Article:

Aguirre-Gutiérrez, J, Rifai, S, Shenkin, A et al. (44 more authors) (2021) Pantropical modelling of canopy functional traits using Sentinel-2 remote sensing data. Remote Sensing of Environment, 252. 112122. ISSN 0034-4257

https://doi.org/10.1016/j.rse.2020.112122

Pantropical modelling of forest functional traits using Sentinel-2 remote sensing data

Jesús Aguirre-Gutiérrez[a,b,*], Sami Rifai[a], Alexander Shenkin[a], Imma Oliveras[a], Lisa Patrick Bentley[c], Martin Svátek[d], Cecile Girardin[a], Sabine Both[e], Terhi Riutta[a], Erika Berenguer[a], W. Daniel Kissling[f], David Bauman[a,g], Nicolas Raab[a], Sam Moore[a], William Farfan-Rios[h,i,j], Axa Figueiredo[k], Simone Matias Reis[a,l], Josué Edzang Ndong[m], Fidèle Evouna Ondo[m], Natacha N'ssi Bengone[n], Vianet Mihinhou[n], Marina Maria Moraes de Seixas[o], Stephen Adu-Bredu[p], Kate Abernethy[q,r], Gregory P. Asner[s], Jos Barlow[t,u], David F.R.P. Burslem[v], David A. Coomes[w], Lucas A. Cernusak[x], Brian Enquist[y], Robert M. Ewers[z], Joice Ferreira[u], Kathryn J. Jeffery[r], Carlos A. Joly[aa], Beatriz Schwantes Marimon[l], Ben Hur Marimon[l], Roberta E. Martin[s], Paulo S. Morandi[l], Oliver L. Phillips[ab], Norma Salinas[a,ac], Miles Silman[ad], Yit Arn Teh[ae], Lee J. T. White[n,q,r], Yadvinder Malhi[a]

[a]Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK

[b]Biodiversity Dynamics, Naturalis Biodiversity Center, Leiden, The Netherlands

[c]Department of Biology, Sonoma State University, 1801 East Cotati Avenue, Rohnert Park, CA 94928, USA

[d]Department of Forest Botany, Dendrology and Geobiocoenology, Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic

[e]Environmental and Rural Science, University of New England, Armidale, 2351 NSW, Australia

[f]Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, Amsterdam, The Netherlands

[g]Laboratoire d'Écologie Végétale et Biogéochimie, CP 244, Université Libre de Bruxelles, Brussels, Belgium

[h]Living Earth Collaborative, Washington University in Saint Louis, St. Louis, MO, USA

[i]Center for Conservation and Sustainable Development, Missouri Botanical Garden, St. Louis, MO, USA

[j]Herbario Vargas (CUZ), Escuela Profesional de Biología, Universidad Nacional de San Antonio Abad del Cusco, Cusco, Peru

[k]National Institute for Amazonian Research – INPA. C.P. 2223, 69080-971, Manaus, AM, Brazil

[l]Laboratorio de Ecologia Vegetal (LABEV), Universidade do Estado de Mato Grosso, Nova Xavantina, Brazil

[m]Agence Nationale des Parcs Nationaux, BP20379, Libreville, Gabon

[n]Ministère des Eaux, des Forêts, de la Mer et de L'Environnement, Libreville, Gabon

[o]Embrapa Amazônia Oriental, Trav. Dr. Enéas Pinheiro, s/n, CP 48, 66095-100 Belém, PA, Brazil

[p]CSIR-Forestry Research Institute of Ghana, University P.O. Box 63, Kumasi, Ghana

[q]Institut de Recherche en Écologie Tropicale, Libreville, Gabon.

[r]Biological and Environmental Sciences, University of Stirling, Stirling, UK.

[s]Center for Global Discovery and Conservation Science, Arizona State University, Tempe, AZ, United States

[t]Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

[u]MCT/Museu Paraense Emílio Goeldi, Av. Magalhães Barata 376, São Braz, 66040-170 Belém, PA, Brazil

[v]School of Biological Sciences, University of Aberdeen, Aberdeen, UK

[w]Conservation Research Institute, Department of Plant Sciences, University of Cambridge, Cambridge CB2 3QZ, UK

[x]College of Science and Engineering, James Cook University, Cairns, Qld, 4878 Australia

[y]University of Arizona, Tucson, Arizona, USA

[z]Department of Life Sciences, Imperial College London, Ascot, UK

[aa]Universidade Estadual de Campinas, Instituto de Biologia, Departamento de Biologia Vegetal, Campinas, São Paulo, Brazil

[ab]Ecology and Global Change, School of Geography, University of Leeds, Leeds, West Yorkshire, UK

[ac]Sección Química, Pontificia Universidad Católica del Perú, Avenida Universitaria 1801, San Miguel, Lima 32, Perú

[ad]Department of Biology, Wake Forest University, Winston-Salem, NC 27109, USA.

[ae]School of Natural and Environmental Sciences, Newcastle University, Newcastle Upon Tyne, UK

*Corresponding author

Highlights

- We use a global array of precisely geolocated plant traits data to assess the ability of Sentinel-2 satellite imagery to map leaf traits in tropical forests.
- Key plant functional traits can be mapped across tropical forests worldwide using Sentinel-2 in combination with soil and climate information
- Leaf photosynthetic and chemical traits, and some morphological traits such as leaf thickness, show the highest detectability
- Textural information makes an important contribution to assessing and mapping leaf traits.

Abstract

Tropical forest ecosystems are undergoing rapid transformation as a result of changing environmental conditions and direct human impacts. However, we cannot adequately understand, monitor or simulate tropical ecosystem responses to environmental changes without capturing the high diversity of plant functional characteristics in the species-rich tropics. Failure to do so can result in oversimplified understanding of responses of ecosystems to environmental disturbances. Innovative methods and data products are needed to track changes in functional trait composition in tropical forest ecosystems through time and space. This study aimed to track key functional traits by coupling Sentinel-2 derived variables with a unique data set of precisely located *in-situ* measurements of canopy functional traits collected to a standardised methodology from field plots in countries spanning the four tropical continents (Australia, Brazil, Peru, Gabon, Ghana, and Malaysia). The spatial positions of individual trees above 10 cm DBH were mapped and their canopy size and shape recorded. From these data, community-level trait values were estimated at the same spatial resolution as Sentinel-2 imagery (i.e. 10m pixels). We use a geographical version of random forest to model and predict functional traits across our plots in the tropics. We demonstrate that key plant functional traits can be measured at a pantropical scale using the high spatial and spectral resolution of Sentinel-2 imagery in conjunction with climatic and soil related information. Pixel texture parameters were found to be key components of remote sensing information for predicting functional traits across tropical forests and woody savannas. Leaf thickness (R^2=0.52) obtained the highest prediction accuracy among the morphological and structural traits and leaf carbon content (R^2=0.70) and A_{max} (R^2=0.67) obtained the highest prediction accuracy for leaf chemistry traits and photosynthesis related traits, respectively. Overall, the highest prediction accuracy was obtained for leaf chemistry and photosynthetic traits (A_{max} and A_{sat}) in comparison to morphological and structural traits. Our approach offers new opportunities for mapping, monitoring and understanding biodiversity and ecosystem change in the most species-rich ecosystems on Earth.

1. Introduction

Some of the most pressing questions in ecology and ecosystem science today focus on how communities of organisms respond to global environmental changes (Naeem et al., 2009), how biodiversity and ecosystem changes across the world can be consistently mapped and monitored (Navarro et al., 2017), and how spatial, temporal and taxonomic variability in biodiversity influences ecosystem resilience to climate change (Oliver et al., 2015). In terms of Earth system science, we need to understand and model how the terrestrial biosphere will respond (and already is responding) to global environmental change, and whether there are dangerous thresholds or “tipping points” beyond which major biomes may not be able to recover. Nowhere is the challenge more urgent or more daunting than in the species-rich tropical forest and woody savanna biomes, which together are home to more than half of global biodiversity and over 60% of terrestrial productivity (Beer et al., 2010). There is already evidence that atmospheric change may have effects on tropical forest productivity and tree functional composition (Esquivel-Muelbert et al., 2019, Hubau et al., 2020). These effects may include a stimulation of productivity (perhaps due to rising CO_2) and/or a degradation or dieback, possibly caused by increased seasonality and incurred intensity of extreme drought events (Malhi, et al., 2008, Malhi, et al., 2018). Such events are partly responsible for the increased tree mortality and decreased carbon residence time in tropical forests worldwide (McDowell et al., 2018). However, to adequately understand such responses we need to capture and map the high diversity of plant ecosystem function in the species-rich tropics and savannas.

