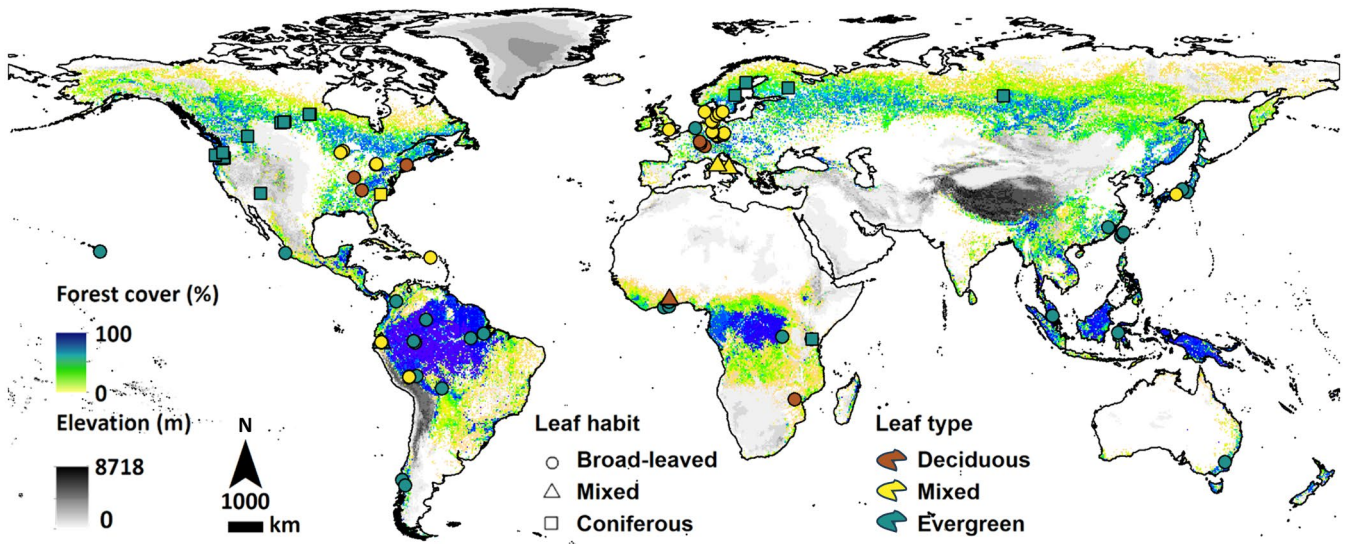
south-facing  $180^{\circ}$ ). Therefore, it was categorised into eight evenly divided nominal classes: North ( $0^{\circ}$ – $22.5^{\circ}$  and  $337.5^{\circ}$ – $360^{\circ}$ ), northeast ( $22.5^{\circ}$ – $67.5^{\circ}$ ), east ( $67.5^{\circ}$ – $112.5^{\circ}$ ), southeast ( $112.5^{\circ}$ – $157.5^{\circ}$ ), south ( $157.5^{\circ}$ – $202.5^{\circ}$ ), southwest ( $202.5^{\circ}$ – $247.5^{\circ}$ ), west ( $247.5^{\circ}$ – $292.5^{\circ}$ ) and northwest ( $292.5^{\circ}$ – $337.5^{\circ}$ ). In addition, we acquired global-scale forest attributes, including MODIS (the Moderate Resolution Imaging Spectroradiometer)-derived mean annual total NPP from 2000 to 2015 ( $\text{Mg C ha}^{-1} \text{ year}^{-1}$ ) (product ID: MOD17A3H) (Nemani et al. 2003) and forest cover (%), by referring to Hansen, Stehman, and Potapov (2010) and the Food and Agriculture Organisation and Global Forest Resources Assessment (FAO 2010). We note that using MODIS NPP should be legitimate since the acquisitions of field NPP and modelled MODIS data were entirely independent. The spatial resolutions of geographical, topographic and vegetation attributes were resampled to match the WorldClim2 (the coarsest resolution) using the nearest neighbourhood method. We conducted spatial analyses using ENVI v. 4.7 (Exelis Visual Information Solutions, Boulder, CO, USA) and ArcGIS v. 10.4 (Environmental Systems Research Institute, Redlands, CA, USA), and statistics and visualisation were performed with R packages ggplot2, ggtern, gridExtra, patchwork and scales (Aguie and Antonov 2017; Hamilton and Ferry 2018; Pedersen 2020; Villanueva and Chen 2019).

## 2.4 | Random Forests

In this study, we chose machine learning over other statistical/mathematical approaches to model  $NPP_{\text{canopy}}$ ,  $NPP_{\text{woody}}$  and  $NPP_{\text{root}}$  ratios ( $NPP_{\text{canopy}}/NPP$ ,  $NPP_{\text{woody}}/NPP$  and  $NPP_{\text{root}}/NPP$ , respectively) due to the spatiotemporal heterogeneity and environmental complexity governing NPP allocation. Machine learning is legitimate for coping with high-dimensional and nonlinear ecological data with correlations (Thessen 2016). Random forests (RF) (Breiman 2001), composed of decision trees, are among the most widely used algorithms. Each tree is based on a random composition of the predictors, and a training data subset is chosen with the bagging (or bootstrap aggregating) sampling method. The samples not utilised for building the tree are ‘out-of-the-bag’ and are used to validate the model performance. RF maintain performance stability by averaging each tree’s branches and thus avoid overfitting. Many variables are allowed, and no prior assumption is required among predictors, such as correlation and nonlinearity (Moore, Lees, and Davey 1991). Operationally, the method is user-friendly with only two commonly adjustable parameters: The number of trees in a forest and the number of predictors of each tree. However, it is also insensitive to both parameters (Liaw and Wiener 2002).

