Manuscript draft

Introduction

Globally, forests play an important role in the carbon cycle and are an important component of global carbon dioxide budgets (Luyssaert et al., 2008). They show higher levels of productivity than non-forest terrestrial ecosystems (Del Grosso et al., 2008), and as a result achieve significant carbon sequestration and storage. Estimating the total role of forests in the carbon cycle is challenging, but studies indicate that old growth forests alone sequester up to 1.4 $GtCyr^{-1}$ (Y. Malhi, Baldocchi, & Jarvis, 1999), while the total sequestration of carbon by established forests globally could be up to 2.4 $GtCyr^{-1}$, with the largest sinks being in old-growth tropical forests (Pan et al., 2011). As atmospheric carbon dioxide levels continue to rise, with consequences for global climate, there is increasing recognition that proper protection and management of forest resources will have an important role to play in mitigating climate change. Understanding the patterns of forest productivity on a global scale, and the drivers behind them, is therefore a priority in forest research.

There are two major questions to understand: firstly, how forest productivity varies globally - and specifically which areas show the greatest peaks in productivity -; and secondly, which climate variables drive this variation. On a global scale, the productivity of forests varies with latitude, with a general trend of increasing productivity towards the tropics (C. Beer et al., 2010; Jung et al., 2011); however the exact nature of this pattern, and how it varies by component of productivity, is poorly understood. This latitudinal gradient is most likely to be explained by climatic gradients in temperature, precipitation, length of growing season, and combinations of the above. Productivity is influenced by a range of climatic drivers, including mean annual temperature (MAT) and mean annual precipitation (MAP) (Del Grosso et al., 2008), but doesn't necessarily respond linearly to these drivers. Disentangling the shape of productivity responses to climate drivers will enable better predictions of future responses under climate change.

What is primary productivity? During photosynthesis, plants capture carbon dioxide from the atmosphere. The gross primary productivity (GPP) of an ecosystem is the gross uptake, via photosynthesis, of carbon dioxide by plants in that ecosystem. Only a fraction of the carbon captured is assimilated into plant tissue; the rest is used in autotrophic respiration (R_a). The component of GPP that is stored as plant material is the net primary productivity (NPP) of an ecosystem. Net primary productivity can therefore be expressed as:

$$NPP = GPP + R\ a$$

Currently, GPP cannot be measured directly by observing total ecosystem photosynthesis. Instead field estimates of GPP have to be derived based on modelling and extrapolation of eddy-covariance studies and measurements of net ecosystem exchange (NEE) (Deborah A. Clark et al., 2017).

In contrast, NPP can be calculated through direct field observations. In order to achieve greater accuracy in estimating NPP, NPP is often broken down into its component parts, with aboveground NPP (ANPP) and belowground NPP (BNPP) considered separately to each other. The components included when estimating ANPP and BNPP often vary between studies, depending on the intensity of fieldwork effort. At its most basic level, ANPP can be expressed as:

$$ANPP = NPP\ stem\ + NPP\ branch\ + NPP\ canopy$$

where NPP_{stem} is the annual woody increment of all stems above a specified diameter at breast height (DBH), NPP_{branch} is annual woody branch turnover, and NPP_{canopy} is annual foliage production, including leaves, twigs, and reproductive structures. ANPP may also include NPP_{VOC}, the annual emission of volatile organic compounds, and $NPP_{herbivory}$, the annual consumption of plant matter by herbivores, but these components are often excluded from field observations as they are much harder to quantify. Other components of aboveground productivity that remain largely unquantified include epiphytes, hemiepiphytes, and understory plants (Deborah A. Clark et al., 2017). All current ANPP estimates are based on the assumption that the contribution of these components to overall NPP is insignificant.

There are two major subcomponents of BNPP, which can be expressed as:

$$BNPP = NPP\ coarseroot\ + NPP\ fineroot$$

where NPP~coarse root~ is the annual production of coarse roots (typically roots >2mm diameter), and NPP~fine root~ is the annual production of fine roots (typically roots <2mm diameter) (L. E. O. C. Aragão et al., 2009). Calculations of BNPP may also include $NPP_{exudation}$, a measure of annual carbon losses through root exudation, and $NPP_{symbionts}$, the annual carbon allocation to mycorrhizae and legumes, but, as before, this is challenging to quantify and is often excluded from field observations.