Species functional traits are defined as the morphological, physiological or phenological attributes which determine the fitness of organisms, their response to changes in the environment and their influence on ecosystem functions (Kissling et al., 2018, Dıaz & Cabido, 2001). Functional traits provide tangible and mechanistic means of assessing the ability of communities to adapt to climate change (Pacifici et al., 2015) and play a major role in determining ecosystem productivity, functioning and notably nature’s contribution to people (NCP; e.g. water and wood availability) (Díaz et al., 2019, Carmona et al., 2016). Hence, any tools or methods that facilitate quantification of functional traits across large spatial scales and at high spatial resolution would be invaluable for quantifying ecosystem functioning and ecological responses to disturbance at scales relevant for policy and management (Kissling et al., 2018). However, it is still challenging to map functional trait diversity in tropical regions given the lack of plant trait data available for most of those locations (Jetz et al., 2016). Additional challenges come from different and often incompatible trait collection protocols and the lack of systematic high spatial, spectral and temporal resolution remote sensing imagery that coincides with data for functional traits at the canopy level.

Ultimately, tracking functional traits can shed light on differences in ecosystem functioning across broad spatial extents and therefore aids policy and decision making, e.g. for creating adequate biodiversity conservation policies or for providing early warning of directional shifts in ecosystems. The key challenges of any functional traits approach are scalability and monitoring: how can functional shifts in highly diverse tropical forests and woody savannas be monitored and tracked over large spatial scales? Intensive field sampling of plant functional traits at a pantropical scale is time-consuming and economically unviable. There are large gaps in the availability of plant trait data globally, and the largest gaps are in the tropics (Jetz et al., 2016). Large plant trait datasets aim to overcome this issue and have advanced our ability to carry out plant functional trait analysis in an unprecedented way (Kattge et al., 2020, Gallagher et al., 2020). However, as with any database, the plant trait values from such databases will represent the local trait-environment relationships for the site where they were collected, which may not be the area of interest. A key assumption in trait-based ecology is that the environment is filtering for an optimal set of trait characteristics so that the resulting communities are best adapted to the environment where they are distributed (Fell & Ogle, 2018, Lebrija-Trejos et al., 2010, Lortie et al. 2004). Hence, we might expect an optimal set of trait characteristics for a given location, which when analysed over time could quantify the dynamics of community trait distributions or shifts in functional composition relating to environmental change.

High-resolution multispectral approaches have been carried out across large spatial extents to detect functional traits but have been limited by their spectral resolution and low frequency of measurements for the same location. With a few exceptions (see Tollefson, 2011), hyperspectral remote sensing has only been conducted across small spatial extents given the logistical difficulties involved in obtaining these measurements using airborne sensors. High temporal resolution is particularly important in the wet tropics, where clear days can be infrequent and several images may be required to construct a cloud-free composite. The field is on the brink of a step change in this area, through the Copernicus mission from the European Space Agency's (ESA; www.esa.int). The Sentinel-2 multispectral imager satellites are part of the Copernicus programme, which has the potential to provide new opportunities to evaluate canopy traits remotely. Sentinel-2 has 13 spectral channels covering the visible, near-infrared, and short-wave infrared, a spatial resolution of 10m for visible and near-infrared, 20m for short-wave infrared, revisit period of 5 days and it provides open data availability. The numerous wavebands and imagery have the potential to elucidate leaf chemistry, morphology and water content, although this remains largely untested. Multispectral sensors do not provide the rich information available from hyperspectral sensors, which have been used in numerous studies to map functional traits at small spatial extents (Townsend et al., 2003, Laurin et al., 2016, Asner et al., 2015), but high resolution open-access hyperspectral imagery is not currently available from space. Although the Landsat imagery has been used to predict a few functional traits at a local scale (Wallis et al., 2019), the superior extended spectral, spatial and temporal capabilities of the state-of-the-art sensors onboard the Sentinel-2 satellites provide greater potential for mapping functional trait diversity in tropical forest ecosystems at large extents.

Here, we employ a unique and large dataset of *in-situ* plant functional traits and vegetation census data collected with a standardised protocol at multiple sites across the tropics to calibrate and validate Sentinel-2 imagery for predicting community leaf trait composition. The data provide 14 standardized measurements of *in-situ* collected plant functional traits, precisely geo-located and delineated individual tree crowns and vegetation censuses from Australia, South East Asia, Africa and South America to model and predict functional trait composition at the pixel level. We investigate how functional traits of tropical forests vary within and between these different tropical regions and whether Sentinel-2 spectral data in conjunction with climatic and soil information provide sufficient information to predict such pixel-level trait composition in long-term vegetation plots across the tropics. We expected to find differences in trait variation among sites and regions given the different climatic and soil conditions observed across the tropics. Given the high spectral and spatial resolution of Sentinel-2 imagery we expected that raw spectral bands and pixel textural parameters would prove key predictors of functional traits distributions across the tropics. We predict that given the very high spatial resolution and local origin of the input plant traits and census dataset, which represent traits adapted to local environments, we will be able to produce realistic predictions of functional trait distributions that are potentially generalisable across the tropical forest biome.

2. Methods

2.1 *Vegetation plots*

We collected vegetation census data from 47 permanent vegetation plots that are part of the Global Ecosystems Monitoring network (GEM; www.gem.tropicalforests.ox.ac.uk). These plots encompass wet tropical forests, seasonally dry tropical forests, and tropical forest-savanna transitional vegetation. The sampled vegetation plots have an area ranging from 0.1 to 1 ha, with most (61%) being 1 ha. The plots used are located across four tropical continents, in Australia, Brazil, Gabon, Ghana, Malaysian Borneo (from here onwards referred to as Malaysia) and Peru (Table 1). In each plot all woody plant individuals with a diameter ≥ 10 cm at breast height (DBH) or above buttress roots, except for two plots (NXV-01 and NXV-10) in Nova Xavantina, here onwards referred to as Brazil -NX, where diameter is measured near ground level as is standard in savanna monitoring protocols) were measured and their exact geographic location was recorded (see the ‘Individual tree crowns’ section below for more details).

2.2 *Functional traits*

We collected plant functional trait measurements from all woody plants located in each of the 47 vegetation plots mentioned above (Table 2). All traits were gathered from the Global Ecosystems Monitoring network (GEM; www.gem.tropicalforests.ox.ac.uk) and were collected following a standardized methodology across plots. Forest inventory data were used to stratify tree species by basal area dominance, a proxy for canopy area dominance. The tree species that contributed most to basal area abundance were sampled with 3-5 replicate individuals per species, with a goal of sampling 60-80% of basal area across the sampling region. Eighty percent of basal area was often achieved in low diversity sites (e.g. montane or dry forests) but only around 60% was achieved in some high diversity sites (lowland humid rainforests). For each selected tree a sun and a shade branch were sampled and in each branch three to five leaves were used for traits measurements. In our analysis we only included the sun exposed branches, which represented a total sample of 2434 individual trees across the tropics (Table 1). Below we give an overview of the methods for individual leaf functional trait measurements.

Photosynthetic related traits: Selected branches were immediately recut under water and leaf gas exchange measurements undertaken as soon as possible (within 1-2 hours). Photosynthetic capacity (light-saturated net assimilation rate) was measured at both saturating CO_2 concentration (2000 ppm CO_2; A_{max}), and at ambient CO_2 concentration (400 ppm CO_2; A_{sat}) under saturating light conditions and at a temperature of 25 °C using a LICOR 6400-XT.