Three RF models were deployed to derive  $NPP_{\text{canopy}}$ ,  $NPP_{\text{woody}}$  and  $NPP_{\text{root}}$  allocations separately using 70% ( $n=91$ ) of the field NPP and spatially corresponding environment datasets. The models were trained with the aforementioned 31 environmental variables using the R package randomForest (Liaw and Wiener 2002). For each model, the optimal number of trees and the number of predictors sampled at each split were selected by grid search with the enumeration method. Model performance was assessed by comparison with the remaining 30% ( $n=40$ ) of the data based on squared correlation coefficients ( $r^2$ ) and root mean square error (RMSE) of the simple linear regression between predictions and observations. We





**FIGURE 1** | Forest NPP datasets of 131 study sites (yellow dots) compiled from the literature and collected by the authors, with the background of 2010 forest cover (green monochrome colours) and a global scale digital elevation model (grey monochrome colours).

determined the variable importance and selected the feature subset using the following four algorithms: Built-in cross-validation metrics as (1) decline in mean square error (MSE) and (2) decline in residual sum of squares (RSS) computed from permuting each predictor variable averaged over all trees and cross-validating with 'out-of-the-bag' data, (3) variable selection using RF (Genauer, Poggi, and Tuleau-Malot 2010) and (4) recursive feature elimination provided by caret (Kuhn et al. 2020). After that, the performances of each subset of variables were compared with the original whole-variable model, and the best model was selected. The top five important variables were selected with the lowest sum of ranking by the abovementioned four measurements. The Pearson correlation coefficient ( $r$ ) further showed the directions of each variable impacting the  $NPP_{\text{canopy}}$ ,  $NPP_{\text{woody}}$  and  $NPP_{\text{froot}}$  allocations, as RF could give the variable importance but not the positive or negative sign. With the availability of three valid RF models, the NPP ratios were mapped within the global forested areas. The spatial inter/extrapolation may allow us to estimate NPP allocation of the unsampled areas and further facilitate investigating NPP allocation patterns along the environmental gradients.

### 3 | Results

#### 3.1 | Field NPP

There were 131 sites selected for the study covering Africa ( $n=11$ ), America ( $n=78$ ), Eurasia ( $n=40$ ) and Oceania ( $n=2$ ) and latitudinal ranges of  $-41.53^\circ$  and  $64.21^\circ$  (Figure 1 and Table S1). The means ( $\pm$  standard deviations [SDs]) of  $NPP_{\text{canopy}}$ ,  $NPP_{\text{woody}}$  and  $NPP_{\text{froot}}$  were  $2.10 \pm 1.57 \text{ Mg C ha}^{-1}\text{y}^{-1}$ ,  $3.24 \pm 2.05 \text{ Mg C ha}^{-1}\text{y}^{-1}$  and  $1.83 \pm 1.71 \text{ Mg C ha}^{-1}\text{y}^{-1}$ , respectively, with a total NPP of  $7.20 \pm 3.81 \text{ Mg C ha}^{-1}\text{y}^{-1}$  (Table S3). The mean ( $\pm$  SD) ratios for  $NPP_{\text{canopy}}$ ,  $NPP_{\text{woody}}$  and  $NPP_{\text{froot}}$  were  $0.29 \pm 0.12$ ,  $0.44 \pm 0.14$  and  $0.27 \pm 0.15$ , respectively (Figure S1 and Table 1). Latitudinally, the tropics ( $n=42$ ) maintained the highest  $NPP_{\text{canopy}}$  ratio (mean  $\pm$  SD =  $0.37 \pm 0.10$ ), while temperate forests ( $n=80$ )

**TABLE 1** | Mean ( $\pm$  SD) of NPP ratios of 131 field NPP plots (Figure 1) categorised by biome, leaf type, leaf habit and soil fertility.

Class (n)	NPP ratio		
	Canopy	Woody	Fine-root
<i>Biome</i>			
Tropical forest (42)	$0.37 \pm 0.10$	$0.34 \pm 0.11$	$0.29 \pm 0.15$
Temperate forest (78)	$0.25 \pm 0.10$	$0.50 \pm 0.14$	$0.26 \pm 0.14$
Boreal forest (11)	$0.22 \pm 0.07$	$0.45 \pm 0.09$	$0.33 \pm 0.12$
Overall (131)	$0.29 \pm 0.12$	$0.44 \pm 0.14$	$0.27 \pm 0.15$
<i>Leaf type</i>			
Broadleaved (78)	$0.33 \pm 0.11$	$0.41 \pm 0.14$	$0.26 \pm 0.13$
Mixed (5)	$0.22 \pm 0.05$	$0.48 \pm 0.23$	$0.30 \pm 0.18$
Coniferous (50)	$0.22 \pm 0.08$	$0.49 \pm 0.13$	$0.29 \pm 0.15$
<i>Leaf habit</i>			
Deciduous (11)	$0.28 \pm 0.05$	$0.44 \pm 0.14$	$0.28 \pm 0.16$
Mixed (34)	$0.29 \pm 0.11$	$0.48 \pm 0.16$	$0.23 \pm 0.10$
Evergreen (85)	$0.28 \pm 0.12$	$0.43 \pm 0.14$	$0.29 \pm 0.15$
<i>Soil fertility</i>			
High (14)	$0.31 \pm 0.12$	$0.43 \pm 0.11$	$0.26 \pm 0.13$
Medium (7)	$0.25 \pm 0.10$	$0.53 \pm 0.08$	$0.22 \pm 0.07$
Low (112)	$0.28 \pm 0.12$	$0.44 \pm 0.15$	$0.28 \pm 0.14$

surpassed other biome zones in  $NPP_{\text{woody}}$  fraction ( $0.50 \pm 0.14$ ), and boreal regions ( $n=11$ ) in  $NPP_{\text{froot}}$  ratio ( $0.33 \pm 0.12$ ) (Table 1). Overall, a significant difference in allocating arose among three components ( $p < 0.001$ , ANOVA), also between  $NPP_{\text{canopy}}$  and  $NPP_{\text{woody}}$  ( $p < 0.001$ ) and between  $NPP_{\text{woody}}$  and  $NPP_{\text{froot}}$  ( $p < 0.001$ ), but not between  $NPP_{\text{canopy}}$  and  $NPP_{\text{froot}}$  ( $p = 0.78$ ) by Tukey–Kramer tests. Negative linear correlations

