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Amazon forest biogeography predicts resilience and vulnerability to drought

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Summary paragraph (216 words, target: 200): **Amazonia contains the most extensive tropical**

- **forests on Earth, but Amazon carbon sinks of atmospheric CO² are declining, as**
- **deforestation and climate change-associated droughts**[1–4](https://paperpile.com/c/gDKLkA/DpETc+ANsHP+iy17K+yG3t8) **threaten to push these forests past**

25 a tipping point towards collapse⁵⁻⁸. Forests exhibit complex drought responses, indicating

- **both resilience (photosynthetic "greening") and vulnerability (browning and tree**
- 27 mortality), that are difficult to explain by climate variation alone⁹⁻¹⁷. Here, we combine
- **remotely-sensed photosynthetic indices with ground-measured tree demography to identify**
- **mechanisms underlying drought resilience/vulnerability in different intact forest**
- **'ecotopes'**[18,19](https://paperpile.com/c/gDKLkA/TeqQr+0BEgg) **(defined by water-table depth, soil fertility and texture, and vegetation**
- **characteristics). In higher-fertility southern Amazonia, drought response was structured by**
- **water-table depth, with resilient greening in shallow-water-table-forests (where greater**
- **water availability heightened response to excess sunlight), contrasting with vulnerability**
- **("browning" and excess tree mortality) over deeper water tables. Notably,**
- **shallow-water-table-forest resilience weakened as drought lengthened. By contrast,**
- **lower-fertility northern Amazonia, with slower-growing but hardier trees (or alternatively,**

tall forests, with deep-rooted water access), supported more drought-resilient forests independent of water-table depth. This new functional biogeography of drought response provides a framework for conservation decisions and improved predictions of heterogeneous forest responses to future climate changes, warning that Amazonia's most productive forests are also at greatest risk, and that longer/more frequent droughts are undermining multiple ecohydrological strategies and capacities for Amazon forest resilience.

Three 'once in a century' droughts (Extended Data Fig. 1) occurred in the Amazon basin 45 over a single decade, in 2005, 2010, and 2015-2016^{[20,21](https://paperpile.com/c/gDKLkA/A3Jno+nw4KX)}, provoking multiple difficult-to-explain forest responses (**Fig. 1**, Extended Data Fig. 2). For instance, unexpected overall increases ("green-up") in remotely sensed canopy greenness (a proxy for photosynthetic function) during 48 the 2005 drought^{[9,10](https://paperpile.com/c/gDKLkA/p6yui+5gmaM)} (Fig. 1a, Extended Data Fig. 2a) appear at odds with reports of simultaneous carbon losses from increased tree mortality observed in ground plots^{[16](https://paperpile.com/c/gDKLkA/i3iSm)}. Further, the 2005 50 green-up contrasts with a strong decrease in greenness ("browndown") during the drought^{[11](https://paperpile.com/c/gDKLkA/iVEDO)} (**Fig. 1b**, Extended Data Fig. 2b), while the 2015/2016 El Niño, the largest and most intense 52 drought of the three, provoked an intermediate response that also included significant green-up 53 regions (Fig. 1c, Extended Data Fig. 2c). Climate drivers alone, though important^{[10](https://paperpile.com/c/gDKLkA/5gmaM)}, are evidently 54 insufficient to predict the complexity of drought responses across heterogeneous landscapes^{[22](https://paperpile.com/c/gDKLkA/5XhwX)}. 55 Still missing is a general understanding of what drives differences in drought resilience across 56 Amazonian landscapes, a "functional biogeography"^{[23](https://paperpile.com/c/gDKLkA/Y8kQ8)} of forest drought response that can 57 address the question: why are some forests (or times) resilient (exhibiting green-up, or reduced mortality), while others are vulnerable (exhibiting browndown, or enhanced mortality)?

Here, we used satellite indices of forest photosynthesis to test whether three non-exclusive ecological hypotheses that go beyond climate-only explanations, developed from

forest plot-scale observations, can also predict regional scale responses to these recent droughts 61 62 across intact *terra firme* forest types of the Amazon basin.

The first ("other side of drought"^{[24](https://paperpile.com/c/gDKLkA/32xKg)}) hypothesis is that shallow water table hydrological 64 environments^{[25](https://paperpile.com/c/gDKLkA/465Cp)} provide trees with greater access to water resources, making them more drought 65 resilient (as observed in forest plots near Manaus^{[26,27](https://paperpile.com/c/gDKLkA/7LA7D+2ZZig)}), than trees in forests over deep water 66 tables, whose mortality rates typically increase with drought^{[2,16](https://paperpile.com/c/gDKLkA/i3iSm+ANsHP)}. This hypothesis predicts that 67 shallow water table forests should show less browndown (or even experience green-up with 68 reduced anoxia or more sunlight due to reduced cloud cover during drought) compared to forests 69 with deep water tables. 63

The second ("soil fertility") hypothesis $28,29$ is that in more fertile forests, where tree 71 growth and turnover rates are high, fast growing trees that invest less in drought tolerance have a 72 competitive advantage over trees that invest more. This is because it is easier to simply regrow 73 trees cheaply when resources are plentiful, especially when tree-killing droughts are rare. This 74 hypothesis thus predicts that more fertile forests will exhibit greater drought susceptibility (more 75 browndown or less green-up) than less fertile forests. 70

The third ("rooting depth/traits") hypothesis focuses on the role of tree characteristics 77 themselves. This hypothesis predicts that forests dominated either by species with drought 78 avoidance traits (tall, deeply rooted trees)^{[30–33](https://paperpile.com/c/gDKLkA/EwUsf+Dy8Mm+qawQE+ycA42)}, or drought tolerance traits (high wood density or 79 embolism resistant xylem)^{[29,34–36](https://paperpile.com/c/gDKLkA/bb7bO+t3f2K+7oh5P+ZRaSR)} are more drought tolerant, even over deep water tables. 76

These three dimensions (water table depth, soil fertility, and vegetation properties) define 81 an 'ecotope space', within which different forest ecotopes are located and may interact with and 82 respond to climate in different ways. To the extent such responses are predictably structured by 83 ecotopes (which also vary by geographic region within the Amazon, Extended Data Fig. 3), it 80

84 should be possible to derive a unified functional biogeography of the basin-wide diversity of 85 forest drought responses.

We tested these hypotheses using satellite indices of photosynthetic capacity (the 87 Enhanced Vegetation Index, EVI, corrected for view- and illumination-geometry artifacts)^{[37](https://paperpile.com/c/gDKLkA/Tj9G)} and 88 of photosynthetic activity (the Global OCO-2 Solar Induced Fluorescence product, GOSIF)^{[38](https://paperpile.com/c/gDKLkA/WUcO)}. We 89 focused on drought-affected regions, defined as those whose maximum cumulative water deficit (MCWD, methods §2.3) reached more than one standard deviation below the mean of the remote 90 91 sensing record (from 2000-2020)^{[39](https://paperpile.com/c/gDKLkA/HHtIX)}. Vegetation index anomalies during drought were analyzed as 92 a function of water table depth (as captured by "height above nearest drainage", or $HAND²⁵$ $HAND²⁵$ $HAND²⁵$) and 93 of gridded climate data (photosynthetically active radiation (PAR), vapor pressure deficit (VPD), 94 and precipitation) derived from remote sensing platforms (see methods §2.4, Extended Data Fig. 5). 95 86

We took relative green-up (more positive or less negative vegetation anomalies) as an 97 index of resilient photosynthetic capacity or activity, because it suggests more carbon resources 98 for responding to stress, and, notably, is predictive of outcomes on the ground commonly associated with resilience at the individual tree scale (lower mortality, greater growth, and 99 100 greater xylem embolism resistance, see methods §2.4). 96

101 Southern Amazon forest drought response

Focusing first on the locale of the 2005 drought (in the Southern Amazon, one of three 103 regions identified in methods $\S2.2$, Extended Data Fig. 6), we found substantial structuring of the 2005 greening by water table depth across the drought-impacted region. This is visually evident 104 105 in the spatial correspondence of 2005 forest green-up/browndown regions (Fig. 1a, ellipse) with 102

shallow/deep water table forests (**Fig. 2a**, ellipse), and is quantified by bin-averaged EVI (**Fig.** 106 **2b**) and GOSIF (Extended Data Fig. 2d, green symbols/lines) observations vs. water table depth. 107 Vegetation green-up in 2005 was concentrated in pixels with shallow water tables, but as water 109 tables deepened, positive vegetation index "greening" anomalies decreased and then reversed to 110 become negative anomalies (Fig. 2b, Extended Data Fig. 2d). The strongest 2005 green-up, 111 intriguingly, was in forests that experienced the strongest drought (Fig. 2b, dark orange points), 112 apparently because these areas experienced a greater frequency of excess sunlight (Fig. 2c 113 histograms), which was particularly advantageous to shallow water table forests (Fig. 2c, 114 blue-hued lines). 108

In order to rigorously quantify the sensitivity of forest response across multiple droughts, 116 we implemented two separate statistical approaches in sequence: non-linear multiple regression 117 (using Generalized Additive Modeling, GAM), to test hypotheses and predict basin-wide drought 118 anomalies, using AIC selection to identify the best predictive models (methods $\S2.6.1)^{40}$ $\S2.6.1)^{40}$ $\S2.6.1)^{40}$, and Structural Causal Modeling (SCM) (using Directed Acyclic Graphs, DAGs) to more 119 120 systematically evaluate the causal relations suggested by the GAM analysis (methods $\S 2.6.2)^{41}$ $\S 2.6.2)^{41}$ $\S 2.6.2)^{41}$, 121 Both modeling approaches were conducted on a 0.4 degree grid, the resolution needed to avoid 122 inflation of statistical significance by accounting for spatial autocorrelation among nearby pixels 123 (methods §2.5, Extended Data Fig. 7). We focus on the multiple regression GAM results below, 124 and report comparisons with SCM results in methods $\S2.6.3$. 115

When all three droughts were modeled simultaneously within Southern Amazonia, using GAM to also account for the effects of climate (**Extended Data Table 1a**), we found that despite 126 127 large differences observed in responses among the years (Fig. 1: a vs b vs c), the overall 128 other-side-of-drought (hypothesis 1) prediction of a negative relationship between remotely 125

129 sensed vegetation anomalies and deepening water tables observed in 2005 was consistently 130 confirmed across all three droughts in this region (Fig. 3a). Notably, though there was an almost 131 universal browning response to the 2010 drought (Fig. 1b), vegetation anomalies remained 132 significantly structured by water table depth (Fig. 3a, purple symbols/lines).

This analysis suggests that the ability of shallow water table forests (but not of deep) to 134 respond positively to excess sunlight (possibly including relief from anoxia^{[24](https://paperpile.com/c/gDKLkA/32xKg)}) was a key general (multi-drought) mechanism of southern Amazon forest drought response (**Fig. 3b** colored 136 curves). Inter-drought differences in climate drivers — not differences in water-table depth 137 distribution of impacted areas (Fig. 3a, distributions did not differ much) — accounted for much 138 of the inter-drought differences in forest response (in Fig. 3a, the observed points correspond 139 well with the model predictions, which differ among droughts only due to climate). Notably, PAR increased during the 2005 and 2015/2016 droughts (Fig. 3b distributions; Extended Data 140 Fig. 5a, g), promoting green-up, but decreased during the 2010 drought (due in part to excess 141 1[42](https://paperpile.com/c/gDKLkA/qBmgd) smoke aerosols from high fire rates⁴², Fig. 3b distribution; Extended Data Fig. 5d). Anomalously 143 high VPD across the droughted region in 2010 (Extended Data Fig. 5e vs Extended Data Fig. 5b, 144 H), may also have contributed to reduced green-up/increased browndown in 2010. 133 135

Importantly, inter-drought differences in Southern Amazon forest responses were 146 mediated by drought length (Fig. 3c) (as hypothesized in Costa et al^{[24](https://paperpile.com/c/gDKLkA/32xKg)}). Despite the even greater 147 sunlight increases in 2015 than in 2005 (Fig. 3b histograms), the overall green-up in 2015/2016 was less than in 2005 (Fig. 3a), apparently due to the exceptional length of the latter drought 148 (Fig. 3c distribution). Initial green-up in shallow-water-table-forests (blue lines in Fig. 3c) 149 150 reversed to browndown in regions experiencing drought longer than three months, with 145

151 increasingly stronger browndown the longer the drought. Sufficiently long droughts thus likely 152 deplete shallow water tables, diminishing and then reversing their protective effect.

