Functional susceptibility of tropical forests to climate change

Jesús Aguirre-Gutiérrez [1,2], Erika Berenguer [1, 38], Imma Oliveras [1], David Bauman [1, 2, 4], Jose Javier Corral-Rivas [5], Maria Guadalupe Nava-Miranda [5], Sabine Both [6], Josué Edzang Ndong [7], Fidèle Evouna Ondo [7], Natacha N'ssi Bengone [8], Vianet Mihinhou [8], James W. Dalling [9, 10], Katherine Heineman [10], Axa Figueiredo [11], Roy González-M [12], Natalia Norden [12], Ana Belén Hurtado-M [12], Diego González [12], Beatriz Salgado-Negret [13], Simone Matias Reis [1, 14], Marina Maria Moraes de Seixas [15], William Farfan-Rios [16, 17, 18], Alexander Shenkin [1], Terhi Riutta [1, 19], Cécile A. J. Girardin [1], Sam Moore [1], Kate Abernethy [20, 21], Gregory P. Asner [22], Lisa Patrick Bentley [23], David F.R.P. Burslem [24], Lucas A. Cernusak [25], Brian J. Enquist [26], Robert M. Ewers [27], Joice Ferreira [28], Kathryn J. Jeffery [27], Carlos A. Joly [29], Ben Hur Marimon-Junior [14], Roberta E. Martin [22], Paulo S. Morandi [14], Oliver L. Phillips [30], Amy C. Bennett [30], Simon L. Lewis [30, 31], Carlos A. Quesada [32], Beatriz Schwantes Marimon [14], W. Daniel Kissling [33], Miles Silman [34], Yit Arn The [35], Lee J. T. White [8, 20, 21], Norma Salinas [1, 36], David A. Coomes [37], Jos Barlow [38], Stephen Adu-Bredu [39], Yadvinder Malhi [1]

[1] Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK
[2] Biodiversity Dynamics, Naturalis Biodiversity Center, Leiden, The Netherlands
[3] Smithsonian Environmental Research Center, Edgewater, Maryland 21037, USA.
[4] AMAP (Botanique et Modélisation de l'Architecture des Plantes et des Végétations), Université de Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France.
[5] Facultad de Ciencias Forestales, Universidad Juárez del Estado de Durango, México
[6] Environmental and Rural Science, University of New England, Armidale, 2351 NSW, Australia
[7] Agence Nationale des Parcs Nationaux, BP20379, Libreville, Gabon
[8] Ministère des Eaux, des Forêts, de la Mer et de L'Environnement, Libreville, Gabon
[9] Smithsonian Tropical Research Institute, Panama City, Republic of Panama
[10] Department of Plant Biology, University of Illinois, Urbana, IL, USA
[11] National Institute of Amazonian Research – INPA. C.P. 2223, 69080-971, Manaus, AM, Brazil
[12] Programa Ciencias Básicas de la Biodiversidad, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Cr. 1 # 16-20, Bogotá, Colombia
[13] Departamento de Biología, Universidad Nacional de Colombia, Bogotá, Colombia
[14] Laboratório de Ecologia Vegetal (LABEV), Universidade do Estado de Mato Grosso, Nova Xavantina, Brazil
[15] Embrapa Amazônia Oriental, Trav. Dr. Enéas Pinheiro, s/n, CP 48, 66095-100 Belém, PA, Brazil
[16] Living Earth Collaborative, Washington University in Saint Louis, St. Louis, MO, USA
[17] Center for Conservation and Sustainable Development, Missouri Botanical Garden, St. Louis, MO, USA
[18] Herbario Vargas (CUZ), Escuela Profesional de Biología, Universidad Nacional de San Antonio Abad del Cusco, Cusco, Peru
[19] College of Life Sciences, University of Exeter, Exeter, UK
[20] Institut de Recherche en Écologie Tropicale, Libreville, Gabon.
[21] Biological and Environmental Sciences, University of Stirling, Stirling, UK.
[22] Center for Global Discovery and Conservation Science, Arizona State University, Tempe, AZ, United States
[23] Department of Biology, Sonoma State University, 1801 East Cotati Avenue, Rohnert Park, CA 94928, USA
[24] School of Biological Sciences, University of Aberdeen, Aberdeen, UK
[25] College of Science and Engineering, James Cook University, Cairns, Qld, 4878 Australia
[26] Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona, USA
[27] Department of Life Sciences, Imperial College London, Ascot, UK
[28] MCT/Museu Paraense Emílio Goeldi, Av. Magalhães Barata376, São Braz, 66040-170, Belém, PA, Brazil
[29] Universidade Estadual de Campinas, Instituto de Biologia, Departamento de Biologia Vegetal, Campinas, São Paulo, Brazil
[30] Ecology and Global Change, School of Geography, University of Leeds, Leeds, UK
[31] Department of Geography, University College London, London, UK
[32] Coordenação de Dinâmica Ambiental, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil
[33] Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, Amsterdam, The Netherlands
[34] Department of Biology, Wake Forest University, Winston-Salem, NC 27109, USA
[35] School of Natural and Environmental Sciences, Newcastle University, Newcastle Upon Tyne, UK
[36] Sección Química, Pontificia Universidad Católica del Perú, Avenida Universitaria 1801, San Miguel, Lima 32, Peru
[37] Department of Plant Sciences and Conservation Research Institute, University of Cambridge, Cambridge CB2 3QZ, UK
[38] Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK
[39] CSIR-Forestry Research Institute of Ghana, University P.O. Box 63, Kumasi, Ghana

Corresponding author : Jesús Aguirre-Gutiérrez; jesus.aguirregutierrez@ouce.ox.ac.uk

ABSTRACT

Tropical forests are some of the most biodiverse ecosystems in the world, yet their functioning is threatened by anthropogenic disturbances and climate change. Global actions to conserve tropical forests could be enhanced by having local knowledge on the forests functional diversity and functional redundancy as proxies for their capacity to respond to global environmental change. Here, we create estimates of plant functional diversity and redundancy across the tropics by combining a dataset of 16 morphological, chemical and photosynthetic plant traits sampled from 2461 individual trees from 74 sites distributed across four continents, together with local climate data for the last half century. Our findings suggest a strong link between climate and functional diversity and redundancy with the three trait groups responding similarly across the tropics and climate gradient. We show that drier tropical forests are overall less functionally diverse than wetter forests and that functional redundancy declines with increasing soil water and vapour pressure deficits. Areas with high functional diversity and high functional redundancy tend to better maintain ecosystem functioning, such as aboveground biomass, after extreme weather events. Our predictions suggest that the lower functional diversity and lower functional redundancy of drier tropical forests, in comparison to wetter forests, may leave them more at risk of shifting towards alternative states in face of further declines in water availability across tropical regions.