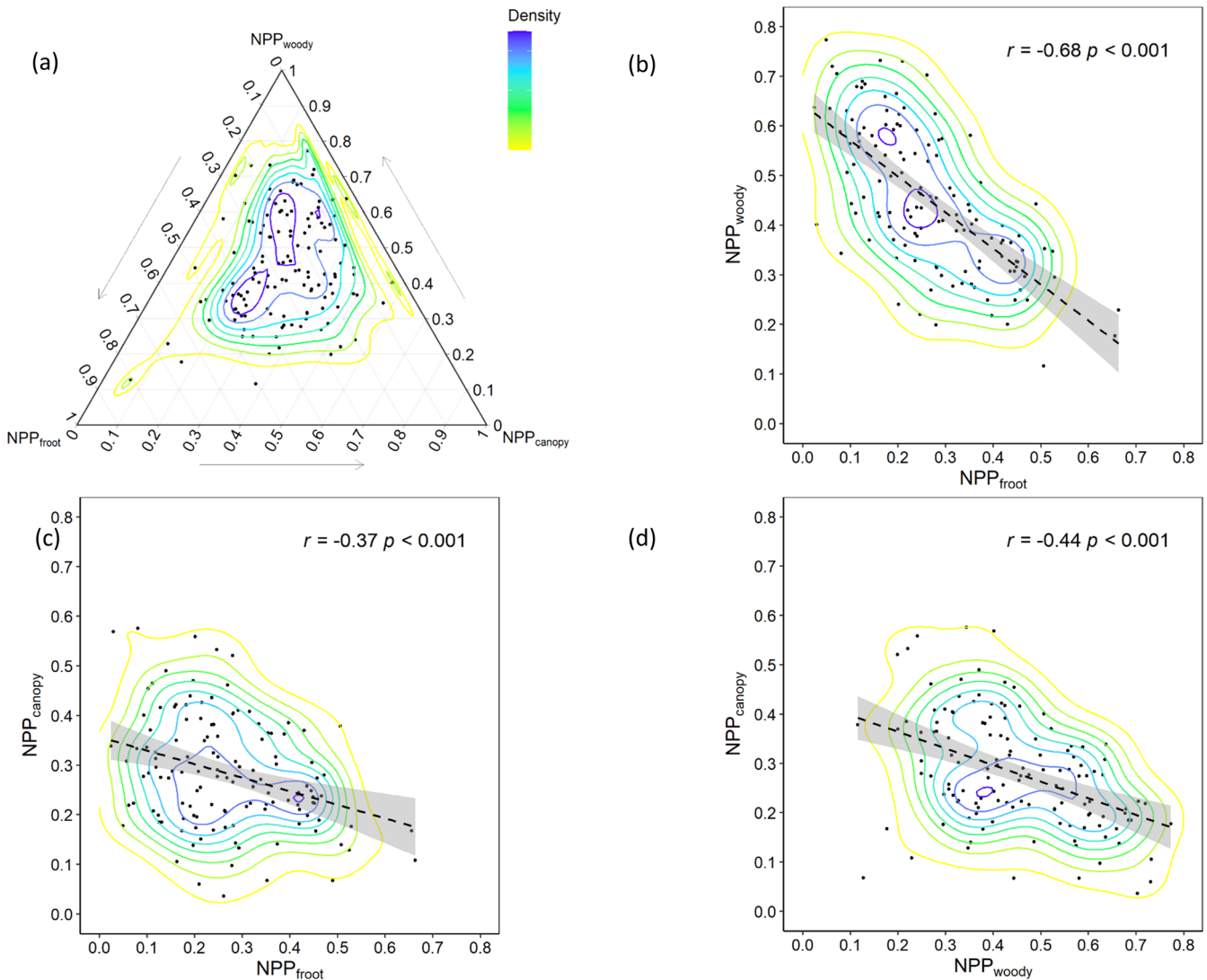
of allocation ( $p < 0.001$ ) were found between  $NPP_{woody}$  and  $NPP_{root}$  ( $r = -0.68$ ), much more significant than those of  $NPP_{canopy}$  and  $NPP_{root}$  ( $r = -0.37$ ) and  $NPP_{canopy}$  and  $NPP_{woody}$  ( $r = -0.44$ ) (Figure 2).