The contrasting responses between shallow and deep water table forests of the southern 154 Amazon support the "other side of drought" (hypothesis 1), and at the same time help reconcile 155 the much-discussed apparent disagreement between remote sensing studies showing 2005 156 drought-associated green-up on average^{[9,10](https://paperpile.com/c/gDKLkA/p6yui+5gmaM)} (interpreted as showing forest resilience to or even 157 benefit from drought) and ground-based plot studies showing 2005 drought-associated excess in 158 tree mortality on average^{[16](https://paperpile.com/c/gDKLkA/i3iSm)} (interpreted as showing forest vulnerability to drought). Our more 159 fine-grained analysis suggests, however, that the excess greening and the excess mortality were 160 not in the same places; it is the locales with shallow water table forests that were benefited by 161 drought, while deep water table forests are vulnerable, a consistent pattern revealed by both 162 remote sensing (Figs. 3a, 2b) and ground-based forest demography (tree mortality drought 163 response increases with water table depth, Fig. 3d). The apparent disagreement arises because 164 the published plot-based sampling efforts^{[2,16](https://paperpile.com/c/gDKLkA/i3iSm+ANsHP)} are not random, but skewed towards the deeper 165 water table regions which experienced browndown during drought (Fig. 3e & Fig. 2b, 166 orange-shaded regions), while the basin as a whole has more shallow water table forests like 167 those that experienced greening (Fig. 3e & Fig. 2b, green-shaded regions) (half of the Amazon 168 basin). Shallow water tables may thus gain (or lose less) carbon during drought (as seen in 169 Esteban et al.^{[27](https://paperpile.com/c/gDKLkA/2ZZig)}) partially offsetting the more negative effect of drought seen on forest mortality 170 and carbon balance in deeper water table forests^{[2,16](https://paperpile.com/c/gDKLkA/ANsHP+i3iSm)}. 153

Basin-wide forest drought response 171

Although we observed consistent support for the "other-side-of-drought" (hypothesis 1) 173 across both time (three droughts) and space in southern Amazon forests (Fig. 3a) (separately 172

174 confirmed by causal modeling analysis, Extended Data Fig. 10a), we found consistently *opposite* 175 drought responses with water table depth (EVI anomalies increased with water table depth) in the 176 everwet Amazon of the northwest and in the lower-fertility Guiana shield in the northeast 177 (Extended Data Fig. 8, where fertility is quantified as exchangeable base cations^{[43](https://paperpile.com/c/gDKLkA/x1zXd)}). These 178 observations falsify hypothesis 1 outside the southern Amazon. We next used forest responses to 179 the 2015/2016 drought (the only drought large enough to substantially impact large portions of 180 all three regions of the basin simultaneously), to test whether joint consideration of all three 181 hypotheses together could explain the biogeography of forest drought response across the basin 182 as a whole.

When gridded ecotope factors (soil fertility and texture^{[43,44](https://paperpile.com/c/gDKLkA/x1zXd+8CpZL)} and vegetation properties 184 such as canopy height^{[34,45](https://paperpile.com/c/gDKLkA/pbgPo+bb7bO)}) were included as predictors in our GAM analyses for the $2015/2016$ 185 drought (Fig. 4, Extended Data Table 1d), coherent differences between southern and northern 186 Amazon regions emerged from interacting effects of water table depth (hypothesis 1^{24} 1^{24} 1^{24}), soil 187 fertility (hypothesis $2^{28,29}$ $2^{28,29}$ $2^{28,29}$) and tree rooting depth (hypothesis 3, using forest canopy height as a 188 rough proxy for rooting depth when water tables are deep, consistent with limited observations 189 of tree height-rooting depth relations $31-33,46$. 183

The effect of water-table depth on drought response across regions depended on soil 191 fertility (Fig. 4a): Highly fertile areas most strongly evinced the protective effect of shallow 192 water tables (Fig. 4a, green portion of the fertility distribution, corresponding to green lines in 193 Fig. 4c), while lower-fertility areas were either less affected by water table depth or showed the 194 opposite response pattern (Fig. 4a, blue portion of the forest height distribution, corresponding to 195 blue lines in Fig. 4c). This is consistent with hypothesis $2^{28,29}$ $2^{28,29}$ $2^{28,29}$ that as soil nutrients become more 196 limiting, trees invest in drought resistance traits (e.g. high xylem embolism resistance), and with 190

197 observations of strong association between regions of low soil fertility and high wood density (Extended Data Table 2). We also noted interactions of water table depth with soil texture 198 (Extended Data Fig. 11), as discussed in methods §2.6.1(ii). 199

The effect of water-table depth on drought response also depended on forest height (Fig. 4b), with the tallest forests, expected to have deeper rooting zones, enabling green-up even in 201 202 regions (like the Guiana shield) with deeper water tables (Fig. 4b red portion of the forest height 203 distribution, corresponding to red lines in Fig. 4d). Meanwhile, taller forests performed worse 204 than shorter tree forests in shallow water table areas (Fig. 4d and Extended Data Fig. 10d, red vs 205 blue lines), consistent with findings that when lacking a deep root advantage, tall trees may 206 suffer higher drought mortality due to greater exposure to atmospheric drought (high VPD)^{[47](https://paperpile.com/c/gDKLkA/74BPM)}. Deep water tables may promote deep-rooted tall trees with resilience to seasonal atmospheric 207 and soil water deficit exposure, with access to more consistently available deep soil water, 209 enabling them (like shallow rooted trees over shallow water tables) to take advantage of extra 210 sunlight during moderate droughts. 200 208

An empirical test of the basin-wide model predictions (Fig. 4a-d) showed that the fully 212 integrated analysis accounting for the differences in the ecotope factors in different regions (Extended Data Fig. 3), was able to consistently predict the different kinds of drought responses 213 214 observed in different regions of the basin (Fig. 4e). 211

Our GAM modeling framework powerfully allows further investigation of additional 216 questions, generating a rich suite of testable hypotheses for future research into forest drought 217 response (methods \S 3). These include the question of whether coarse-scale patterns (like those deriving from the 1-40 km pixels used here) may emerge from such mechanisms as access to 218 water tables, which vary across landscapes, from forest plateaus to adjacent valleys, at fine scales 219215

220 of just a few meters (Extended Data Fig. 12); how individual relatively tall trees may be at 221 greater drought risk^{[48,49](https://paperpile.com/c/gDKLkA/dqt9C+ld6M0)} even within tall forests whose average height is here predicted to be more 222 protective against drought; whether forests are more sensitive to droughts that occur in wet 223 versus dry seasons (Extended Data Fig. 13); the effects of forest degradation on drought 224 sensitivity (Extended Data Fig. 14); and of the generality of these mechanisms in other 225 ecosystem types in the Amazon basin and beyond.

A functional biogeography of Amazon drought 226

We used the GAM predictions (Fig. 4) of different drought responses across different 228 forest ecotopes (here defined by water table depth, soil fertility and texture, and forest height) to map a biogeography of forest drought resilience (where resilient pixels, as defined in methods 229 §2.4, are those in which ecotope factors promote relative green-up) and vulnerability (pixels in 230 which ecotope factors promote browndown) across the Amazon basin (**Fig. 5a**), including the 231 232 ecotope factor combinations conducive (or not) to resilience (Fig. 5b, c). 227

This functional biogeography reveals the importance of ecotopes in structuring forest 234 drought response: first, simply because the GAM models which accouted for forest ecotopes (via 235 the variables HAND, SoilFertility, SoilTexture, and ForestHeight; Extended Data Fig. 3) along 236 with climate had significantly more predictive power (higher R^2 while selected by lower AIC) 237 than climate-only models (Extended Data Table 1). More importantly, the ecotope-defined biogeography allows attribution of greening-inferred resilience in different forests to distinct mechanisms. For example, during the 2015/2016 drought, forest greening was observed both in 239 240 the shallow water table forests of the Rio Negro basin and in deep water table forests of Amapa 241 state ("RN" and "AP" regions, respectively, highlighted in Figs. 1c, 4b and 5a). The 242 biogeography (Fig. 5b) and GAM prediction (Fig. 4b) show both regions sharing infertile soils, 233 238

243 but they point in particular to forest height—and associated deep rooting zones enabling access 244 to deep water—as a key factor supporting resilience/greening in the deep water table forests of AP (coded orange in Fig. 5b, c), whereas the RN forests (coded green in Fig. 5b,c), though short, 245 246 had access to shallow water tables.

This new analysis goes beyond previous climate-based explanations of Amazon forest 248 drought response, and importantly complements the recent map of *external* anthropogenic tipping-point threats (due to combined stresses of droughts, deforestation, fire, roads, etc.)^{[7](https://paperpile.com/c/gDKLkA/WeoKb)} with a biogeography of *intrinsic* ecological resilience/vulnerability (due to characteristics of forests in 250 251 their adapted environments). Interaction among the three different hypotheses—that hydrologic 252 environments, soil fertility, and tree drought resistance traits structure forest drought 253 response—shows that no single factor could explain drought response across the whole basin 254 through different droughts. Thus, shallow water table hydrologic environments do indeed protect 255 against drought^{[24](https://paperpile.com/c/gDKLkA/32xKg)}, but only relatively, especially in regions where high fertility stimulates the fast 256 growth of hydraulically more vulnerable trees^{[28](https://paperpile.com/c/gDKLkA/zXgTd)} (Fig. 5c, where the blue-labeled fertile regions 257 with shallow water tables are the least vulnerable among the first four "more vulnerable" 258 combinations on the left). The most resilient forest types (Fig. 5c) were those with low soil 259 fertility, occupying all categories of the "more resilient" end of the drought-response 260 biogeography (the right side of Fig. 5c). 247 249

Confidence in this new forest biogeography arises from corroboration by ground 262 observations, and by consistent results from different modeling approaches (GAM predictive 263 models, Figs. 3 & 4, suggested causal linkages to driving variables that were confirmed by SCM 264 models that more rigorously test for causation, Extended Data Figs. 9 & 10). Remote sensing 265 observations generally align well with ecosystem photosynthetic fluxes derived from towers on 261

266 the ground (methods $\S1.6$), and here, with tree demography during the three droughts (Fig. 3a vs 3d for 2005 and 2010, and Extended Data Fig. 16, for 2015), with remote photosynthetic 267 anomalies negatively correlated to mortality, and positively to recruitment, as expected if more 268 negative anomalies are associated with increased plant stress. Notably, our GAM-derived remote 269 270 sensing resilience map also independently predicted observations in forest plots of tree xylem 271 hydraulic safety margins to mortality-inducing embolism^{[50](https://paperpile.com/c/gDKLkA/xHuM4)}, a widely-cited physiological drought 272 tolerance trait (Fig. 5a inset).

Implications of a new Biogeography 273

This work has important implications for understanding forest responses to climatic 275 variability and change. First, because shallow water table forests in Amazonia are extensive (30-40% of the southern Amazon where they are found to be protective during drought) but 276 277 neglected by most previous studies of forest drought sensitivity (Fig. 3e histograms), southern 278 Amazon forests are likely more resilient to drought than common estimates of climate sensitivity 279 imply^{[16](https://paperpile.com/c/gDKLkA/i3iSm)}, and large-scale plot-based estimates of a drought-induced decline in the Amazon forest 280 280 carbon sink² may need to be adjusted to account for these more drought resilient but neglected 281 forests. 274

However, this analysis also warns that climate change is likely simultaneously 283 undermining different strategies and capacities for drought resilience, and highlights specific mechanisms and Amazon regions likely to be vulnerable to tipping-point failure: the resilience 284 285 conveyed by shallow water table hydrologic environments in certain regions (or the long-term benefits of a strategy of growing "trees fast in high-fertility environments to replace those easily 286 287 287 lost to drought²⁸) is likely limited under growing climate change. The buffering effect of shallow 288 water tables appears limited to short duration droughts $($ < 3 months, Fig. 3c) that do not last long 282

289 enough to deplete water tables. And the benefits of re-growing trees quickly that are lost to once-in-a-century droughts (whether or not protected by shallow water tables) are much reduced 290 when those drought frequencies increase to become 5 or 10-year droughts (as seen recently and 291 292 as predicted to continue in the near future^{[51,52](https://paperpile.com/c/gDKLkA/snI53+B55Fz)}). Importantly, these fertility results imply 293 293 (consistent with a recent ground-based study of hydraulic traits²⁹) that it is Amazonia's most 294 productive higher-fertility forests that are actually those most vulnerable to future climate 295 change.