MAIN TEXT

Tropical forests are amongst the most biodiverse ecosystems on the planet [1], they harbour more than 50% of global biodiversity including between 67-88% of all tree species and are responsible for more than 30% of terrestrial productivity [2, 3]. Given the large distribution of tropical forests on earth, small but widespread changes in their tree community composition can have global impacts in the removal of CO_2 from the atmosphere [4]. Tropical forests are also essential to help mitigate the effects of climate change, as intact tropical forests are carbon sinks of around 1.26 Pg C yr^{-1} [5]. However, carbon storage can be negatively impacted by changes in water availability [6]. For example, the Amazon forest, which contains close to 123 Pg C of above and belowground biomass[7] lost 1.2-1.6 Pg C [8] – the equivalent of 1% of its total carbon stocks [9] – during the extreme drought of 2005 and it is now suggested to be a carbon source [10]. Besides impacting the carbon storage capacity of forests, changes in climate mean states and variability are key potential drivers of biodiversity declines around the world [11, 12]. Understanding how climate may affect tropical forests' capacity to store carbon thereby requires evaluation of how plants respond to drought stress. To do so, the Maximum Climatic Water Deficit (MCWD) and Vapour Pressure Deficit (VPD) are two fundamental proxies of hydric stress for plants [13, 14], with increases in VPD leading to greater plant transpiration stress [15, 16] (but see Costa et al.[17] for a review on the water table depth as another highly relevant metric under drought). Although it has been generally expected that communities historically adapted to high MCWD and VPD should be better adapted to increasing drier conditions, it could also be that such communities might already be at their climatic physiological limits and thus further droughts may increase water stress to such an extent that they are driven towards alternative states [18, 19]. To disentangle these two possibilities, evaluating functional trait composition may provide clues on their possible historical adaptations to water stress

100 conditions [20, 21]. Although changes in MCWD and VPD are prominent features of climate
101 change across tropical forests, detailed analyses that show their relationship with plant
102 morphology/structure, leaf chemistry and photosynthesis related traits across climatic and
103 elevation gradients at a pantropical scale remain scarce. Thus, understanding the functional-
104 climatic gradients relationship is key to disentangling the long-term role of tropical forests for
105 mitigating climate change and is crucial for deciphering the resilience of key ecosystem
106 properties such as diversity and carbon stocks under a changing climate.

107 Ecosystem resilience may increase through different pathways, for example, by
108 species having the same traits that affect a given ecosystem process, such as carbon capture,
109 but different traits to respond to environmental changes, such as droughts. Arguably
110 functional traits may respond differently to diverse drivers of change (e.g. temperature or
111 precipitation change) which may be reflected in trait diversity but not necessarily in species
112 richness [22] given that there is not always a tight relation between species richness and
113 functional trait diversity [23, 24]. According to the biodiversity-ecosystem functioning insurance
114 hypothesis [25], ecosystem functions should be less affected by a changing environment when
115 1) the ecosystem possesses both high functional diversity (e.g. large range of trait values; FD),
116 2) but also a wide set of species with similar functional characteristics [23] conferring the system
117 with high functional redundancy (FRed) [26, 27]. Thus, in communities with high functional
118 diversity and high functional redundancy, the loss of a given species is less likely to result in
119 the disruption of the ecosystem function [28], as other species will probably continue carrying
120 out the same functions, compensating the lost species [29, 30]. High FD and high FRed may
121 enhance the temporal stability of ecosystem functions (e.g., biomass productivity) [31] and thus
122 provide a buffering effect against environmental changes [25], conferring higher resilience.
123 Nonetheless, these hypotheses have never been tested across the tropics, and the role of FD
124 and FRed for maintaining the tropical forests ability to capture and store carbon remains to
125 be tested and quantified at this global scale. Quantifying the FD and FRed is crucial to
126 advancing our understanding of the resilience of these forests in the Anthropocene.

127 Here, we address this knowledge gap by combining a new pantropical dataset of 16
128 plant traits related to morphology/structure (leaf area, leaf dry and fresh mass, leaf dry
129 matter content, leaf water content, specific leaf area, leaf thickness, wood density), foliar
130 nutrients (leaf calcium, potassium, magnesium, nitrogen and phosphorus content) and
131 photosynthesis (photosynthetic rate, dark respiration). These plant traits are hypothesised to
132 be of importance for tropical forests to adapt or respond to a drying climate (see Table S1 for
133 a description of their hypothesised importance). The importance of such traits relies on their
134 influence on the capacity of species to capture energy for growth and conserve resources (e.g.
135 water) for survival under stressful environmental conditions, such as droughts, and have been
136 shown to change in response to a changing climate [32, 33, 34]. The plant traits were collected
137 from 2461 individual trees belonging to 1611 species distributed across 74 plots that
138 contained 32,464 individual trees equal to or greater than 10 cm diameter at breast height
139 from 2497 species (Extended Data Figure 1, Table S2, See Methods). The vegetation plots are
140 free of obvious local anthropogenic disturbance (i.e., far from forest edges, and no evidence

141 of logging or fires) and cover a wide range of the climatic conditions found across tropical and
142 subtropical dry and moist broadleaf forests (Extended Data Figure 2; Extended Data Figure 3).
143 This dataset was combined with estimates of MCWD and VPD from 1958-2017 and of soil
144 chemistry (cation exchange capacity) and texture (clay content) (Extended Data Figure 3).

145 We address three fundamental questions: 1) Does the long-term mean ambient water
146 stress environment (MCWD and VPD) or its changes (ΔMCWD and ΔVPD) over the last half-
147 century determine current functional diversity (Extended Data Figure 3)? First, we examine
148 the relationship between the functional diversity (here calculated as functional dispersion [35])
149 and redundancy levels across tropical regions. The relationship between changes in climate and
150 long-term FD and FRed can be understood as a proxies of the effects of climate change on the
151 functional diversity levels of the ecosystem given that we do not quantify their direct effect on
152 changes in FD and FRed. 2) What is the spatial distribution of functional diversity and
153 redundancy across tropical forests? 3) Is there a relationship between functional diversity or
154 functional redundancy and one metric of ecosystem functioning (above ground biomass)
155 during extreme drought events? We expect that: 1) Communities that are found in drier
156 climate conditions and that have experienced stronger decreases in water availability across
157 the last half century will be less functionally diverse but may be more functionally redundant
158 as a result of climate filtering for better adapted traits than communities in less extreme
159 conditions such as wetter forests; 2) Across the full spatial distribution of tropical forests,
160 tropical wet forests communities, which are more species-rich than drier tropical forests,
161 have higher functional diversity given a broader set of ecological strategies available as a
162 result of more stable and favourable climate; 3) There is a positive relationship between
163 functional diversity, functional redundancy and ecosystem functioning (i.e. above ground
164 biomass) as more functionally diverse and redundant communities may attenuate the
165 negative effects of a changing climate and may be therefore be considered to be more
166 resilient.

167 **Results**

168 **Functional diversity, redundancy and forest susceptibility**

169 Fundamental knowledge on the climate-FD and climate-FRed relationships across tropical
170 forest ecosystems has been missing. To fill this knowledge gap, we calculated, for vegetation
171 plots distributed across the tropics, the FD and FRed for morphological/structural, leaf
172 chemistry and photosynthetic traits that are hypothesised to be of importance for tropical
173 forests to respond to a drying climate. The selected traits play a role in plant establishment,
174 growth and/or survival [20, 21, 36] (Table S1). Then, we investigated variation in FD and FRed
175 across tropical forests by modelling their relation with MCWD, VPD and their interaction,
176 the ΔMCWD and ΔVPD and their interaction (see Methods section), where more positive
177 values in MCWD and VPD reflect stronger water deficits. In our models, we also accounted
178 for soil characteristics (see Methods) such as texture (Clay %) and chemistry (cation
179 exchange capacity, CEC). Soils high in clay content may have high water holding capacity
180 over longer periods of time which is important for vegetation under drought conditions [32].
181 Moreover, it is widely acknowledged that tropical forests in drier regions are generally
182 associated with soils that are richer in nutrients in comparison to wet tropical forests [37]. The

183 feedbacks between soil–rainfall and their effects on plant distributions could be disrupted
184 under a changing climate and therefore have adverse effects on the functioning of tropical
185 forest ecosystems. A principal component analysis (PCA) of climate conditions (long-term
186 trends and recent changes) indicated that the first two axes explained 71.3% of the variation
187 among plots (Extended Data Figure 4a) and the first two axes of the soil-based PCA (with soil
188 chemistry and texture) account for 83% of the variation among plots (Extended Data Figure
189 4b).