### 3.2 | Site Characteristics

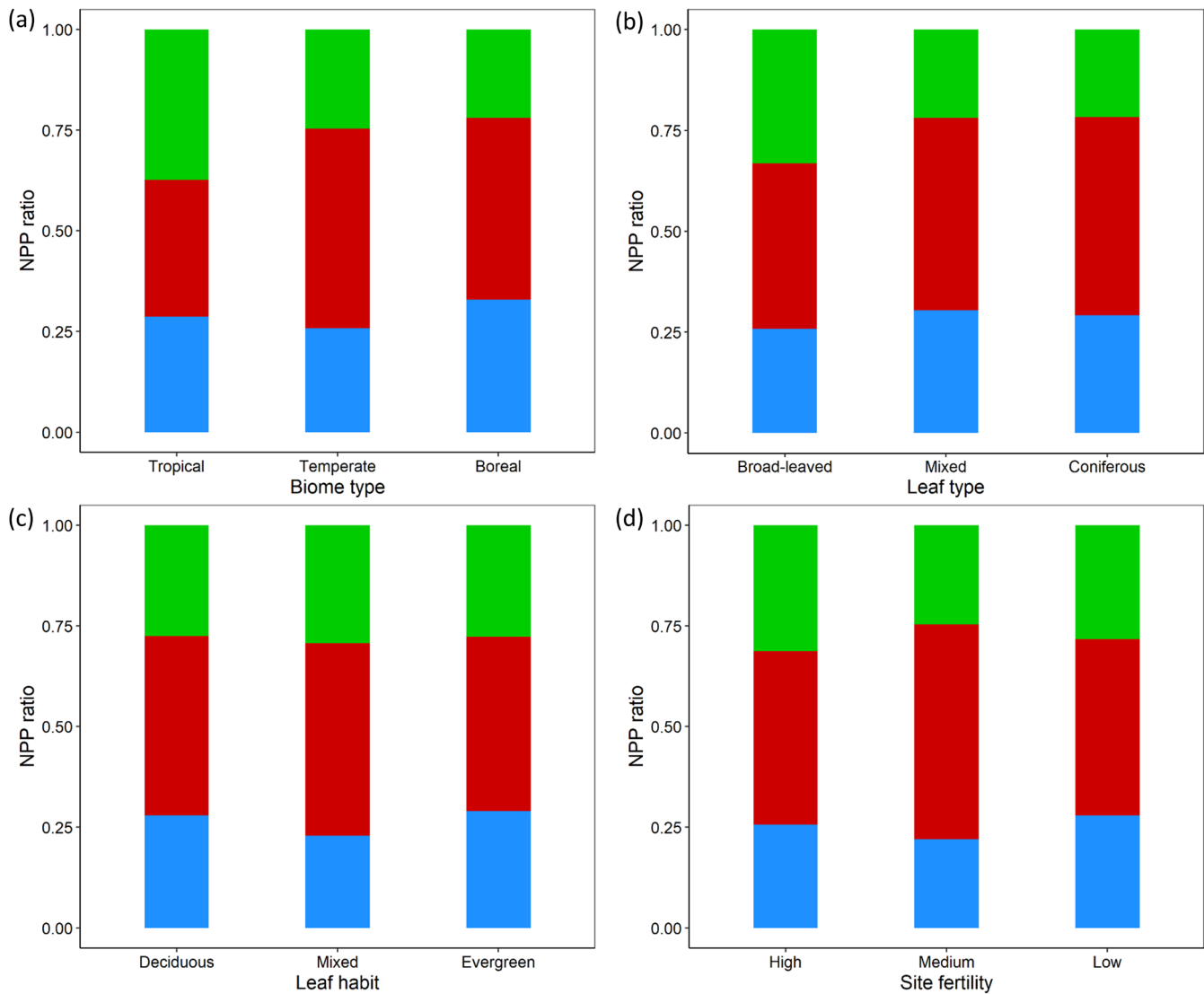
Based upon the field observation, biome type ( $p < 0.001$  for  $NPP_{canopy}$  and  $NPP_{woody}$ ) and leaf type ( $p < 0.001$  for  $NPP_{canopy}$ ,  $p < 0.01$  for  $NPP_{woody}$ ) had significant effects but not on  $NPP_{root}$  ratios, while leaf habit and soil fertility hardly accounted for it, according to a one-way ANOVA (Figure 3 and Table 1). Coniferous and broadleaved forests diverged in  $NPP_{canopy}$  ratios ( $p < 0.001$  for broadleaved and coniferous,  $p < 0.05$  for broadleaved and mixed) and  $NPP_{woody}$  fractions ( $p < 0.01$  for broadleaved and coniferous) based on Tukey–Kramer tests.  $NPP_{canopy}$  ratios differed across biome types ( $p < 0.001$  for tropical and boreal, and  $p < 0.001$  for tropical and temperate), and  $NPP_{woody}$  allocations varied among regions ( $p < 0.05$  for tropical and boreal, and  $p < 0.001$  for tropical and temperate). Leaf habit and soil

fertility were insignificant to NPP allocation. Cross-comparing those environmental settings, it was further observed that the canopy, in terms of NPP ratios, tended to flourish at low latitudes with broad leaves and fertile soil. However, coniferous and less fertile forests allocated more fine-root carbon belowground, while forests produced more woody tissues under intermediate conditions such as temperate regions, mixed leaf type and habit and moderate fertility (Table 1, also see Figure 3 and Figure S2).

Broadleaf forests allocated more NPP in the canopy than conifers, which allocated more carbon to woody and fine-root components (Figure 3b). The correlation coefficient between  $NPP_{root}$  and  $NPP_{woody}$  ratios was evident in all groups ( $|r| \geq 0.67$ ,  $p < 0.001$ ) (Figure S4). However, the negative allocation between  $NPP_{root}$  and  $NPP_{canopy}$  was only found moderate in conifer and between  $NPP_{woody}$  and  $NPP_{canopy}$  in broadleaf forests ( $|r|$  of 0.49,  $p < 0.001$ ) (Figure S4). Similar results were found for biome type, leaf habit and soil fertility, in which allocating fine roots against woody plants was robust. The trade-off in allocating between  $NPP_{root}$  and  $NPP_{canopy}$  was found to be the highest in tropical, evergreen and fertile sites among categories ( $|r| \geq 0.46$ ,  $p < 0.05$ ),



**FIGURE 2** | (a) NPP ratio pattern of 131 field sites. (b–d) Trade-offs between each pair of canopy, woody and fine-root NPP ratios with a red (higher density)-blue (lower density) colour gradient.