Finally, we note that the geographic distribution of these most-vulnerable forests (Fig. 5a 297 reddish regions) has important warnings for sustaining the integrity of critical ecosystems both in 298 the basin and beyond. First, these vulnerable forests are at high risk of deforestation (substantially overlapping with the "arc of deforestation," Extended Data Fig. 18). More 299 300 importantly, because they are predominantly situated under prevailing winds that bring moist Amazonian air to the south (Extended Data Fig. 18) they are critical to maintaining the 301 302 evapotranspiration that feeds (and likely amplifies^{[53](https://paperpile.com/c/gDKLkA/TqlQZ)}) the "atmospheric rivers" that bring 303 forest-recycled precipitable water from the Amazon regions to sustain South America's 304 breadbasket in the agricultural regions of Brazil^{[54](https://paperpile.com/c/gDKLkA/Cut6I)}. 296

This unified understanding of the functional biogeography of Amazon drought response 306 provides a basis both for establishing basin-wide priorities for conservation planning and for 307 achieving improved understanding and predictions of tropical forest vulnerability to current 308 droughts, threatened tipping points, and future climate change. 305

FIGURE CAPTIONS 309

Fig. 1. Amazon forest remotely-sensed responses to the droughts of (a) 2005, (b) 2010, and 310 **(c) 2015/2016, expressed as** standardized anomalies of Enhanced Vegetation Index (EVI, a 311 312 proxy of photosynthetic capacity) in drought-affected pixels (defined in Extended Data Fig. 1). 313 (note: panel A highlights an ellipse of green-up and browndown patterns that correspond to 314 shallow and deep water tables in Fig. 2a; panel C highlights two areas exhibiting green-up—RN, 315 in Rio Negro catchment, and AP in Amapa state—for comparison to Figs. 4-5). Insets: 316 Frequency distributions of MAIAC EVI anomalies in drought regions for (a) 2005 (\triangle *EVI* = $_{317}$ +0.14, p<0.001, df =916, (b) 2010 (\triangle EVI = -1.06, p<0.001, df =1057) and (c) 2015 (\triangle EVI = 318 -0.57, p<0.001, df=2218) droughts. Statistics are from student's t-test, where, following the 319 variogram analysis (Methods $\S2.5$) the degrees of freedom, df=n-1, were adjusted for 320 autocorrelation based on $n =$ number of statistically independent $0.4^\circ \times 0.4^\circ$ drought-affected 321 pixels in each drought region.

Fig. 2. Amazon forest response to 2005 drought is structured by water-table depth: (**a**) 322

Water-table depth map (indexed by Height Above Nearest Drainage, HAND, in meters, Andes 323 324 excluded^{[25](https://paperpile.com/c/gDKLkA/465Cp)}) with ellipse highlighting shallow and deep water tables that correspond to green-up and browndown patterns in Fig. 1a. (**b**) Observed EVI anomalies (solid symbols±SE, from Fig. 325 326 1a, left axis) bin-averaged by water-table depth (HAND), and by moderate, medium, and severe 327 drought pixels (those with MCWD 1-1.5 SD, 1.5-2 SD, and >2 SD below mean, respectively); 328 area histogram of drought-affected HAND (right axis). Average EVI anomaly across all 329 severities (horizontal lines) for shallow (0-8 m, green band) and deep water-table forests $(222 \text{ m},$ orange band). (**c**) Observed EVI anomalies (solid symbols±SE, from Fig. 1a) bin-averaged by 330 PAR anomalies and by different water-table depths (HAND values) (upper panel); histograms of 331 332 PAR anomaly (lower panels) according to drought severity.

Fig. 3. Southern Amazon forest responses to multiple droughts: (a-c) GAM (Extended 333 **Data Table 1a) predictions**: (**a**) Climate-adjusted EVI responses vs. water-table depths (indexed 334 335 by HAND) support hypothesis 1 (with consistent negative slopes) for observations (points $\pm 95\%$ CI and solid regression line) and GAM predictions for the 2005 (green, slope=-0.019±0.001 SD 336 337 m^{-1}), 2010 (purple, slope=-0.020±0.002 SD m⁻¹), and 2015 (blue, slope=-0.028±0.002 SD m⁻¹) 338 droughts (shading and dashed regression lines), paired with HAND distributions in each drought 339 region(bottom graphs, right axis); (b) PAR sensitivity, by HAND class, of (climate-adjusted) EVI 340 drought responses, paired with drought-specific area distributions of PAR anomalies (right axis), 341 show greater PAR sensitivity for shallower water tables. (c) Drought-length sensitivity, by 342 HAND class, of (climate-adjusted) EVI drought response, paired with drought-specific area 343 distributions of duration (in months) (bottom graphs, right axis) show that shallow-water-table 344 protection is diminished for long droughts. 'Climate-adjusted' responses use southern Amazon 345 drought-specific average climate to predict responses or adjust observations. Each drought's 346 distribution occupies equal area across the three panels. (d) Above-ground biomass (AGB) 347 mortality drought responses (mortality-associated carbon flux, in percent change relative to 348 long-term MgC ha⁻¹ y⁻¹ in RAINFOR plots^{[2](https://paperpile.com/c/gDKLkA/ANsHP)}) vs. water-table depth (HAND) (points \pm 95% CI, 349 regression line for depths less than 30 meters) support hypothesis 1 (with consistent positive 350 slopes) for the 2005 (green, slope=1.4 % m⁻¹, p=0.051) and 2010 (purple, slope=1.8 % m⁻¹, p=0.015) droughts, paired with (**e**) cumulative distributions of HAND area across basin (gray 351 352 bars, left axis), and distribution of plot-based sampling efforts (fractional effort, RAINFOR plot 353 area \times years monitored, per HAND bin, divided by fractional basin area per HAND bin, blue 354 bars, right axis). This shows that plot sampling efforts underrepresent prevalent shallow 355 water-table forests that greened up (green band, \sim 55% of the basin, but 16% of the effort) and 356 over-represent deep water-table forests that browned down (orange band, \sim 20% of the basin but 55% of the effort). 357

Fig. 4. Basin-wide Amazon forest responses to the 2015 drought, structured by ecotopes 358 **and predicted by whole-basin GAM analysis (Extended Data Table 1d):** GAM partial 359 360 predictions of EVI anomalies (color scale) for (a) soil fertility^{[43](https://paperpile.com/c/gDKLkA/x1zXd)} (vertical axis) and HAND^{[25](https://paperpile.com/c/gDKLkA/465Cp)} 361 (horizontal axis) terms only, and for (b) forest height^{[45](https://paperpile.com/c/gDKLkA/pbgPo)} and $HAND²⁵$ $HAND²⁵$ $HAND²⁵$ terms only. Ecotope 362 distributions in southern, everwet, and Guiana shield forests are in A-B margins, and associated 99% confidence ellipses are in the graphs. Mean values of two areas exhibiting green-up in Fig. 363 364 1c (RN, in Rio Negro catchment, and AP in Amapa state) illustrate differing mechanisms of 365 green-up (especially evident in B, where tall trees, despite deep water tables, promote green-up in AP, while shallow water tables promote green-up for RN). (**c**)(**d**) adjusted EVI anomaly versus 366 367 HAND with increasing (c) fertility (blue to green, corresponding to colored areas in fertility 368 distributions in a) or (d) forest height (blue to red, corresponding to colored areas in forest height distributions in b). (**e**) Region-specific EVI anomaly sensitivities to HAND, comparing adjusted 369 370 observations (symbols) to adjusted GAM predictions (lines and 95% confidence shaded area). 371 Note: 'adjusted' EVI anomalies indicate that climate and ecotope factors not displayed in the 372 graph are held constant at basin-wide (a-d) or regional average values (e).

Fig. 5. A biogeography of Amazon forest drought resilience and vulnerability: (**a**) Regions 373 374 relatively more resilient (likely to exhibit EVI green-up) (green) or more vulnerable (red) to 375 drought, based on standardized GAM drought response predictions of EVI anomaly from 376 ecotope factors only (from Fig. 4, Extended Data Table 1d) (removing effects of climate 377 variability by setting climate equal to its basin-wide average) (see methods $\S2.8$). Crosses are 378 validation sites where remote sensing-derived resilience predicts plot-based physiological 379 drought tolerance (tree hydraulic safety margins, HSM_{50}) as seen in the inset ($R^2=0.65$; p=0.008); (**b**) Overlapping strategies and ecotopes structuring the distribution of relative drought resilience 380 mapped in (a), as promoted by presence of resilience factors: shallow water tables 381 382 (HAND<10m, blue), low-fertility soils (cation concentrations<10 \cdot ^{0.35} cmol \cdot /kg, yellow), or tall 383 deep-rooted trees (heights>32.5 m, red), with overlap indicated by the primary color mixing rules 384 in the legend, and white indicating no resilience factor (which notably corresponds well to the most vulnerable red regions in a). (**c**) Distribution of resilience factor groups, and the proportion 385 386 of relatively vulnerable, resilient, or neutral forest associated with each (left axis) and mean 387 relative resilience (blue horizontal lines, right axis), ordered from most vulnerable to most 388 resilient.

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Methods 506

In this study, we applied a hypothesis-testing framework^{[55,56](https://paperpile.com/c/gDKLkA/Ytisa+xdvJm)}, using remote sensing methods 508 to test a sequence of three key ecological hypotheses that predict how different forest types 509 respond to drought. To conduct these tests, we assembled key datasets (Section 1), including two 510 classic satellite products of vegetation photosynthetic function (the most recent version of the Enhanced Vegetation Index, EVI, and Solar Induced Fluorescence, SIF) (section 1.1, including 511 512 their validation), gridded products of climate (section 1.2), water table depth, soil fertility and 513 texture, and vegetation properties defining ecotopes (section 1.3). We focused on intact 514 evergreen forests, mapping data in areas corresponding to evergreen forest cover in 515 non-floodplain, non-deforested forest regions (section 1.4). We assembled field datasets of forest 516 demography (from RAINFOR^{[2](https://paperpile.com/c/gDKLkA/ANsHP)} and from Sousa et al.^{[26](https://paperpile.com/c/gDKLkA/7LA7D)}) and of physiological drought tolerance 517 (Tavares et. al^{[50](https://paperpile.com/c/gDKLkA/xHuM4)}) (section 1.5) to test remote sensing skill at capturing ground-measured metrics 518 for forest drought response (section 1.6). 507

To conduct the statistical analysis (**Section 2**), we first interpolated data products onto grids 520 of appropriate spatial resolution (section 2.1), and conducted a supervised classification analysis 521 of Amazon forests into three distinct regions defined by ecotope (section 2.2). We defined 522 climate anomalies and drought characteristics and duration on a pixel-by-pixel basis (section 2.3), defined forest drought resilience in terms of anomalies in vegetation function (section 2.4), 523 524 conducted a variogram analysis to remove effects of spatial autocorrelation (section 2.5), and 525 then evaluated the scale dependence, or sensitivity of key results to the pixel size/spatial 526 resolution (section 3). We derived statistical models of drought response (section 2.6) using two 527 independent approaches: predictive regression modeling (General Additive Modeling, GAM, a 528 non-linear multiple regression technique where the most predictive models are selected by an 529 information criterion) (section 2.6.1), and Structural Causal Modeling (SCM, using Directed Acyclic Graphs, DAG, section 2.6.2). We tested GAM predictions by comparison to adjusted 530 531 observations (section 2.7) and then used the basin-wide GAM predictive model (from section 2.6.1) to derive a functional biogeography of drought response (section 2.8). 532 519