Leaf chemistry traits: On a different branch, all leaves were removed for bulk chemical analysis. Leaf area (hereafter referred to as Area) was determined by scanning the adaxial side of the leaf lamina on a flatbed scanner Canon LiDE220® and analysing images with Matlab code available at https://github.com/bblonder/leafarea (see Neyret et al. 2016 for a full description of methodology). Trait values for compound leaves were analysed at the leaflet level.

Morphological and structural traits: Specific leaf area (SLA) was determined by dividing leaf area by leaf dry mass. Leaf fresh mass (Fresh mass) was calculated as the fresh weight of the recently obtained leaves. Leaf dry mass (Dry mass) was determined after oven drying at 60 °C leaves for 72 hours or until constant weight. Leaf water content (LWC) was determined by subtracting the dry mass content from the fresh mass, multiplying by 100 and dividing by the fresh mass to obtain percentage water content.

The thickness of leaf lamina (Thickness) was measured by taking four micrometre measurements halfway between the mid-vein and the edge of the leaf, avoiding major secondary veins.

Further details of measurements for the Peruvian Andes campaign are given in Martin et al. (2020) and Enquist et al. (2017), for the Malaysian campaign in Both et al. (2019), for the Ghana and Brazil campaigns in Oliveras et al. (2020) and Gvozdevaite et al. (2018).

Given the trait sampling protocol some individuals from species not sampled in the plot lacked functional trait values. To assign representative trait values to individuals belonging to species sampled elsewhere in the same region and that were missing such information we did the following: 1) individuals from which traits were measured kept their original trait information, 2) for individuals with no trait information we randomly sampled trait values from other individuals from the same species present in the same plot, 3) if the species was not sampled in the given plot then we randomly sampled an individual from the same species that had trait information in other plots from the same region (Table 1). This protocol for trait values allocation allowed us to work with the existing range of trait values at the species level and avoid creating average values per species (Cadotte et al., 2011, Schneider et al., 2017). We did not assign trait values to the remaining individuals belonging to species from which no trait collection was obtained at the regional level.

2.3 *Individual tree crowns*

Tree crown locations and structural attributes were recorded for each tree, where crown area and shape were measured by direct crown field measurements in the case of plots in Malaysia and Peru (see protocol below), or by means of regional level allometric equations developed by Shenkin et al. (2019) (all other plots). In the latter case the crown's shape was assumed to be circular. The direct field crown measurements were as follows: all trees ≥ 10 cm DBH (stem diameter at breast height, i.e., 1.3 m from the ground) were mapped using a ground-based Field-Map laser technology (IFER, Ltd., Jílové u Prahy, Czech Republic) (Hédl et al., 2009). The Field-Map technology was based on a combination of Impulse 200 Standard laser rangefinder (with in-built tilt sensor for measuring vertical angles), MapStar

Module II electronic compass (both Laser Technology Inc., Colorado, USA), and the specialized mapping software Field-Map v. 11 (IFER, Czech Republic). The technology was used to record spatial positions of tree stems in three-dimensional space (x, y, z-coordinates) as well as to map individual horizontal projections of tree crowns in the plots. The horizontal crown projection of every tree was obtained by measuring spatial positions (x and y-coordinates) of series of points (ranging from 5 to 30 points depending on the size of the crown) at the boundary of a crown projected to the horizontal plane. The shape of crown projection was subsequently smoothed using the "smooth contour line" feature of Field-Map software v. 11. Heights of all trees with DBH ≥ 10 cm were measured by the Impulse and TruPulse 360 R laser rangefinders (both Laser Technology Inc., Colorado, USA). Thus, each individual crown was accurately geolocated rendering information about its shape and vertical and horizontal position.

2.4 *Calculating pixel level trait composition*

We calculated the community weighted mean of each trait for each 10×10m subplot (matching the highest pixel spatial resolution of the Sentinel-2 imagery) based on the mass ratio hypothesis, which states that the most dominant species drive the ecosystem processes by means of their functional traits (Grime, 1998). To this end we first geolocated the vegetation plot, with its already mapped tree crowns (see protocol above), to the Sentinel-2 imagery based on the plot's corner coordinates. Then for each of the traits, t, and pixels, p, we calculated their community level weighted mean (CWM) using the individual tree crown horizontal area as the weighting factor (Fig. 1) as follows:

$$CWM_{tp} = \frac{\sum_{i=1}^{N} \quad CA_{ip} \times t_{ip}}{CA_p}$$

(Eq. 1)

Where CA_{ip} is the crown area of individual i in pixel p, t_{ip} is the trait value of individual i in pixel p, N is the total number of individuals per pixel and CA_p is the crown area of pixel p. The crown contribution to the CWM was weighted by its proportional cover of the corresponding pixel. The total number of pixels used in our calculations are 403 for Australia, 449 for Brazil -NX (Nova Xavantina), 302 for Brazil -ST (Santarem), 464 for Gabon, 620 for Ghana, 976 for Malaysia and 1280 for Peru.

2.5 Sentinel-2 data, vegetation indices and canopy texture metrics

We gathered Sentinel-2 imagery that was closest in time and season to the sampling dates of functional traits and vegetation census across the tropics for each of the study locations (Table S1). The Sentinel-2 imagery was first selected using the European Space Agency (ESA) ScienceHub (scihub.copernicus.eu) choosing images with high pixel quality and low cloud cover (<10%). Atmospheric, radiometric and topographic corrections were applied to the selected imagery (Level 1C) using the Sen2Cor algorithm in the Sentinel SNAP toolbox (step.esa.int), thereby removing clouds and cirrus effects. The above-mentioned steps allowed us to obtain level 2A imagery with surface reflectance values. We then resampled the 20m bands to 10m spatial resolution using bilinear interpolation. The Sentinel-2 60m resolution bands (B01, B09, B10) were not used as these are designed for cirrus, water vapour and cloud detection (Table 3). Band 8A was not used as it covers an overlapping spectral window with band 8 and has a lower spatial resolution. Vegetation indices may increase prediction accuracy when modelling community weighted traits (Wallis et al., 2019), therefore we calculated three vegetation indices (Table 3) that we hypothesised may inform traits distributions given their quantification of chlorophyll and nutrients levels in the leaves and their use of the visible to red edge spectral bands.

Canopy structure may play an important role in separating different vegetation types and differences in canopy spectral composition. To characterize canopy structure, we calculated the Grey Level Co-Occurrence Matrix (GLCM) (Haralick et al., 1973). The GLCM analyses the spectral relationship between pixel pairs. Based on the GLCM we calculated two variables that are least correlated with each other, the Entropy and Correlation, for each of the vegetation indices using a 3 x 3 pixel kernel window. While Entropy measures the homogeneity level for a given area, the Correlation measures the correlation between spectral reflectance across pixels in the analysis window (Haralick et al., 1973, Wallis et al., 2019). The texture metrics were calculated in ENVI (Exelis Visual Information Solutions, Boulder, Colorado, v.5.5). All other remote sensing analyses were carried out using the Sentinel SNAP toolbox and the R statistical environment (R Development Core Team, 2014) with the ‘Sen2R’ package.

2.6 *Environmental and soil data*

Climatic, topographic and soil characteristics may vary across regions and could at least partly determine the region’s vegetation and intrinsic trait composition. We obtained information on these three components for each sampling location. The three components were grouped as belonging to environmental (climate) or soil-terrain (texture, pH, cation exchange capacity and topography) drivers (Table 3).

