1 **Pantropical modelling of canopy functional traits using Sentinel-2 remote sensing data**

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

12
13 [a]Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford,
14 UK

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

39   [w]Conservation Research Institute, Department of Plant Sciences, University of Cambridge, Cambridge CB2
40   3QZ, UK

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

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

43   [z]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona, USA

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

45   [ab]Universidade Estadual de Campinas, Instituto de Biologia, Departamento de Biologia Vegetal, Campinas,
46   São Paulo, Brazil

47   [ac]Department of Geography, University College London, London, UK

48   [ad]Coordenação de Dinâmica Ambiental, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil

49   [ae]Sección Química, Pontificia Universidad Católica del Perú, Avenida Universitaria 1801, San Miguel, Lima
50   32, Peru

51   [af]Department of Biology, Wake Forest University, Winston-Salem, NC 27109, USA

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

53   *Corresponding author

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55   **Abstract**

56   Tropical forest ecosystems are undergoing rapid transformation as a result of changing environmental

57   conditions and direct human impacts. However, we cannot adequately understand, monitor or simulate

58   tropical ecosystem responses to environmental changes without capturing the high diversity of plant

59   functional characteristics in the species-rich tropics. Failure to do so can oversimplify our understanding

60   of ecosystems responses to environmental disturbances. Innovative methods and data products are

61   needed to track changes in functional trait composition in tropical forest ecosystems through time and

62   space. This study aimed to track key functional traits by coupling Sentinel-2 derived variables with a

63   unique data set of precisely located *in-situ* measurements of canopy functional traits collected from 2434

64   individual trees across the tropics using a standardised methodology. The functional traits and vegetation

65   censuses were collected from 47 field plots in the countries of Australia, Brazil, Peru, Gabon, Ghana, and

66   Malaysia, which span the four tropical continents. The spatial positions of individual trees above 10 cm

67   diameter at breast height (DBH) were mapped and their canopy size and shape recorded. Using geo-

68　located tree canopy size and shape data, community-level trait values were estimated at the same spatial

69　resolution as Sentinel-2 imagery (i.e. 10 m pixels). We then used the Geographic Random Forest (GRF) to

70　model and predict functional traits across our plots. We demonstrate that key plant functional traits can

71　be measured at a pantropical scale using the high spatial and spectral resolution of Sentinel-2 imagery in

72　conjunction with climatic and soil information. Image textural parameters were found to be key

73　components of remote sensing information for predicting functional traits across tropical forests and

74　woody savannas. Leaf thickness (R^2=0.52) obtained the highest prediction accuracy among the

75　morphological and structural traits and leaf carbon content (R^2 = 0.70) and maximum rates of

76　photosynthesis (R^2 = 0.67) obtained the highest prediction accuracy for leaf chemistry and photosynthesis

77　related traits, respectively. Overall, the highest prediction accuracy was obtained for leaf chemistry and

78　photosynthetic traits in comparison to morphological and structural traits. Our approach offers new

79　opportunities for mapping, monitoring and understanding biodiversity and ecosystem change in the most

80　species-rich ecosystems on Earth.

81　Keywords: Plant traits, Sentinel-2, Tropical forests, Random Forest, Pixel-level predictions, Image texture

82　**1. Introduction**

83　Some of the most urgent questions in ecology and ecosystem science today focus on how communities

84　of organisms respond to global environmental changes (Naeem et al., 2009), how biodiversity and

85　ecosystem changes across the world can be consistently mapped and monitored (Navarro et al., 2017),

86　and how spatial, temporal and taxonomic variability in biodiversity influences ecosystem resilience to

87　climate change (Oliver et al., 2015). In terms of Earth system science, we need to understand and model

88　how the terrestrial biosphere will respond (and already is responding) to global environmental change,

89　and whether there are critical thresholds or "tipping points" beyond which major biomes may not be able

90　to recover. Nowhere is the challenge more urgent than in the species-rich tropical forest and woody

91　savanna biomes, which together are home to more than half of global biodiversity and over 60% of

92　terrestrial productivity (Beer et al., 2010). There is evidence that atmospheric change may have effects on

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93   tropical forest productivity and tree functional composition (Esquivel-Muelbert et al., 2019, Hubau et al.,

94   2020). These effects may include a stimulation of productivity (perhaps due to rising CO_2) and/or a

95   degradation or dieback, possibly caused by increased seasonality and incurred intensity of extreme

96   drought events (Malhi et al., 2008, Malhi et al., 2018). Such events are partly responsible for the increased

97   tree mortality and decreased carbon residence time in tropical forests worldwide (McDowell et al., 2018).

98   However, to adequately understand such responses we need to capture and map the high diversity of

99   plant ecosystem function in the species-rich tropics and savannas.

100   Species functional traits are defined as the morphological, physiological or phenological attributes

101   which determine the fitness of organisms, their response to changes in the environment and their

102   influence on ecosystem functions (Kissling et al., 2018, Díaz & Cabido, 2001). Functional traits provide

103   tangible and mechanistic means of assessing the ability of communities to adapt to climate change

104   (Pacifici et al., 2015) and play a major role in determining ecosystem productivity, functioning and notably

105   nature's contribution to people (e.g. water and wood availability) (Díaz et al., 2019, Carmona et al., 2016).

106   Any tools or methods that facilitate quantification of functional traits across large spatial scales and at

107   high spatial resolution would be invaluable for quantifying ecosystem functioning and ecological

108   responses to disturbance at scales relevant for policy and management (Kissling et al., 2018). However, it

109   is still challenging to map functional trait diversity in tropical regions given the lack of plant trait data

110   available for most of those locations (Jetz et al., 2016). Additional challenges come from different and

111   often incompatible trait collection protocols and the lack of systematic high spatial, spectral and temporal

112   resolution remote sensing imagery that coincides with data for functional traits at the canopy level and

113   the lack of geo-located tree stems at the plot level. Thus, there is a need for spatially-explicit methods to

114   map and quantify plant functional traits at high spatial resolution in tropical forest and woody savanna

115   ecosystems.

116   Tracking functional traits can shed light on differences in ecosystem functioning across broad

117   spatial extents and therefore aid policy and decision making, e.g. for creating adequate biodiversity

118   conservation policies or for providing early warning of directional shifts in ecosystems. The key challenges

119 of any functional trait approach are scalability and monitoring: how can functional shifts in highly diverse

120 tropical forests and woody savannas be monitored and tracked over large spatial extents? Intensive field

121 sampling of plant functional traits at a pantropical scale is time-consuming and economically unviable.

122 There are large gaps in the availability of plant trait data globally, and the largest gaps are in the tropics

123 (Jetz et al., 2016). Large plant trait datasets aim to overcome this issue and have advanced our ability to

124 carry out plant functional trait analysis in an unprecedented way (Kattge et al., 2020, Gallagher et al.,

125 2020). However, as with any database, the plant trait values from such databases will represent the local

126 trait-environment relationships for the site where they were collected, which may not be the area of

127 interest. A key assumption in trait-based ecology is that the environment is filtering for an optimal set of

128 trait characteristics so that the resulting communities are adapted to the environment where they are

129 distributed (Fell & Ogle, 2018, Lebrija-Trejos et al., 2010, Lortie et al., 2004). Hence, we might expect an

130 optimal set of trait characteristics for a given location, which when analysed over time could quantify the

131 dynamics of community trait distributions or shifts in functional composition relating to environmental

132 changes (Enquist et al. 2015).

133   Recently, there has been an increasing investment into mapping plant functional trait

134 distributions given economic and data availability constraints such efforts have mostly focused on

135 hyperspectral imagery at local (Schneider et al., 2017) to regional scales (Asner et al., 2015, Asner et al.,

136 2016). However, high resolution hyperspectral imagery is not widely available (Clark, 2017, Szabó et al.,

137 2019). Landsat-8 imagery at coarser spatial (30 m pixel), spectral and temporal resolution than Sentinel-2

138 imagery has been used to map four traits over small (20 × 20 m) vegetation plots covering small spatial

139 extents (Wallis et al. 2019). The spatial mismatch between site-level trait sampling and the spatial

140 resolution of pixels may partly affect overall model predictions (Wallis et al. 2019). Other studies restricted

141 to European forests (Ma et al., 2019) show how Sentinel-2 imagery could be used to map functional trait

142 diversity in the comparatively low tree diversity forests of Europe (Ma et al., 2019) and to retrieve specific

143 leaf area from Landsat-8 imagery (Ali et al., 2017). However, the tropics present a different set of

144 challenges, such as the high species richness, low accessibility and comparatively low availability of trait

145   data, plus the low coverage of remote sensing data because of persistent high cloud cover. These

146   challenges have hampered developments in mapping plant functional trait distributions across most

147   tropical areas.