190 Based on the long-term mean MCWD, our results show that drier tropical forests are
191 clearly morphologically less diverse (*slope*= -0.18 [-0.31, -0.05], median and 90% highest
192 density intervals) than wet forests (Table S2). The effect of MCWD on morphological FD was
193 modulated by atmospheric VPD, where the FD of communities with low VPD (blue fitted line
194 in Fig. 1a) strongly decreased as MCWD increased, but FD tended to increase with MCWD in
195 communities where VPD was high (red fitted line in Fig. 1a). Morphological/structural FD
196 increased linearly with increases in clay content (*slope*= 0.08 [0.01, 0.16]; Fig. 1b). Foliar
197 nutrients FD also tended to decrease towards drier forests (*slope*= -0.15 [-0.24, -0.05]; Fig.
198 1c). Overall, foliar nutrients FD increased towards communities with higher soil CEC (*slope*=
199 0.17 [0.12, 0.22]; Fig. 1d), while photosynthetic FD also increased towards areas that
200 experienced stronger increases in MCWD (*slope*= 0.14 [0.02, 0.25]; Fig. 1e) but did not
201 respond to the long-term mean MCWD. For the trait groups (morphology, nutrients,
202 photosynthesis) for which a clear relationship with climate and soil was found (90% Highest
203 Density Interval, HDI, of the posterior distribution does not overlap 0; Table S3), the models
204 explained (R^2) 44%, 75% and 75% of the variation in morphology/structure, nutrients and
205 photosynthetic FD, respectively.

206 The models of FRed as a function of climate and soil explained 53%, 73% and 33% of
207 the variation in morphology/structure, nutrients and photosynthetic functional redundancy
208 respectively across the tropical forest. The FRed models (Table S3) showed that redundancy
209 of morphological/structural (*slope*= -0.06 [-0.11, -0.01]) traits declines with higher long-term
210 mean MCWD and that photosynthetic FRed declines as long-term VPD increases (*slope*= -0.11
211 [-0.23, -0.01]; Fig. 2a and Fig. 2e respectively). While redundancy of morphological/structural
212 and foliar nutrients traits decreased with increases in MCWD through time (ΔMCWD) in areas
213 that also increased the most in VPD (ΔVPD; Fig. 2b and Fig. 2d red fitted line) the opposite
214 was predicted for areas that experienced larger increases in MCWD but smallest increases in
215 VPD (Fig. 2b and Fig. 2d blue fitted line). FRed of morphological/structural traits also tended
216 to decrease with increases in soil clay content (*slope*= -0.04 [-0.07, -0.003]; Fig. 2c).

217 **Mapping functional diversity and functional redundancy**

218 Based on our understanding of the relation of FD and FRed of morphological/structural, leaf
219 nutrients and photosynthetic trait groups with climate and soil (Fig. 1 and Fig. 2), and to fill
220 the knowledge gap on the pantropical distribution of functional diversity and redundancy we
221 created pantropical maps of both FD (Fig. 3) and FRed (Fig. 4) distribution. With our map
222 predictions we aim to uncover the locations of forests with potentially higher and lower
223 resilience to a changing climate. To this end, we used the statistical models built above (Table
224 S3) to predict FD and FRed across the pantropical dry and moist broadleaf forests, for which

our field sampling locations have a wide representation of the climatic conditions across those tropical forests (Extended Data Figure 2; Extended Data Figure 5 and Extended Data Figure 6). Based on the FD and FRed predictions, we calculated the percent area that had 'low', 'intermediate' and 'high' diversity and redundancy for each trait group (see methods). We also created bivariate maps that combine the FD and FRed scores in a single map to visualise where FD and FRed are both maximized and minimized across the tropics (Fig. 5). We further developed the same statistical models as described above but by removing from the analysis all plots from each continent (Asia and Australia out at the same time) to determine which regions have higher contribution to determining the observed spatial predictions (those of Fig. 5). For morphology/structure, foliar nutrients and photosynthesis we found high correlations between the bivariate maps developed with the full dataset and when Asia and Australia were left out (r= 0.96, 0.82 and 0.94; Extended Data Figure 7, Extended Data Figure 8, and Extended Data Figure 9 respectively; Also Supplementary Figure 1). For morphology/structure and photosynthesis there were also high correlations between the patterns based on the full dataset and those based on the one where Africa was removed (r= 0.92 and 0.93 respectively; Extended Data Figure 7 and Extended Data Figure 9 respectively). Low correlations between the maps generated with the full dataset and those based on smaller datasets depict those regions contributed significantly for the full model predictions (Supplementary Figure 1), which is also correlated to the number of observations available for each continent (Table S2 and Table S4).

As predicted, our results show that wetter tropical forests tend to be more functionally diverse than drier tropical forests, especially for morphological/ structural traits and foliar nutrients traits, but also more functionally redundant for foliar nutrients and photosynthetic traits than drier tropical forests (Fig. 3 and Fig. 4). While FD levels across our sampling locations are not significantly related to their taxonomic diversity (number of species, genera and families; $P\text{-}val$ > 0.05), $FRed_{NU}$ appears to be positively correlated to taxonomic diversity ($P\text{-}val$ < 0.05; Table S5). Our results suggest that given the lower FD (Fig. 3) and FRed (Fig. 4) of drier tropical forests for most of the analysed trait groups, these forests may be more at risk in the face of further water availability reductions.

The bivariate predictions maps combining FD and FRed (Fig. 5) highlight how wet tropical regions, such as the Western Amazon, Central Africa, and several regions in South East Asia maintain high functional diversity and high functional redundancy of morphological/structural (FD_{MO} max=3.5, $FRed_{MO}$ max=1.5) and leaf nutrients traits (FD_{NU} max=2.5, $FRed_{NU}$ max=1.5), and also in several wet regions for leaf photosynthetic traits (FD_{PHO} max=2.5, $FRed_{PHO}$ max=1.5). We expect these wet tropical regions to be more resilient to a changing climate given their large combined FD (Fig. 3) and FRed (Fig. 4). To evaluate which are the different levels FD and FRed across tropical and subtropical dry and moist broadleaf forests, we distinguished low, intermediate and high scores based on the range of the spatial predictions (Table S6; see methods section). We predicted that only 2.4% of the tropical and subtropical dry and moist broadleaf forests have high morphological FD and 2.3% high morphological FRed. In contrast, the drier tropical forests show a functional diversity of morphological/structural traits that reach only about half of that in the wet tropics (FD_{MO} min=~1.5) and some of the lowest FRed (<0.6). From the total area of tropical and subtropical

268 dry and moist broadleaf forests, 30.4% shows low morphological/structural FD and 5.5% have
269 low morphological/structural FRed. Moreover, FD and FRed of leaf nutrients traits are lowest
270 to intermediate across the tropical dry forest regions, such as the southernmost parts of the
271 forests in Brazil, in parts of Mexico, and West Africa (Fig. 3 and Fig. 4).