**FIGURE 3** | NPP ratios of 131 field sites grouped by (a) biome type, (b) leaf type, (c) leaf habit and (d) soil fertility.

and that between  $NPP_{\text{woody}}$  and  $NPP_{\text{canopy}}$  was found in temperate, mixed and infertile sites ( $|r| \geq 0.41$ ,  $p < 0.001$ ) (Figures S3, S5 and S6).

### 3.3 | Random Forests

In this study, we employed RF to unravel the complex relationships between NPP ratios and a comprehensive set of variables (Table S2), which allowed us to decipher the pivotal environmental variables to estimate NPP ratios. We found that the most important 14 predictors.

Were all but wind speed, warmest quarter precipitation and longitude associated with temperature variation (e.g. seasonality, isothermality and range), annual (minimum) and extreme (coldest month minimum and driest quarter) (Table 2; the complete result see Table S4). Temperature variation attributes had significant ( $p \leq 0.05$ ) effects on the  $NPP_{\text{canopy}}$  ratio. Most temperature variables except the mean diurnal range, maximum warmest month and mean driest quarter, annual maximum and minimum were significantly related to the  $NPP_{\text{woody}}$  ratio (Figure S7).

Range and seasonality were positive with  $NPP_{\text{woody}}$  and  $NPP_{\text{froot}}$  but negative with  $NPP_{\text{canopy}}$  ratios (Figure S7 and Table 2). Finally, all important variables (but longitude) for the  $NPP_{\text{froot}}$  RF model were associated with temperature (Table 2), but none of them with significant ( $p > 0.05$ ) correlation (Figure S7).

### 3.4 | Global Forest NPP Ratio Mapping

The model fitness ( $r^2$  [RMSE]) for  $NPP_{\text{canopy}}$ ,  $NPP_{\text{woody}}$  and  $NPP_{\text{froot}}$  ratios were 0.94 (0.10), 0.93 (0.12), and 0.85 (0.11), respectively (Figure 4b), which allowed us to generate a global forest NPP ratio map (Figure 4a). Regarding latitudes, NPP allocation to  $NPP_{\text{canopy}}$  was higher in the tropics, whereas  $NPP_{\text{woody}}$  and  $NPP_{\text{froot}}$  ratios were higher in temperate and boreal regions based on visual assessment (Figure 4a). Generally, the spatial patterns of NPP ratios were dominated by temperature and can be further investigated within important variable (Table 2) spaces. For example,  $NPP_{\text{canopy}}$  occupied large fractions in regions with low temperature seasonality. The components of  $NPP_{\text{woody}}$  and  $NPP_{\text{froot}}$  were dominant with moderate wind speed and pronounced seasonality, respectively (Figure 4c). Another

**TABLE 2** | The most important variables (see Table S2 for units) of optimal random forests (RF) models in the canopy (variables selected by recursive feature elimination), woody (by variable selection using RF in prediction) and fine-root (recursive feature elimination) NPP ratio predictions, and their directions shown by the Pearson correlation coefficients.

Canopy			Woody			Fine root		
Predictor	Correlation	Type	Predictor	Correlation	Type	Predictor	Correlation	Type
Temperature seasonality	-0.4335*	Variation	Range	0.2618*	Variation	Temperature minimum	-0.0607	Annual
Isothermality	0.4781*	Variation	Coldest month minimum	-0.2729*	Extreme	Isothermality	0.0075	Variation
Range	-0.4674*	Variation				Coldest month minimum	-0.0847	Extreme
Wind speed	-0.3369*	Annual				Longitude	-0.1661	Geography
Warmest quarter precipitation	0.5024*	Extreme				Range	0.0964	Variation
Temperature minimum	0.5164*	Annual				Driest quarter temperature	-0.1046	Extreme

Note: Significance with the  $p < 0.05$  noted by \*.

example shows both the high coldest month minimum temperature and the low annual temperature range (e.g. tropics) for canopy growth (Figure 4d) and vice versa for  $NPP_{woody}$  and  $NPP_{root}$ . Finally, high monthly minimum temperature and isothermality may facilitate canopy growth. However, more carbon was allocated to woody and fine-root parts once both variables went opposite directions (Figure 4e).