148   Satellite imagery with high spectral, spatial and temporal resolution is particularly needed in the

149   wet tropics (Asner et al., 2017), where clear days can be infrequent and several images may be required

150   to construct a cloud-free composite. The Copernicus mission from the European Space Agency's (ESA;

151   www.esa.int) aids in the improvement in this area. The Sentinel-2 multispectral imager satellites are part

152   of the Copernicus programme, which has the potential to provide new opportunities to evaluate canopy

153   traits remotely. Sentinel-2 has 13 spectral channels covering the visible, near-infrared, and short-wave

154   infrared, a spatial resolution of 10 m for visible and near-infrared, 20 m for short-wave infrared, revisit

155   period of 5 days and it provides open data availability. The improved spectral sampling (13 bands, 10

156   excluding the 60 m atmospheric bands) and fine spatial resolution of the Sentinel-2 images have the

157   potential to elucidate leaf chemistry, morphology, photosynthesis and water content at the pixel-level,

158   although this remains largely untested. Multispectral sensors do not provide the rich information available

159   from hyperspectral sensors, which have been used in numerous studies to map functional traits at small

160   spatial extents (Townsend et al., 2003, Laurin et al., 2016, Asner et al., 2015, Martin, M. E. et al., 2008).

161   However, high resolution open-access hyperspectral imagery is not currently available from space.

162   Although Landsat images have been used to predict a few functional traits at a local scale (Wallis et al.,

163   2019), the extended spectral, spatial and temporal capabilities of the state-of-the-art sensors onboard the

164   Sentinel-2 satellites provide greater potential for mapping functional trait diversity in tropical forest

165   ecosystems at large extents.

166   Here, we employ a unique and large dataset of *in-situ* plant canopy traits and vegetation census

167   data collected with a standardised protocol at multiple sites across the tropics to calibrate and validate

168   Sentinel-2 imagery for predicting community leaf trait composition. The data provide 14 standardized

169   measurements of *in-situ* collected plant functional traits, precisely geo-located and delineated individual

170   tree crowns and vegetation censuses from Australia, South East Asia, Africa and South America to model

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171   and predict functional trait composition at the pixel-level. We investigate how functional traits of tropical

172   forests vary within and between these different tropical regions and whether Sentinel-2 spectral data in

173   conjunction with climatic and soil information provide sufficient information to predict such pixel-level

174   trait composition in long-term vegetation plots across the tropics. We hypothesised that there would be

175   differences in trait variation among sites and regions given the range of climatic and soil conditions across

176   the tropics. Given the high spectral and spatial resolution of Sentinel-2 imagery we further hypothesised

177   that raw spectral bands and textural information will prove to be key predictors of functional trait

178   distributions across the tropics. The very high spatial resolution and local origin of the input plant traits

179   and census dataset, which represent traits adapted to local environments, plus the use of the Sentinel-2

180   data will allow us to accurately predict plant functional trait distributions that are potentially generalisable

181   across the tropical forest biome.

182   **2. Methods**

183   2.1 *Vegetation plots*

184   We collected vegetation census data from 47 permanent vegetation plots that are part of the Global

185   Ecosystems Monitoring network (GEM; www.gem.tropicalforests.ox.ac.uk). These plots encompass wet

186   tropical forests, seasonally dry tropical forests, and tropical forest-savanna transitional vegetation. The

187   sampled vegetation plots have an area ranging from 0.1 to 1 ha, with most (61%) being 1 ha. The plots

188   used are located across four tropical continents and specifically in the countries of Australia, Brazil, Gabon,

189   Ghana, Malaysian Borneo (from here onwards referred to as Malaysia) and Peru (Table 1). In each plot all

190   woody plant individuals with a diameter ≥ 10 cm at breast height (DBH) or above buttress roots were

191   measured and their exact geographic location was recorded (see the 'Individual tree crowns' section

192   below for more details). In two plots (NXV-01 and NXV-10) in Nova Xavantina, here onwards referred to

193   as Brazil-NX, the DBH was measured near ground level as is standard in savanna monitoring protocols.

194   2.2 *Functional traits*

195   We collected plant functional trait measurements from all woody plants located in each of the 47

196   vegetation plots mentioned above (Table 2). All traits were gathered from the GEM network and were

197   collected following a standardized methodology across plots. Forest inventory data were used to stratify

198   tree species by basal area dominance, a proxy for canopy area dominance. The tree species that

199   contributed most to basal area abundance were sampled with 3-5 replicate individuals per species, with

200   a goal of sampling 60-80% of basal area across the sampling region. Eighty percent of basal area was often

201   achieved in low diversity sites (e.g. montane or dry forests) but only around 60% was achieved in some

202   high diversity sites (lowland humid rainforests). For each selected tree a sun and a shade branch were

203   sampled and in each branch 3-5 leaves were used for trait measurements. We only included the sun

204   exposed branches in our analysis because we were interested in the branches that could potentially be

205   receiving direct sun radiation and thus show direct spectral reflectance. This represented a total sample

206   of 2434 individual trees across the tropics (Table 1). The plant functional traits collected were those

207   related to photosynthetic capacity at both saturating CO_2 concentration (2000 ppm CO_2; A_{max}) and

208   ambient CO_2 concentration (400 ppm CO_2; A_{sat}); leaf chemistry (nitrogen, phosphorus, carbon, calcium,

209   potassium and magnesium content); and leaf morphological and structural traits (area, specific leaf area,

210   thickness, dry mass, fresh mass and water content). An overview of the methods for individual leaf

211   functional trait measurements is provided in the Supplementary Information (see full traits collection

212   protocol section). Further details of measurements for the Peruvian Andes campaign are given in Martin

213   et al. (2020) and Enquist et al. (2017), for the Malaysian campaign in Both et al. (2019), and for the Ghana

214   and Brazil campaigns in Oliveras et al. (2020) and Gvozdevaite et al. (2018).

215   Some individuals in the plots lacked functional trait values. To assign representative trait values

216   to unsampled individuals we did the following: 1) individuals from which traits were measured kept their

217   original trait information, 2) for individuals with no trait information we randomly sampled trait values

218   from other individuals from the same species present in the same plot, 3) if the species was not sampled

219   in the given plot then we randomly sampled an individual from the same species that had trait information

220   in other plots from the same region (Table 1). This protocol for trait value allocation allowed us to work

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221   with the existing range of trait values at the species level and avoided to create average values per species

222   (Cadotte et al., 2011, Schneider et al., 2017). We did not assign trait values to the remaining individuals

223   belonging to species from which no trait collection was obtained at the regional level.

224   2.3 *Individual tree crowns*

225   Tree crown locations and structural attributes were recorded for each tree, where crown area and shape

226   were measured by direct crown field measurements in the case of plots in Malaysia and Peru (see protocol

227   below), or by means of regional level allometric equations developed by Shenkin et al. (2019) (all other

228   plots). In the latter case, the crown's shape was assumed to be circular. The direct field crown

229   measurements were as follows: all trees ≥ 10 cm DBH (i.e., 1.3 m from the ground) were mapped using a

230   ground-based Field-Map laser technology (IFER, Ltd., Jílové u Prahy, Czech Republic) (Hédl et al., 2009).

231   The Field-Map technology was based on a combination of Impulse 200 Standard laser rangefinder (with

232   in-built tilt sensor for measuring vertical angles), MapStar module II electronic compass (both Laser

233   Technology Inc., Colorado, USA), and the specialized mapping software Field-Map v. 11 (IFER, Czech

234   Republic). The technology was used to record spatial positions of tree stems in three-dimensional space

235   (x, y, z-coordinates) as well as to map individual horizontal projections of tree crowns in the plots. The

236   horizontal crown projection of every tree was obtained by measuring spatial positions (x and y-

237   coordinates) of series of points (ranging from 5 to 30 points depending on the size of the crown) at the

238   boundary of a crown projected to the horizontal plane. The shape of crown projection was subsequently

239   smoothed using the "smooth contour line" feature of Field-Map software v. 11. Heights of all trees with

240   DBH ≥ 10 cm were measured by the Impulse and TruPulse 360 R laser rangefinders (both Laser Technology

241   Inc., Colorado, USA). Thus, each individual crown was accurately geolocated rendering information about

242   its shape and vertical and horizontal position.
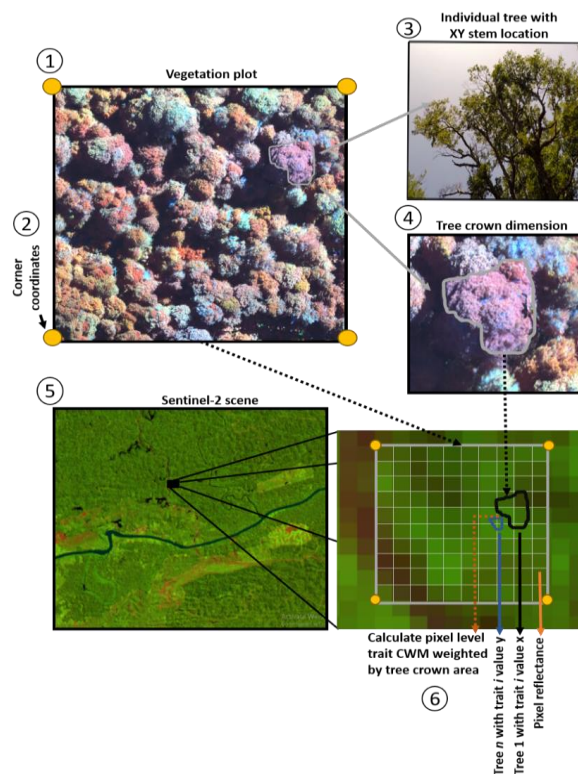
243   2.4 *Calculating pixel-level trait composition*