Finally (**Section 3**), we addressed confidence in our interpretations by exploring potential 534 alternative mechanisms and caveats, and by using the predictive GAM framework to conduct 535 tests of alternative hypotheses that could either support or reject those presented in the main text. These provided evidence in support of our interpretation, but also pointed to future research 536 537 needs. 533

1. Datasets 538

539 1.1. Remote sensing indices of photosynthesis

We applied two widely used, ground-validated remote sensing indices of photosynthesis 541 to provide a sensitivity analysis that brackets the plausible range of forest canopy response to 542 drought: the Enhanced Vegetation Index (EVI), constructed from observations of surface 543 reflectance by the MODerate resolution Imaging Spectroradiometer (MODIS) onboard the Terra/Aqua satellites; and the global OCO-2 Solar-induced Fluorescence (GOSIF) product 544 545 derived from observations by the Orbiting Carbon Observatory 2 satellite. EVI, derived from the spectra of light reflected from surface vegetation, is designed as an index of the *photosynthetic* 546 547 capacity^{[57](https://paperpile.com/c/gDKLkA/lnNzK)}. GOSIF is designed to represent the active light emission from fluorescing chlorophyll molecules during photosynthesis, which is often well-correlated with canopy-scale instantaneous 548 549 *photosynthetic activity⁵⁷*. This distinction (between reflected light used to construct EVI as a 540

550 proxy for capacity, versus actively emitted light used to construct GOSIF as a proxy for activity) means that these indices may be expected to display divergent responses. 551

We chose these indices because they aim to capture different end-members of a spectrum 553 of canopy responses: from transient physiological changes in photosynthesizing/fluorescing 554 leaves (which might be due, for example, to stomatal regulation in response to changing 555 atmospheric VPD) which affect photosynthetic activity for a given capacity^{[58](https://paperpile.com/c/gDKLkA/luHda)}, versus more 556 structural responses associated with leaf turnover such as leaf flushing or shedding which also 557 change canopy photosynthetic capacity^{[59](https://paperpile.com/c/gDKLkA/ZcED2)}. We primarily focus here on EVI responses, which have 558 been shown to remotely capture seasonal canopy greenup dynamics that are consistent with 559 underlying mechanisms of leaf development and demography^{[60](https://paperpile.com/c/gDKLkA/frCbw)}. However, GOSIF corroboration 560 of EVI drought responses at broadscales would suggest that ecophysiological and structural canopy responses to drought are aligned in the Amazon, increasing confidence in the robustness 561 562 of remotely observed drought responses. 552

MAIAC EVI: The Multi-Angle Implementation of Atmospheric Correction (MAIAC) algorithm rigorously accounts for sun-sensor geometry, as represented in a bidirectional 564 565 reflectance distribution function (BRDF), estimating reflectance at a nadir view and 45° solar 566 zenith angle, with strict atmosphere, aerosol, and cloud corrections^{[61](https://paperpile.com/c/gDKLkA/yZ3zl)}. We used the 8-day MCD19A3 (MAIAC) 1-km product from MODIS collection six, a level 3 product composited 567 from cloud-free and low aerosol conditions. We applied the coefficients (weights) of the 568 RossThick/Li-Sparse (RTLS) Bidirectional Reflectance Distribution Function (BRDF) model 569 570 (available at [https://e4ftl01.cr.usgs.gov/MOTA/MCD19A3.006/\)](https://e4ftl01.cr.usgs.gov/MOTA/MCD19A3.006/). We calculated the 8-day EVI 571 571 from the MAIAC surface reflectances of red, blue, and near-infrared bands as in Huete et al.⁵⁷ 572 from 2001-2019. The 8-day EVI is then aggregated to a monthly time step. *GOSIF*: Solar induced fluorescence (SIF), emitted by chlorophyll molecules in green plants 574 that have been excited by absorption of sunlight, provides a direct index of the current 575 physiological state of a photosynthesizing canopy^{[62](https://paperpile.com/c/gDKLkA/Wl3bw)}. The OCO-2 satellite observes SIF at coarse 576 resolutions^{[63](https://paperpile.com/c/gDKLkA/AT7FJ)}, and these are used to create the modeled GOSIF data product^{[64](https://paperpile.com/c/gDKLkA/6LNG5)} available at 577 http://data.globalecology.unh.edu/data/GOSIF_v2), which simulates higher resolution SIF 578 dynamics over longer time periods by interpolating among discrete OCO-2 SIF soundings using 579 the MODIS surface reflectance product MCD43C4 (BRDF-corrected to nadir view and to the 580 solar zenith angle at local noon), and meteorological reanalysis data^{[64](https://paperpile.com/c/gDKLkA/6LNG5)}. We used the monthly 581 composite GOSIF product with high spatial resolution of 0.05° over the period from 2001 to 2019. Among SIF-related products, GOSIF has been found to be the best predictor of GPP across 582 583 land cover types^{[65](https://paperpile.com/c/gDKLkA/mwrB7)}. 563 573

584 1.2. Climate variables

To explore climate effects on forest drought responses, we used monthly precipitation, 586 Maximum Cumulative Water Deficit (MCWD), surface downwelling shortwave radiation and 587 Vapor Pressure Deficit (VPD) resampled at 0.4°. Precipitation and MCWD are from the Global Precipitation Mission (GPM) and Tropical Rainfall Measuring Mission (TRMM) 3B43-v7 for 2000-2020 at 0.25° resolution (~25 km x 25 km) 585 588 589

(https://disc2.gesdisc.eosdis.nasa.gov/data/TRMM_L3/TRMM_3B43.7/)^{[66](https://paperpile.com/c/gDKLkA/zihxb)}. 590

MCWD measures local drought intensity, defined as the maximum deficit reached in the 592 last month of a string of dry months for each grid cell within the year^{[39](https://paperpile.com/c/gDKLkA/HHtIX)}, treating forest water 593 deficit as analogous to a bucket whose deficit is zero when the bucket is full. To avoid splitting a 591

594 string of dry months between two years, we used a 12-month 'hydrological year' running from 595 May to the following April (e.g., MCWD for 2004 was calculated using CWD data from May 2004 to April 2005). We also used monthly surface downwelling shortwave radiation from 596 597 Modern-Era Retrospective analysis for Research and Applications version 2 (MERRA-2 598 Reanalysis) for 2000 to 2019 as a proxy for PAR at spatial resolution of 0.5° x 0.625° 599 ([https://goldsmr4.gesdisc.eosdis.nasa.gov/data/MERRA2_MONTHLY/M2TMNXRAD.5.12.4/\)](https://goldsmr4.gesdisc.eosdis.nasa.gov/data/MERRA2_MONTHLY/M2TMNXRAD.5.12.4/)^{[67](https://paperpile.com/c/gDKLkA/GBlpD)} . Vapor Pressure Deficit (VPD) was calculated based on surface air temperature and relative 600 humidity (L3 Standard Monthly Product, AIRS3STM) from version 6 of the Atmospheric 601 602 Infrared Sounder (AIRS) at the spatial resolution of 1 degree for 2003-2017 (\sim 100 km, 603 <https://airs.jpl.nasa.gov/data/get-data/standard-data/>)⁶⁸⁻⁷¹.

604 1.3. Ecotope variables

We follow the ecosystem ecology approach^{[18,19](https://paperpile.com/c/gDKLkA/TeqQr+0BEgg)} of characterizing different ecosystem types (in this case, forest ecosystems) by their "ecotopes", that is, by the combination of biotic 606 607 characteristics and abiotic environments that define them, here including their hydrological environment (water table depth), soil types (fertility and texture), vegetation characteristics, and 608 609 other factors^{[72](https://paperpile.com/c/gDKLkA/WwPel)}. 605

We used the Height Above the Nearest Drainage (HAND) normalized terrain model^{[25,73](https://paperpile.com/c/gDKLkA/465Cp+8zNlf)} as a proxy of water table depth and for plant access to groundwater, rederived at 100m resolution 611 612 from digital elevation model-Shuttle Radar Topography Mission (SRTM) data for this study^{[26,74](https://paperpile.com/c/gDKLkA/OK4pb+7LA7D)}. The HAND normalization is relative to the local drainage height, using the flow paths to connect 613 all cells (pixels) with the cells of the nearest drainage. The HAND model has been validated over 614 615 an area of 18,000 km² in the lower Rio Negro catchment^{[25](https://paperpile.com/c/gDKLkA/465Cp)} and used for a wide range of 616 ecohydrological studies^{[27,75,76](https://paperpile.com/c/gDKLkA/38cqI+b73Ja+2ZZig)}. HAND is comparable to the water table depth (WTD) model-based 617 product of Fan & Miguez-Macho^{[77](https://paperpile.com/c/gDKLkA/0ESYS)}, which gave broadly similar results to those reported here with HAND. For this study the HAND normalized terrain model was derived from SRTM-DEM 618 at 100 m resolution. 619 610

For soil fertility, we used a map $(0.1^{\circ}$ spatial resolution) of exchangeable base cations $(Ca^+$ $621 + Mg⁺ + K⁺$ measured in cmol(+)/kg) for the Amazon basin^{[43](https://paperpile.com/c/gDKLkA/x1zXd)}, the most extensive 622 empirically-validated gridded soil fertility product currently available. Soil cation concentrations 623 estimated from this product achieved good agreement with an independent dataset of 624 field-measured values (correlation of $r = 0.71^{43}$ $r = 0.71^{43}$ $r = 0.71^{43}$). 620

Our analysis does not include phosphorus, generally considered to be limiting to tropical 626 forest productivity^{[78,79](https://paperpile.com/c/gDKLkA/AGBb2+sRQI4)}, but not currently available as a high-quality validated gridded data 627 product. We expect base cations to be a partial index of phosphorus availability, as both cations and phosphorus become available though weathering of young soils arising from Andean parent 628 material or runoff sediment, but are eventually leached, leaving older highly weathered soils in 629 630 the Guiana Shields depleted of both. Cation concentration should also be directly relevant to 631 drought tolerance, as high concentrations should improve osmotic regulation of stomatal conductance, an important regulator of drought response^{[80](https://paperpile.com/c/gDKLkA/tQsvY)}. 625 632

For soil texture, we used soil sand/clay fractions from "SoilGrids" system released by 634 ISRIC (International Soil Reference Information Centre) World Soil Information^{[44](https://paperpile.com/c/gDKLkA/8CpZL)}. 633

For forest height, we used a canopy height metric derived from spaceborne lidar 636 measurements^{[45](https://paperpile.com/c/gDKLkA/pbgPo)} [\(https://webmap.ornl.gov/ogc/dataset.jsp?dg_id=10023_1\)](https://webmap.ornl.gov/ogc/dataset.jsp?dg_id=10023_1) and validated by field 637 measurements, with an increased accuracy in the Amazon compared to previous metrics^{[33](https://paperpile.com/c/gDKLkA/ycA42)}). This 638 wall-to-wall global map of canopy height is at 1-km spatial resolution, interpolated from lidar 639 observations by the Geoscience Laser Altimeter System (GLAS) aboard ICESat (Ice, Cloud, and 635

Land Elevation Satellite). We take forest canopy height as a proxy of rooting depth, based on 640 641 standard allometries backed by observations in Brazilian tree plantations^{[31,32,46](https://paperpile.com/c/gDKLkA/uVIEh+Dy8Mm+qawQE)}, in a central 642 Amazon forest^{[31,32,46](https://paperpile.com/c/gDKLkA/uVIEh+Dy8Mm+qawQE)} and across biomes^{31,32,46} that show they are correlated^{31,32,46}. However, 643 observations of the tree height-rooting depth allometry are limited, especially in tropical forests 644 (although one study cited here^{[31](https://paperpile.com/c/gDKLkA/Dy8Mm)} is directly relevant, as it is from central-eastern Amazon upland 645 forest, conducted during the 2015 drought); this limitation remains a key uncertainty in our 646 ability to confidently attribute variations in drought response to rooting depth, as opposed to canopy height itself, or other (as yet unidentified) correlates of canopy height. We also note that 647 shallow WTD limits rooting depth such that canopy height correlations to rooting depth in these 648 649 forests may be diminished 81 .