272 While 14.8% of the forest area has low foliar nutrients FD and 3.7% low FRed, 14.1%
273 shows high nutrients FD and 7% high FRed. Drier tropical forests in Western Mexico, the
274 southern forest portion of Brazil and parts of central and West Africa show intermediate to
275 high photosynthetic FD (max=2.5) but they also tend to show intermediate to low levels of
276 FRed ($FRed_{Pho}$ min=0.3). However, photosynthesis FD and FRed do not seem to have a clear
277 difference between wetter and drier forests. About 36.8% of the tropical and subtropical dry
278 and moist broadleaf forest area is predicted to have low photosynthetic FD and 16.9% to have
279 low photosynthetic FRed, while only 2.4% is expected to have high photosynthetic FD and
280 6.8% high photosynthetic FRed. Overall, a large amount of forest area has intermediate
281 photosynthetic FD and/or FRed levels (60.7% and 76.3% respectively). The bivariate FD-FRed
282 predictions show that most tropical forests across West Amazon and Central Africa reach
283 some of the highest predicted morphological and photosynthesis FD and FRed, while a smaller
284 area of western South America reaches some of the highest predicted nutrients FD and FRed
285 (Fig. 5). In general forests in drier areas show lower FD and FRed combined scores (grey
286 colour; Fig. 5 bottom panel) for the three functional groups (morphology/structure, nutrients
287 and photosynthesis) but this is more evident for the photosynthesis traits (Fig. 5).

Linking functional diversity, redundancy and resilience

289 We tested to what extent the long-term FD and FRed model predictions (Fig. 3 and Fig. 4),
290 could capture the functioning of tropical forests after climatic disturbances such as El Niño
291 events. By obtaining the above ground biomass data (AGB) from a set of 86 vegetation plots
292 in tropical Africa before and after the 2015 El Niño event [38], we calculated the change in
293 aboveground biomass (ΔAGB) and modelled it as a function of the predicted long-term FD
294 and FRed map scores. Bennett et al. [38] did not detect a strong decline in AGB for most forests
295 they analysed after the 2015 El Niño event. We show that, on average, smaller decreases or
296 larger increases in AGB (Fig. 6; Table S7) can be found at locations that are predicted to have
297 higher long-term FD and FRed of morphology/structure (*slope*= 1.97, [0.28, 3.65]; Fig. 6a) and
298 nutrients traits (*slope*= 2.94, [0.25, 5.69]; Fig. 6b) and also higher FRed of photosynthesis traits
299 (*slope*= 2.96, [0.94, 5.13]; Fig. 6d) (Table S9). The effect of FD_{NU} on ΔAGB was mediated by
300 recent changes in MCWD (ΔMCWD), with positive FD_{NU} effects found in areas that
301 experienced larger increases in mean MCWD (Fig. 6b). There was no strong effect of FD_{PHO} in
302 areas where ΔVPD was smaller (blue fitted line in Fig. 6c) but the effect became negative for
303 areas where ΔVPD was larger (becoming drier, red fitted line in Fig. 6c). The effect of $FRed_{NU}$
304 on ΔAGB was mediated by ΔMCWD with a positive effect only in regions that experienced
305 increases in water availability (Fig. 6e blue fitted line; *slope*= 2.94 [0.25, 5.69]).

Discussion

307 Changes in forest cover affect the local surface temperature by means of the exchanges of
308 water and energy [39]. At the same time climate change is altering land conditions affecting the

309 regional climate and in the near future global warming is likely to cause the emergence of
310 unprecedented climatic conditions in tropical regions [39]. Therefore, determining the
311 distribution of more and less resilient tropical forests (e.g. regarding the maintenance of their
312 functioning) to a changing climate and understanding the mechanisms causing such changes
313 in resilience is pivotal for the conservation of biodiversity and ecosystem functioning. Here
314 we provide spatially explicit models of forest functional diversity and functional redundancy
315 that may aid on this endeavour. However, such predictions may not directly reflect the actual
316 resilience of forest towards climate change as other biological (e.g. competition, dispersal)
317 and climatic (e.g. ground water depth, microclimate) may also play a pivotal role on the
318 responses of tropical forests to a changing environment.

319   Theory on niche complementarity predicts that more diverse systems make more
320 efficient use of ecosystem properties given the complementarity of species in the use of
321 resources available [40, 41]. High functional complementarity and functional redundancy may be
322 more easily achieved in areas with high taxonomic richness. Such complementarity may also
323 increase the performance of diverse communities in the face of more stressful environments
324 given facilitative interaction between species [42]. It can be therefore expected that more
325 functionally diverse and more functionally redundant communities would experience lower
326 change in performance (e.g. lower mortality, lower biomass decrease) with changes in
327 environmental conditions (e.g. ΔMCWD, ΔVPD). In our study we observed that the functional
328 diversity levels are not significantly related to the taxonomic diversity found in the study sites
329 across the tropics but that functional redundancy tends to be, especially for redundancy in
330 morphological/structure and foliar nutrients traits. This points to the role of taxonomic
331 diversity on the possible resilience of tropical ecosystems. We show that forest communities
332 located in areas with lower soil and atmospheric water stress are generally more functionally
333 diverse and more functionally redundant in morphological/structural, nutrients and
334 photosynthetic traits than communities in drier areas. Such higher functional diversity and
335 higher functional redundancy may be one reason why such forests have experienced weaker
336 compositional and ecosystem functioning changes (e.g. carbon capture) as a result of a drying
337 climate in comparison to forests in drier areas, as shown for forests across water availability
338 gradients in West Africa [32, 33] and the Amazon [25, 34]. The higher functional diversity in these
339 wetter forests can be the result of their high water availability (low MCWD and VPD, Table
340 S2) [43, 44]. These conditions facilitate the adaptation, by means of a varied species morphology
341 and structure [45], to a diverse set of light and moisture conditions under and at the canopy.
342 Overall, our results support our expectation of lower functional diversity in the sites with
343 lower long-term water availability, and are in agreement with what has been recently found
344 not only for functional diversity but also for taxonomic and phylogenetic diversity in some
345 local forests [32, 46]. Higher diversity and higher redundancy in functional traits may enhance
346 ecosystem functioning, such as the ability of plant communities for carbon capture [47, 48], and
347 thus show smaller reductions in biomass and lower mortality [49] under changes in climatic
348 conditions. Our results are consistent with recent studies carried out in temperate forests [48]
349 and with few tree taxa [26], which suggest a positive functional diversity-productivity
350 relationship.

351   Tropical forests that experienced the largest decreases in soil water availability across
352   the last half century, which corresponds to intermediate to high long-term average MCWD
353   (e.g. some forests in Panama, Peru and southern Mexico), tend to have high
354   morphology/structure and nutrients FD and FRed and high photosynthetic FD. The high
355   functional diversity and high functional redundancy potentially points to the capabilities of
356   such forests to better withstand the effects of a drying environment than other locations with
357   low FD and FRed levels. Our findings show that atmospheric water availability (VPD) and its
358   changes in the last decades mediate the FD and FRed levels across tropical forest ecosystems.
359   Forests that experienced larger decreases in VPD over the last half century tend to be
360   functionally redundant in morphological and nutrients traits even with increases in soil water
361   availability (here the MCWD). However, such forests are not necessarily redundant in
362   photosynthesis traits. One explanation for this pattern of higher redundancy of forests that
363   experienced larger increases in MCWD and VPD is that such increases in water stress occurred
364   in a variety of forests which are located all across the long-term mean MCWD and VPD
365   spectrum (See Table S2). That means that these forests may well be composed of species with
366   a wide range of functional adaptations to local conditions, adaptations that could have a
367   possible mechanistic link via leaf phenology [50], some adapted to long periods of droughts but
368   also others adapted to high water availability across the year. As tropical forests that
369   increased the most in soil and atmospheric water availability are located across the long-term
370   water availability gradient, these forests might be composed of species that have evolved
371   with different leaf strategies ranging from evergreen to sclerophyllous and deciduous [21]. Leaf
372   adaptations to different environments may thus also explain the pattern of increasing
373   diversity and redundancy of leaf nutrients and photosynthesis traits in these forests that
374   experienced larger decreases in water availability. An important further step in future
375   analyses will be to include as much information as possible not only on the changes in climate
376   but also on the contemporary changes in functional diversity and functional redundancy. This
377   would allow establishing a more direct link between the effects of a changing climate on
378   forest functioning. Moreover, while our study showed clear relations with proxies of water
379   availability at a pantropical scale (MCWD and VPD), other environmental variables at fine
380   scale including local topography and ground water availability may also contribute for
381   determining local FD and FRed levels.