244   We calculated the community weighted mean of each trait for each 10 × 10 m subplot (matching the

245   highest pixel spatial resolution of the Sentinel-2 imagery) based on the mass ratio hypothesis, which

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246 states that the most dominant species drive the ecosystem processes by means of their functional traits

247 (Grime, 1998). We first geolocated the vegetation plot, with its already mapped tree crowns (see

248 protocol above), to the Sentinel-2 imagery based on the corner coordinates of the plots. This is an

249 important step as geolocation errors between the vegetation plot and the correct location in the

250 satellite image could represent a large proportion of a given plot depending on the plots' area. Then for

251 each of the traits, *t*, and pixels, *p*, we calculated their community level weighted mean (CWM) using the

252 individual tree crown horizontal area as the weighting factor (Fig. 1) as follows:

253
$$CWM_{tp} = \frac{\sum_{i=1}^{N} CA_{ip} \times t_{ip}}{CA_p}$$

254 (Eq. 1)

255 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

256 total number of individuals per pixel and CA_p is the crown area of pixel *p*. The crown contribution to the

257 CWM was weighted by its proportional cover of the corresponding pixel. The total number of pixels used

258 in our calculations are 403 for Australia, 449 for Brazil -NX (Nova Xavantina), 302 for Brazil -ST (Santarem),

259 464 for Gabon, 620 for Ghana, 976 for Malaysia and 1280 for Peru.

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Figure 1. Diagram summarising the steps followed to assign trait values per Sentinel-2 pixel. 1) First the vegetation plots are defined based on the GEM (Global Environmental Monitoring) dataset and 2) from each vegetation plot the corner coordinates are extracted. 3) From each vegetation plot the XY position of each stem ≥10 cm DBH is extracted and 4) the crown horizontal area is calculated based on the protocol described in the methods section. 5) Then the Sentinel-2 imagery for the study area is processed to level 2A using the ESA SNAP toolbox and 6) the vegetation plot is overlaid in the Sentinel-2 image based on its corner coordinates. In this last step (6) each pixel defines a 'subplot' which is the unit used to calculate the trait community weighted mean based on the crown area of the trees that are contained by that pixel. In 6) *n* refers to a given tree in a given pixel, trait *i* represents a given trait and *x* and *y* are values for that trait. The image used as an example in step (1) was taken by Jesus Aguirre-Gutierrez over a vegetation plot using a multispectral ALTUM camera mounted on an Inspire 1 drone."

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

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). Our overlapping imagery with the vegetation plots appeared free of clouds and cirrus effects. The above-mentioned steps allowed us to obtain level 2A imagery with surface reflectance values. We then resampled the 20 m bands to 10 m spatial resolution using bilinear interpolation. The Sentinel-2 60 m 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. Since vegetation indices may increase prediction accuracy when modelling community weighted traits (Wallis et al., 2019), we calculated three of them (Table 3) which we hypothesised to inform trait distributions given their association with chlorophyll and nutrient 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) based texture features (Haralick et al., 1973). The desired texture metrics are computed from a grey tone matrix that is spatially dependent. The co-occurrence matrix

11

292 depends on the angular relationship and distance between two neighbouring pixels and depicts the

293 number of occurrences of the relationship between a pixel and its neighbour. After trials with smaller

294 windows size (5 x 5) we opted to use a 9 x 9 pixel kernel window which was sufficient to render enough

295 canopy contrast information during the modelling step (see section 2.7 below) without taking large

296 periods of time for its calculation. The texture results obtained with the used kernel window was highly

297 correlated to the smaller kernel window (*Cor* = 0.94, *P* =< 0.0001). Based on the GLCM we calculated two

298 variables that are least correlated with each other, the Entropy and Correlation, for each of the vegetation

299 indices. While Entropy measures the homogeneity level for a given area, the Correlation measures

300 probability of occurrence of the specified pixel pairs across the image (Haralick et al., 1973, Wallis et al.,

301 2019). All remote sensing analyses related to the generation of vegetation indices and texture metrics

302 were carried out using the Sentinel SNAP toolbox (step.esa.int) and the R statistical environment (R

303 Development Core Team, 2014) with the 'Sen2R' package.

304 2.6 *Environmental and soil data*

305 Climatic, topographic and soil characteristics may vary across regions and could at least partly determine

306 the region's vegetation and intrinsic trait composition. We obtained information on these three

307 components for each sampling location. The three components were grouped as belonging to

308 environmental (climate) or soil-terrain (texture, pH, cation exchange capacity and topography) drivers

309 (Table 3).

310   For climate and for each sampling location we gathered gridded data on the mean annual climatic

311 water deficit (MCWD), which is a metric of drought intensity and severity, mean annual maximum

312 temperature (MATmax), solar radiation (SRAD) and soil moisture (SM) (Table 3). All climatic data with a

313 spatial resolution of ~4km were obtained from the TerraClimate gridded climate product (Abatzoglou et

314 al., 2018). To characterise the climatic conditions for each location we used a climatology of 30 years

315 (1986-2015)   as   suggested   by   the   World   Meteorological   Organization   (WMO;

316 www.wmo.int/pages/prog/wcp/ccl/faqs.php). We used the terrain slope to characterise the plot's

317 topography, as it has been shown that topography may shape the composition and structure of tropical

318 forests (Jucker et al., 2018) and may affect the vegetation spectral reflectance by modifying soil water and

319 nutrient availability. Terrain slope was calculated using a high-resolution digital elevation model, ~30m

320 pixel size at the equator, from the Shuttle Topography Mission (Farr et al., 2007). At most sites soil data

321 were sampled locally, and analysed to a standardised protocol in labs in either INPA, Manaus, Brazil or the

322 University of Leeds, UK, following the RAINFOR soil protocol (Quesada et al., 2012). From these data we

323 summarised plot level soil data averaged over the first 30 cm for texture (Sand% and Clay%), cation

324 exchange capacity (eCEC) and pH-H_2O (pH). Plot level texture data were not available for plots in Australia

325 and the NXV-10 plots and were thus derived from the SoilGrids dataset at 250m pixel spatial resolution

326 for those plots only (Hengl et al., 2017).

327 2.7 *Comparing community level trait distributions across regions*

328 We tested if and to what extent the community-level trait distributions differed among regions. We

329 square-root transformed the trait value to improve normality and applied an analysis of variance

330 (ANOVA). We then applied a Tukey's Honest Significant Difference (Tukey HSD) test to investigate the

331 significance of the differences between the means of the community weighted mean (CWM) trait values

332 among locations. The ANOVA and Tukey test were carried out using the 'stats' package for R (R

333 Development Core Team, 2014).

334 2.7 *Relating pixel-level trait composition to spectral reflectance, environment and soil conditions*

335 We modelled the community weighted mean (CWM) of each trait at the pixel-level (10×10 m) as a function

336 of the Sentinel-2 remote sensing, environmental and soil covariates (Table 3) using a 'spatial' version of

337 the machine learning Random Forest (RF) algorithm (Breiman, 2001) named Geographic Random Forests

338 (GRF) (Georganos et al., 2019). RF is a nonparametric algorithm that has been shown to be robust to

339 overfitting and variable inputs thanks to the bagging process and its random feature selection (Hastie et

340 al., 2009). Moreover, it has been extensively used to model and predict ecological and remote sensing

data within and across ecosystems (e.g. Asner et al., 2016, Van der Plas et al., 2018). In contrast to RF, GRF disaggregates the underlying data in geographic space, in this case based on the spatial coordinates of the Sentinel-2 pixels, building global and local sub-models (plot level), making the modelling framework thus 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 fusion 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.
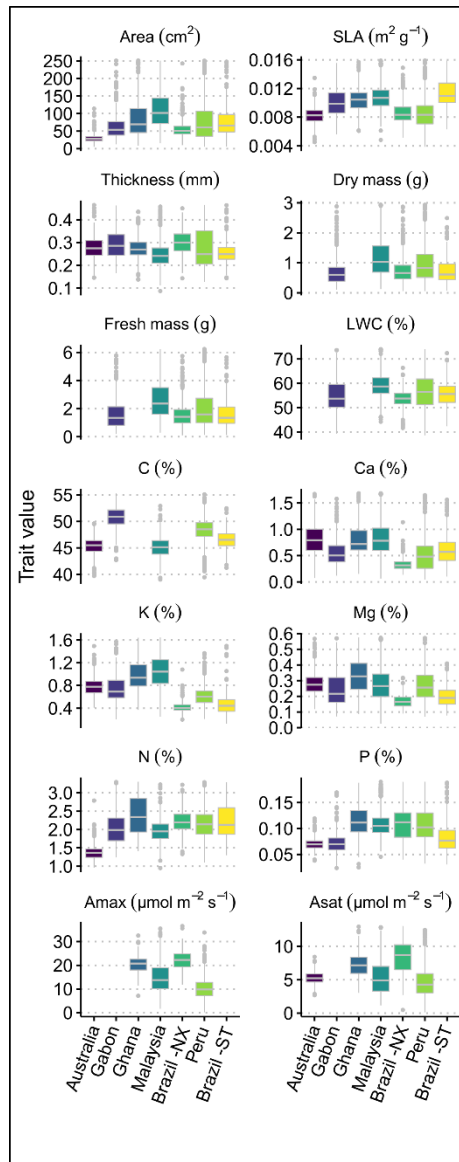
We performed an extensive set of model optimization and regularization procedures to reduce over-fitting. For the CWM models we selected the number of trees to fit by 10-fold cross-validation analysis with number of trees ranging between 500 and 1500 and the number of variables randomly sampled as candidates 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.