BNPP is a poorly understood component of total ecosystem productivity, primarily because of the challenges in gaining accurate field measurements. Coarse root productivity is often estimated via extrapolation of NPP_{stem} estimates using allometries that may not have been empirically verified (Deborah A Clark et al., 2001). NPP~fine root~ is easier to quantify through soil cores and minirhizotrons, however, sampling tends to be limited to the surface soils, with very few studies sampling to depths below 3 metres [cite]. As a result, it is possible that BNPP is currently significantly underestimated, despite being a hugely significant component of total ecosystem productivity (Pan et al., 2011).

Which factors influence primary productivity? Primary productivity is influenced by many factors, which often act across a range of scales, and may show interactive effects with each other. On a local scale, stand age (Gillman et al., 2015; Litton, Raich, & Ryan, 2007), management (Šímová & Storch, 2017); nutrient availability (L. E. O. C. Aragão et al., 2009); and altitude (C. A. J. Girardin et al., 2010; Y. Malhi et al., 2017) all impact forest productivity. On a global scale, changes in primary productivity are influenced by climatic variables and abiotic gradients, such as the length of growing season (Michaletz, Cheng, Kerkhoff, & Enquist, 2014). There is some debate over the precise relationship between these drivers and productivity; While mean annual precipitation (MAP) and mean annual temperature (MAT) have been argued to be significant predictors of productivity (Chu et al., 2016), other studies have found that the correlation between productivity and MAT is a factor of the relationship between productivity and growing season length (Kerkhoff, Enquist, Elser, & Fagan, 2005; Y. Malhi, 2012; Michaletz et al., 2014; Michaletz, Kerkhoff, & Enquist, 2018). Improving understanding of how these factors interact to control global patterns in primary productivity is essential to understanding the global carbon cycle.

Current research into how primary productivity varies with latitude is inconclusive, and - though it has primarily focussed on patterns of GPP, NPP, and ANPP - indicates that different components of productivity may show different relationships to latitude. Gross primary productivity is generally thought to be highest in the tropics. Modelling of global terrestrial ecosystem GPP though upscaling and calibration of eddy flux measurements indicates a peak in GPP in the tropics, with the highest levels in tropical forests (C. Beer et al., 2010; Jung et al., 2011). This is corroborated by analysis of site-level GPP measurements, which show a strong positive correlation between GPP and MAT and MAP (Luyssaert et al., 2007), with the highest GPP values reported in tropical forests. The influence of latitude on global patterns of NPP is less clear than that of GPP. Simova and Storch (2017) found that, as with GPP, NPP decreases with latitude, peaking in the tropics. However, other studies have found the highest values of NPP in temperate forests (Huston & Wolverton, 2009; Luyssaert et al., 2007). Because of the challenges in accurately obtaining unbiased measures of belowground productivity, many studies focus on ANPP in preference to measures of NPP. Studies on global patterns of ANPP are equally inconclusive: Gillman et al. (2015) found a weak negative relationship between ANPP and latitude, with the relationship becoming stronger in older forest stands. These findings were echoed in other studies, which have found weak or no relationships between ANPP and latitude (Huston & Wolverton, 2009).

Furthermore, there is evidence that different components of productivity show individual responses to drivers of productivity. For example, increases in GPP have been reported to saturate above 25°C MAT (Larjavaara & Muller-Landau, 2012), while increases in NPP are recorded to saturate above 10°C MAT (Luyssaert et al., 2007). Similarly, allocation to different components of ANPP varies with climate. Within the tropics, allocation to canopy NPP appears fairly consistent, with significantly greater variation in allocation to woody and belowground NPP (Litton et al., 2007; Y. Malhi, Doughty, & Galbraith, 2011). Allocation to these structural biomass components has been shown to increase with water availability (Bloom, Exbrayat, Velde, Feng, & Williams, 2016; Litton et al., 2007), and is highest in the wet tropics, indicating that control of woody productivity by MAP may be more significant than control of foliar productivity. However, these studies are regional, meaning that our understanding of variation in allocation and its relationship to climate on a global scale remains limited. In addition, allocation is also influenced by stand age (De Lucia, Drake, Thomas, & Gonzalez-Meler, 2007), nutrient availability (Litton et al., 2007) and forest structure (Taylor et al., 2019), which can make it challenging to disentangle the effects of climate.