For climate and for each sampling location we gathered gridded data on the mean annual climatic water deficit (MCWD), which is a metric of drought intensity and severity, mean annual maximum temperature (MATmax), solar radiation (SRAD) and soil moisture (SM) (Table 3). All climatic data were obtained from the TerraClimate high resolution gridded climate product (Abatzoglou et al., 2018). To characterise the climatic conditions for each location we used a climatology of 30 years (1986-2015) as suggested by the World Meteorological Organization (WMO; www.wmo.int/pages/prog/wcp/ccl/faqs.php). We used the terrain slope to characterise the plot’s topography, as it has been shown that topography may shape the composition and structure of tropical forests (Jucker et al., 2018) and may affect the vegetation spectral reflectance by modifying soil water and nutrient availability. Terrain slope was calculated using a high-resolution digital elevation model, ~30m pixel size at the equator, from the Shuttle Topography Mission (Farr et al., 2007). At most sites soil data were sampled locally, and analysed to a standardised protocol in labs in either INPA, Manaus, Brazil or the University of Leeds, UK, following the RAINFOR soil protocol (Quesada et al 2012). From these data we summarised plot level soil data averaged over the first 30 cm for texture (Sand% and Clay%), cation exchange capacity (eCEC) and pH-H_2O (pH). Plot level texture data were not available for plots in Australia and the NXV-10 plots and was thus derived from the SoilGrids dataset for those plots only (Hengl et al., 2017).

2.7 *Comparing community level trait distributions across regions*

We tested if and to what extent the community-level trait distributions differed among regions. To this end we square-root transformed the trait value to improve normality and applied an analysis of variance (ANOVA). We then applied a Tukey's Honest Significant Difference (Tukey HSD) test to investigate the significance of the differences between the means of the community weighted mean (CWM) trait values among locations. The ANOVA and Tukey test were carried out using the 'stats' package for R (R Development Core Team, 2014).

2.7 *Relating pixel level trait composition to spectral reflectance, environment and soil conditions*

We modelled the community weighted mean (CWM) of each trait at the pixel level (10×10 m) as a function of the Sentinel-2 remote sensing, environmental and soil covariates (Table 3) using a 'spatial' version of the machine learning Random Forest (RF) algorithm (Breiman, 2001) named Geographic Random Forests (GRF) (Georganos et al., 2019). RF is a nonparametric algorithm that has been shown to be robust to overfitting and variable inputs thanks to the bagging process and its random feature selection (Hastie et al., 2009). Moreover, it has been extensively used to model and predict ecological and remote sensing data within and across ecosystems (Asner et al., 2016, Van der Plas et al., 2018). In contrast to RF, GRF disaggregates the underlying data into geographic space, in this case based on the spatial coordinates of the Sentinel-2 pixels, building global and local sub-models (plot level), thus making the modelling framework spatially explicit. The explicit inclusion of the spatial component (XY pixel location) in the models, which are sequentially fitted with different sets of the training data (the bagging process) may contribute to the observed reduced spatial autocorrelation of GRF in comparison to the common RF (Georganos et al. 2019). In the GRF a global model is built as in other RF applications. However, GRF also generates a local RF for each location, which includes a specified number of nearby observations, here defined by all pixels in the vegetation plot (mostly 1 ha; Table 1), called 'neighbourhood', obtaining in this way metrics of local and global model predictive power and variable importance. For model predictions, a fuse between the global model (that uses more data) and local models (with low bias) can be applied, weighting the contributions of the global and local models based on the parameters that increase the predictive accuracy and decrease the model's Root Mean Square Error (RMSE). We used the spatial GRF to fit a global model for each functional trait and also fit a specific model for each region (Australia, Brazil -ST, Brazil -NX, Gabon, Ghana, Malaysia and Peru) using the SpatialML package in R.

We performed an extensive set of model optimization and regularization procedures to reduce over-fitting. For the CWM models we selected the number of trees to fit by 10-fold cross-validation analysis with number of trees ranging between 500 and 1500 and the number of variables randomly sampled as candidates at each split (mtry) ranging between 1 to 10, using in the final model the combination of terms that generated the lowest RMSE. All covariates included in the models had pairwise Pearson correlation coefficients $r \leq 0.82$ (Table 3). For the final global and local models, we used 80% of the data for model fitting and the remaining 20% for model evaluation. Variable importance for each model was computed as the decrease in node impurities from splitting on the variable, averaged over all trees and derived from the Out of Bag (OOB) error. Then the resulting importance was standardised to a 0–1 scale for comparison purposes.

We carried out all analyses stated above with the full set of tree individuals present in each vegetation plot with functional traits assuming that the contribution of small individuals to the trait CWM value, and thus to the community reflectance at the pixel level, would be minimal given the weighting factor used (i.e. the individual's crown area). However, to corroborate this we carried out all analyses on two smaller datasets, one where the 25th and other where the 50th percentile of the smallest trees per region were removed. All analyses were carried out in the R statistical environment (R Development Core Team, 2014) with the 'caret', 'tidyverse' and 'SpatialML' packages.

3. Results

3.1 *Variation in trait composition across tropical forests*

Most leaf functional traits exhibited significant differences across the tropics (Fig. 2) including wide trait range variation within the same region (Fig. S1), with leaf fresh mass and leaf thickness being on average less variable among locations (Table S4). Leaf chemistry and photosynthetic capacity (A_{max} and A_{sat}) often showed significant differences among locations (Table S4). Drier locations as in Nova Xavantina (Brazil -NX) display trait adaptations to such seasonal rainfall and temperature environment with on average thicker and smaller (30 ± 0.05 mm and 56.2 ± 24.7 cm^2 respectively) leaves at the community level, with some of the highest community level leaf nitrogen concentration (2.2 ± 0.3 %) and high photosynthetic capacity (mean A_{max}= 21.9 ± 4.3 $\mu mol\ m^{-2}\ s^{-1}$, and A_{sat}= 8.3 ± 2.5 $\mu mol\ m^{-2}\ s^{-1}$). In contrast, wetter regions such as Malaysia display on average some of the biggest (113.5 ± 55 cm^2) and thinner (0.25 ± 0.05 mm) leaves with high leaf water content (59.1 ± 5 %). The Peruvian altitudinal transect showed large variation in community level traits values, which often overlapped with trait values from all other sampled locations across the tropics (Fig. 2). For most nutrients, leaf nutrient concentration was often highest in forests found in Ghana (e.g. K%= 0.97 ± 0.27 and Mg%= 0.33 ± 0.1) and Malaysia (K%= 1.05 ± 0.27 and Mg%= 0.27 ± 0.1) across the study regions, and Australian forests showed on average some of the lowest community level N (1.3 ± 0.21 %) and P (0.07 ± 0.01%) leaf concentrations.

3.2 *Pantropical and local community level functional trait models*

The analyses carried out with the full dataset and the dataset where the 25th and 50th percentile of the smallest trees per region were removed gave similar results for the global (R^2=0.95 and R^2=0.97 respectively; Table S2) and local (R^2=0.81 and R^2=0.80 respectively; Table S3) models of plant trait distributions. Therefore, in the following we only present the results for the models carried out with the full vegetation dataset.

The accuracy of the pantropical prediction of functional traits ranged between a minimum of R^2=0.26, for leaf fresh mass, and a maximum of R^2=0.70 for leaf carbon content (C%) based on the out-of-sampled (testing) data across the tropics (Table 4). The predictive accuracies of leaf chemistry and photosynthetic traits were often higher than for morphological and structural traits such as leaf dry mass (R^2=0.27) and leaf area (R^2=0.43) (Fig. 3). At the pantropical level, the highest prediction accuracy was obtained for leaf thickness (R^2=0.52) for morphological and structural traits, for leaf Ca (Ca%; R^2=0.64) and leaf K (K%; R^2=0.63) for the chemical traits other than carbon. Leaf N and P concentrations were also predicted with high accuracy (R^2=0.59). Leaf photosynthetic capacity traits, A_{max} and A_{sat}, showed some of the highest prediction accuracies ranging from R^2=0.55 to 0.67, respectively. Model spatial predictions for several traits and locations is shown in Fig. 4.