We also applied community-weighted mean wood density and the abundance of Fabaceae 651 (legumes)^{[34](https://paperpile.com/c/gDKLkA/bb7bO)}. Fabaceae refers to a large, nearly cosmopolitan family that relates woody plants 652 with nitrogen-fixing nodulation, usually assumed adaptations to low-fertility soils^{[82](https://paperpile.com/c/gDKLkA/ysapK)}. 650

653 1.4. Identification of terra firme Amazon basin forests using land cover maps

In order to focus our analysis on the desired domain of terra firme forests, we used a 655 forest map at 1 km spatial resolution (MOD12Q1.006) to identify evergreen forest pixels within 656 the Amazon basin^{[83](https://paperpile.com/c/gDKLkA/NNlni)}, excluding open water, deforested forests, and non-forest vegetation types. A 657 floodplain map was also used in order to identify targeted non-flooded forests, and exclude 658 floodplain forests^{[84](https://paperpile.com/c/gDKLkA/W3uM1)}. We used the map of Gomez et al.^{[85](https://paperpile.com/c/gDKLkA/U0dcW)} to define the boundary of the Amazon 659 basin, an inclusive definition encompassing all forested parts of the Amazon river catchment and Amazon forests technically within the Orinoco river catchment. We used a recently published 660 forest cover classification that now includes a category for "degraded" forests at 30 meter spatial 661 662 resolution (Vancutsem et al.^{[86](https://paperpile.com/c/gDKLkA/fMhzl)}, updated to 2022), to test drought sensitivity (methods 3). 654

663 1.5. Forest Plot Data

RAINFOR long-term forest plots: We used demographic datasets over the period 1983-2011 from all of the 321 re-censused forest plots that were published and used to estimate 665 Amazon basin-wide carbon balance (most, but not all, of these were from the RAINFOR 666 667 network)^{[2](https://paperpile.com/c/gDKLkA/ANsHP)}, for three purposes: (1) to characterize the spatial representativity of the reported plot-based sampling efforts (area-weighted frequency**×**duration that plots were monitored) with 668 669 respect to the distribution of water table depths (HAND) across the Amazon basin (Fig. 3e); (2) 670 to test whether forest mortality anomalies (% deviation from long term mean) in 247 plots 671 subject to the 2005 and 2010 droughts were associated with water table depth (Fig. 3d); and (3) 672 to validate EVI remote sensing with spatial variations in long term (2000-2011) average 673 above-ground net primary productivity (ANPP) rates across the Amazon basin (section 1.6.b, Extended Data Fig. 15). The full RAINFOR and related networks sample more plots than these, 674 675 likely including a greater range of environments^{[87](https://paperpile.com/c/gDKLkA/ZMBC)}, but published results representing drought 676 response of "the Amazon rainforest"^{[16](https://paperpile.com/c/gDKLkA/i3iSm)} and "the Amazon carbon sink"^{[2](https://paperpile.com/c/gDKLkA/ANsHP)} are the ones whose sample plot distributions are analyzed here for their representivity. 664 677

Shallow water table forest plots: For remote sensing validation, we also used mortality and recruitment data from 25 1-ha plots distributed across eight research sites along the BR-319 679 680 road in the southern Amazon between Manaus and Porto Velho (from 62.5° W, 5.9° S to 60.9° W, 681 4.4°S) as analyzed in Sousa et al.^{[26](https://paperpile.com/c/gDKLkA/7LA7D)} These are shallow water table sites (2.81 m \pm 2.38 deep [M \pm 682 SD]) intended to complement the on average deeper water table sites of the RAINFOR network 678

(above). These more recent data focused on mortality and recruitment rates calculated for the 683 2015-2016 drought (section 1.6.b, Extended Data Fig. 16). 684

Forest plot hydraulic safety margins. We used a published pan-Amazon hydraulic trait dataset (hydraulic safety margins, HSM, the difference between water potentials experienced by 686 a species in the field and the water potentials leading to hydraulic failure, with narrower margins 687 688 indicating greater mortality risk)^{[50](https://paperpile.com/c/gDKLkA/xHuM4)}, including 108 species distributed across 9 forest sites across western, central eastern and southern Amazon, to validate our derived resilience map (Fig. 5). 689 These sites belong to old-growth lowland forests, little disturbed by human activities, spanning 690 691 the Amazonian precipitation gradient and encompassing the principal axes of species 692 composition in the Amazon^{[50](https://paperpile.com/c/gDKLkA/xHuM4)}. The HSM was calculated with respect to P50/88 (HSM50/88) at 693 species level, and then basal-area weighted averaged occurring at sites^{[50](https://paperpile.com/c/gDKLkA/xHuM4)}. 685 694

695 1.6. Remote sensing validation and consistency

1.6.1 Validation by ecosystem flux measurements (eddy flux towers) 696

MAIAC EVI: EVI has been extensively validated against measurements of ecosystem 698 photosynthesis (Gross Primary Productivity, GPP) from eddy flux towers across land types 699 world-wide^{[88](https://paperpile.com/c/gDKLkA/iDzAC)}, including temperate^{[89–91](https://paperpile.com/c/gDKLkA/wXWDd+GW25c+DVKM2)} and tropical biomes^{[92–94](https://paperpile.com/c/gDKLkA/ooK3T+WU5y2+NDDFx)}. Earlier versions of MODIS EVI 700 were criticized as influenced by aerosol or sun-sensor geometry artifacts when detecting tropical 701 forest greening^{[95,96](https://paperpile.com/c/gDKLkA/jKqsW+TC3d7)}, but such effects are largely eliminated in the current MAIAC EVI product 702 used here (which corrects artifacts from aerosol contamination and sun-sensor geometry) 61 . 703 Particularly relevant for this study, MAIAC EVI well-detected Amazon forest seasonal green-up 704 dynamics across a network of eddy flux tower sites in the Brazilian Amazon^{[97,98](https://paperpile.com/c/gDKLkA/PFdXY+QfZai)}, with patterns 705 shown to be consistent with understandings of leaf development and demography derived from 706 flux towers and phenocam studies on the ground^{[60](https://paperpile.com/c/gDKLkA/frCbw)}. 697

EVI or EVI-based models predict independent tower measurements of monthly GPP with 708 R²~0.5-0.7 for tropical^{92-94,97}, and R²~0.7-0.8+ for temperate biomes⁸⁹⁻⁹¹. 707

GOSIF: Despite non-linear and sometimes decoupled relationships between chlorophyll 710 fluorescence and photosynthesis at leaf scales^{[99](https://paperpile.com/c/gDKLkA/PRORn)}, satellite observations of SIF from OCO-2 have 711 been shown to be linearly related to canopy scale GPP 63 63 63 , suggesting that canopy scale processes 712 can effectively average over leafscale complexities. GOSIF modeled datasets built from SIF 713 observations have been multiply validated by tower-based CO2 flux estimates of GPP, achieving 714 good correlation ($R^2 = 0.73$ globally) with the 91 sites of global Fluxnet GPP (2015 Tier 1 715 dataset)^{[64](https://paperpile.com/c/gDKLkA/6LNG5)}, with somewhat lower correlations (R^2 =0.51, comparable to EVI in the tropics) for the 716 evergreen broadleaf forest biome, including sites in the Amazon^{[65](https://paperpile.com/c/gDKLkA/mwrB7)}. 709

Note on lower R² for Tropical vs Temperate forest GPP detection: Although both indices (GOSIF and EVI) capture GPP comparably in deciduous broadleaf (temperate) versus evergreen 718 719 broadleaf (tropical) forests *within* active growing seasons, most statistical assessments are of full 720 annual cycles, which typically show substantially better statistics ($R^2 > 0.8$) for temperate zone 721 forests, simply because temperate forests include easily detectable dormant periods when GPP \sim 722 0, which make total annual variability (hence R^2) higher, while tropical evergreen forests are 723 active year round. 717

724

725 1.6.2. Validation by forest plot metrics of demography and of physiological drought tolerance We investigated the effect of variations in remotely sensed photosynthesis on downstream 727 forest demographic effects (growth, recruitment, and mortality, section 1.5). We should expect 728 remote sensing skill in predicting demography to be weaker than for predicting photosynthetic 726

729 fluxes, because demography emerges, not from photosynthesis alone, but from the balance of 730 photosynthesis and autotrophic respiration, and is also influenced by other factors such as disturbance. 731

We nevertheless found validation at multiple scales: MAIAC EVI significantly predicted 733 spatial variations in decadal forest ANPP (during 2000-2011) across the Amazon basin (RAINFOR network, methods section 1.5, Extended Data Fig. 15). Using more recent data, we 734 735 also confirmed consistent detection by EVI and GOSIF of short-term demographic drought-response metrics during the 2015/2016 drought (mortality, recruitment, and the 736 737 mortality: recruitment ratio, Extended Data Fig. 16), as expected if excess mortality (or a decline 738 in recruitment) follows declines in photosynthetic carbon assimilation. The R^2 values of 0.25 to 0.35 for remote detection of demography (Extended Data Figs. 15-16) are consistent with our 739 740 expectation that they should be about half of the remote detection \mathbb{R}^2 for GPP (0.5 to 0.6, 741 discussed in 1.6.1), since GPP is about one-half the determinant of the NPP driver of 742 demography. 732

With respect to remote detection of the physiological drought tolerance of trees, we 744 investigated the ability of our remote sensing-derived forest photosynthetic "resilience" map (Fig. 5a, see methods section 2.8) to predict a metric of the resilience of individual trees to 745 746 drought, hydraulic safety margins (HSM) for xylem embolism. Individual tree HSM -- the 747 difference between observed stem water potentials and the stem water potentials at which trees 748 become vulnerable to xylem embolism -- are widely regarded as predictors of tree mortality risk 749 under drought^{[50](https://paperpile.com/c/gDKLkA/xHuM4)}, with narrower HSMs indicating greater mortality risk^{[36](https://paperpile.com/c/gDKLkA/ZRaSR)}. We found that our 750 remote sensing-derived estimates of forest resilience (Fig. 5a) could significantly predict 751 basal-area weighted tree HSM measured on the ground at forest plots across the Amazon basin 752 (Fig. 5a inset) (reported in Tavares et al.^{[50](https://paperpile.com/c/gDKLkA/xHuM4)}, as summarized in section 1.5). (Note that forest 753 resilience was estimated as in methods section 2.8, but using canopy height mapped at 0.1 degree 754 resolution--instead of the baseline model resolution of 0.4 degrees--in order to avoid mixing the 755 height signal of intact HSM plot forests with that of occasionally nearby deforested areas.) This 756 validation strongly supports the validity of using remotely sensed photosynthetic indices to 757 derive a definition of photosynthetic resilience to drought. 743

758

1.6.3. Consistency between EVI and GOSIF 759

Are the two remote sensing metrics showing consistent response to drought? The spatial 761 locations of the drought anomalies appear similar, though not the same (Fig. 1 vs Extended Data 762 Fig. 2) – but since EVI and GOSIF are intended to be sensitive to distinct dimensions of canopy 763 photosynthetic function -- i.e., to photosynthetic capacity versus activity, respectively (as 764 discussed in section 1.1), we should not expect sameness. 760

We do expect *activity* to be generally more sensitive to drought than *capacity*, because activity-based responses encompass both transient/reversible physiological responses (e.g. 766 767 stomatal adjustment) as well as slower structural effects due to changes in capacity (e.g. 768 biochemical inhibition, leaf growth or shedding)^{[58,100](https://paperpile.com/c/gDKLkA/luHda+DEuV5)}. We indeed see this expectation reflected in 769 observed drought response, with the range of GOSIF (activity) anomalies (from -9.6 to $+4.8$ 770 standard deviations, excluding 0.1% of the distribution in each tail) 30% greater than the range 771 of EVI anomalies (-6.5 to +4.5 standard deviations, Extended Data Fig. 2 vs Fig. 1 insets). More important, we ask whether there is consistency in terms of support for or rejection of 773 hypotheses that are the focus of this analysis -- for example, whether the "other side of drought" 774 prediction that drought response anomalies should decline with water table depth, and here we 765 772

775 do see broad support for this hypothesis from both EVI and GOSIF: for the 2005 drought 776 "ellipse" region that was discussed in the main text (Extended Data Fig. 2d), and for the three 777 droughts considered together (Fig. 3a vs Extended Data Fig. 2e). We also see similar ability of 778 the two metrics to predict tree demographic responses to drought on the ground (Extended Data 779 Fig. 16). Together, these comparisons increase confidence that forest drought response 780 hypotheses are robustly supported by the two indices.