382   Forests with larger functional diversity and larger functional redundancy pools may be
383   more resilient to further climate change. Extreme El Niño events bring about higher
384   temperatures and droughts across tropical forests which can impact the establishment,
385   survival and persistence of tropical forest vegetation, thus also impacting their functioning [38].
386   The 2015-2016 El Niño event did not seem to strongly reduce carbon gains in African tropical
387   forests. Although we did not measure the functional composition of those tropical forests in
388   Africa before and after the El Niño event, our modelling framework provides a general
389   understanding of the functional diversity and functional redundancy of such forest given long-
390   term climate conditions. Our results show that areas with higher long-term functional
391   diversity and functional redundancy tended to show smaller decreases or larger increases in
392   AGB, thus being more resilient to changes in environmental conditions caused by the 2015-
393   2016 El Niño event. Overall, our results highlight that tropical dry forests, such as those in

drier parts of Mexico, Colombia, south-eastern Amazonia and much of West Africa, which have experienced high long-term soil water and atmospheric water stress over the last half century, could be at higher risk than wetter forests of further functional declines given the projected changes in climatic conditions for the coming decades [51]. Further droughts may increase the water stress of drier tropical forests, which may already be at their climatic physiological limits, and could potentially drive them towards alternative stable states [19]. This is in agreement with recent findings for West African [32] and South American drier tropical forests [6, 50], where large and consistent changes in functional diversity [34] and functioning [6] have been observed. It has been hypothesised that low functional diversity and low functional redundancy may pinpoint areas that could be less resilient to further changes in environmental conditions [52]. Recent work in the wet tropics of Australia shows that tree growth has been reduced the most by positive anomalies in atmospheric water deficits in drier forests and for species growing faster in drier conditions than in wetter ones [36]. The net carbon sink of tropical seasonal forests in Brazil has decreased by 0.13 Mg C ha^{-1} year^{-1} amounting to carbon losses of 3.4% per year (on average over a 15 year period) [6], highlighting how the driest and warmest sites are experiencing some of the largest carbon sink declines and becoming carbon sources. Moreover, the effects of a changing climate on drier tropical forest ecosystems may not only affect tree growth and survival but also strongly decrease their functional trait space available, possibly also affecting their functioning [50]. Both the species-level and forest-level differential demographic sensitivities to a drying climate support this hypothesis of potentially less resilience in already-drier environments.

We also highlight the need for measuring more widely other plant functional traits that have a more direct link to the availability, accessibility and transport of water resources and to adaptations to a drying climate such as plant hydraulic traits (e.g. vessel density, P_{50}, hydraulic safety margin, hydraulic conductivity, osmotic potential, root size and depth) which are seldom available for most tropical plant species but that may shed more light into the possible responses of tropical forest to a changing climate [53, 54]. However, recent work has shown there is strong correlation between plant hydraulics and economic traits. For instance wood density may serve as a proxy for hydraulic traits [55] and has been shown to corelated with vessel diameter, branch and tree leaf specific conductivity [56, 57, 58], resistance to embolism [57, 59], sapwood capacitance [60, 61], minimum leaf water potential [62] and leaf water potential at turgor loss [60]. Also, significant relationships between SLA and conduit diameter, seasonal change in pre-dawn leaf water potential and stomatal conductance have been found [62], together with significant correlation between leaf P_{50} and leaf mass per area (LMA) and leaf hydraulic conductivity and LMA [63]. Moreover, the leaf osmotic potential at full turgor and leaf nitrogen content have been shown to be largely correlated [64]. Given that within the hydraulics traits, and thus their leaf and wood economics correlates, and in face of a changing environment, there is a trade-off involving drought avoidance and hydraulic safety. Such trade-off forms an important axis of variation across tropical forests where it is expected that fast-growing species have lower hydraulic safety compared to slow-growing species [54]. Across the tropics species that can quickly transport water resources would tend to be the ones with low wood density, short leaf life span and high rates of resources acquisition [53]. We expect

this relationship to scale up from the individual to the ecosystem level and that this is thus reflected in ecosystem characteristics such as above ground biomass.

In summary, this study addresses the need to understand and monitor the responses of tropical forest ecosystems to climate change, such as the negative impacts of a drying climate on the capacity of tropical forests to sequester and store carbon. Current models of ecosystem contribution to climate mitigation lack information on earth systems feedbacks. Our results show how contemporary climate shapes the functional diversity and functional redundancy of tropical forest communities. Across the tropics a diverse set of environmental conditions support a myriad of tropical tree communities with diverse combinations of plant functional traits and different functional diversity and functional redundancy levels. Tropical communities more at risk of shifting towards alternative states could be expected to be currently the ones where lower functional diversity and redundancy is found and that are under already high water stress, such as in the drier tropical forests. From the ecosystems conservation point of view, it is of critical importance to inform decisions by mapping tropical regions in terms of their resilience to future changes in the environment. Conservation efforts need to prioritise and manage ecosystems accordingly, especially including drier tropical forests in the conservation agenda, but also considering that wet tropical forests with higher functional diversity and higher functional redundancy are likely to continue to be long term carbon stores and be more resilient in the face of climate extremes and pathogens.

Methods

Vegetation plots. We collected vegetation census data from 74 permanent vegetation plots that are part of the Global Ecosystems Monitoring network (GEM; www.gem.tropicalforests.ox.ac.uk) [65]. These plots are located in wet tropical forests, seasonally dry tropical forests, and tropical forest-savanna transitional vegetation. The sampled vegetation plots ranged in area from 0.1 to 1 ha, with most (67%) being 1 ha and only one of them being 0.1 ha (Table S2). The plots are located in Australia, Brazil, Colombia, Gabon, Ghana, Malaysian Borneo, Mexico and Peru across the four tropical continents (Table S2). In each plot, all woody plant individuals with a diameter ≥ 10 cm at breast height (DBH) or above buttress roots were measured. In the plots NXV-01 and NXV-10 in Nova Xavantina, here onwards referred to as Brazil-NX, the diameter was measured at 30 cm from the ground level as is standard in drier shorter vegetation monitoring protocols.