Models built for each location uncovered marked differences in prediction accuracy among tropical regions depending on traits (Fig. 5; Table 5 and Table S5). Leaf area prediction accuracy ranged from R^2=0.04 (Brazil -ST) to 0.35 (Australia), and that of SLA ranged from R^2=0.06 for Malaysia to 0.54 for Brazil -NX (Table S5). The local models showed a higher accuracy for predicting local level leaf chemical nutrients (up to R^2=0.68), especially for P, Ca, and N concentrations in comparison to morphological (e.g. leaf area and SLA) traits (Table 5; Fig. 5). Traits related to photosynthetic capacity showed an overall better prediction accuracy than leaf area and SLA with prediction values ranging between 0.36 (Peru) to 0.49 (Ghana) for A_{max} and up to 0.52 for A_{sat} (Brazil -NX; Fig. 5). On average the highest prediction accuracy across regions for a given trait were reached for leaf P concentration (R^2=0.47) and A_{max} (R^2=0.44) and the locations with the highest average prediction accuracy across traits were the Nova Xavantina savanna (Brazil -NX, R^2=0.40) and the Peru elevation gradient (R^2=0.38; Table 5), both sites encompassing strong gradients in vegetation morphology and structure.

3.3 *Importance of spectral remote sensing, climatic and soil data for mapping trait distributions*

We included Sentinel-2 band derived reflectance values, vegetation indices, their canopy texture components, climatic and soil variables in the general trait models to predict community level traits at the pixel level (Table 3). The importance of these variables for predicting traits depended on the specific trait being addressed (Fig. 6). In the global model, the textural remote sensing derived variables were the first or second major contributor for predicting nine of the functional traits across the tropics

(Fig. 6 and Fig. S2). Raw spectral variables were the second most important group for predicting four of such functional traits but often lower in importance than the textural parameters. In the global model, soil and terrain factors were on average some of the most important for predicting photosynthetic traits and foliar P concentration. On average, climatic variables were important for predicting 11 out of 14 functional traits but their contribution was lower for predicting leaf dry and fresh mass and leaf water content (Fig. 6). However, it is evident that a combination of textural, spectral, climatic and soil information is required to obtain the best general model predictions across functional traits and no single variable appears as the most important across all traits (Fig. S2).

The local models provide a site-specific view of the most important remote sensing derived variables, environmental and soil conditions for deriving community level traits composition (Fig. S3). Sentinel-2 remote sensing related variables were more important for detecting leaf morphology and nutrient values than environmental and soil related variables 88% of the time (in 75 out of 85 possible traits by region combinations). From those, 81% of the times (69 location by trait combinations) the canopy texture derived variables were more important than the raw spectral reflectance factors. In 5.9% and 4.7% of the possible trait and region combinations, climatic or soil-topography related variables respectively were the most important for detecting community traits (Fig. S3).

4. Discussion

To the best of our knowledge this is the first study evaluating the ability of Sentinel-2 to map plant functional traits across tropical ecosystems using the Sentinel-2 satellites. Tropical forest trait mapping is fundamental for understanding of plant responses to global change, and notably the plant functional traits we predict in this study are relevant to plant species responses to a changing environment (Both et al., 2019, Nunes et al., 2019, Soudzilovskaia et al., 2013, Aguirre-Gutiérrez et al., 2019). We have demonstrated how accurate pixel level (10×10m) predictions of tropical forest functional trait distributions across the tropics can be generated by making use of extensive *in-situ* collected plant functional traits, geo-located canopy structure, vegetation censuses and high spectral and spatial resolution remote sensing data from the Sentinel-2 satellites.

4.1 *Tropical forest trait distributions*

Plant functional traits are the characteristics that aid species to thrive in their environment or adapt to new conditions. Given such adaptations to specific environments it might be expected that trait variation would be higher in regions that encompass more varied environmental conditions (Enquist et al., 2015). Environmental adaptation is exemplified by the strong variation in values for most traits in Peru and Malaysia. In Peru the data represent a climatic and altitudinal gradient ranging from the lowland Amazon in the Tambopata National Park at an elevation of 200-225 masl to plots in Acjanaco at above 3000 masl. In Malaysia the vegetation plots are distributed across a land-use gradient ranging from undisturbed to heavily logged forests (Both et al., 2019). Environmental adaptation may be also shown by the observed differences in trait distributions between different regions across the tropics (e.g. Australia and Gabon; see also Fig. 2). The pixel-based community trait values in the Peruvian transect often extend across much of the range in trait values observed in other locations (Fig. 2). We detected an overall significant difference among locations in terms of morphological, chemical and photosynthetic traits (Table S4). This wide variation in traits suggests the presence of local biotic and abiotic controls of trait distributions and plant species adaptations that may differ even among tropical regions. For instance, it is widely known that African tropical forests are in general less species diverse than their Asian and South American counterparts but that they have some of the highest biomass carbon storage capacity per unit area (Sullivan et al., 2017). Tropical forests in West Africa are in general drier in comparison to Amazonian tropical forests (Parmentier et al., 2007) and some African regions such as Gabon have experienced increases in temperature and decreases in precipitation over the last 30 years (Bush et al., 2020). Thus, such changes in climatic conditions as those observed in West African tropical forest may also underlie variations in species composition and the locally observed functional trait pool as shown in this study. It is also worth noting that two caveats of the community-weighted mean trait approach may account for part of the unexplained trait variation. First, it makes the assumption of a unique functional optimum in a given environment, while multiple optimal strategies – potentially corresponding to contrasting trait values – could coexist (Laughlin et al., 2018). Secondly, it does not account for the dynamic nature of communities, so that a community weighted mean at a given time point might not encompass the optimum at equilibrium (Laughlin et al., 2018).

Morphological and structural traits such as leaf area, fresh and dry mass, leaf thickness, SLA and LWC, resemble trade-offs between energy acquisition, consumption and survival and form a main part of the global spectrum of plant functioning (Díaz et al., 2016). Besides investigating the predictability of such plant structural traits, we further analysed the potential for predicting leaf chemistry (C, K, Mg, Ca, N, P) and photosynthesis related traits (A_{max} and A_{sat}). Mapping chemical and photosynthetic traits at a pantropical scale has the potential for increasing our understanding of how photosynthetic capacity shifts across tropical regions and on possible impacts of a changing environment on tropical forests productivity (but see Guan et al., 2015, Mueller et al., 2014).

4.2 *Sentinel-2 remote sensing for mapping community level trait distributions across the tropics*

Recently, there has been a great effort toward mapping plant functional trait distributions; however, given economic and data availability constraints such efforts have mostly concentrated at the local (Schneider et al., 2017) to regional scales (Asner et al., 2015, Asner et al., 2016) and employed hyperspectral imagery. However, high resolution hyperspectral imagery is not widely available (e.g. Clark, 2017, Szabó et al., 2019). Wallis et al. (2019) used Landsat-8 imagery which has coarser spatial (30m pixel), spectral and temporal resolution than Sentinel-2 imagery to map four traits over small (20×20m) vegetation plots at small spatial extent. Such spatial mismatch between site level trait sampling and pixel spatial resolution may in some situations, as the authors discuss, affect overall model predictions. Another study restricted to European forests (Ma et al. 2019) shows how Sentinel-2 imagery could be used to map functional trait diversity in the comparatively lower tree diversity forests of Europe. However, the tropics present a different set of challenges, such as the high species richness, low accessibility and comparatively lower availability of trait data, plus the lower coverage of remote sensing data because of persistent high cloud cover. These challenges have hampered developments in mapping plant functional trait distributions across most tropical areas.