## 4 | Discussion

### 4.1 | Forest NPP Allocation

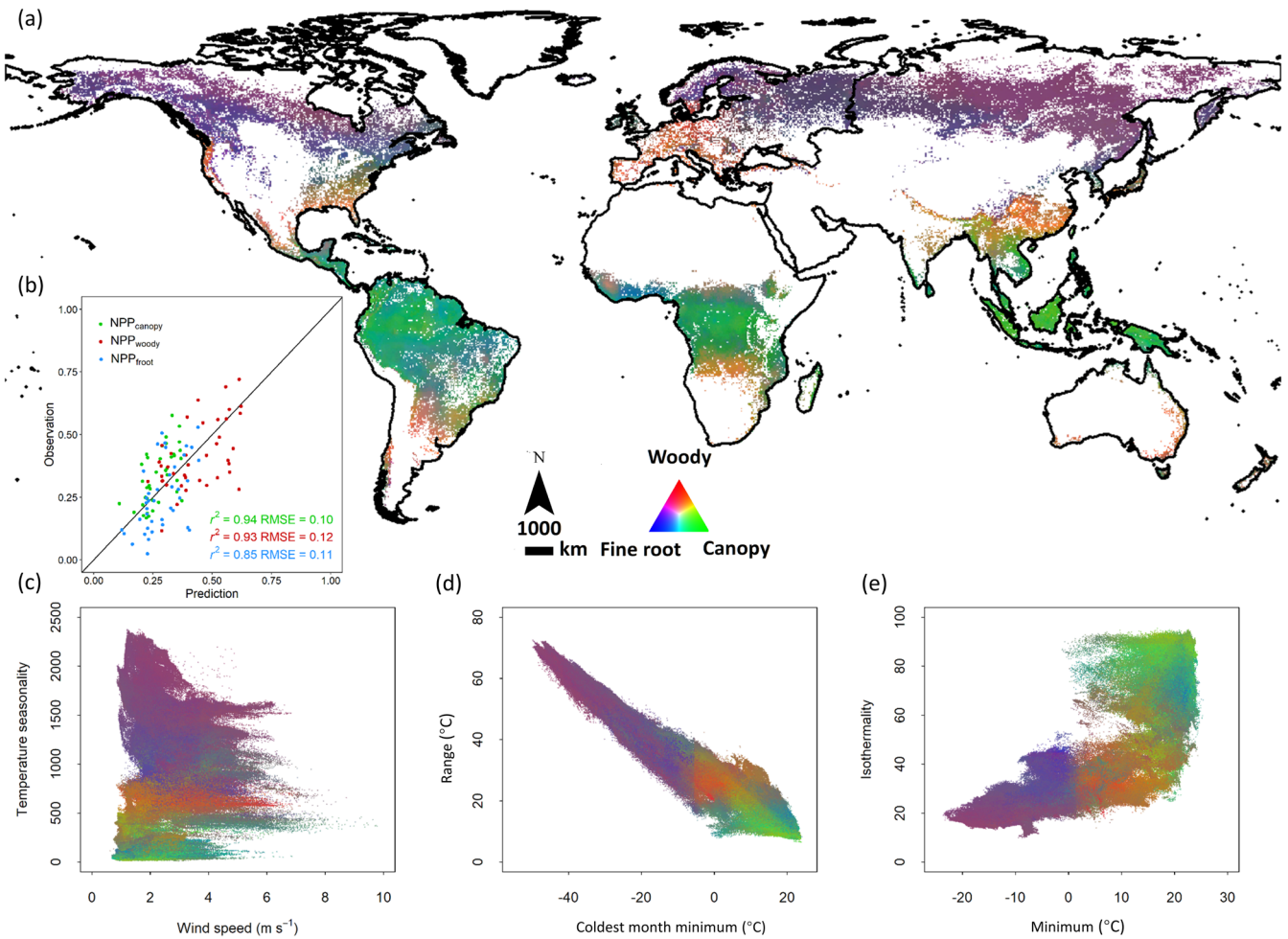
According to our global synthesis, the more sequestered carbon went to woody than canopy and fine-root tissues (Figure S1, Table 1 and Table S1). Wolf, Field, and Berry (2011) suggested that forests of the FLUXNET (Luyssaert et al. 2007) in rich resource environments were characterised by intense competition for light, as individual trees ascended through increasing partitioning toward wood, rather than growing short-lived tissues, such as leaves and fine roots. It is, therefore, plausible to assume that carbon stored in forests might have benefited from primary anthropogenic effects such as elevated temperatures and nitrogen deposition (Dewar et al. 2009), which might have resulted in an increase in NPP allocated to wood (Chen, Yang, and Robinson 2013). Hence, these effects may enhance the  $NPP_{woody}$  ratio.

Our global synthesis depicts that  $NPP_{canopy}$  and its allocation held the overall slightest variation among components through environmental gradients, naturally followed by a shift between  $NPP_{root}$  and  $NPP_{woody}$  ratios (Figure 2 and Figures S3–S6, Table 1), which agrees with Malhi, Doughty, and Galbraith (2011) on tropical forests. Shifts between  $NPP_{woody}$  and  $NPP_{canopy}$  or between  $NPP_{root}$  and  $NPP_{canopy}$  were relatively less obvious. Previous meta-analyses on allocation patterns of forest ecosystems (Litton, Raich, and Ryan 2007; Wolf, Field, and Berry 2011) revealed that increasing nutrient availability led to little change in canopy production, whereas the proportions of wood flux increased and

belowground decreased. In addition, with the increment of stand biomass, there were considerable declines in fine roots and slight declines in the canopy but increases in stem and coarse root production. In perturbed settings, Aragão et al. (2009) found that highly dynamic tropical forests prioritised woody growth by reducing fine-root production. Doughty et al. (2015) also found that during the dry season, the Amazonian forests responded to water availability changes through investment toward leaf and fine-root tissues but decreased woody growth with stable total NPP. Nonstructural carbohydrates allowed forests to reallocate growth based on ecological benefits despite the reduced photosynthate caused by drought (Hartmann and Trumbore 2016). The relationship between  $NPP_{root}$  and  $NPP_{woody}$  in our result (Figure 2b) points to a global ‘root-wood’ (fine root vs. stem and coarse root) trade-off (Chen, Yang, and Robinson 2013; Dybzinski et al. 2011; Malhi, Doughty, and Galbraith 2011) rather than a ‘root-leaf’ (fine root vs. foliage) or a ‘belowground-aboveground’ (fine and coarse roots vs. stem, woody shoot and foliage) trade-off, as previously suggested (Reich 2002; Reynolds and Pacala 1993). The insensitivity of canopy and the predominant trade-off between fine-root and wood production were also adopted in vegetation models in the view of optimization (Dewar et al. 2009; Mäkelä, Valentine, and Helmisaari 2008), as trees intended to acquire more significant amounts of limiting nutrients via short-lived components (i.e. fine roots) or to compete for light via long-term components, maintaining greater overall productivity.