Plant functional traits. We directly collected plant functional trait measurements from the most abundant species that would cover at least 70% of plot basal area and that were located in most of the 74 vegetation plots mentioned above (Extended Data Figure 1; Table S1). All traits were collected following the GEM network standardised methodology across plots. Forest inventory data were used to stratify tree species by basal area dominance. The tree species that contributed most to basal area abundance were sampled with 3–5 replicate individuals per species. Eighty percent or more of basal area was often achieved in low diversity sites (e.g., montane or dry forests). For each selected tree a sun and a shade branch were sampled and in each branch 3–5 leaves were used for trait measurements. This represented a total sample of 2461 individual trees across the tropics (Extended Data Figure 1). We collected plant functional traits related to photosynthetic capacity A_{max} (μmol m^{-2} s^{-1}):

478 light-saturated maximum rates of net photosynthesis at saturated CO_2 (2000 ppm CO_2), A_{sat}
479 ($\mu mol\ m^{-2}\ s^{-1}$): light-saturated rates of net photosynthesis at ambient CO_2 concentration
480 (400 ppm CO_2), R_{Dark} ($\mu mol\ m^{-2}\ s^{-1}$): dark respiration. Leaf nutrient concentration traits (%) of
481 Ca: leaf calcium, K: leaf potassium, Mg: leaf magnesium, N: leaf nitrogen and P: leaf
482 phosphorus. Plant morphological and structural traits, A (cm^2): leaf area, DM (g): leaf dry
483 mass, FM (g): leaf fresh mass, LDMC (mg/g): leaf dry matter content, LWC (%): leaf water
484 content, SLA (g/m^2): specific leaf area, T (mm): leaf thickness and WD (g/cm^3): wood density.
485 Further details of measurements for the Peruvian Andes campaign are given in Martin et al.
486 [66] and Enquist et al. [67], for the Malaysian campaign in Both et al. [68], and for the Ghana and
487 Brazil campaigns in Oliveras et al. [69], Gvozdevaite et al. [70] and for Colombia campaigns in
488 González-M. et al. [50]. For the specific dates of plant functional traits collection see ref. [71]. For
489 the FD and FRed calculations, as both only accept one trait value per species, from the
490 individual level plant functional traits, we averaged the values at species level and when the
491 species had no trait values available, we filled the gaps by averaging the trait values at the
492 genus level. This protocol allowed us to have at least 70% of the plot's basal area covered by
493 traits but often more. Thus, in our analysis the inclusion of plots is trait dependent in the
494 sense that only plots with at least 70% of the BA covered by the focus trait were included in
495 the analysis (see Table S2).

496 **Community level functional diversity and redundancy**

497 We calculated the functional diversity and functional redundancy of morphological/structural
498 traits, leaf chemistry and photosynthetic traits, which are hypothesised to be of importance
499 for tropical forests to respond to a drying climate (Table S1) [14, 21], based on data for species
500 covering at least 70% of the plot basal area (Table S2) and following equations from refs. [35,
501 72, 73, 74]. The morphological/structural and nutrient related traits used for this analysis are A,
502 FM, DM, LDMC, T, LWC, SLA, WD, Ca, K, Mg, N, P; and A_{sat}, A_{max} and R_{Dark} for photosynthesis.
503 We did not build an index including all functional traits together as this would make their
504 interpretation rather difficult as they point to different axes of the global spectrum of plant
505 form and function [75] and also because of the difference in number of records available for
506 each trait group. Plant functional trait diversity (FD) was calculated at the plot level using the
507 functional dispersion metric, which is closely related to the RaoQ and which represents the
508 mean distance, in trait space, of each single species to the weighted centroid of all species [35].
509 We used the FD as it can handle any number and type of traits, because it is unaffected by
510 species richness, it weighs the values based on the abundance of species, it is not influenced
511 by outliers and is relatively insensitive to the effects of undersampling [76]. To calculate FD we
512 applied the equation presented by Laliberté and Legendre [35]:

513 eq. 1 $$FD = \frac{\sum BA_{ip}\ z_{ip}}{\sum BA_{ip}}$$

514 where BA_{ip} reflects the total plot level basal area of species i in plot p and z_{ip} is the distance
515 of species i in plot p to the weighted centroid of the n species in trait space. The plant traits
516 were weighted by the relative basal area (in m^2) of each of the species in the plot. Therefore,
517 FD summarises the trait diversity and represents the mean distance in trait space of each

species to the centroid of all species in a given community. All numeric traits were standardised during the FD calculation.

We calculated the functional trait redundancy in the community (vegetation plots), FRed, as in Pavoine and Ricotta [73] and Ricotta et al. (*'Rstar'*) [74] and as developed in the 'uniqueness' function of the R 'adiv' package [72]. *'Rstar'* quantifies how redundant a plant community is compared to a scenario where all species would have the most distinct trait values possible. As in the case of FD, *'Rstar'* as calculated in Ricotta et al. [72, 73] works with multiple traits and takes into account species abundances. The *'Rstar'* index is complementary to the community-level functional uniqueness index *Ustar* described by Ricotta et al. [73] which is the ratio of the Rao quadratic diversity index Q [77, 78], that accounts for species trait dissimilarities and the Simpson index D, which considers the species in the community as equally and maximally dissimilar. Thus *Ustar* measures the uniqueness of the community in functional space which is obtained by including interspecies dissimilarities in the calculations of the index. *Rstar*, which is the complement of *Ustar*, represents thus a measure of community-level functional redundancy and is quantified as:

eq. 2 $$Ustar = \frac{1-D}{1-Q}$$

eq. 3 $$Rstar = 1 - Ustar$$

For an in-depth description of the functional redundancy index see refs. [72, 73, 74].

All above-mentioned analyses were carried in the R statistical environment [79] with the 'FD' and 'adiv' packages.

Climatic and soil data

In order to investigate the role that long-term climate plays on determining the community trait composition and functional diversity and redundancy across tropical forests we gathered climatic data on the potential evapotranspiration (PET in mm), precipitation accumulation (mm) and VPD (kPa) from the TerraClimate project [80] at a spatial resolution of ~4 × 4 km. The data were obtained for the period from 1958 to 2017. Using the full-term climatic dataset (1958-2017) we calculated the mean annual VPD, PET, precipitation coefficient of variation (CV; as a measure of seasonality in water availability) and the maximum climatological water deficit (MCWD). The MCWD is a metric for drought intensity and severity and is defined as the most negative value of the climatological water deficit (CWD) over each calendar year. The VPD is an indicator of plant transpiration and water loss [14]. CWD is defined as precipitation (P) (mm/month) – PET (mm/month) with a minimum deficit of 0. The MCWD was calculated as in Malhi et al.[13] where MCWD=min(CWD1...CWD12). As a final step we converted the MCWD so that positive values indicate increases in water stress. We also calculated the change in the climatic variables (ΔMCWD, ΔVPD and ΔCV) between a first period corresponding to a climatology of 30 years encompassing 1958-1987 and a second period encompassing the years 1988-2017. The climatology of 30 years to calculate the different time periods climate was selected as recommended by the World Meteorological Organization in order to characterise the average weather conditions for a given area

557 (www.wmo.int/pages/prog/wcp/ccl/faqs.php). There are other possibly relevant predictors
558 of water stress for plants in tropical forests such as the water table depth [17,81]. It has been
559 hypothesised that water table depth drives the distribution of plant species and functional
560 composition, and where it is expected that forest in shallow water table areas show higher
561 mortality during strong drought events (e.g. El Niño) given the presence of species with
562 shallower roots and less adapted traits [17,81]. However, we did not include the water table
563 depth in our analysis given the lack of spatially explicit predictions across the tropics.

564 We also obtained soil texture (percent clay and sand) and chemistry (soil pH and cation
565 exchange capacity, CEC) gridded data from the SoilGrids project (www.soilgrids.org) and used
566 this as extra covariates in our modelling framework. Although the CEC includes the acid
567 aluminium, which is not a plant nutrient and may be toxic to plants, this is one of the best
568 estimates of the overall potential of the soil to exchange cations (Ca, Mg, and K) that is
569 available at a pantropical extent [82].