In their pioneering work with hyperspectral imagery and simulated multispectral Sentinel-2 data over Ghana, Laurin et al. (2016) demonstrated that Sentinel-2 imagery could be used to discriminate tropical forest types and map plant functional types. The authors argued that the full band set and vegetation indices derived from the Sentinel-2 would be advantageous for accurately mapping plant functional guilds in the tropics. By using functional trait collected *in situ* data across tropical forests and modelling at high spatial resolution (pixel level) we show that most of our global trait distribution models present a high predictive power for most traits analysed, with prediction accuracy on the testing datasets being highest for predicting leaf chemical and photosynthetic capacity traits. Some of the leaf chemistry we modelled can be directly related to the reflectance obtained from the Sentinel-2 remote sensor in the visible, infrared and red-edge regions which capture the leaf biogeochemistry (Ustin & Gamon, 2010). Our models show how Sentinel-2 imagery, and especially the canopy texture metrics derived from it, can be especially useful for mapping traits related to leaf chemistry (Fig. 2 and Fig. S2). Moreover, our high predictive accuracy for photosynthetic capacity (A_{max}, A_{sat}) is consistent with studies carried out in other vegetation types (e.g. agroecosystems; Serbin et al., 2015) where a strong association was shown between photosynthesis related traits and the red-edge spectral region. Sentinel-2 has 3 bands over the red-edge spectral region (bands 5, 6, 7) and two over the near infrared (bands 8 and 8a) with different bandwidths, which as shown by Shiklomanov et al. (2016) can be advantageous for detecting foliar nutrients such as leaf N (Schlemmer et al., 2013), as small differences in wavelength position in different bands may impact their capacity to retrieve canopy trait characteristics. Moreover, the strong relationship between photosynthetic capacity and spectral reflectance can be partly captured from the leaf N signal, as leaf N concentrations are strongly associated with photosynthetic capacity (Reich, 2012; Vincent, 2001). This reflectance signal is often best obtained in wavebands centred between 440 and 570 nm (Ferwerda et al., 2005). This is of relevance for informing policies for monitoring biodiversity and ecosystem change as we show we can accurately predict relevant functional traits distributions in highly biodiverse areas such as the tropics. Our approach thus facilitates tracking possible shifts in trait distributions and composition across large spatial extents as a response to environmental changes using the Sentinel-2 satellites.

In this study we leverage evidence on covariation among traits to estimate and predict values of traits that have no clear physical effects on spectral reflectance. There is ample evidence of the existence of covariation among plant traits, as for instance between leaf N concentration, specific leaf area and leaf longevity (Walker et al., 2017). Such covariation among traits may in principle also represent covariation in the spectral reflectance patterns across vegetation types (Ma et al. 2019), especially if such individuals vary in leaf structural tissue that drive energy scattering and reflectance (Ollinger, 2011). Such covariation between traits can be helpful for mapping functional trait diversity across large spatial extents that include diverse vegetation types (Townsend et al., 2003, Both et al., 2019).

We show that often the spectral reflectance, pixel textural parameters as Entropy and Correlation, climate and soil, are highly relevant for modelling plant trait distributions across the tropics with high prediction accuracy. However, the canopy texture parameters (Entropy and Correlation) are some of the most important for attaining high trait prediction accuracies across plant functional traits (see also Sarker & Nichol, 2011, Wallis et al., 2019) and differences in spectral, climatic and soil conditions between different regions are key components for improving model predictions across broad spatial extents. The role of texture parameters for modelling biomass and functional traits has also been recognised by other studies focusing not only on mapping functional traits along elevation gradients but also for estimating standing biomass (Wallis et al. 2019). Moreover, soil properties can be informative when modelling trait distributions across regions in the tropics as they partly drive the plant functional and species compositional turnover (e.g. Asner et al., 2016, Prada et al., 2017). In our study different vegetation plots appeared to be on soils with different parent materials resulting in varying cation exchange capacity, pH and soil texture, and thus including differences between sites contributes to increasing the prediction accuracy of trait distributions.

Although in the past it was thought not to be possible to map individual plant species or functional traits (see Price, 1994, Ustin & Gamon, 2010), the advent of remotely sensed data with high spectral, spatial and temporal resolution has made it possible to extract information on the chemical and structural composition of forest canopies even in highly biodiverse tropical forests. This has been demonstrated with the use of hyperspectral sensors (Asner et al., 2015, Asner et al., 2017, Jetz et al., 2016) which often collect hundreds of spectral bands at very high spatial and spectral resolutions but at relatively small spatial extents and often without temporal replication. More research is needed to disentangle to what extent hyperspectral data offers more information to that offered by the Sentinel-2 sensors for an increased mapping accuracy of functional traits of tropical forests. As shown by Laurin et al. (2016), results obtained with simulated Sentinel-2 data are highly comparable to those obtained from hyperspectral imagery for mapping forest types, dominant tree species and functional guilds. Being able to monitor functional traits at high spatial and temporal resolution with multispectral data ranging from the visible to the shortwave infrared across the tropics and with freely available data opens new opportunities for understanding the effects of environmental changes on biodiversity at a local scale. This is because functional traits play a major role in determining ecosystem productivity and functioning, e.g. carbon capture (Díaz et al., 2019, Carmona et al., 2016). Moreover, spatially explicit models of functional traits shift across the tropics can help decipher how ecosystem functioning varies even among tropical areas, providing a cost-effective pathway to identifying regions of high conservation value and hence aid in the creation of locally adequate biodiversity conservation policies.

5. Conclusions

Tropical forest ecosystems are witnessing a fast transformation as a result of changing environmental conditions and direct human impacts (Lewis et al., 2015, Taubert et al., 2018, Aguirre-Gutiérrez et al., 2019). However, we cannot adequately understand or simulate tropical ecosystem responses to environmental changes based solely on current ecosystem model approaches as these are unable to capture the high diversity of plant ecosystem functions in the species-rich tropics. Neglect of functional biodiversity can oversimplify the simulated response of an ecosystem to an environmental disturbance. Here we show the high variation in functional traits that exists among tropical regions, which hints at the different capabilities of such forests to respond to a changing environment. We demonstrate the opportunities for measuring the distribution of key functional traits across tropical forest ecosystems at the pixel level using the Sentinel-2 satellites, which if done across time could reveal areas where functional shifts have occurred and likely where biodiversity conservation/amelioration measures are needed. Although the Sentinel-2 satellites show high promise for this endeavour, our approach is limited by the short time interval since they were launched (i.e. 2015) and the lower spectral resolution of Sentinel-2 imagery in comparison to that derived from hyperspectral sensors. Methods and data products are needed to track changes in functional composition in forest ecosystems across time and space. We demonstrate a new approach to develop a rapid monitoring tool for capturing the effects of a changing environment across the tropics. This new tool has the potential to contribute to a more robust and evidence-based policy-making for conservation of tropical forest ecosystems.

Authorship contribution statement

J.A.G. conceived the study, designed and carried out the analysis and wrote the first draft of the paper. Y.M. conceived and implemented the GEM Network, obtained funding for most of the GEM traits field campaigns and commented on earlier versions of the manuscript. S.R. advised on statistical and remote sensing analysis and commented on earlier versions of the manuscript. All co-authors participated in or coordinated vegetation, trait data and/or soil data collection or processed field data.

The authors named between S.A.B. and L.J.T.W. are listed alphabetically. All co-authors commented on and approved the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work is a product of the Global Ecosystems Monitoring (GEM) network (gem.tropicalforests.ox.ac.uk). J.A.G. was funded by the Netherlands Organisation for Scientific Research (NWO) under the Rubicon programme with project number 019.162LW.010 and by the Natural Environment Research Council (NERC) 'Arboles' project (NE/S011811/1). The traits field campaign was funded by a grant to Y.M. from the European Research Council (Advanced Grant GEM-TRAIT: 321131) under the European Union's Seventh Framework Programme (FP7/2007-2013), with additional support from NERC Grant NE/D014174/1 and NE/J022616/1 for traits work in Peru, NERC Grant ECOFOR (NE/K016385/1) for traits work in Santarem, NERC Grant BALI (NE/K016369/1) for plot and traits work in Malaysia and ERC Advanced Grant T-FORCES (291585) to Phillips for traits work in Australia. Plot setup in Ghana and Gabon were funded by a NERC Grant NE/I014705/1 and by the Royal Society-Leverhulme Africa Capacity Building Programme. The Malaysia campaign was also funded by NERC Grant NE/K016253/1. Plot inventories in Peru were supported by funding from the US National Science Foundation Long-Term Research in Environmental Biology program (LTREB; DEB 1754647) and the Gordon and Betty Moore Foundation Andes-Amazon Program. During data collection, I.O. was supported by a Marie Curie Fellowship (FP7-PEOPLE-2012-IEF-327990). GEM trait data in Gabon was collected under authorisation to YM and supported by the Gabon National Parks Agency. D.B. was funded by the Fondation Wiener-Anspach. W.D.K. acknowledges support from the Faculty Research Cluster 'Global Ecology' of the University of Amsterdam. M.S. was funded by a grant from the Ministry of Education, Youth and Sports of the Czech Republic (INTER-TRANSFER LTT19018).