Data that control for stand age and standardize methodologies are required to resolve this question. Here, we use a comprehensive global database to explore global patterns in productivity. We explore three questions:
1. **Which climatic variables are the most important drivers behind the latitudinal pattern in primary productivity?** To date, the majority of studies have focussed on productivity responses to precipitation and temperature, while the influence of other climate variables on productivity remains under-explored. We utilise global climate datasets to investigate the relationships between productivity and a range of climate variables.
2. **Do the components of primary productivity show variation in their responses to these climatic drivers?** Allocation to components of primary productivity appears to show some variation across climate and latitudinal gradients. We use global datasets of a range of primary productivity components to explore how significant this variation in allocation is.
3. **Does climate explain the same proportion of variation in different components of primary productivity?** Review of current research shows that, while the relationship between GPP and latitude is consistent, NPP and ANPP show weaker relationships with latitude. This may be a result of varying sensitivities to climate drivers. We use mixed models to estimate the proportion of variation explained by climate for different components of productivity, to investigate how the relative importance of climatic drivers varies across components.

Methods

Analyses were conducted on data contained in the open-access ForC database (Anderson-Teixeira, Wang, Mcgarvey, & Lebauer, 2016; Anderson-Teixeira et al., 2018). This database contains records of field-based measurements of forest carbon stocks and annual fluxes, compiled from original publications and existing data compilations and databases. Associated data, such as stand age, measurement methodologies, and disturbance history, are also included. For each site, site geographic co-ordinates were used to extract the Koeppen-Geiger zone from the ESRI Koeppen-Geiger map [cite], and the FAO Global Ecological Zone from the ???. Additional targeted literature searches were conducted to identify any further available data on primary productivity, with particular focus on old-growth forests in temperate and boreal regions. ForC currently contains [] records from [] plots, representing [] distinct geographic areas across all forested biogeographic and climate zones.

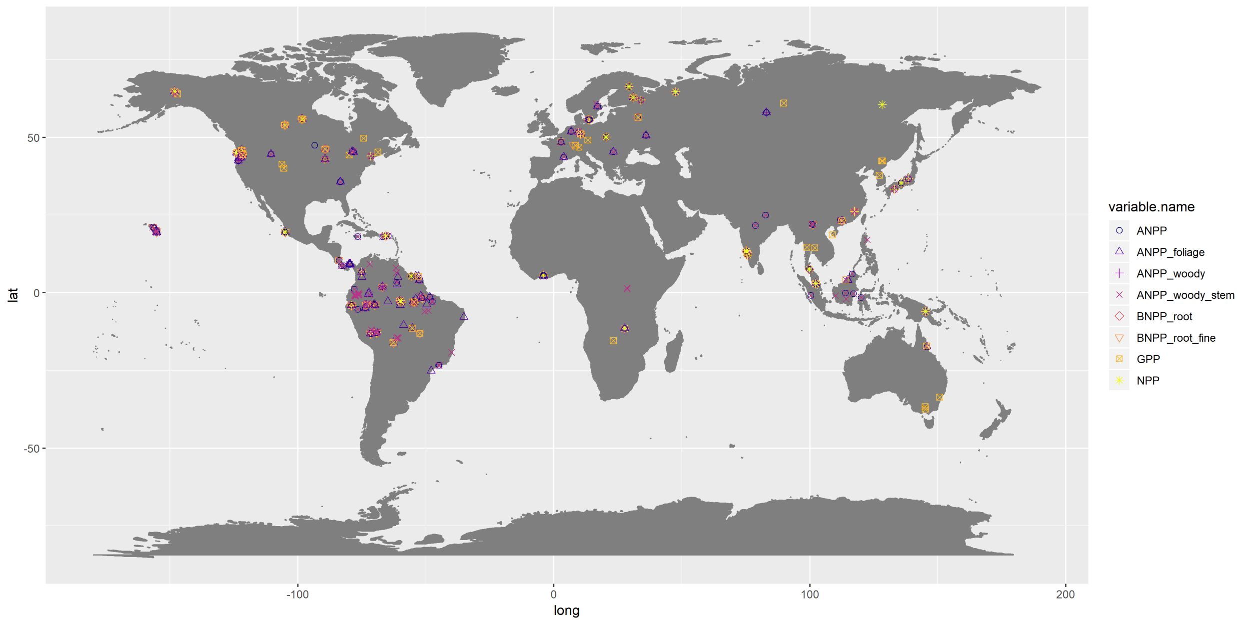

Figure 1: Map showing all data used in the analysis, coded by variable

Data selection. Over 50 variables of forest carbon stocks and annual fluxes are represented in the ForC database; this analysis focussed on measures of primary productivity. Table 1 contains details of the variables selected for analysis.