Within the broadscale consistency, there is also substantial finescale differences in spatial 782 location of anomalies (Fig. 1 vs Extended Data Fig. 2) and the detailed structure of responses (the pattern of residuals in Fig. 3a vs. Extended Data Fig. 2e), suggesting that more nuanced 783 784 study of these finer-scale differences could reveal additional insights into the biogeography of 785 forest drought response 101 . 781

786

2. Mapping and Statistical Analysis 787

788 2.1. Spatial Grid resolutions

We interpolated the differently resolved data products to different grid resolutions as needed 790 for mapping and modeling. Native resolutions were used to display most maps (exceptions 791 noted): 789

- 1 km for MAIAC EVI (Figs. 1-2, Extended Data Figs. 12b, 15, 16a-c); 792
- 100 m for HAND, composited to 1 km for mapping (Fig. 2a, Extended Data Fig. 3a); 793
- 0.05 degrees for GOSIF (Extended Data Figs. 2, 16d-f); 794
- 0.25 degrees for precipitation-derived products (Extended Data Figs. 3f-g, 4-5); 795
- $-$ 0.625×0.5 degrees for PAR; 796
- 1 degree for VPD (Extended Data Fig. 5); 797
- 0.1 degrees for soil fertility (Extended Data Fig. 3b); 798
- 0.25 km for soil sand content (Extended Data Fig. 3h), 799
- 1 km for forest canopy height (Extended Data Fig. 3c); and 800
- 1 degree for wood density and proportion of Fabaceae (Extended Data Fig. 3d-e). 801

For statistical modeling we interpolated different datasets to common grid resolutions, 803 according to the resolution of the model. For this we initially downscaled all maps to the native 804 resolution of the EVI product (1km), then aggregated to the desired coarser resolution, typically 805 0.4°, that was needed to avoid inflation of statistical significance of drought responses in models 806 by accounting for spatial autocorrelation among nearby pixels using variogram analysis (section 807 2.5, Extended Data Fig. 7). Grid cells in the drought-affected domain that included no intact 808 forest were excluded from analysis. When an analyzed grid cell (at coarse resolution, typically 0.4°) included a mix of intact forests and non-forest or deforested regions, we selected and 809 810 aggregated all intact forest pixels at the smaller (1km) subgrid scale to accurately represent intact 811 vegetation properties (EVI, canopy height, etc), and represented the coarser model grid cell by 812 those intact forest properties. 802

813

2.2. Classification of forest regions according to ecotopes 814

We investigated whether the distribution of factors defining forest types (ecotopes) across 816 Amazonia could lead to a coherent clustering of different forest ecotopes into different regions, 817 each with different broadscale forest drought responses. To this end, we conducted a supervised 818 forest classification, using factors identified in previous studies as important:^{[17,34,102,103](https://paperpile.com/c/gDKLkA/yyNc4+b4cnQ+bb7bO+fBlmh)} two 819 climate variables (average minimum monthly precipitation and MCWD variability), soil fertility 815

 820 (concentration of exchangeable base cations^{[43](https://paperpile.com/c/gDKLkA/x1zXd)}) and three tree functional characteristics (forest 821 height, wood density, and proportion of trees in the family Fabaceae).

We conducted the classification in four steps: *First*, the six ecotope factors, standardized by 823 their mean and SD, were mapped, with each grid cell considered to occupy a point in a six 824 dimensional space, and each dimension indexed in comparable units of standard deviations. 825 Second, a principal component analysis (PCA)^{[104](https://paperpile.com/c/gDKLkA/hH6ge)} ("FactoMineR" package in R, Extended Data 826 Fig. 6a) identified three complementary dimensions of forests in this space: a dimension defined 827 by *vegetation* characteristics (wood density, and proportions of the family Fabaceae), nearly 828 coincident with the first principal component (horizontal axis, Extended Data Fig. 6a); a 829 dimension defined by water availability (minimum monthly precipitation and MCWD 830 variability), nearly coincident with the second principal component (vertical axis, Extended Data Fig. 6a), and a third dimension defined mainly by *soil fertility* (Extended Data Fig. 6a). Based on 831 832 these initial PCA results suggesting three relatively distinct dimensions, we chose to cluster 833 Amazon basin pixels into three classes. Given their diversity, Amazon forests could likely be 834 classified into more than three, but we judged that three would be sufficient to capture substantial 835 functional variation, without being so complex as to prevent intuitive understanding. *Third*, an automatic procedure extracted endmember characteristics based on percentile 837 thresholds^{[105](https://paperpile.com/c/gDKLkA/Nhqun)} from the PCA space^{[106](https://paperpile.com/c/gDKLkA/9pQaU)}. Pixels with low climate variability had high minimum 838 precipitation and long wet seasons (in the 90th percentile), and were identified as a water 839 availability spectrum end-member. Grid cells with the highest proportion of Fabaceae, 840 overlaying with tall, dense-wooded trees (in the 90th percentile) and low-fertility soils, were 841 identified as another endmember. A third endmember was defined by a combination of high 842 variability climates and moderately high (67th percentile) soil fertility. *Finally*, supervised 843 classification via the Minimum Distance method was used in ENVI 5.3 software^{[107](https://paperpile.com/c/gDKLkA/G2070)} to cluster 844 each region based on proximity to the endmembers selected in Step three. This process identified three clusters of pixels in functional PCA space that turned out to 846 also correspond to geographically distinct Amazonian regions that were mostly contiguous (Extended Data Fig. 6b): an *Ever-wet Amazon* region in the northwest, a *Guiana shield* region 847 848 in the northeast, and *the southern Amazon*. The standardized values within each cluster, of each 849 of the characteristics defining the regional clustering (ordered by water availability, soil fertility, 850 and tree traits), exhibit the distinct niches of each region (Extended Data Fig. 6c). The ever-wet 851 Amazon is differentiated by lack of dry seasons (periods with months ≤ 100 mm rainfall, 852 Extended Data Fig. 3a). Forests in this region might be composed of species that do not 853 well-tolerate climate conditions (such as droughts), compared to tree assemblies (in other 854 regions) adapted to regular droughts or dry seasons. The Guiana shield region is distinct in 855 having old, highly weathered, low-fertility soils, with tree communities containing the largest 856 proportion of trees in the family Fabaceae, with dense wood and high seed mass (Extended Data 857 Fig. 3c-e)^{[34](https://paperpile.com/c/gDKLkA/bb7bO)}. The southern Amazon is then differentiated further from the Guiana shield as 858 slightly dryer, with soil fertility that was both higher on average but also more variable. This three-region classification (which we use to define the regions depicted in the main 860 text figures) is independent of the results (Figs. 3-4) of the basin-wide modeling investigation 822 836 845 859

(described in sections 2.6-2.7 below) because model predictions depend on pixel-pixel variations 861 862 of environmental factors regardless of what region they are in. However, the three region 863 Amazon is useful for presenting model results because it illustrates how different functional 864 responses emerge from different ecotope regions (as shown in Fig. 4e).

865 2.3. Climate anomalies for Drought definition and Mapping

The spatial extent for each of the three droughts (*d*) was taken to be all grid cells where the 867 MCWD anomaly was more than one standard deviation below the long-term mean for that cell (Extended Data Fig. 1). MCWD anomaly for each grid cell is calculated by Eqn. (1): 868 866

$$
MCWD_{anomaly} = \frac{MCWD_d - MCWD}{\sigma_{MCWD}}
$$
 (1)

870 where $MCWD_d$ is the data value in drought year (*d*), $MCWD$ is the average of 19 yearly MCWD 871 values for hydrological years 2000-2019 (May 2000 to April 2020) and σ_{MCWD} is the standard 872 deviation for the same time period. Anomalies of the other climate variables were calculated 873 analogously.

Drought severity in each grid cell was classified into three levels by standardized MCWD 875 anomaly: modest drought (-1.5 to -1 standard deviations relative to the mean), medium drought 876 (-2 to -1.5 standard deviations relative to the mean) and severe drought (greater magnitude than 877 -2 deviations) (Extended Data Fig. 1). 874

Drought duration (for each of the three droughts separately for each grid cell) was measured $\frac{879}{10}$ in terms of number of drought months (*i*) for a particular drought (*d*) for each grid cell within the 880 period (May to the following April) for the droughts of 2005 and 2010; and from May to October 881 of the following year for the El Nino drought of 2015/2016. The drought onset month is found 882 where the following is true, recalling that CWD and MCWD are more negative with greater 883 water deficit: 878

if
$$
CWD_{d,i-1} \geq \overline{M C WD}
$$
,
\n $CWD_{d,i} < \overline{M C WD}$,
\nand $CWD_{d,i+1} < \overline{M C WD}$,
\nthen $Onset_d = i$ (2)

884

869

The end month of drought interval (*i*) for each grid cell for each of the three droughts is 886 defined as follows: 885

if
$$
CWD_{d,j} < \overline{M CWD}
$$
,
\n $CWD_{d,j+1} \ge \overline{M CWD}$,
\nand $End_d \ge \overline{Onset}_d$,
\nthen $End_d = j$ (3)

887

Then for each grid cell, $duration_d = End_d - Onset_d + 1$ as shown in Extended Data Fig. 4. 888

2.4. Drought resilience and Vegetation Anomalies 889

We defined drought resilience as a forest's ability to increase (or relatively better maintain) 891 photosynthetic capacity or activity during a perturbation -- that is, by its tendency to exhibit more 892 positive/less negative anomalies in vegetation indices (relative green-up) during drought. There 893 is a broad literature on resilience^{[108,109](https://paperpile.com/c/gDKLkA/QlT1S+6lXAG)}, and our definition (which can also be characterized as 894 "resistance" or ability to resist changes in function with perturbation^{[108](https://paperpile.com/c/gDKLkA/QlT1S)}) is nominally distinct for 895 example, from another common definition, the capacity of a system to return to its equilibrium 896 state following a disturbance^{[110](https://paperpile.com/c/gDKLkA/d1rqz)}. We chose relative green-up here for conceptual and practical 897 reasons. Conceptually, greater relative green-up implies relatively more photosynthesis and 898 hence, all else equal, more carbon resources to respond to stress, encompassing different 890

899 strategies (likely including system capacity to return to equilibrium following disturbance), 900 making it a logical general metric of resilience. Practically, greening has been widely cited and 901 discussed in the literature, and, notably, is predictive of outcomes on the ground commonly 902 associated with resilience at the individual tree and plot scale (lower mortality, greater growth, 903 and greater xylem embolism resistance, see methods section 1.6, Extended Data Fig. 16). In order to quantify photosynthetic resilience, we extracted from each grid cell for each of 905 the three droughts, the anomalies in photosynthetic indices for the period of drought (Figs. 1, 2b-c; Extended Data Fig. 2, 4-5), calculated as the departure (in standard deviations from their 906 non-drought-year means) across a 9-year window centered on each drought (for example, 907 2001-2009 for the 2005 drought and 2011-2019 for the 2015 drought): 908 904

909

Anomaly_{d, du} = $\frac{X_{d,du} - \overline{X_{du}}}{\sigma}$ (4) 910 where $X_{d,du}$ is the value of the index in a grid cell during drought *d*, averaged over the duration *du* 911 (extracted by Eqn. (2) and (3)) – and X_{du} and σ_{du} are the average and standard deviation, 912 respectively, of the same 'du' period across the years of data availability (with the drought years

2005, 2010 and 2015 excluded). Including pixel-specific drought duration introduces greater 913 914 realism in drought response metrics by capturing pixel-pixel variability in drought response due $\frac{915}{10}$ to duration *du*, which has been treated in some previous analyses as fixed (e.g. in analyses of the 2005 drought, *du* was assumed to be the three months of July-August-September for all 916 917 pixels)^{[9,10,111](https://paperpile.com/c/gDKLkA/p6yui+5gmaM+zxBmH)}.