570 We then tested the correlation between all pairs of climatic variables (full-term and
571 their changes) and also between the soil variables. We observed that MCWD and CV had
572 Pearson's correlation coefficients $|>0.70|$ and also CEC and pH and Clay and Sand had
573 correlation coefficients $|>0.70|$ (Supplementary Figure 2) and we thus dropped CV and its
574 change, Sand and pH from the analyses as to avoid distorting model coefficients in the
575 modelling stage [83]. We then carried out a principal component analysis (PCA) using the MCWD
576 and VPD climatic variables (average of full-term and their changes) and another with the soil
577 variables to investigate the distribution of the vegetation plots in climate and soil space and
578 to describe how much of this distribution can be explained by each of these. For the PCA
579 analysis we used the 'stats' package in R.

Statistical analysis

Functional diversity and redundancy statistical analysis

582 We investigated the variation in morphological/structural, leaf chemistry and photosynthetic
583 FD and FRed across tropical forests by modelling their relation with mean MCWD, VPD for the
584 period 1958-2017 and their interaction, the ΔMCWD and ΔVPD between the first and second
585 periods and their interaction and soil chemistry (CEC) and texture (Clay%). For the
586 photosynthesis statistical models, given their lower sample size (n=22; Table S2), interaction
587 terms were not included and to avoid overfitting we first tested by means of leave-one-out
588 cross-validation (LOO) [84] if the soil covariates improved or not the models with only climate
589 information. We found soil data did not improve our models (Table S8) and thus left CEC and
590 Clay out of the photosynthesis models. We also calculated the relative change (%) in climatic
591 conditions but this did not improve model predictions and thus we only present results that
592 include the absolute changes in MCWD and VPD. We included the change in MCWD and VPD
593 as we wanted to understand if areas that have experienced stronger changes in climate
594 showed lower or higher functional diversity and functional redundancy than others that have
595 experienced milder climate changes. In the same way we included the interaction between
596 MCWD and VPD (and also between ΔMCWD and ΔVPD) as there may be regions where high

597 values of one of these variables may not be related to the values of the other, e.g. high MCWD
598 may not be related to high VPD. Prior to the statistical modelling we centred and standardised
599 (generated z-scores) all climatic and soil variables.

600   We tested for spatial autocorrelation effects in the FD and FRed model residuals using
601 the Moran's I test and found a significant effect for the photosynthesis and nutrients FD
602 models and for the FRed nutrients model (Table S9). Thus, for those data we calculated the
603 spatial distance at which such spatial effect decreased and found that a distance of 2 km was
604 sufficient. We then generated an ID for each group of plots (group ID) that were at most 2 km
605 away from each other and included such group ID as a random factor in those statistical
606 models. As some plots were smaller than 1 ha (Table S2) we included the z-scores of plot size
607 as a covariate in all statistical models to account for its possible effect. We log transformed
608 the FD and FRed indices to improve the normality of the data and applied linear mixed-effects
609 models with a Gaussian error structure accounting for difference in plot size and spatial
610 autocorrelation as described above under a Bayesian framework. The mixed-effects models
611 were run with normal diffuse priors with mean 0 and 2.5 standard deviation to adjust the
612 scale of coefficients and 10 standard deviations to adjust the scale of the intercept, three
613 chains and 10000 iterations to avoid issues with model convergence. We computed the
614 highest density intervals (HDI) rendering the range containing the 90% most probable effect
615 values and calculated the ROPE values using such HDI as suggested in Makowski et al. [85]. The
616 95% HDI was not used as this range has been shown to be unstable with ESS < 10,000
617 (effective sample size) [86]. We considered a climatic variable had an important (significant)
618 effect on the response variable if the 90% HDI did not overlap 0. Posterior density
619 distributions for all models and covariates included in the models are shown in
620 Supplementary Figure 3 and Supplementary Figure 4.

621   Based on the statistical models described above we created spatial predictions of
622 Functional Diversity (FD) and Functional Redundancy (FRed) at a pantropical scale. We
623 defined the 'low', 'intermediate' and 'high' FD and FRed groups by defining the range in FD
624 and FRed values and dividing that range between three in order to allocate the FD and FRed
625 predicted values to each of these groups and be able to state what is the predicted percent
626 area of tropical and subtropical dry and moist broadleaf forests with low, medium and high
627 FD and FRed. We also tested the robustness of the spatial predictions of FD and FRed by also
628 developing the models by leaving out the data from one continent (South East Asia and
629 Australia together), fitting the model again, and comparing the resulting spatial predictions
630 to the full model prediction maps by means of Spearman correlations. In Extended Data Figure
631 10 we also highlight locations across the tropics with climate and soil conditions outside of
632 our climatic and soil calibration space, thus not covered by the range in our sampling
633 locations, which may represent locations where our models are extrapolating the
634 relationships found.

635 ***Relating functional diversity, redundancy and biomass***

636 We obtained the above ground biomass data (AGB) from an independent set of 100
637 vegetation plots in Africa before (AGB$_{pre}$) and after (AGB$_{post}$) the 2015 El Niño event from
638 Bennett et al. [38]. The plots from Bennet et al. include censuses from 2000 onward where the
639 median plot size is 1 ha, the mean initial census was May 2008, with the mean pre-El Niño
640 census in April 2014, and mean post-El Niño census in February 2017. The plots have a mean
641 monitoring length pre-El Niño of 8.3 years, with a mean length of the El Niño interval being
642 2.7 years. To calculate AGB Bennet et al. [38] used the BiomasaFP R package, including the
643 calculation of the census interval corrections for AGB where Pre-El Niño means of these
644 variables are time weighted using the census interval lengths. For a full description of the AGB
645 data see Bennett et al. [38]. We calculated the ΔAGB as:

646 eq. 4 ΔAGB= (AGB$_{post}$ - AGB$_{pre}$)

647 Before modelling we eliminated statistical outliers in the AGB values, this is values more
648 than 1.5 the interquartile range above the third quartile or below the first quartile. We
649 therefore only used 86 plots in our analysis. We modelled the ΔAGB as a function of the
650 predicted (see methods above) FD and FRed maps scores from each functional group
651 (morphology/structure, nutrients and photosynthesis; Fig. 3 and Fig. 4), one model was built
652 per functional group. Each model included the FD and FRed index (e.g. FD and FRed of
653 nutrients) and their interaction with ΔMCWD and ΔVPD as to test the effect of a changing
654 climate on the effects of FD and FRed on above ground biomass change. We accounted for
655 plot size by including as a covariate in the models and used a Gaussian error structure model
656 under a Bayesian framework. The ΔAGB statistical models were run with normal diffuse priors
657 with three chains and 5000 iterations.

658 We carried out all statistical analysis in the R statistical environment [79] using the, 'rstanarm',
659 'loo', 'bayestestR', 'egg' and 'BEST' packages.