366   We carried out all analyses stated above with the full set of tree individuals present in each

367   vegetation plot with functional traits assuming that the contribution of small individuals to the trait CWM

368   value, and thus to the community reflectance at the pixel-level, would be minimal given the weighting

369   factor used (i.e. the individual's crown area). However, to underpin this we carried out all analyses on two

370   smaller datasets, one where the 25th and other where the 50th percentile of the smallest trees per region

371   were removed. All analyses were carried out in the R statistical environment with the 'caret', 'tidyverse'

372   and 'SpatialML' packages.

373   **3. Results**

374   3.1 *Variation in trait composition across tropical forests*

375   Most leaf functional traits exhibited significant differences across the tropics (Fig. 2) including wide trait

376   range variation within the same region (Fig. S8), with leaf fresh mass and leaf thickness being on average

377   less variable among locations (Table S2).

Figure 2. Comparison of trait distributions across tropical regions. The boxplots are based on the pixel-level (10×10 m) community trait values for each trait and region (n=403 for Australia, 449 for Brazil-NX, 302 for Brazil-ST, 464 for Gabon, 620 for Ghana, 976 for Malaysia and 1280 for Peru). Horizontal lines in each boxplot show the median value and vertical lines are the whiskers that extend to the largest value or not further than 1.5 times the inter-quartile range. For some locations information for all traits was not available. For full details in significant differences in mean trait values among locations see Table S4. Brazil -NX: Nova Xavantina; Brazil -ST: Santarem.

Leaf chemistry and photosynthetic capacity (A_{max} and A_{sat}) often showed significant differences among locations (Table S2). Drier locations as in Nova Xavantina (Brazil -NX) displayed trait adaptations to seasonal rainfall and temperature 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 highest photosynthetic capacity (mean A_{max}= 21.9 ± 4.3 µmol m^{-2} s^{-1}, and A_{sat}= 8.3 ± 2.5 µmol m^{-2} s^{-1}). In contrast, wetter regions such as Malaysia displayed on average some of

392   the biggest (113.5 ± 55 cm^2) and thinnest (0.25 ± 0.05 mm) leaves with high leaf water content (59.1 ± 5

393   %). The Peruvian altitudinal transect showed large variation in community-level traits values, which often

394   overlapped with trait values from all other sampled locations across the tropics (Fig. 2). For most nutrients,

395   leaf nutrient concentration was often highest in forests found in Ghana (e.g. K% = 0.97 ± 0.27 and Mg% =

396   0.33 ± 0.1) and Malaysia (K% = 1.05 ± 0.27 and Mg% = 0.27 ± 0.1). Australian forests showed on average

397   some of the lowest community-level N (1.3 ± 0.21 %) and P (0.07 ± 0.01%) leaf concentrations.

398   3.2 *Pantropical and local community level functional trait models*

399   The analyses carried out with the full dataset and the dataset where the 25th and 50th percentile of the

400   smallest trees per region were removed gave similar results for the global (R^2 = 0.95 and R^2 = 0.97

401   respectively; Table S3) and local (R^2 = 0.81 and R^2 = 0.80 respectively; Table S4) models of plant trait

402   distributions. Therefore, in the following we only present the results for the models carried out with the
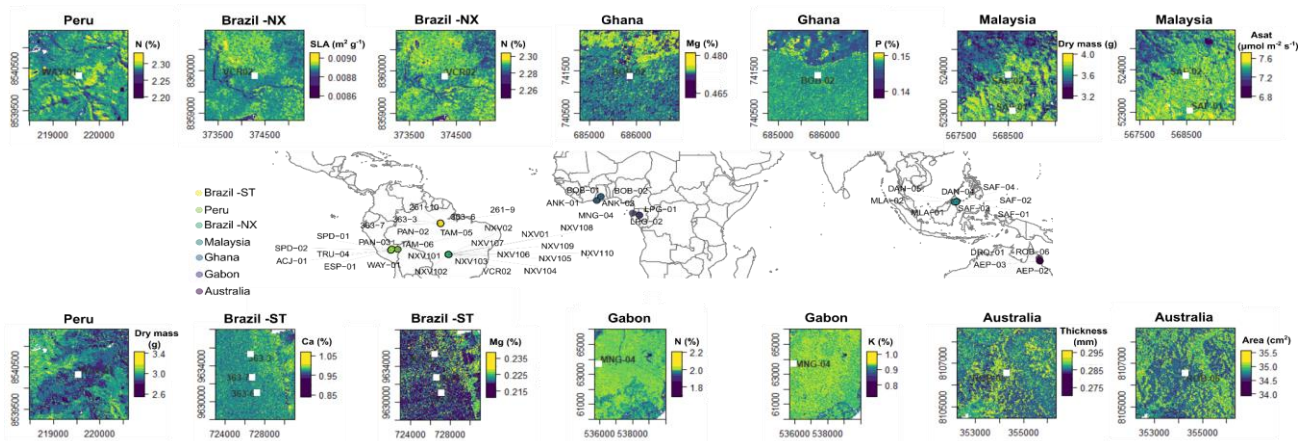
403   full vegetation dataset.

404   The accuracy of the pantropical prediction of functional traits ranged between a minimum of R^2 =

405   0.26, for leaf fresh mass, and a maximum of R^2 = 0.70 for leaf carbon content (C%) based on the out-of-

406   sampled (testing) data across the tropics (Table 4). The predictive accuracies of leaf chemistry and

407   photosynthetic traits were often higher than for morphological and structural traits such as leaf dry mass

408   (R^2 = 0.27) and leaf area (R^2 = 0.43) (Fig. 3). At the pantropical level, the highest prediction accuracy was

409   obtained for leaf thickness (R^2 = 0.52) for morphological and structural traits, for leaf Ca (Ca%; R^2 = 0.64)

410   and leaf K (K%; R^2 = 0.63) for the chemical traits other than carbon. Leaf N and P concentrations were also

411   predicted with high accuracy (R^2 = 0.59). Leaf photosynthetic capacity traits, A_{max} and A_{sat}, showed some

412   of the highest prediction accuracies ranging from R^2 = 0.55 to 0.67, respectively. Model spatial predictions

413   for several traits and locations are shown in Fig. 4 and others can be seen in Fig. S1-Fig. S7.

414   Models built for each tropical region and trait uncovered marked differences in prediction

415   accuracy among them (Fig. 5; Table 5 and Table S5). Leaf area prediction accuracy ranged from R^2 = 0.04

416   (Brazil -ST) to 0.35 (Australia), and that of specific leaf area (SLA) ranged from R^2 = 0.06 for Malaysia to

417 0.54 for Brazil -NX (Table S5). The local models showed a higher accuracy for predicting local level leaf

418 chemical nutrients (up to R^2 = 0.68), especially for P, Ca, and N concentrations in comparison to

419 morphological (e.g. leaf area and SLA) traits (Table 5; Fig. 5). Traits related to photosynthetic capacity

420 showed an overall better prediction accuracy than leaf area and SLA with prediction values ranging

421 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

422 highest prediction accuracy across regions for a given trait were reached for leaf P concentration (R^2 =

423 0.47) and A_{max} (R^2 = 0.44) and the locations with the highest average prediction accuracy across traits were

424 the Nova Xavantina savanna (Brazil -NX, R^2=0.40) and the Peru elevation gradient (R^2 = 0.38; Table 5), both