Y.M. is supported by the Jackson Foundation.

References

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*, 170191

Aguirre-Gutiérrez, J., Oliveras, I., Rifai, S., Fauset, S., Adu-Bredu, S., Affum-Baffoe, K., et al. (2019). Drier tropical forests are susceptible to functional changes in response to a long-term drought. *Ecology Letters, 22*, 855-865

Asner, G.P., Martin, R.E., Anderson, C.B., & Knapp, D.E. (2015). Quantifying forest canopy traits: Imaging spectroscopy versus field survey. *Remote Sensing of Environment, 158*, 15-27

Asner, G.P., Knapp, D.E., Anderson, C.B., Martin, R.E., & Vaughn, N. (2016). Large-scale climatic and geophysical controls on the leaf economics spectrum. *Proceedings of the National Academy of Sciences, 113*, E4043-E4051

Asner, G.P., Martin, R.E., Knapp, D.E., Tupayachi, R., Anderson, C.B., Sinca, F., et al. (2017). Airborne laser-guided imaging spectroscopy to map forest trait diversity and guide conservation. *Science, 355*, 385-389

Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., et al. (2010). Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. *Science, 329*, 834-838

Both, S., Riutta, T., Paine, C.E.T., Elias, D.M., Cruz, R.S., Jain, A., et al. (2019). Logging and soil nutrients independently explain plant trait expression in tropical forests. *New Phytologist, 221*, 1853-1865

Breiman, L. (2001). Random forests. *Machine Learning, 45*, 5-32

Bush, E.R., Jeffery, K., Bunnefeld, N., Tutin, C., Musgrave, R., Moussavou, G., et al. (2020). Rare ground data confirm significant warming and drying in western equatorial Africa. *PeerJ, 8*, e8732

Cadotte, M.W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology, 48*, 1079-1087

Carmona, C.P., de Bello, F., Mason, N.W., & Lepš, J. (2016). Traits without borders: integrating functional diversity across scales. *Trends in ecology & evolution, 31*, 382-394

Clark, M.L. (2017). Comparison of simulated hyperspectral HyspIRI and multispectral Landsat 8 and Sentinel-2 imagery for multi-seasonal, regional land-cover mapping. *Remote Sensing of Environment, 200*, 311-325

Díaz, S., Kattge, J., Cornelissen, J.H., Wright, I.J., Lavorel, S., Dray, S., et al. (2016). The global spectrum of plant form and function. *Nature, 529*, 167-171

Díaz, S., Settele, J., Brondízio, E., Ngo, H.T., Guèze, M., Agard, J., et al. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. https://www.ipbes.net/sites/default/files/downloads/spm_unedited_advance_for_posting_htn.pdf, *- ADVANCE UNEDITED VERSION –*

Dıaz, S., & Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in ecology & evolution, 16*, 646-655

Enquist, B.J., Norberg, J., Bonser, S.P., Violle, C., Webb, C.T., Henderson, A., et al. (2015). Scaling from traits to ecosystems: developing a general trait driver theory via integrating trait-based and metabolic scaling theories. In Anonymous *Advances in ecological research* (pp. 249-318). : Elsevier

Enquist, B.J., Bentley, L.P., Shenkin, A., Maitner, B., Savage, V., Michaletz, S., et al. (2017). Assessing trait-based scaling theory in tropical forests spanning a broad temperature gradient. *Global Ecology and Biogeography, 26*, 1357-1373

Esquivel-Muelbert, A., Baker, T.R., Dexter, K.G., Lewis, S.L., Brienen, R.J., Feldpausch, T.R., et al. (2019). Compositional response of Amazon forests to climate change. *Global Change Biology, 25*, 39-56

Farr, T.G., Rosen, P.A., Caro, E., Crippen, R., Duren, R., Hensley, S., et al. (2007). The shuttle radar topography mission. *Reviews of Geophysics, 45*

Fell, M., & Ogle, K. (2018). Refinement of a theoretical trait space for North American trees via environmental filtering. *Ecological Monographs, 88*, 372-384

Ferwerda, J.G., Skidmore, A.K., & Mutanga, O. (2005). Nitrogen detection with hyperspectral normalized ratio indices across multiple plant species. *International Journal of Remote Sensing, 26*, 4083-4095

Gallagher, R.V., Falster, D.S., Maitner, B.S., Salguero-Gómez, R., Vandvik, V., Pearse, W.D., et al. (2020). Open Science principles for accelerating trait-based science across the Tree of Life. *Nature ecology & evolution, 4*, 294-303

Georganos, S., Grippa, T., Gadiaga, A.N., Linard, C., Lennert, M., Vanhuysse, S., et al. (2019). Geographical Random Forests: A Spatial Extension of the Random Forest Algorithm to Address Spatial Heterogeneity in Remote Sensing and Population Modelling. *Geocarto International*, 1-12

Grime, J.P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology, 86*, 902-910

Guan, K., Pan, M., Li, H., Wolf, A., Wu, J., Medvigy, D., et al. (2015). Photosynthetic seasonality of global tropical forests constrained by hydroclimate. *Nature Geoscience, 8*, 284

Gvozdevaite, A., Oliveras, I., Domingues, T.F., Peprah, T., Boakye, M., Afriyie, L., et al. (2018). Leaf-level photosynthetic capacity dynamics in relation to soil and foliar nutrients along forest–savanna boundaries in Ghana and Brazil. *Tree physiology, 38*, 1912-1925

Haralick, R.M., Shanmugam, K., & Dinstein, I.H. (1973). Textural features for image classification. *IEEE transactions on systems, man, and cybernetics*, 610-621

Hastie, T., Tibshirani, R., & Friedman, J. (2009). *The elements of statistical learning, 2nd edn New York.*

Hédl, R., Svátek, M., Dančák, M., Rodzay, A.W., Salleh, A.B., & Kamariah, A.S. (2009). A new technique for inventory of permanent plots in tropical forests: a case study from lowland dipterocarp forest in Kuala Belalong, Brunei Darussalam. *Blumea-Biodiversity, Evolution and Biogeography of Plants, 54*, 124-130

Hengl, T., de Jesus, J.M., Heuvelink, G.B., Gonzalez, M.R., Kilibarda, M., Blagotić, A., et al. (2017). SoilGrids250m: Global gridded soil information based on machine learning. *PLoS one, 12*, e0169748

Hubau, W., Lewis, S.L., Phillips, O.L., Affum-Baffoe, K., Beeckman, H., Cuní-Sanchez, A., et al. (2020). Asynchronous carbon sink saturation in African and Amazonian tropical forests. *Nature, 579*, 80-87

Jetz, W., Cavender-Bares, J., Pavlick, R., Schimel, D., Davis, F.W., Asner, G.P., et al. (2016). Monitoring plant functional diversity from space. *Nature Plants, 2*, 16024

Jucker, T., Bongalov, B., Burslem, D.F., Nilus, R., Dalponte, M., Lewis, S.L., et al. (2018). Topography shapes the structure, composition and function of tropical forest landscapes. *Ecology Letters, 21*, 989-1000

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., et al. (2020). TRY plant trait database–enhanced coverage and open access. *Global Change Biology*

Kissling, W.D., Walls, R., Bowser, A., Jones, M.O., Kattge, J., Agosti, D., et al. (2018). Towards global data products of Essential Biodiversity Variables on species traits. *Nature ecology & evolution, 2*, 1531-1540

Laughlin, D.C., Strahan, R.T., Adler, P.B., & Moore, M.M. (2018). Survival rates indicate that correlations between community-weighted mean traits and environments can be unreliable estimates of the adaptive value of traits. *Ecology Letters, 21*, 411-421