There have been debates on the allocation of patterns and strategies among NPP components. Contrary to our finding, the leaf-initiated variation in NPP allocation was raised in some studies. Dybzinski et al. (2011) utilised the theory of evolutionary stability to investigate carbon allocation by hypothesizing that the most competitive strategy for plants was to create a harsh situation for their competitors for resources. This game theory explains the investment in canopy growth against the cost of metabolism, maintenance and defence. Considering temporal heterogeneity, Sloan, Fletcher, and Phoenix (2016) also suggested leaf and root growth were asynchronous in woody communities of the sub-arctic trees,





**FIGURE 4** | (a) Global forest canopy, woody and fine-root NPP ratios, with the normalised NPP fractions shown in the red (woody)-green (canopy)-blue (fine root) scale. (b) Performance of random forests (RF) for NPP ratio modelling using 31 environmental variables (Table S2) by referring to squared correlation coefficients ( $r^2$ ) and root mean square error (RMSE) of the 1:1 line (the black solid line). (c–e) NPP allocating patterns depicted in the two-dimensional bioclimate spaces among the most important variables (without repetition, Table 2) to model canopy, woody and fine-root NPP ratios. Due to the large data size, we applied uniform sampling from only 10% of latitudes and longitudes forested pixels for the display.

as they tended to allocate carbon to leaves at the beginning and to roots at the end of the growing season. Doughty et al. (2015) showed that the year after a drought in the Amazon forests, allocation shifted toward the canopy but away from fine roots, while total NPP remained constant. However, the aforementioned ‘root-woody’ trade-off could have been a prerequisite for old-growth forest stands free of climatic and edaphic constraints, where the canopy might encounter diminishing returns of carbon investment of lofting foliage into the sunlit canopy and allocating more photosynthate (Dybzinski et al. 2011; Malhi, Doughty, and Galbraith 2011; Wolf, Field, and Berry 2011). We note that some previous works (e.g. Litton, Raich, and Ryan (2007) and Wolf, Field, and Berry (2011)) might not subdivide roots into fine and coarse components or from belowground parts, which are functionally distinct. These aforementioned regional scale findings may induce the uncertainty of the analysis.

## 4.2 | Bioclimate Ramifications

We hypothesize that temperature attributes (particularly related to seasonality) but not precipitation play significant roles

in influencing NPP ratios, which is supported by our results. The NPP ratio might change due to seasonal variability (Table 2, Doughty et al. 2014); stand biomass was pivotal in regulating total NPP via allometric allocation (Enquist et al. 2007). On the other hand, Wolf, Field and Berry (2011) indicated that resource availability including climatic and edaphic factors (water, nutrients) can change total primary productivity and NPP partitioning in the face of climate change. We found that leaves flushed under favourable climates where temperature and other resources were likely unlimited (Figure 4). In contrast,  $NPP_{woody}$  and  $NPP_{froot}$  could sustain relatively harsher conditions, in terms of lower annual means and periodic extremes of temperature and sharp fluctuation, to compete for light and nutrients (Figure 4 and Table S4).

As for individual climatic effects, our results showed that the  $NPP_{canopy}$  ratio was positively correlated to most temperature and precipitation variables, such as the mean annual temperature and annual precipitation, while  $NPP_{woody}$  and  $NPP_{froot}$  ratios were negatively correlated to these variables (Figure S7 and Table S4). Chen, Yang and Robinson (2013) depicted that increasing rainfall shifted  $NPP_{woody}$  to  $NPP_{canopy}$ . Moreover,



NPP allocation was more influenced by bioclimatic variables (mainly temperature) grouped in temperature-related factors. For instance,  $NPP_{\text{woody}}$  and  $NPP_{\text{froot}}$  allocations were related to the minimum temperature of the coldest month rather than by water terms, except for the mean temperature of the driest quarter's impact on the  $NPP_{\text{froot}}$  ratio (Table 2). However, the coupling impact of temperature and precipitation on NPP allocation was found by Taylor et al. (2017), stating that rainfall in warm sites increased aboveground NPP but slowed carbon cycling rates in cool forests. Hofhansl et al. (2015) also manifested this interaction by showing that precipitation increased the proportion of woody production in tropical lowland forests but had an adverse effect in montane forests. Another study on the sensitivity of tropical lowland carbon sequestration stated that the rising temperature and dry season length during the El Niño–Southern Oscillation anomaly would not affect  $NPP_{\text{canopy}}$  but would shift away from wood, thus reducing the carbon storage of highly productive forests (Hofhansl et al. 2014). Drought-induced  $NPP_{\text{woody}}$  deduction was then overcompensated during the subsequent La Niña wet period. Therefore, in warm climates, precipitation positively affected  $NPP_{\text{woody}}$ ; in cold temperatures, precipitation negatively influenced  $NPP_{\text{woody}}$ .

Other meteorological variables also played some roles in altering NPP ratios. Solar radiation and water vapour pressure (related to air temperatures) facilitate the growth of foliar tissues (Figure S7 and Table S4). Contrarily, wind speed, indicating the harshness of the environment may be against the canopy growth. We also found that the ‘wood-leaf’ trade-off may be influenced by meteorological factors, affecting how plants adapt to environments and vie for resources. The allocation of NPP could also follow some geographic gradients, where the environments differentiated dramatically; geographic patterns could be inconsistent with temperature rules (see the above section). Surprisingly, topography (elevation, slope and aspect) did not significantly impact NPP allocation of different pools in the analysis (Figure S7 and Table S4). This could result from the coarse spatial resolution obscuring these relatively fine-scale factors. The  $NPP_{\text{canopy}}$  ratio increased with satellite-derived NPP, while the  $NPP_{\text{woody}}$  ratio went opposite (Figure S7 and Table S4). There could also be a temporal decoupling between total photosynthesis and total carbon usage, such as NPP and respiration, where nonstructural carbohydrate storage allows continued growth during drought (Doughty et al. 2015).