Correspondingly, we also calculated the field-based demographic mortality anomalies for 919 drought years [2](https://paperpile.com/c/gDKLkA/ANsHP)005 and 2010 from RAINFOR plots,² as above-ground biomass (AGB) mortality 920 drought responses (mortality carbon flux following drought, in percent change relative to 921 long-term mean MgC ha⁻¹ y ⁻¹. 918

922 2.5. Variogram analysis for removal of spatial autocorrelation

Observations from spatial samples are not independent, due to spatial autocorrelation 924 among grid cells that are near to each other^{[112](https://paperpile.com/c/gDKLkA/fLgAO)}. To obtain independent observations for general 925 additive models (GAM) and for statistical quantification of average drought response (Fig. 1), 926 we resampled grid cells at increasingly coarse resolutions, until response differences (between 927 forests with different water table depths) were no longer spatially autocorrelated -- that is, a sill 928 (plateau) was reached in the variogram (Extended Data Fig. 7) at around 40 km, indicating a 929 scale at which samples could be treated as statistically independent. The variogram was 930 calculated from the covariance of the difference between drought responses in shallow and deep water table grid cells: 931 923

$$
2\gamma(h) = \frac{1}{N(h)} \sum_{m,n \in N(h)} (z_m - z_n)^2
$$
\n(5)

932 933

$$
z_m = Anomaly_{EVI, \,SWTD_m} \tag{6}
$$

$$
z_n = Anomaly_{EVI, \, DWTD_n}
$$
\n⁽⁷⁾

935 where $N(h)$ was the number of grid-cell pairs (m, n) separated by distance h . Each z_m is the 936 standardized EVI anomaly of the first member of a grid cell pair, drawn only from cells having 937 shallow water table depths $(0, 1, 2, ..., 9)$, while z_n is the second member of each pair, drawn 938 only from cells with deep water tables $(10, 11, 12, ..., 19)$.

2.6. Statistical analyses for inferring causes of, and predicting, drought response 939

Our statistical analysis had two main goals: first, to test the three core hypotheses presented in the main text introduction (causal inference), and to develop the best possible 941 942 predictions of regional to basin-wide drought response by combining ecotope factors with 943 climate (predictive inference). 940

For this, we implemented two sequential statistical approaches: First $(\S 2.6.1)$, we used 945 GAM statistical regression^{[110](https://paperpile.com/c/gDKLkA/LHorB)}, selecting among ecologically-informed models by the Akaike 946 information criterion (AIC) to both test hypotheses about variables thought to influence forest 947 drought response and to identify the best predictive models of regional to basin-wide drought 948 response^{[111,112](https://paperpile.com/c/gDKLkA/hiA0N+z673)}. To avoid known inferential biases of building large regression models out of many 949 variables selected blindly by information criteria like $AIC^{111,113,114}$, we construct our moderate-sized models within a hypothesis-testing framework, where causal hypotheses are 950 951 specified based on ecological considerations and the selected regression fits test the predictions 952 made by those hypotheses. Second ($\S2.6.2$), we also employed structural causal modeling 953 (SCM)^{[40,113](https://paperpile.com/c/gDKLkA/6mJto+LEqb)} an approach which formalizes hypothesis testing as part of the model structure (e.g., 954 using Directed Acyclic Graphs, DAG^{[114,115](https://paperpile.com/c/gDKLkA/xV5A0+l06Rv)}). SCM reduces risk from confounding variables that 955 can mask or dilute (or magnify) true causal relationships between the 'exposure' variables (e.g., 956 climate, soil types) and the 'outcome' variable (e.g., forest greening/browning). We note that in 957 both approaches, accurate inference of the relative magnitude or importance of inferred relations 958 is conditional on the model being true. 944

Finally, we compare the two approaches $(\S2.6.3)$, based on the idea that if the inferences 960 from the two approaches are consistent with each other in terms of their conclusions about 961 hypotheses, this increases confidence in those conclusions. 959

2.6.1. AIC-selected General Additive Models (GAM) for hypothesis testing and prediction 962 We developed GAM regression models of forest drought response as a function of climate 964 variables and ecotope factors^{[10,18,37](https://paperpile.com/c/Loc88a/lAKi+wIzT+SBQn)} to represent our three core hypotheses of water table depth^{[28](https://paperpile.com/c/Loc88a/VBBc)}, 965 soil fertility^{[32,33](https://paperpile.com/c/Loc88a/JmJs+sWkN)}, and tree characteristics^{[34–36,49](https://paperpile.com/c/Loc88a/5ukH+OuUG+rbs3+IMa4K)}. GAMs allow for non-linear relationships between 966 response and multiple explanatory variables, in which underlying model structure can be 967 analyzed to understand why they make the predictions they make -- in contrast, for example, to 968 machine learning techniques, like boosted regression trees or neural networks^{[40,113](https://paperpile.com/c/gDKLkA/LHorB+c71u5)}. GAM links 969 response variables to explanatory variables with a smoothing function, or a spline, which can 970 take a variety of shapes, which are then added together. 963

We developed GAMs of two types: *(i) regional models—fit within regions—*designed to 972 test the "other side of drought" hypothesis 1, by including hydrological environments (as 973 represented by HAND) in addition to climate variables used in previous climate-only regression 974 models of forest drought response^{[10](https://paperpile.com/c/gDKLkA/5gmaM)}; and *(ii) basin-wide models* designed to test all three of our 975 hypotheses together (including effects of soil fertility and tree characteristics), and in particular 976 to understand the opposite sensitivity of forest responses to water tables across different regions 977 (Fig. 3a vs Extended Data Fig. 8). 971

(i) Effect of local hydrological environment and climate on drought response (**regional GAMs).** 978 979 GAMs were fit separately for the southern Amazon, Guiana shield, and ever-wet Amazon 980 regions, and for all three droughts together, as:

+*ti*(pairwise interactions of every two predictors)+ ε

$$
\Delta EVI = s(HAND) + s(\Delta PAR) + s(\Delta VPD) + s(\Delta P) + s(\Delta M CWD) + s(DL)
$$

981

(8)

where *∆EVI* is the vegetation response anomaly, *∆PAR*, *∆VPD*, *∆P* and *∆MCWD* are the 982 983 radiation, VPD, precipitation, and MCWD anomalies, respectively; *DL* denotes the drought 984 length; ε is the normally distributed residual; $s()$ and $ti()$ are the smoothing functions of predictor 985 variables, obtained using a scatterplot smoothing algorithm with a back-fitting procedure for the 986 appropriate smoothing function for each predictor. The degree of freedom (df) for the smoothers 987 is determined with "REML" with gaussian distribution implemented by Wood's R package 988 "mgcv"^{[113](https://paperpile.com/c/gDKLkA/c71u5)}. Models were implemented with gam.check function by R package "mgcv"¹¹³ for 989 diagnostics of residual, distribution and k basis dimension as well as concurvity. All the predictors were scaled to the same range and unit (40 kms, or ~0.4 degree). 990

The smooth functions were determined by thin plate splines^{[114,115](https://paperpile.com/c/gDKLkA/ivNf6+rmUx4)}. Here, we fitted thin plate 992 regression splines using automatically optimized smoothing parameters using the restricted maximum likelihood, or REML method. Three optimal models were selected for the 993 corresponding three regions, with all three model selection procedures evaluated by delta AIC 994 995 and R square^{[116](https://paperpile.com/c/gDKLkA/hiA0N)} using the "dredge" function in the mgcv package in R^{113} R^{113} R^{113} , with results reported in **Extended Data Table 1** (models a, b, and c). 996 991

(ii) Effect of hydrological environment interacting with regional ecotopes (**basin-wide GAM).** 997 We included soil types (fertility and texture) and vegetation characteristics (forest height, wood 998 999 density) into the GAM of section (i). Without specifying regions, we aimed to explore whether 1000 soil and vegetation characteristics (Extended Data Fig. 3) are able to explain regional differences 1001 in the sensitivity of forest response to water table depth. GAMs were fitted across the whole 1002 basin for the 2015/2016 El Niño drought, the only drought that had substantial simultaneous 1003 impacts on all three regions of the Amazon basin. The forest responses were comprised of three 1004 components: (I) the climate predictor variables (PAR anomaly, VPD anomaly, precipitation 1005 anomaly and MCWD anomaly); (II) the ecotope-based environmental predictor variables, in 1006 addition to HAND, associated with regional differences: soil fertility, soil texture, forest height 1007 and wood density; (III) error terms assumed to be a Gaussian distribution. Specifically, GAMs 1008 were fitted as below:

 $\Delta EVI = s(HAND) + s(SF) + s(ST) + s(FH) + s(DSL) + s(\Delta PAR) + s(\Delta VPD)$

 $+ s(\Delta P) + s(\Delta M CWD) + ti$ (pairwise interactions of every two climate variables)

+ *ti*(pairwise interactions of HAND with other ecotope-based variables and Δ *PAR*) + ε (9) 1009

where *DSL* denotes dry season length, *FH* denotes forest height, *ST* denotes soil texture and *SF* 1010 1011 denotes soil fertility. Considering variable correlations (Extended Data Table 2), we avoided 1012 choosing highly correlated variables for the same model (which for example excluded wood 1013 density when soil fertility was in the model). Considering the complexity of the model and 1014 computational cost, the pairwise interactions were included separately among ecotope factors, 1015 among climate variables, and between HAND and PAR, but did not traverse interactions among 1016 every possible pair of variables. The fitting process was the same as for the regional GAMs of 1017 (i): smoother determined with "REML" as implemented by "mgcv"^{[113](https://paperpile.com/c/gDKLkA/c71u5)}, and models evaluated by 1018 delta AIC and R square^{[116](https://paperpile.com/c/gDKLkA/hiA0N)} coded by the "dredge" function in the "mgcv" package in R, with final 1019 results reported in Extended Data Table 1 (model d). Basin-wide modeled forest response for 1020 the 2015/2016 drought is presented in Extended Data Fig. 17 where the GAM well-predicts the 1021 pattern of response (Extended Data Fig. 17b), but under-estimates the extremes of the responses 1022 (as evident from residuals in Extended Data Fig. 17c showing greening/browning patterns 1023 beyond the predictions).