425 sites encompassing strong gradients in vegetation morphology and structure.
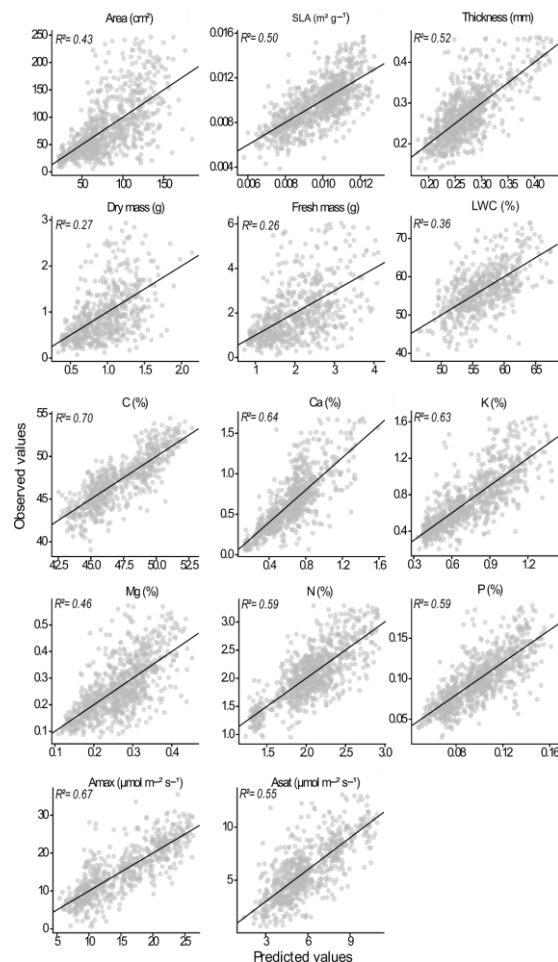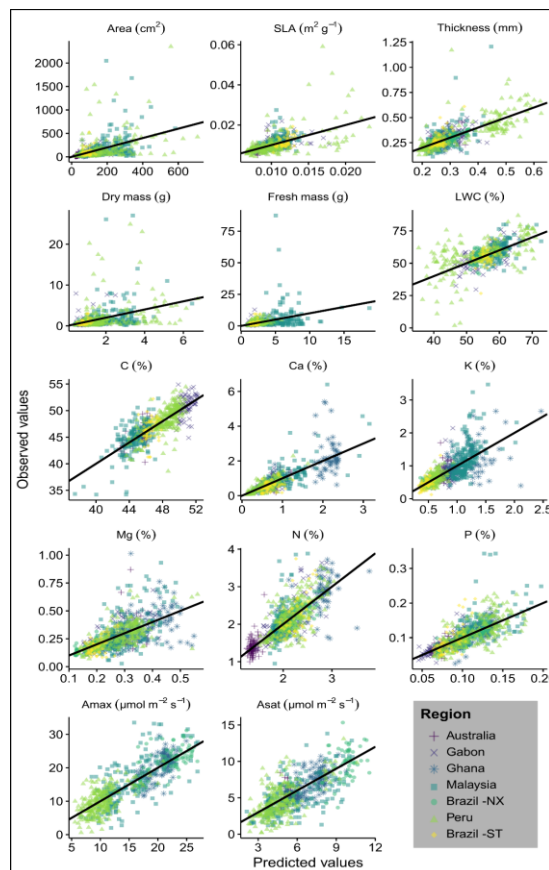

426

427 **Figure 3. Model predictions to the 20% test data from the general model which was fitted with 80% of**
428 **the trait data from across the tropics.** Grey dots are the observed against predicted trait values of the
429 pixel-level (10 × 10 m) community weighted mean traits from the test dataset. The black line shows the
430 1:1 relationship between observed and predicted values. Model prediction accuracy is shown in the top
431 left. Full model results are shown in Table 4.

432

Figure 4. Spatial predictions of trait distributions for a selected subset of plant traits and locations.
The map (middle) shows the locations of vegetation plots that were used during the modelling
framework. The spatial predictions (top and bottom rows) were obtained using the general models
(Table 4) for each of the traits and locations at a 10 × 10 m pixel resolution. The approximated location
of each vegetation plot used is shown as a white square within each spatial prediction map (for
visualisation purposes white squares are not scaled to the plot's real size). Spatial predictions for other
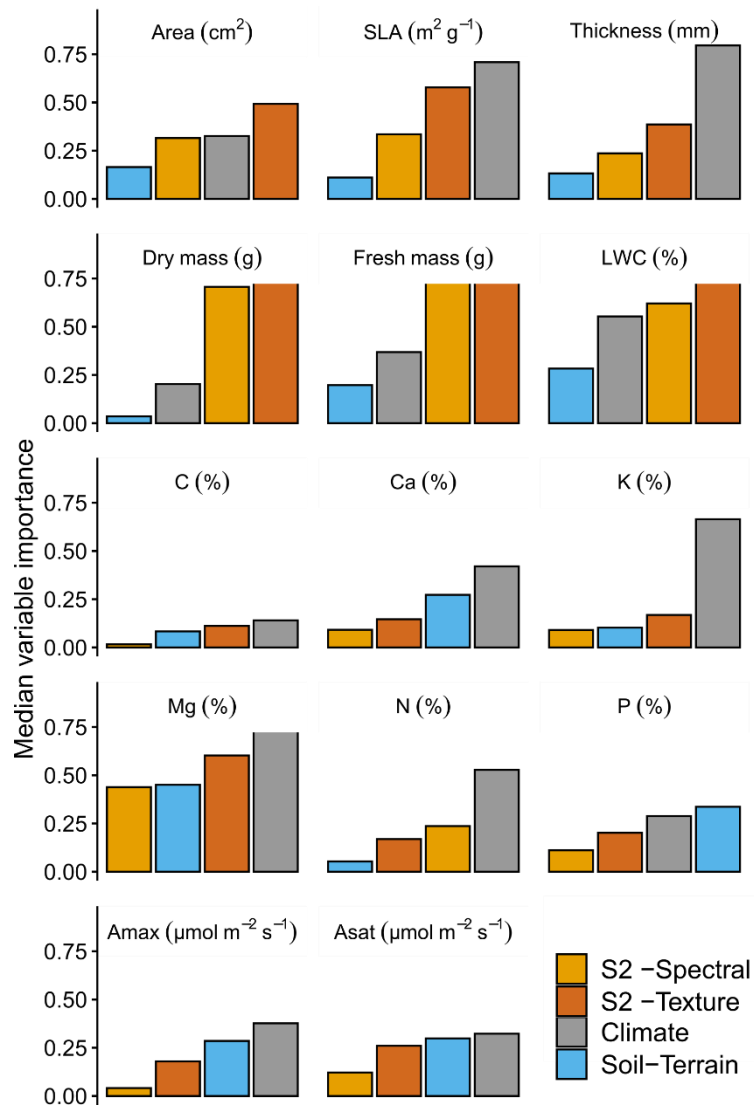traits can be found in Fig. S1-S7.

440

**Figure 5. Models predictions to the 20% test data from the regional models fitted with 80% of the trait
data from each region across the tropics.** Each colour represents an individual regional model and the
coloured symbols are the observed against predicted trait values of the pixel-level (10 × 10 m) community
weighted mean traits from the test dataset. The black line shows the 1:1 relationship between observed
and predicted values. Model prediction accuracy is shown in Table 5. Full model results are shown in Table
S5. Brazil -NX: Nova Xavantina; Brazil -ST: Santarem.

447   3.3 *Importance of spectral remote sensing, climatic and soil data for mapping trait distributions*

448   We included Sentinel-2 band derived reflectance values, vegetation indices, their canopy texture

449   parameters, climatic and soil variables in the general trait models to predict community level traits at the

450   pixel-level (Table 3). The importance of these variables for predicting traits depended on the specific trait

451   being addressed (Fig. 6). In the global model, the remote sensing texture parameters were the first or

452   second major contributor for predicting nine of the functional traits across the tropics (Fig. 6 and Fig. S9).

453   Raw spectral variables were the second most important group for predicting four of such functional traits

454   but often lower in importance than the textural parameters. In the global model, soil and terrain factors

455   were on average some of the most important for predicting photosynthetic traits and foliar P

456   concentration. On average, climatic variables were important for predicting 11 out of 14 functional traits

457   but their contribution was lower for predicting leaf dry and fresh mass and leaf water content (Fig. 6).

458   However, it is evident that a combination of textural, spectral, climatic and soil information is required to

459   obtain the best general model predictions across functional traits and no single variable appears as the

460   most important across all traits (Fig. S9).

461   The local models provided a site-specific view of the most important remote sensing derived

462   variables, environmental and soil conditions for deriving community level traits composition (Fig. S10).

463   Sentinel-2 remote sensing related variables were more important for detecting leaf morphology and

464   nutrient values than environmental and soil related variables in 88% of the trait models (in 75 out of 85

465   possible traits by region combinations). Eighty-one percent of the time (69 location by trait combinations)

466   the canopy texture parameters were more important than the raw spectral reflectance factors. In 5.9%

467   and 4.7% of the possible trait and region combinations, climatic or soil-topography related variables

468   respectively were the most important for detecting community traits (Fig. S10).

Figure 6. Group median variable importance of spectral remote sensing, environmental and soil related variables for determining functional trait predictions in the global model. Variable importance (Y axis) ranges from 0 (no importance) to 1 (highest importance) and represents the decrease in node impurities from splitting on the variable, averaged over all trees and derived from the Out of Bag error, the resulting value has been standardised to a 0-1 scale for comparison purposes. The spectral group (S2 -Spectral) contains the select raw bands from the Sentinel-2 and the vegetation indices; Texture parameters (S2 -Texture) contain the Correlation and Entropy metrics from the grey level co-occurrence matrix obtained from the vegetation indices; Climate contains all climatic variables; Soil-Terrain contains all soil characteristics and slope. All variables are described in Table

4. Discussion

To the best of our knowledge, this is the first study evaluating the ability of Sentinel-2 satellite data to map plant functional traits across tropical ecosystems. 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

484   al., 2019, Soudzilovskaia et al., 2013, Aguirre-Gutiérrez et al., 2019). We have demonstrated that accurate

485   pixel-level (10×10 m) predictions of tropical forest functional trait distributions across the tropics can be

486   generated by making use of extensive *in-situ* collected plant functional traits, geo-located canopy

487   structure, vegetation censuses and high spectral and spatial resolution remote sensing data from the

488   Sentinel-2 satellites.

489   4.1 *Tropical forest trait distributions*

490   Plant functional traits are characteristics that aid species to thrive in their environment or adapt to new

491   conditions. Given such adaptations to specific environments it might be expected that trait variation

492   would be higher in regions that encompass more varied environmental conditions (Enquist et al., 2015).