### 4.3 | Local Site Influences

We grouped field NPP datasets by bioclimate zones, plant species and communities since these attributes may directly impact carbon allocation (Figure 3). Hofhansl et al. (2014) observed that tropical aboveground NPP was influenced by topography and disturbance history, affecting water availability and species composition; Araujo-Murakami et al. (2013) found that NPP allocation patterns were similar between forests on humid and dry soils at the dry margin of Amazon (e.g. the dry one may function as a down-scaled version of the wetter forest) even with different physiognomy and floristic composition. Malhi et al. (2013) further suggested that their productivity was driven by phenological rhythms rather than directly by water stress. Finally, demographic details such as tree age or life stage in the selected

plots could also play a pivotal role in allocating NPP (e.g. saplings and mature trees may have different allocation priorities) (Enquist et al. 2007), but unfortunately, such detailed information was often missing preventing global-scale analysis.

Soil fertility is another crucial driver of  $CO_2$  exchange in forests (Capioli et al. 2016). This study shows that soil fertility positively influences  $NPP_{\text{canopy}}$  and its ratio, which was moderate to  $NPP_{\text{woody}}$  and negative to  $NPP_{\text{froot}}$  ratios in most cases (Figure 3, Tables 1 and Figure S3). A cross-continental comparison in tropical forests by Banin et al. (2014) suggested that aboveground woody production was positively associated with soil fertility (e.g. total phosphorus). Similarly, in modelling Scots pine (*Pinus sylvestris* L.) in boreal regions, the allocation was insensitive to foliage and was prone to woody NPP in response to increased soil nitrogen, whereas fine-root growth favoured nitrogen-poor sites (Mäkelä, Valentine, and Helmisaari 2008). However, in temperate deciduous forests, Tateno, Hishi, and Takeda (2004) found that belowground production showed no apparent change as soil nitrogen availability went opposite the topographic gradient of the nitrification rate.

Plants tended to maximise the capture of the most limiting resource, and growth was limited to one resource at a time (Chapin et al. 2002). The root-wood trade-off was generally found in all conditions (Figure 2b), which could occur in forests limited by nutrients such as nitrogen and light as total NPP increased (Dybzinski et al. 2011; Wolf, Field, and Berry 2011). Based on our results, the root-shoot trade-off was only in uncompetitive environments such as tropical, boreal, evergreen, and fertile sites (Figures S3, S5 and S6). However, the root-leaf trade-off occurred in conifers, and the wood-leaf trade-off occurred in broadleaf forests (Figure S4), possibly because forests were not under the old-growth stage for foliage construction, in addition to cold and warm climates for roots and wood in competing nutrients and light, respectively.

### 4.4 | Global Forest NPP Ratio Mapping

RF provided robust prediction (Figure 4b), and mapping global forest NPP allocating using machine learning is the first of its kind (Figure 4a). NPP allocations of a finer division, especially involving the belowground, were subject to field measurement, and thus, data were limited to a small coverage. A large-scale spatial estimation should, therefore, be given importance by using machine learning. Nevertheless, a more comprehensive and extensive dataset with more data points from Africa and Oceania may moderate the ramifications of spatial data gaps and modelling extrapolation to improve the global forest NPP ratio mapping further. With the availability of spatial coverage, the constraint of limited field samples could be alleviated to facilitate sophisticated analysis, such as further investigating the effects of leaf types and habits, biome types and soil fertilities on the NPP ratios and the underlying mechanisms.

## 5 | Conclusions

The majority of annual net carbon gain was found to be allocated to woody tissues, while the proportion allocated to the canopy was stable due to a ‘root-wood’ relationship rather than

a ‘root-leaf’ trade-off as previously thought. Trees differentiated NPP allocation due to the climatic and environmental variability strategically for adaptation and competition and thus different resource limits. Generally, NPP allocation was temperature-driven, as temperature was the most limiting factor over water, light and nutrients. Thus, spatial preferences of three NPP components straddled boreal, temperate and tropical areas. High and stable temperature seems to promote higher NPP allocation to the canopy. Woody tissue and fine roots could bear relatively varying and limiting environmental conditions. These prominent insights would facilitate the understanding, mapping and modelling efforts, such as dynamic global vegetation models, of terrestrial carbon budgets and dynamics in a changing climate.

### Author Contributions

Xiancheng Lu and Cho-ying Huang conceived the ideas; Xiancheng Lu, Yadvinder Malhi and Cho-ying Huang collected and compiled global NPP data; Xiancheng Lu and Chi-Hsin Chung analysed the data; Xiancheng Lu and Cho-ying Huang led the writing with contributions of all co-authors.

### Acknowledgements

This work was supported by the National Science and Technology Council (NSTC 112-2321-B-002-016, 112-2313-B-002-012-MY3), National Taiwan University (NTU-AS-112L104303) and the Research Center for Future Earth, the Featured Areas Research Center Program, the Higher Education Sprout Project, and the Ministry of Education in Taiwan. We thank Iain Collin Prentice for discussing and recommending the ForC global carbon database.

### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

The data that support the findings of this study are openly available in Zenodo at <https://zenodo.org/records/10408419>.

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### Supporting Information

Additional supporting information can be found online in the Supporting Information section.