Laurin, G.V., Puletti, N., Hawthorne, W., Liesenberg, V., Corona, P., Papale, D., et al. (2016). Discrimination of tropical forest types, dominant species, and mapping of functional guilds by hyperspectral and simulated multispectral Sentinel-2 data. *Remote Sensing of Environment, 176*, 163-176

Lebrija-Trejos, E., Pérez-García, E.A., Meave, J.A., Bongers, F., & Poorter, L. (2010). Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology, 91*, 386-398

Lewis, S.L., Edwards, D.P., & Galbraith, D. (2015). Increasing human dominance of tropical forests. *Science, 349*, 827-832

Malhi, Y., Rowland, L., Aragao, L. E. O. C., & Fisher, R.A. (2018). New insights into the variability of the tropical land carbon cycle from the El Nino of 2015/2016. *Philosophical transactions of the Royal Society of London.Series B, Biological sciences, 373*, 10.1098/rstb.2017.0298

Malhi, Y., Roberts, J.T., Betts, R.A., Killeen, T.J., Li, W., & Nobre, C.A. (2008). Climate change, deforestation, and the fate of the Amazon. *Science, 319*, 169-172

Martin, R.E., Asner, G.P., Bentley, L.P., Shenkin, A., Salinas, N., Huaypar, K.Q., et al. (2020). Covariance of Sun and Shade Leaf Traits Along a Tropical Forest Elevation Gradient. *Frontiers in plant science, 10*, 1810

McDowell, N., Allen, C.D., Anderson-Teixeira, K., Brando, P., Brienen, R., Chambers, J., et al. (2018). Drivers and mechanisms of tree mortality in moist tropical forests. *New Phytologist, 219*, 851-869

Mueller, T., Dressler, G., Tucker, C., Pinzon, J., Leimgruber, P., Dubayah, R., et al. (2014). Human land-use practices lead to global long-term increases in photosynthetic capacity. *Remote Sensing, 6*, 5717-5731

Naeem, S., Bunker, D.E., Hector, A., Loreau, M., & Perrings, C. (2009). *Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective.* (pp. 388). : Oxford University Press

Navarro, L.M., Fernández, N., Guerra, C., Guralnick, R., Kissling, W.D., Londoño, M.C., et al. (2017). Monitoring biodiversity change through effective global coordination. *Current opinion in environmental sustainability, 29*, 158-169

Nunes, M.H., Both, S., Bongalov, B., Brelsford, C., Khoury, S., Burslem, D.F., et al. (2019). Changes in leaf functional traits of rainforest canopy trees associated with an El Niño event in Borneo. *Environmental Research Letters, 14*, 085005

Oliver, T.H., Heard, M.S., Isaac, N.J., Roy, D.B., Procter, D., Eigenbrod, F., et al. (2015). Biodiversity and resilience of ecosystem functions. *Trends in Ecology & Evolution, 30*, 673-684

Oliveras, I., Bentley, L., Fyllas, N.M., Gvozdevaite, A., Shenkin, A.F., Prepah, T., et al. (2020). The influence of taxonomy and environment on leaf trait variation along tropical abiotic gradients. *Frontiers in Forests and Global Change, 3*, 18

Ollinger, S.V. (2011). Sources of variability in canopy reflectance and the convergent properties of plants. *New Phytologist, 189*, 375-394

Pacifici, M., Foden, W.B., Visconti, P., Watson, J.E., Butchart, S.H., Kovacs, K.M., et al. (2015). Assessing species vulnerability to climate change. *Nature Climate Change, 5*, 215-224

Parmentier, I., Malhi, Y., Senterre, B., Whittaker, R.J., ATDN, Alonso, A., et al. (2007). The odd man out? Might climate explain the lower tree α-diversity of African rain forests relative to Amazonian rain forests? *Journal of Ecology, 95*, 1058-1071

Prada, C.M., Morris, A., Andersen, K.M., Turner, B.L., Caballero, P., & Dalling, J.W. (2017). Soils and rainfall drive landscape-scale changes in the diversity and functional composition of tree communities in premontane tropical forest. *Journal of vegetation science, 28*, 859-870

Price, J.C. (1994). How unique are spectral signatures? *Remote Sensing of Environment, 49*, 181-186

R Development Core Team. (2014). R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Ranghetti, L., Boschetti, M., Nutini, F., & Busetto, L. (2020). “sen2r”: An R toolbox for automatically downloading and preprocessing Sentinel-2 satellite data. *Computers & Geosciences*, 104473

Sarker, L.R., & Nichol, J.E. (2011). Improved forest biomass estimates using ALOS AVNIR-2 texture indices. *Remote Sensing of Environment, 115*, 968-977

Schlemmer, M., Gitelson, A., Schepers, J., Ferguson, R., Peng, Y., Shanahan, J., et al. (2013). Remote estimation of nitrogen and chlorophyll contents in maize at leaf and canopy levels. *International Journal of Applied Earth Observation and Geoinformation, 25*, 47-54

Schneider, F.D., Morsdorf, F., Schmid, B., Petchey, O.L., Hueni, A., Schimel, D.S., et al. (2017). Mapping functional diversity from remotely sensed morphological and physiological forest traits. *Nature communications, 8*, 1441

Shenkin, A., Bentley, L.P., Oliveras, I., Salinas, N., Adu-Bredu, S., Marimon, B.H., et al. (2019). The Influence of Ecosystem and Phylogeny on Tropical Tree Crown Size and Shape. *bioRxiv*, 789255

Shiklomanov, A.N., Dietze, M.C., Viskari, T., Townsend, P.A., & Serbin, S.P. (2016). Quantifying the influences of spectral resolution on uncertainty in leaf trait estimates through a Bayesian approach to RTM inversion. *Remote Sensing of Environment, 183*, 226-238

Soudzilovskaia, N.A., Elumeeva, T.G., Onipchenko, V.G., Shidakov, I.I., Salpagarova, F.S., Khubiev, A.B., et al. (2013). Functional traits predict relationship between plant abundance dynamic and long-term climate warming. *Proceedings of the National Academy of Sciences, 110*, 18180-18184

Sullivan, M.J., Talbot, J., Lewis, S.L., Phillips, O.L., Qie, L., Begne, S.K., et al. (2017). Diversity and carbon storage across the tropical forest biome. *Scientific Reports, 7*, 39102

Szabó, L., Burai, P., Deák, B., Dyke, G.J., & Szabó, S. (2019). Assessing the efficiency of multispectral satellite and airborne hyperspectral images for land cover mapping in an aquatic environment with emphasis on the water caltrop (Trapa natans). *International Journal of Remote Sensing, 40*, 5192-5215

Taubert, F., Fischer, R., Groeneveld, J., Lehmann, S., Müller, M.S., Rödig, E., et al. (2018). Global patterns of tropical forest fragmentation. *Nature, 554*, 519

Tollefson, J. (2011). A new eye on biodiversity: airborne observatory will use chemical clues to map and assess tropical ecosystems. *Nature, 474*, 13-15

Townsend, P.A., Foster, J.R., Chastain, R.A., & Currie, W.S. (2003). Application of imaging spectroscopy to mapping canopy nitrogen in the forests of the central Appalachian Mountains using Hyperion and AVIRIS. *IEEE Transactions on Geoscience and Remote Sensing, 41*, 1347-1354

Ustin, S.L., & Gamon, J.A. (2010). Remote sensing of plant functional types. *New Phytologist, 186*, 795-816

Van der Plas, F., Ratcliffe, S., Ruiz-Benito, P., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., et al. (2018). Continental mapping of forest ecosystem functions reveals a high but unrealised potential for forest multifunctionality. *Ecology Letters, 21*, 31-42

Walker, A.P., McCormack, M.L., Messier, J., Myers-Smith, I.H., & Wullschleger, S.D. (2017). Trait covariance: the functional warp of plant diversity? *New Phytologist, 216*, 976-980

Wallis, C.I., Homeier, J., Peña, J., Brandl, R., Farwig, N., & Bendix, J. (2019). Modeling tropical montane forest biomass, productivity and canopy traits with multispectral remote sensing data. *Remote Sensing of Environment, 225*, 77-92