493   Environmental adaptation is exemplified by the strong variation in values for most traits in Peru and

494   Malaysia. In Peru, the data represent a climatic and altitudinal gradient ranging from the lowland Amazon

495   in the Tambopata National Park at an elevation of 200-225 masl to plots in Acjanaco at above 3000 masl.

496   In Malaysia, the vegetation plots are distributed across a land-use gradient ranging from undisturbed to

497   heavily logged forests (Both et al., 2019). Environmental adaptation may be also shown by the observed

498   differences in trait distributions between different regions across the tropics (e.g. Australia and Gabon;

499   see also Fig. 2). The pixel-based community trait values in the Peruvian transect often extend across much

500   of the range in trait values observed in other locations (Fig. 2). We detected an overall significant

501   difference among locations in terms of morphological, chemical and photosynthetic traits (Table S2). This

502   wide variation in traits suggests the presence of local biotic and abiotic controls of trait distributions and

503   plant species adaptations that may differ among tropical regions. Such differences in trait composition

504   highlight the importance and the challenge of sampling as fully as possible the functional trait diversity

505   across different tropical forests. This is of pivotal importance when comparing forest responses to

506   changing environments across multiple regions. We thus suggest that further field trait survey campaigns

507   across the tropics are needed to improve pantropical trait predictions. As for the local biotic and abiotic

508   controls of trait distributions, for instance, it is widely known that African tropical forests are in general

509   less species diverse than their Asian and South American counterparts but that they have some of the

510   highest biomass carbon storage capacity per unit area (Sullivan et al., 2017). Tropical forests in West Africa

511   are in general drier in comparison to Amazonian tropical forests (Parmentier et al., 2007) and some African

512   regions such as Gabon have experienced increases in temperature and decreases in precipitation over the

513   last 30 years (Bush et al., 2020). Thus, such changes in climatic conditions as those observed in West

514   African tropical forest may also underlie variations in species composition and the locally observed

515   functional trait pool as shown in this study. It is also worth noting that two caveats of the community-

516   weighted mean trait approach may account for part of the unexplained trait variation. First, it makes the

517   assumption of a unique functional optimum in a given environment, while multiple optimal strategies –

518   potentially corresponding to contrasting trait values – could coexist (Laughlin et al., 2018). Secondly, it

519   does not account for the dynamic nature of communities, so that a community weighted mean at a given

520   time point might not encompass the optimum at equilibrium (Laughlin et al., 2018).

521   Morphological and structural traits such as leaf area, fresh and dry mass, leaf thickness, SLA and

522   LWC, represent trade-offs between energy acquisition, consumption and survival and form a main part of

523   the global spectrum of plant functioning (Díaz et al., 2016). Besides investigating the predictability of such

524   plant structural traits, we further analysed the potential for predicting leaf chemistry (C, K, Mg, Ca, N, P)

525   and photosynthesis related traits (A_{max} and A_{sat}). Mapping chemical and photosynthetic traits at a

526   pantropical scale has the potential for increasing our understanding of how photosynthetic capacity shifts

527   across tropical regions and on possible impacts of a changing environment on tropical forests productivity

528   (Guan et al., 2015, Mueller et al., 2014).

529   4.2 *Sentinel-2 remote sensing for mapping community level trait distributions across the tropics*

530   In their pioneering work with hyperspectral imagery and simulated multispectral Sentinel-2 data over

531   Ghana, Laurin et al. (2016) demonstrated that Sentinel-2 imagery could be used to discriminate tropical

532   forest types and map plant functional types. The authors argued that the full band set and vegetation

533   indices derived from the Sentinel-2 would be advantageous for accurately mapping plant functional guilds

534   in the tropics. By using functional trait data collected *in situ* across tropical forests and modelling at high

535   spatial resolution (pixel-level) we show that most of our global trait distribution models present a high

536   predictive power for most traits analysed, with prediction accuracy on the testing datasets being highest

537   for predicting leaf chemical and photosynthetic capacity traits. However, we also show that the local level

538   trait models produced less accurate predictions than the global models, probably as a result of the

539   narrower range of in plant trait values found at the local region in comparison to across the regions,

540   something also shown by Wallis et al. (2019). The prediction accuracy obtained from our models using

541   Sentinel-2 multispectral data is similar and in some cases higher than that shown by recent studies that

542   make use of hyperspectral imagery and other multispectral sensors to map functional traits (Martin et al.,

543   2018, Asner et al., 2017, Asner et al., 2015). For instance our predictions on test data for leaf nitrogen,

544   phosphorus and carbon are comparable or higher than those obtained by other innovative studies in

545   Malaysia (R^2 = 0.46, 0.44 and 0.48 respectively; Martin et al., 2018), Peru (R^2 = 0.48, 0.39 and 0.44; Asner

546   et al., 2015) and temperate forests (R^2 = 0.55, 0.22, 0.46; Nunes et al., 2017), and closely related to those

547   obtained by Wallis et al. (2019) with other multispectral sensor for nitrogen and phosphorus (R^2 = 0.65

548   and 0.65). Specially the work of Asner et al. (2017) has shown how such plant trait predictions (with its

549   inherent accuracies) can be used for other applications such as to guide biodiversity conservation actions.

550   In our approach we resample the 20m spatial resolution bands from the Sentinel-2 to 10m pixels as to

551   work with the highest spatial resolution available for most spectral bands. Such resampling could in

552   principle have an effect on the match between the tree canopies' reflectance signal and the spectral signal

553   from the Sentinel-2 pixel and could thus influence the textural parameters, by for instance, detecting

554   lower heterogeneity.

555   Some of the leaf chemistry we modelled can be directly related to the reflectance obtained from

556   the Sentinel-2 remote sensor in the visible, infrared and red-edge regions which capture the leaf

557   biogeochemistry (Ustin & Gamon, 2010). For instance, it has been shown how carbon and carbon

558   containing metabolites peak in reflectance at around 550 nm (band 3 in the Senitnel-2) and at the lower

559   part of the 702–715 nm (Ely et al., 2019), which would be depicted best by the red-edge band 5 in the

560   Sentinel-2. such spectral behaviour captured by the Sentinel-2 bands contributed to the high prediction

561   accuracy of leaf carbon in our study. Our models show how Sentinel-2 imagery, and especially the canopy

562   texture parameters derived from it, can be especially useful for mapping traits related to leaf chemistry

563   (Fig. 2 and Fig. S9). Moreover, our high predictive accuracy for photosynthetic capacity (A_{max}, A_{sat}) is

564   consistent with studies carried out in other vegetation types (e.g. agroecosystems; Serbin et al., 2015)

565   where a strong association was shown between photosynthesis related traits and the red-edge spectral

566   region. Sentinel-2 has 3 bands over the red-edge spectral region (bands 5, 6, 7) and two over the near

567   infrared (bands 8 and 8a) with different bandwidths, which as shown by Shiklomanov et al. (2016) can be

568   advantageous for detecting foliar nutrients such as leaf N (Schlemmer et al., 2013) , as small differences

569   in wavelength position in different bands may impact their capacity to retrieve canopy trait

570   characteristics. Moreover, the strong relationship between photosynthetic capacity and spectral

571   reflectance can be partly captured from the leaf N signal, as leaf N concentrations are strongly associated

572   with photosynthetic capacity (Reich, 2012, Vincent, 2001). The N reflectance signal is often best obtained

573   in wavebands centred between 440 and 570 nm (Ferwerda et al., 2005).

574   In this study we leverage evidence on covariation among traits to estimate and predict values of

575   traits that have no clear physical effects on spectral reflectance. There is ample evidence of the existence

576   of covariation among plant traits, as for instance between leaf N concentration, specific leaf area and leaf

577   longevity (Walker et al., 2017). Such covariation among traits may in principle also represent covariation

578   in the spectral reflectance patterns across vegetation types (Ma et al., 2019), especially if such individuals

579   vary in leaf structural tissue that drive energy scattering and reflectance (Ollinger, 2011). Such covariation

580   between traits can be helpful for mapping functional trait diversity across large spatial extents that include

581   diverse vegetation types (Townsend et al., 2003, Both et al., 2019). We show that the spectral reflectance,

582   image textural parameters (Entropy and Correlation), climate and soil, are highly relevant for modelling

583   plant trait distributions across the tropics with high prediction accuracy. However, the canopy texture

584   parameters (Entropy and Correlation) are some of the most important for attaining high trait prediction

585   accuracies across plant functional traits (Sarker & Nichol, 2011, Wallis et al., 2019) and differences in

586 spectral, climatic and soil conditions between different regions are key components for improving model

587 predictions across broad spatial extents.