Table 1: Definitions of variables used in analysis

Variable	Definition	Components included	Methodologies used
GPP	Annual gross primary production; annual uptake of carbon dioxide by an ecosystem	NA	Flux partitioning of eddy covariance
NPP	Annual net primary production; the component of GPP that is stored in plant tissue; GPP minus ecosystem respiration	Foliage, branch, stem, coarse root, fine root, and optionally understory	Direct measurement of annual increments of components
ANPP	Aboveground net primary production	Foliage, stem, and optionally branch	Direct measurement of annual increments of components
ANPP_foliage	Net primary production of foliage	Foliage	Direct measurement of litterfall, correcting for changes in leaf biomass when measured
ANPP_woody	Net primary production of woody components	Stems and branches	Direct measurement of stem growth and branch fall
ANPP_woody_stem	Net primary production of woody stems	Woody stems	Direct measurement of stem growth increment

Variable	Definition	Components included	Methodologies used
BNPP_root	Belowground net primary production	Coarse and fine roots	Direct measurement of one or more of: fine root turnover, soil cores, root ingrowth cores, minirhizotrons; indirect estimates of coarse roots using allometries based on aboveground stem increment measures
BNPP_root_fine	Net primary production of fine roots	Fine roots	Direct measurement of one or more of: minirhizotrons, fine root turnover, soil cores, root ingrowth cores

A subset of the ForC database was generated for the purposes of this analysis, in order to control for data quality and remove biasing factors. Since management can alter observed patterns of primary productivity (Šímová & Storch, 2017), sites were excluded from analysis if they were managed, defined as plots that were planted, managed as plantations, irrigated, fertilised or including the term "managed" in their site description. Sites that had experienced significant disturbance were also excluded. Disturbances that justified site exclusion were major cutting or harvesting, and/or burning, flooding, drought and storm events with site mortality >10% of trees. Grazed sites were retained.
There is evidence that stand age influences patterns of primary productivity and carbon allocation in forest ecosystems, and can confound relationships between latitude and primary productivity (De Lucia et al., 2007; Gillman et al., 2015). To reduce any biasing effects of stand age, stands under 100 years of age were excluded from analysis. Sites for which stand age was unknown were excluded from analysis.

Methodological consistency. The data in ForC is derived from a range of studies, often employing different methods. For this reason, criteria were introduced to standardise for differences in methodology. Where data was based on forest plot census measurements, studies which used a minimum diameter at breast height (DBH) measure of 10cm or greater were excluded from analysis. It would be preferable to standardise by minimum area sampled; however x% of plots in the database are 1 ha or under in size; excluding these plots would place significant constraints on sample size.

As discussed above, estimates of NPP, ANPP, and BNPP are generated through summing measurements of their component parts. Since the components included in productivity estimates vary between studies, estimates of productivity were classified within the ForC database according to their components, and then filtered for analysis. Estimates of NPP were selected if they included foliage, branch, stem, coarse root, fine root and optionally understory. Measures of NPP which included additional components were excluded. Estimates of ANPP were selected if they included foliage, stem growth and branch turnover. Any measures of primary productivity where components were unknown were excluded from analysis.

Climate datasets. Where site-level data on mean annual temperature, mean annual precipitation, and latitude were available in the primary literature, this data was compiled and entered directly into the ForC database. In addition to this data, climate data for each site was extracted from five open-access climate datasets based on site geographic co-ordinates.

Table 2: Sources of climate data

Database	Variables downloaded	Citation
WorldClim	Mean annual temperature; temperature seasonality; annual temperature range; mean annual precipitation	(Hijmans, Cameron, Parra, Jones, & Jarvis, 2005)

Database	Variables downloaded	Citation
WorldClim2	Vapour pressure; solar radiation	(Fick & Hijmans, 2017)
Climate Research Unit (CRU) time-series dataset v 4.03	Cloud cover; annual frost days; annual wet days; potential evapotranspiration	(Harris, Jones, Osborn, & Lister, 2014)
Global Aridity Index and Potential Evapo-transpiration Climate Database	Aridity; potential evapotranspiration	(Trabucco & Zomer, 2018)
TerraClimate	Vapour pressure deficit	(Abatzoglou, Dobrowski, Parks, & Hegewisch, 2018)

Model specification. The effects of climate and latitude on primary productivity were analysed using mixed effects models using the package 'lme4' in RStudio v. 1.1.463 (cite). The effect of each extracted climate variable on each measure of primary productivity was modelled by specifying the climate variable as a fixed effect. Site altitude was also included as a fixed effect. Random effect was stand nested within area. Data from the temperate regions was heavily skewed towards studies from the old-growth forests of the Pacific Northwest. These forests have very high productivity, and so to reduce any bias from over-sampling of this region, the proportion of global forest cover contributed by each Koeppen climate zone was calculated, and the models weighted according these proportions.