660 **Data availability**

661 The vegetation census and plant functional traits data that support the findings of this study are
662 available from their sources (www.ForestPlots.net and gem.tropicalforests.ox.ac.uk/). To comply
663 with the original data owners the processed community-level data used in this study can be
664 accessed through the corresponding author upon request.
665
666 **Code availability**

667 All relevant R-functions and code used in this study are referred to in the Method section and can be
668 accessed through the DOI 10.5281/zenodo.6367982.
669

710

711 **Author contributions statement**

712 J.A.-G. conceived the study, designed and carried out the analysis and wrote the first draft of the
713 paper. E.B. contributed to the main ideas and design of the study. Y.M. conceived and implemented
714 the GEM Network, obtained funding for most of the GEM traits field campaigns and commented on
715 earlier versions of the manuscript. J.A.-G., E.B., I.O., D.B, J.J.C.-R.,M.G.N.-M., S.B., J.E.N., F.E.O.,
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718 R.E.M., P.S.M., O.L.P., A.C.B., S.L.L., C.A.Q., B.S.M., W.D.K., M.S., Y.A.T., L.J.T.W., N.S., D.A.C., J.B.,
719 S.A.-B. and Y.M. participated in or coordinated vegetation, trait data and/or soil data collection or
720 processed field data and commented on and approved the manuscript.
721

722 **Competing interests statement**

723 The authors declare no competing interests

724

725 **Figure legends**

726

727 **Figure 1. Long-term water availability and its recent changes and soil conditions drive functional diversity of**
728 **plant traits across the tropics.** Model results for functional diversity of morphological (a, b), leaf nutrients (c-d)
729 and photosynthetic (e) traits are shown. Only climatic variables (X-axis) with a clearly important relationship (90%
730 Highest Density Interval, HDI, of the posterior distribution does not overlap 0) with functional diversity (FD) are

731 shown. Models for each group (morphology/structure, leaf nutrients, photosynthetic) were fitted as a function of
732 long-term and recent changes in climate and of soil chemistry (CEC) and texture (Clay). Thick black lines show
733 the average response and shaded lines show 300 random draws from the model posterior distribution
734 representing variability of the expected model fit. The blue fitted line in a) shows the effect of MCWD at the
735 lowest value of VPD and the red fitted line at the highest values of VPD. Larger positive values in MCWD and VPD
736 reflect stronger water deficits. MCWD: maximum climatic water deficit, VPD: vapour pressure deficit, CEC: cation
737 exchange capacity. Δ: change. The Y-axis shows the FD of morphology/structure (FD_{MO}), leaf nutrients (FD_{NU})
738 and photosynthetic (FD_{PHO}) traits. For details about the single traits that form each of the groups
739 (morphology/structure, leaf nutrients, photosynthetic) see Table S1. For full statistical results see Table S3.
740
741 **Figure 2. Long-term water availability and its recent changes and soil texture drive functional redundancy of**
742 **plant traits across the tropics.** Model results for functional redundancy of morphological (a-c), leaf nutrients (d)
743 and photosynthetic (e) traits are shown. Only climatic variables (X-axis) with a clearly important relationship (90%
744 Highest Density Interval, HDI, of the posterior distribution does not overlap 0) with functional redundancy are shown
745 but in e) where the effect of VPD on $FRed_{PHO}$ is marginal. Models for each group (morphology/structure, leaf
746 nutrients, photosynthetic) were fitted as a function of long-term and changes in climate and of soil chemistry (CEC)
747 and texture (Clay). Thick black lines show the average response and shaded lines show 300 random draws from
748 the model posterior distribution representing variability of the expected model fit. The blue fitted line in b) and d)
749 shows the effect of ΔMCWD at the largest decrease in ΔVPD and the red fitted line at the larger increase in ΔVPD.
750 Larger positive values in MCWD reflect stronger water deficits. MCWD: maximum climatic water deficit, VPD:
751 vapour pressure deficit, Δ: change. The Y-axis shows the FRed of morphology/structure ($FRed_{MO}$), leaf nutrients
752 ($FRed_{NU}$) and photosynthetic ($FRed_{PHO}$) traits. For details about the single traits that form each of the groups
753 (morphology/structure, leaf nutrients, photosynthetic) see Table S1. For full statistical results see Table S3.
754
755 **Figure 3. Global predictions of functional diversity (FD) across the tropical and subtropical dry and moist broadleaf forests.**
756 FD predictions for morphological/structural (top panel), leaf nutrients (middle panel) and photosynthetic (bottom panel)
757 traits are shown. Dark brown colours depict areas where FD is lowest, light brown and light blue where FD is intermediate
758 and dark blue where FD is predicted to be highest. Functional diversity predictions across the tropics were made using the
759 statistical models for which details are shown in Table S3. The location of field sites whose data informed this analysis is
760 shown in Figure S5.

761 **Figure 4. Global predictions of functional redundancy (FRed) across the tropical and subtropical dry and moist broadleaf**
762 **forests.** FRed predictions for morphological/structural (top panel), leaf nutrients (middle panel) and photosynthetic (bottom
763 panel) traits are shown. Dark brown colours depict areas where FRed is lowest, light brown and light blue where FRed is
764 intermediate and dark blue where FRed is predicted to be highest. Functional redundancy predictions across the tropics were
765 made using the statistical models for which details are shown in Table S3.

766 **Figure 5. Global bivariate maps combining the scores of the Functional Diversity (FD) and Functional Redundancy (FRed)**
767 **across the tropical and subtropical dry and moist broadleaf forests.** Bivariate maps for morphological/structural (top panel),
768 leaf nutrients (second panel) and photosynthetic (third panel) traits are shown. The bottom panel shows the combination of
769 the morphological/structural, nutrient and photosynthesis bivariate maps, after standardizing (with values 0 to 1) and
770 summing them to obtain a general bivariate map of global functional diversity and functional redundancy. Purple-red colours
771 depict areas where both FD and FRed are highest, while yellow points to areas with higher FD and blue to areas with higher
772 FRed. Gray colours show areas where both FD and FRed are predicted to be lowest. See full details of the statistical models
773 underlying these predictions in Table S3.

774 **Figure 6. The strength of changes in aboveground biomass (ΔAGB) after extreme events such as the 2015 El Niño (from**
775 **Bennett et al. [38]) are related to the local functional diversity (FD) and functional redundancy (FRed) for sites in Africa.** The
776 relation between ΔAGB and FD are shown in a-c and between ΔAGB and FRed in d-e. The x axis shows the FD or FRed scores
777 for the morphological/structural (MO), nutrients (NU) and photosynthetic (PHO) traits as extracted from the predictions
778 shown in Fig. 3 and Fig. 4 and the Y axis shows the relation with ΔAGB. The ΔAGB shows a clear relation (90% Highest Density
779 Interval, HDI, does not overlap 0) with the diversity indices (Table S7). Thick black lines show the average response and grey
780 shaded lines show 700 random draws from the posterior distribution representing variability of the expected model fit. The
781 blue fitted line in b) shows the effect of FD_{NU} at the largest decrease in ΔMCWD and the red fitted line at the larger increase
782 in ΔMCWD. The blue fitted line in c) shows the effect of FD_{PHO} at the largest decrease in ΔVPD and the red fitted line at the
783 larger increase in ΔVPD. In e) the effect of $FRed_{NU}$ is shown for the largest decrease in ΔMCWD with the blue fitted line, and
784 the red fitted line shows the effect at the largest increase in ΔMCWD. In b, c and e the thick blue and red fitted lines represent
785 the slopes of the interaction between the variable in the X axis and the moderator (i.e. ΔMCWD or ΔVPD). The FD and FRed
786 scores for each trait group (i.e. morphology/structure, nutrients and photosynthetic) are predictions extracted from Fig. 3
787 and Fig. 4 for the vegetation plots where the ΔAGB was collected. Only model covariates with a clear relationship with the
788 ΔAGB are shown. For full statistical results see Table S7.

789

790

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