588 Image texture parameters were derived from the vegetation indices that we calculated, which in

589 turn were derived from the raw spectral bands of the Sentinel-2. Thus, the texture metrics besides taking

590 advantage of the high spectral resolution of the sensor also take advantage of its high spatial resolution.

591 Although the raw spectral bands of the Sentinel-2 were not as important for predicting some functional

592 traits as image texture, it is relevant to consider that texture values tend to differ based on the spatial

593 resolution of the underlying data on which they are based. A larger pixel (e.g. Landsat's 30 × 30 m pixels)

594 may thus mask differences in the landscape that could in principle be captured by the Sentinel 10 × 10 m

595 resolution texture generated metrics. This therefore highlights the relevance of Sentinel-2 imagery for

596 functional plant functional trait predictions in comparison to others with lower spectral and spatial

597 resolution. Image texture parameters can help characterise the upper surface of the vegetation, which in

598 our study is composed of varied sets of functional trait characteristics that confer them different spectral

599 responses. When such spectral differences are analysed with grey level co-occurrence matrices, the

600 generated image texture parameters (e.g. entropy and correlation) can help differentiate contrasting

601 vegetation in the landscape. The role of texture parameters for modelling biomass and functional traits

602 has also been recognised by other studies focusing not only on mapping functional traits along elevation

603 gradients but also for estimating standing biomass (Wallis et al., 2019). Moreover, such relevance of

604 texture parameters does not seem to be limited to the spatial resolution of the Sentinel-2 imagery as

605 shown when using high spatial resolution SPOT imagery for modelling forest aboveground biomass

606 (Hlatshwayo et al., 2019) and WorldView-3 for tree species identification (Ferreira et al., 2019), or lower

607 spatial resolution data as that from the Landsat (Wallis et al., 2019). Other added value of the Sentinel-2

608 in contrast to finer spatial resolution satellites (e.g. SPOT and WorldView-3) is its high revisit period, to

609 obtain cloud free imagery, and it's free availability. Moreover, soil properties can be informative when

610 modelling trait distributions across regions in the tropics as they partly drive the plant functional and

611 species compositional turnover (Prada et al., 2017, Asner et al., 2016). In our study different vegetation

612 plots appeared to be on soils with different parent materials resulting in varying cation exchange capacity,

613 pH and soil texture, and thus including differences between sites contributes to increasing the prediction

614 accuracy of trait distributions.

615   Although in the past it was thought not to be possible to map individual plant species or functional

616 traits (Price, 1994, Ustin & Gamon, 2010), the advent of remotely sensed data with high spectral, spatial

617 and temporal resolution has made it possible to extract information on the chemical and structural

618 composition of forest canopies even in highly biodiverse tropical forests. This has been demonstrated with

619 the use of hyperspectral sensors (Asner et al., 2017, Asner et al., 2015, Jetz et al., 2016), which often

620 collect hundreds of spectral bands at very high spatial and spectral resolutions but at relatively small

621 spatial extents and often without temporal replication. More research is needed to disentangle to what

622 extent hyperspectral data offers more information to that offered by the Sentinel-2 sensors for an

623 increased mapping accuracy of functional traits of tropical forests. As shown by Laurin et al. (Laurin et al.,

624 2016), results obtained with simulated Sentinel-2 data are highly comparable to those obtained from

625 hyperspectral imagery for mapping forest types, dominant tree species and functional guilds. Being able

626 to monitor functional traits at high spatial and temporal resolution with multispectral data ranging from

627 the visible to the shortwave infrared across the tropics and with freely available data opens new

628 opportunities for understanding the effects of environmental changes on biodiversity at a local scale. This

629 is because functional traits play a major role in determining ecosystem productivity and functioning, e.g.

630 carbon capture (Díaz et al., 2019, Carmona et al., 2016). Moreover, spatially explicit models of functional

631 traits shift across the tropics can help decipher how ecosystem functioning varies even among tropical

632 areas, providing a cost-effective pathway to identifying regions of high conservation value and hence aid

633 in the creation of locally adequate biodiversity conservation policies. Overall, our findings are of relevance

634 for informing biodiversity monitoring policies under ecosystem change as we show that accurate

635 predictions of relevant plant functional traits can be obtained in high biodiversity areas such as the tropics.

636 Our approach thus facilitates tracking possible shifts in trait distributions and composition across large

637 spatial extents as a response to environmental changes using the Sentinel-2 satellites.

5. Conclusions

Tropical forest ecosystems are witnessing a rapid 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 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

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

664　manuscript.

Declaration of competing interest

666　The authors declare that they have no known competing financial interests or personal relationships that

667　could have appeared to influence the work reported in this paper.

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Figure 1. Diagram summarising the steps followed to assign trait values per Sentinel-2 pixel. 1) First the vegetation plots are defined based on the GEM (Global Environmental Monitoring) dataset and 2) from each vegetation plot the corner coordinates are extracted. 3) From each vegetation plot the XY position of each stem ≥10 cm DBH is extracted and 4) the crown horizontal area is calculated based on the protocol described in the methods section. 5) Then the Sentinel-2 imagery for the study area is processed to level 2A using the ESA SNAP toolbox and 6) the vegetation plot is overlaid in the Sentinel-2 image based on its corner coordinates. In this last step (6) each pixel defines a 'subplot' which is the unit used to calculate the trait community weighted mean based on the crown area of the trees that are contained by that pixel. In 6) n refers to a given tree in a given pixel, trait i represents a given trait and x and y are values for that trait. The image used as an example in step (1) was taken by Jesus Aguirre-Gutierrez over a vegetation plot using a multispectral ALTUM camera mounted on an Inspire 1 drone."

Figure 2. Comparison of trait distributions across tropical regions. The boxplots are based on the pixel-level (10×10 m) community trait values for each trait and region (n=403 for Australia, 449 for Brazil-NX, 302 for Brazil-ST, 464 for Gabon, 620 for Ghana, 976 for Malaysia and 1280 for Peru). Horizontal lines in each boxplot show the median value and vertical lines are the whiskers that extend to the largest value or not further than 1.5 times the inter-quartile range. For some locations information for all traits was not available. For full details in significant differences in mean trait values among locations see Table S4. Brazil -NX: Nova Xavantina; Brazil -ST: Santarem.

Figure 3. Model predictions to the 20% test data from the general model which was fitted with 80% of the trait data from across the tropics. Grey dots are the observed against predicted trait values of the pixel-level (10 × 10 m) community weighted mean traits from the test dataset. The black line shows the 1:1 relationship between observed and predicted values. Model prediction accuracy is shown in the top left. Full model results are shown in Table 4.

Figure 4. Spatial predictions of trait distributions for a selected subset of plant traits and locations. The map (middle) shows the locations of vegetation plots that were used during the modelling framework. The spatial predictions (top and bottom rows) were obtained using the general models (Table 4) for each of the traits and locations at a 10 × 10 m pixel resolution. The approximated location of each vegetation plot used is shown as a white square within each spatial prediction map (for visualisation purposes white squares are not scaled to the plot's real size). Spatial predictions for other traits can be found in Fig. S1-S7.

Figure 5. Models predictions to the 20% test data from the regional models fitted with 80% of the trait data from each region across the tropics. Each colour represents an individual regional model and the coloured symbols are the observed against predicted trait values of the pixel-level (10 × 10 m) community weighted mean traits from the test dataset. The black line shows the 1:1 relationship between observed and predicted values. Model prediction accuracy is shown in Table 5. Full model results are shown in Table S5. Brazil -NX: Nova Xavantina; Brazil -ST: Santarem.

Figure 6. Group median variable importance of spectral remote sensing, environmental and soil related variables for determining functional trait predictions in the global model. Variable importance (Y axis) ranges from 0 (no importance) to 1 (highest importance) and represents the decrease in node impurities from splitting on the variable, averaged over all trees and derived from the Out of Bag error, the resulting value has been standardised to a 0-1 scale for comparison purposes. The spectral group (S2 -Spectral) contains the select raw bands from the Sentinel-2 and the vegetation indices; Texture parameters (S2 -Texture) contain the Correlation and Entropy metrics from the grey level co-occurrence matrix obtained from the vegetation indices; Climate contains all climatic variables; Soil-Terrain contains all soil characteristics and slope. All variables are described in Table 3.

Table 1. Collection details for vegetation plots and plant functional traits. A total of 2434 individual trees were sampled for functional traits.