Two models were specified: one with the climate variable as a linear term, and one with the climate variable as a polynomial term. AIC values were calculated for the models and used to select the best model. R-squared values were calculated for the best model. In addition, slope values were calculated for the linear models.

Abatzoglou, J. T., Dobrowski, S. Z., Parks, S. A., & Hegewisch, K. C. (2018). TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958-2015. *Scientific Data*, *5*, 1–12. https://doi.org/10.1038/sdata.2017.191

Anderson-Teixeira, K. J., Wang, M. M., Mcgarvey, J. C., & Lebauer, D. S. (2016). Carbon dynamics of mature and regrowth tropical forests derived from a pantropical database (TropForC-db). *Global Change Biology*, *22*(5), 1690–1709. https://doi.org/10.1111/gcb.13226

Anderson-Teixeira, K. J., Wang, M. M., McGarvey, J. C., Herrmann, V., Tepley, A. J., Bond-Lamberty, B., & LeBauer, D. S. (2018). ForC: a global database of forest carbon stocks and fluxes. *Ecology*, *99*(6), 1507. https://doi.org/10.1002/ecy.2229

Aragão, L. E. O. C., Malhi, Y., Metcalfe, D. B., Silva-Espejo, J. E., Jiménez, E., Navarrete, D., … Vásquez, R. (2009). Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. *Biogeosciences Discussions*, *6*(1), 2441–2488. https://doi.org/10.5194/bgd-6-2441-2009

Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., … Papale, D. (2010). Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate. *Science*, *329*(5993), 834–838. https://doi.org/10.1126/science.1184984

Bloom, A. A., Exbrayat, J.-F., Velde, I. R. van der, Feng, L., & Williams, M. (2016). The decadal state of the terrestrial carbon cycle: Global retrievals of terrestrial carbon allocation, pools, and residence times. *Proceedings of the National Academy of Sciences*, *113*(5), 1285–1290. https://doi.org/10.1073/pnas.1515160113

Chu, C., Bartlett, M., Wang, Y., He, F., Weiner, J., Chave, J., & Sack, L. (2016). Does climate directly influence NPP globally? *Global Change Biology*, *22*(1), 12–24. https://doi.org/10.1111/gcb.13079

Clark, D. A., Asao, S., Fisher, R., Reed, S., Reich, P. B., Ryan, M. G., … Yang, X. (2017). Reviews and syntheses: Field data to benchmark the carbon cycle models for tropical forests. *Biogeosciences*, *14*(20), 4663–4690. https://doi.org/10.5194/bg-14-4663-2017

Clark, D. A., Brown, S., Kicklighter, D. W., Chambers, J. Q., Thomlinson, J. R., Ni, J., & Holland, E. A. (2001). Net Primary Production in Tropical Forests : An Evaluation and Synthesis of Existing Field Data. *Ecological Applications*, *11*(2), 371–384.

De Lucia, E. H., Drake, J. E., Thomas, R. B., & Gonzalez-Meler, M. (2007). Forest carbon use efficiency: Is respiration a constant fraction of gross primary production? *Global Change Biology*, *13*(6), 1157–1167. https://doi.org/10.1111/j.1365-2486.2007.01365.x

Del Grosso, S., Parton, W., Stohlgren, T., Zheng, D., Bachelet, D., Prince, S., … Olson, R. (2008). Global potential net primary production predicted from vegetation class, precipitation, and temperature. *Ecology*, *89*(8), 2117–2126.

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315. https://doi.org/10.1002/joc.5086

Gillman, L. N., Wright, S. D., Cusens, J., Mcbride, P. D., Malhi, Y., & Whittaker, R. J. (2015). Latitude, productivity and species richness. *Global Ecology and Biogeography*, *24*(1), 107–117. https://doi.org/10.1111/geb.12245

Girardin, C. A. J., Malhi, Y., Aragão, L. E., Mamani, M., Huaraca Huasco, W., Durand, L., … Whittaker, R. J. (2010). Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. *Global Change Biology*, *16*(12), 3176–3192. https://doi.org/10.1111/j.1365-2486.2010.02235.x

Harris, I., Jones, P. D., Osborn, T. J., & Lister, D. H. (2014). Updated high-resolution grids of monthly climatic observations - the CRU TS3.10 Dataset. *International Journal of Climatology*, *34*(3), 623–642. https://doi.org/10.1002/joc.3711

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*(15), 1965–1978. https://doi.org/10.1002/joc.1276

Huston, M. A., & Wolverton, S. (2009). The global distribution of net primary production: resolving the paradox. *Ecological Monographs*, *79*(3), 343–377.