Location	Species sampled for traits	Plot code	Size (ha)	Centroid coordinates		Date of collection	
				X	Y	Vegetation census	Traits
Australia	81	AEP-02	0.5	145.586	-17.146	2011	June-September 2015
		AEP-03	0.5	145.592	-17.088		
		DRO-01	0.9	145.430	-16.103		
		ROB-06	1	145.630	-17.121		
Ghana	63	ANK-01	1	-2.696	5.268	2013	October-March 2015/2016gramm
		ANK-03	1	-2.692	5.271		
		BOB-01	1	-1.339	6.691	2015	
		BOB-02	1	-1.319	6.704		
Gabon	41	LPG-01	1	11.574	-0.174	2014	February-March 2017
		LPG-02	1	11.615	-0.216		
		MNG-04	1	9.324	0.577	2016	
Brazil -NX	64	NXV-01	1	-52.352	-14.708	2015	March-May 2014
		NXV-02	1	-52.351	-14.701		
		VCR-02	1	-52.168	-14.832		
		NXV-10-1	0.1	-52.353	-14.713		
		NXV-10-2	0.1	-52.352	-14.713		
		NXV-10-3	0.1	-52.351	-14.713		
		NXV-10-4	0.1	-52.349	-14.713		
		NXV-10-5	0.1	-52.346	-14.713	2014	
		NXV-10-6	0.1	-52.349	-14.712		
		NXV-10-7	0.1	-52.348	-14.711		
		NXV-10-8	0.1	-52.347	-14.711		
		NXV-10-9	0.1	-52.347	-14.711		
		NXV-10-10	0.1	-52.346	-14.712		
Brazil -ST	136	261-10	0.25	-55.005	-3.019	2014	

Country							
		261-9	0.25	-55.015	-3.040		
		363-6	0.25	-54.956	-3.337		August-September 2015
		363-3	0.25	-54.963	-3.297		
		363-7	0.25	-54.961	-3.321		
		ESP-01	1	-71.595	-13.176		
		PAN-02	1	-71.263	-12.650		
		SPD-01	1	-71.542	-13.047	2013	
		SPD-02	1	-71.537	-13.049		
Peru	159	TRU-04	1	-71.589	-13.106		April-November 2013
		WAY-01	1	-71.587	-13.191		
		ACJ-01	1	-71.632	-13.147		
		PAN-03	1	-71.274	-12.638	2014	
		TAM-05	1	-69.271	-12.830		
		TAM-06	1	-69.296	-12.839		
		SAF-01	1	4.732	117.619		
		SAF-02	1	4.739	117.617		
		SAF-03	1	4.691	117.588		
Malaysia	283	SAF-04	1	4.765	117.700	2016	July-December 2015
		DAN-04	1	4.951	117.796		
		DAN-05	1	4.953	117.793		
		MLA-01	1	4.747	116.970		
		MLA-02	1	4.754	116.950		

Brazil -NX: Nova Xavantina; Brazil -ST: Santarem; Malaysia: Malaysian Borneo.

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Table 2. Description of plant functional traits collected across the tropics and their relevance under a changing environment.

Trait	Abbreviation	Units	Description	Relevance	References*
Leaf area	Area	cm^2	One-sided area of the leaf	Higher leaf area could result in higher levels of light capture and photosynthetic activity.	(Walker et al., 2014, Wright et al., 2004, Juneau & Tarasoff, 2012, Díaz et al., 2016, Hawthorne, 1995, Chave et al., 2006, Huang et al., 2019)
Specific leaf area	SLA	$m^2\,g^{-1}$	One-sided area of a leaf divided by dry mass	Relevant for photosynthetic capacity, light capture, water loss, net assimilation rate, leaf life span.	
Leaf thickness	Thickness	mm	Thickness of a fresh leaf	Trade-off between decreasing water transpiration at the expense of higher construction investment and probably lower photosynthetic efficiency in thicker leaves.	
Leaf nitrogen content	N	%	Content per unit dry leaf mass	Nutrient relevant for metabolic reactions, including light capture, related to photosynthetic capacity and growth. Restricted availability of some nutrients may limit plant carbon acquisition and growth.	
Leaf phosphorus content	P	%			
Leaf carbon content	C	%			
Leaf calcium content	Ca	%			
Leaf potassium content	K	%			
Leaf magnesium content	Mg	%			
Leaf water content	LWC	%	Amount of water in the leaf relative to its dry and fresh mass	Leaf mass is a proxy of leaf biomass investment which may vary depending on environmental conditions and phenology of species. It has been considered relevant for photosynthetic potential.	
Leaf dry mass	Dry mass	g	Mass of a dry leaf		
Leaf fresh mass	Fresh mass	g	Mass of a fresh leaf		
A_{max}	A_{max}	$\mu mol\ m^{-2}\,s^{-1}$	Light-saturated maximum rates of net photosynthesis at saturated CO_2 (2000 ppm CO_2)	Indicate the maximum CO_2 assimilation and are thus indices of leaf photosynthetic capacity	
A_{sat}	A_{sat}	$\mu mol\ m^{-2}\,s^{-1}$	Light-saturated rates of net photosynthesis at ambient CO_2 concentration (2000 ppm CO_2)		

*References are not exhaustive.

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Table 3. Spectral remote sensing, environmental and soil related variables used during the modelling protocol. All climatic variables but slope were calculated using a climatology of 30 years (1986-2015). All soil variables were calculated for the top 30cm soil layer. Sentinel-2 band wavelengths (nm) are given in parenthesis after the band name.

Type	Variable	Description	References
RS	B2 (490), B3 (560), B4 (665), B8 (842)	Sentinel-2 bands with spatial resolution of 10m	
	B5 (705), B6 (740), B7 (783), B11 (1610), B12 (2190)	Sentinel-2 bands with spatial resolution of 20m	www.esa.int
	MCARI	Modified Chlorophyll Absorption in Reflectance Index	(Daughtry et al., 2000)
	MSAVI2	Modified Soil Adjusted Vegetation Index 2	(Qi et al., 1994)
	NDRE	Normalized Difference Red edge Index	(Barnes et al., 2000)
	Texture	Entropy, calculated for vegetation indices	(Haralick et al. 1973)
		Correlation, calculated for vegetation indices	
Climate	MCWD	Mean annual climatic water deficit	
	MATmax	Mean maximum annual temperature	(Abatzoglou et al. 2018)
	SM	Soil moisture as a water balance indicator	
	SRAD	Downward Solar Radiation	
Soil-Terrain	eCEC	Cation Exchange Capacity (mmol$^+$ /kg^{-1})	Plot level soil data from the Global Environmental Monitoring (GEM) database
	pH	Soil pH (H2O solution)	
	Clay (%)	Amount of clay (weight %)	
	Sand (%)	Amount of sand (weight %)	
	Slope	Terrain slope (30 m resolution)	(Farr et al. 2007)

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Table 4. Statistical results on the test data (20% of full dataset) for the global trait distribution models. The prediction accuracy is shown by the R^2 score.

Type	Trait	MAE	RMSE	R^2
Morphological and structural	Area (cm^2)	28.32	39.854	0.43
	Dry mass (g)	0.349	0.48	0.27
	Fresh mass (g)	0.799	1.075	0.26
	SLA (m^2 g^{-1})	0.001	0.001	0.50
	Thickness (mm)	0.034	0.046	0.52
Chemistry	LWC (%)	3.718	4.886	0.36
	C (%)	1.237	1.615	0.70
	Ca (%)	0.14	0.204	0.64
	K (%)	0.133	0.186	0.63
	Mg (%)	0.055	0.075	0.46
	N (%)	0.23	0.3	0.59
	P (%)	0.015	0.02	0.59
Photosynthetic	Amax (μmol m^{-2} s^{-1})	2.89	3.937	0.67
	Asat (μmol m^{-2} s^{-1})	1.297	1.734	0.55

MAE: Mean Absolute Error; RMSE: Root mean square error.

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Table 5. Prediction accuracy (R^2) on the testing data among regions (shaded Region mean R^2 column) and functional traits (shaded Trait mean R^2 row). Not shaded values in the table show the prediction accuracy (R^2) on the test data per region and trait.

Location	P (%)	Amax (μmol m^{-2} s^{-1})	Ca (%)	N (%)	Thickness (mm)	Asat (μmol m^{-2} s^{-1})	Mg (%)	C (%)	SLA (m^2 g^{-1})	LWC (%)	K (%)	Dry mass (g)	Area (cm^2)	Fresh mass (g)	Region mean R^2
Australia	0.21	-	0.33	0.17	0.21	0.03	0.12	0.34	0.25	-	0.06	-	0.35	-	*0.21*
Brazil -NX	0.68	0.42	0.49	0.52	0.66	0.52	0.46	-	0.54	0.07	0.07	0.38	0.08	0.31	*0.40*
Brazil -ST	0.47	-	0.15	0.30	0.42	-	0.28	0.07	0.29	0.05	0.29	0.25	0.04	0.18	*0.23*
Gabon	0.60	-	0.39	0.50	0.23	-	0.52	0.22	0.15	0.38	0.24	0.22	0.11	0.11	*0.31*
Ghana	0.47	0.49	0.53	0.52	0.22	0.36	0.15	-	0.14	-	0.23	-	0.29	-	*0.34*
Malaysia	0.34	0.48	0.50	0.27	0.31	0.36	0.31	0.38	0.06	0.24	0.28	0.07	0.11	0.03	*0.27*
Peru	0.49	0.36	0.69	0.44	0.64	0.38	0.46	0.47	0.32	0.34	0.30	0.09	0.18	0.20	*0.38*
Trait mean R^2	*0.47*	*0.44*	*0.44*	*0.39*	*0.38*	*0.33*	*0.33*	*0.30*	*0.25*	*0.22*	*0.21*	*0.20*	*0.17*	*0.17*	

976   - :no data available; Brazil -NX: Nova Xavantina; Brazil -ST: Santarem.

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