Jung, M., Reichstein, M., Margolis, H. A., Cescatti, A., Richardson, A. D., Arain, M. A., … Williams, C. (2011). Global patterns of land-atmosphere fluxes of carbon dioxide, latent heat, and sensible heat derived from eddy covariance, satellite, and meteorological observations. *Journal of Geophysical Research: Biogeosciences*, *116*(3), 1–16. https://doi.org/10.1029/2010JG001566

Kerkhoff, A. J., Enquist, B. J., Elser, J. J., & Fagan, W. F. (2005). Plant allometry, stoichiometry and the temperature-dependence of primary productivity. *Global Ecology and Biogeography*, *14*(6), 585–598. https://doi.org/10.1111/j.1466-822X.2005.00187.x

Larjavaara, M., & Muller-Landau, H. C. (2012). Temperature explains global variation in biomass among humid old-growth forests. *Global Ecology and Biogeography*, *21*(10), 998–1006. https://doi.org/10.1111/j.1466-8238.2011.00740.x

Litton, C. M., Raich, J. W., & Ryan, M. G. (2007). Carbon allocation in forest ecosystems. *Global Change Biology*, *13*(10), 2089–2109. https://doi.org/10.1111/j.1365-2486.2007.01420.x

Luyssaert, S., Inglima, I., Jung, M., Richardson, A. D., Reichstein, M., Papale, D., … Janssens, I. A. (2007). CO2 balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology*, *13*(12), 2509–2537. https://doi.org/10.1111/j.1365-2486.2007.01439.x

Luyssaert, S., Schulze, E. D., Börner, A., Knohl, A., Hessenmöller, D., Law, B. E., … Grace, J. (2008). Old-growth forests as global carbon sinks. *Nature*, *455*(7210), 213–215. https://doi.org/10.1038/nature07276

Malhi, Y. (2012). The productivity, metabolism and carbon cycle of tropical forest vegetation. *Journal of*

Ecology, *100*(1), 65–75. https://doi.org/10.1111/j.1365-2745.2011.01916.x

Malhi, Y., Baldocchi, D. D., & Jarvis, P. G. (1999). *The carbon balance of tropical, temperate and boreal forests*. 715–740.

Malhi, Y., Doughty, C., & Galbraith, D. (2011). The allocation of ecosystem net primary productivity in tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1582), 3225–3245. https://doi.org/10.1098/rstb.2011.0062

Malhi, Y., Girardin, C. A., Goldsmith, G. R., Doughty, C. E., Salinas, N., Metcalfe, D. B., … Silman, M. (2017). The variation of productivity and its allocation along a tropical elevation gradient: a whole carbon budget perspective. *New Phytologist*, *214*(3), 1019–1032. https://doi.org/10.1111/nph.14189

Michaletz, S. T., Cheng, D., Kerkhoff, A. J., & Enquist, B. J. (2014). Convergence of terrestrial plant production across global climate gradients. *Nature*, *512*(1), 39–43. https://doi.org/10.1038/nature13470

Michaletz, S. T., Kerkhoff, A. J., & Enquist, B. J. (2018). Drivers of terrestrial plant production across broad geographical gradients. *Global Ecology and Biogeography*, *27*(2), 166–174. https://doi.org/10.1111/geb.12685

Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., … Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science*, *333*(August), 988–993.

Šímová, I., & Storch, D. (2017). The enigma of terrestrial primary productivity: measurements, models, scales and the diversity–productivity relationship. *Ecography*, *40*(2), 239–252. https://doi.org/10.1111/ecog.02482

Taylor, P. G., Cleveland, C. C., Soper, F., Wieder, W. R., Dobrowski, S. Z., Doughty, C. E., & Townsend, A. R. (2019). Greater stem growth, woody allocation, and aboveground biomass in Paleotropical forests than in Neotropical forests. *Ecology*, *100*(3), 1–9. https://doi.org/10.1002/ecy.2589

Trabucco, A., & Zomer, R. J. (2018). Global Aridity Index and Potential Evapotranspiration (ET0) Climate Database v2. *CGIAR Consortium for Spatial Information (CGIAR-CSI)*, (November), 10. https://doi.org/10.6084/m9.figshare.7504448.v3