Beyond the three more recent hypotheses discussed in the main text, soil texture was also 1025 expected to affect soil hydraulic properties and forest ecosystem response to drought $102,117$. We 1026 found that forests on sandy soils were more resilient (i.e., higher relative green-up) than those on 1027 clay soils (which bind water more closely), consistent with findings of process model studies^{[22](https://paperpile.com/c/gDKLkA/5XhwX)} of 1028 clays that bring soils more quickly to wilting points^{[23](https://paperpile.com/c/Loc88a/v79L)}. But again, this depended on water table 1029 depth, and deep water table forests also became more vulnerable with increasing sand content 1030 (Extended Data Fig. 11), perhaps because in the absence of a shallow water resource, sandy soils 1031 drained water too quickly 1024

This final basin-wide GAM model (Extended Data Table 1d) including soil texture (along 1033 with WTD, forest height, and soil fertility) suggests a further hypothesis for how soil texture 1034 moderates the effects of forest height and water table depth on drought response (Extended Data 1035 Fig. 11). The potential counteracting effects of the positively correlated forest height (which 1036 increases resilience when water tables are deep) and soil clay fraction (which generally decreases 1037 resilience due to binding water more tightly to soil particles) may explain the otherwise puzzling 1038 result that the tall forest advantage in deep water table forests does not just disappear but reverses 1039 in shallow water table environments (Fig. 4d). As shown in Extended Data Fig. 11, the reversal 1040 of the general trend (of decreasing resilience as clay fraction increases = sand fraction decreases) 1041 in deep water table forests (red lines in Extended Data Fig. 11 reverse as sand content falls below 50%), is associated with increasing forest height, especially in deep water table forests. Thus, at 1042 1043 the low sand (=high clay) end of the spectrum, the effect of soil texture depends strongly on 1044 WTD: in shallow WTD forests where tall trees are not advantaged, the negative effect of clay 1045 depresses forest drought response, but in deep WTD forests drought resilience increases again, 1046 even with increasing clay (decreasing sand), possibly because the associated taller tree effect 1047 outweighs the negative effect of clay soils. This mechanism could serve to improve models of 1048 how soil texture modulates drought response^{[118,119](https://paperpile.com/c/gDKLkA/M8m9h+RZBy5)}. 1032

2.6.2. Structural Causal Modeling (SCM) using Directed Acyclic Graphs (DAG) 1049

In order to further test the causal mechanisms proposed by our three core hypotheses, we 1051 used a framework for causal inference from $SCM^{40,118}$ $SCM^{40,118}$ $SCM^{40,118}$, DAG analysis^{[119,120](https://paperpile.com/c/gDKLkA/l06Rv+79rbG)}. We proposed and 1052 tested hypothesized causal relationships (represented by DAG diagrams, as in Extended Data 1053 Fig. 9a). 1050

Implementing DAG analysis with 'dagitty' (R package^{[120](https://paperpile.com/c/gDKLkA/rSRtL)}, we first developed a DAG 1055 diagram for Amazon forest drought response with relevant climate variables and ecotope factors 1056 expected from the literature^{[10,17,34](https://paperpile.com/c/gDKLkA/bb7bO+5gmaM+fBlmh)}, including our three core hypotheses of water table depth^{[24](https://paperpile.com/c/gDKLkA/32xKg)}, soil 1057 fertility^{[28,29](https://paperpile.com/c/gDKLkA/zXgTd+7oh5P)}, and tree characteristics^{[30–32,50](https://paperpile.com/c/gDKLkA/EwUsf+Dy8Mm+qawQE+xHuM4)} (Extended Data Fig. 9a). We assessed 'DAG-data 1058 consistency', testing to ensure that unconnected nodes are not correlated, applying root mean 1059 square error of approximation (RMSEA) (R functions "localTests" and "cis.loess" to allow 1060 potential non-linear correlations using loess fits^{[120](https://paperpile.com/c/gDKLkA/rSRtL)}; Extended Data Fig. 9b). 1054

We iteratively tested and revised the DAG by repairing detected independence violations 1062 between unconnected nodes (i.e. where RMSEA was greater than 0.30, as in Ankan et al.^{[121](https://paperpile.com/c/gDKLkA/xV5A0)}), by 1063 adding either a new direct causal link between such nodes (after first verifying an ecological 1064 basis for the link), or new links to each of the correlated nodes from a common causal node 1065 (again, if they made ecological sense). For example, longer dry season length should promote 1066 generally drier conditions, including greater VPD and MCWD; positive precipitation anomalies 1067 will cause higher relative humidity and therefore lower VPD anomaly^{[33](https://paperpile.com/c/gDKLkA/ycA42)}; more clayey soils allow 1068 taller trees^{[122](https://paperpile.com/c/gDKLkA/MzLtI)}, supporting the addition of links between these nodes. These adjustments gave a 1069 final DAG with a greater number of links (Extended Data Fig. 9c) and no independence 1061

1070 violations among the remaining unconnected nodes (Extended Data Fig. 9d). We next utilized the 1071 "backdoor criterion" to test the causal effects of key predictors, exposing the influence of each 1072 variable on drought response, one-by-one, while blocking (or adjusting for) the influence of 1073 "backdoor" variables on non-causal pathways (i.e., pathways in which at least one arrow points 1074 in a direction opposite to the hypothesized causal influence)^{[123,124](https://paperpile.com/c/gDKLkA/6mJto+l06Rv)}. Extended Data Fig. 9c 1075 illustrates blocking the confounding 'backdoor path' influence of average dry-season length 1076 [DSL] on the causal relationship between drought length [DL] and drought response [DR]; 1077 Extended Data Fig. 10 shows non-linear (GAM) model results for causal relationships 1078 addressing our hypotheses identified this way. Completing these steps, we accepted our finalized 1079 DAG (Extended Data Fig. 9c) as representing detected causal links for forest drought response 1080 and blocked all backdoor paths in subsequent analysis by including the confounding variables in 1081 multiple regression (in GAM analysis), as reported in Extended Data Fig. 10.

1082 2.6.3. Comparing inferences from SCM with predictive GAM regressions

We found that both modeling approaches consistently supported the "other side of 1084 drought" hypothesis (hypothesis 1) for forest drought response in the southern Amazon across all 1085 three droughts (negative dependence on water table depth, Fig. 3a and Extended Data Fig. 10a), 1086 with associated consistent climate dependencies (positive dependence on sunlight, Fig. 3b and 1087 Extended Data Fig.10b, and declining overall dependence on drought length, but with a peak at $1088 \sim 3$ months duration, Fig. 3c, Extended Data Fig. 10c). Across the basin for the 2015/2016 1089 drought, both modeling approaches supported hypothesis 2, that increasing soil fertility (past a 1090 moderate fertility level) would negatively affect drought response (Fig. 4a,c and Extended Data 1091 Fig. 10e), and both supported a "hypothesis 1- hypothesis 3" interaction, finding that increasing 1092 forest height (and presumed deeper rooting depth) positively affected drought response in deep 1093 water-table forests, but had the opposite effect in shallow water-table forests (Fig. 4b,d and Extended Data Fig. 10d). Finally, though not part of the three core hypotheses, both modeling 1094 1095 approaches found similar effects of soil texture on drought response (Extended Data Fig. 10f and 1096 Extended Data Fig. 11). 1083

2.7. Comparing adjusted observations to GAM predictions for different predictor variables 1097 The observed vegetation indices (MAIAC EVI, and GOSIF) were graphed in adjusted form 1099 (as "climate adjusted" or "ecotope-adjusted" observations) in order to compare observed versus 1100 predicted relationships with one predictor variable at a time (e.g. water table depth) while 1101 adjusting for the effect of the other, potentially influential, predictor variables represented in the GAM models (section 2.6.1, above). This is analogous to partial regression plots or adjusted 1102 1103 variable plots in conventional regression models^{[125](https://paperpile.com/c/gDKLkA/m2n4s)}. EVI (Figs. 3a, 4e, Extended Data Fig. 8a, b) 1104 or GOSIF (Extended Data Fig. 8c, d) observations of anomalies were adjusted by the difference 1105 between the full GAM predictions at each pixel and the partial prediction for the median 1106 conditions. For example, to plot climate-adjusted EVI/GOSIF versus water table depth (across 1107 different HAND bins) as in Fig. 3a and Extended Data Fig. 8, the adjustment (shown for EVI) 1108 was: 1098

1109

Adjusted $\Delta EVI_i = \Delta EVI_i - Correction_i$

Correction_i = $f(HAND_i, Climates_i) - f(HAND_i, Climates)$ (10) 1110

1111 where ΔEVI_i is the observed *i*th *EVI* anomaly, $I($ *HAND*_{*i*}, *Cumates*_{*i*}) is the prediction of the *i*th *EVI* anomaly from GAM (model function for Eqn. 8 denoted as *f()* here) and 1112

 $\int f(HAND_i, \overline{Climates})$ is the prediction when holding climates constant at the median value of the 1114 domain of the prediction (in this case, the median climate within each drought). 1113

Similar calculations are applied to observations in Fig. 4e to account for the regional 1116 differences in climates and ecotopes (Ever-wet, Guiana shield, and southern Amazon), while 1117 isolating the effects of water-table depth (HAND) on EVI anomalies with the basin-wide GAM 1118 model. The correction term applied to Eqn. 9 in the case of Fig. 4e was 1115

Correction $_{i}$ = f $(HAND_{i}$, Climates $_{i}$, SF_{i} , ST_{i} , FH_{i}) - f $(HAND_{i}$, Climates, $\overline{SF}, \overline{ST}, \overline{FH}$) (11) where *SF* denotes soil fertility, *ST* denotes soil texture, and *FH* denotes forest height. The 1120 1121 domain of the prediction for which median values of ecotope distributions were taken was, in 1122 this case, each of the three regions, considered separately. 1119

1123 2.8. Deriving the basin-wide biogeography of forest drought resilience/vulnerability

Classic biogeography in ecology focuses on the drivers of the distribution of species and 1125 their phylogenies over space and time, as an emergent consequence of their evolutionary 1126 histories^{[126,127](https://paperpile.com/c/gDKLkA/yGQmB+uvBcW)}. Here, following recent ideas in the emerging field of functional biogeography^{[23,128](https://paperpile.com/c/gDKLkA/Y8kQ8+Kceqt)}, 1127 we extend classic species-based biogeography to derive a functional biogeography of Amazon 1128 forest drought resilience and vulnerability. To accomplish this, we used the GAM analysis that 1129 included ecotopes and was derived for the whole basin (section 2.6.1, Eqn. 9, Extended Data 1130 Table 1d, Extended Data Fig. 17). Resilience (as plotted in Fig. 5a) was defined as the 1131 standardized GAM prediction (positive values corresponding to greening and resilience) from 1132 the spatially varying ecotope factors alone (with effects of spatial variation in climate removed 1133 by setting each pixel's climate factors equal to their basin wide average during the 2015 1134 drought): 1124

Standardized *resilience*
$$
{i} = \frac{Resilience}{SD}{resilience}
$$

\nAssilience
$$
{i} = f\left(HAND{i}, SF_{i}, ST_{i}, FH_{i}, \overline{Climates}\right)
$$

\n(12)

1137 where *Resilience_i* is the prediction for pixel *i* using Eqn. 9 as function $f(t)$, and *Resilience* and 1138 SD _{resilience} denote mean and standard deviation across the basin, respectively.

We defined thresholds conducive to resilience to define ecotope factor groups associated 1140 with resilience or vulnerability. Overlapping ecotope factors generally conducive to resilience 1141 (shallow water tables, low soil fertility, and tall trees) were distributed across the basin (Fig. 5b, 1142 C). The resilience thresholds for the different factors were: shallow water table forests: <10m, 1143 taken from Nobre et al.^{[25](https://paperpile.com/c/gDKLkA/465Cp)}, <u>low soil fertility</u>: exchangeable base cation concentrations <10^{-0.35} 1144 cmol⁺/kg; and tall forests: heights>32.5 m. The thresholds for soil fertility and forest height were 1145 chosen as the level where average slope of EVI anomaly sensitivity to HAND changed sign (in 1146 Fig. 4a, b, respectively). 1139

3. **Testing alternative interpretations and considering caveats** 1147

To address potential questions about whether alternative interpretations might either 1149 undermine or further illuminate our reported results, we identified additional hypotheses posing 1150 alternative interpretations. Among the additional hypotheses we considered were the following 1151 five, the first four of which we were able to partially test here with the functional biogeography GAM model: 11521148

H1. That spatial scaling artifacts contaminate the results. In particular, it might be that the 1154 primary spatial scale of our analysis $(\sim 40 \text{km})$, in order to achieve statistical independence, see 1155 section 2.5) is too large and does not reflect the fine scale of individual tree response to drought 1156 in distinct environments, raising the question of whether the effects reported here can be 1157 confidently attributed to the aggregation of these fine scale responses, or to some other effect. In order to test this hypothesis, we investigated how sensitivity of forest drought response to 1159 water table depth depended on the scale of the analysis (Extended Data Fig. 12), from 40 km (Fig. 3a, reproduced in Extended Data Fig. 12a) to the native MODIS scale (1km) (Extended 1160 Data Fig. 12b), and across the finer scales (resolved to 30 meters using Landsat OLI 8 land 1161 1162 surface reflectance, see Extended Data Fig. 12c) available for a region near Manaus^{[129](https://paperpile.com/c/gDKLkA/Vpl3I)} (at scales 1163 below 40 km, spatial autocorrelation is evident; this artificially narrows confidence intervals, but 1164 does not hinder the scaling comparisons). These analyses showed that sensitivity of forest 1165 drought response to water table depth did not detectably depend on scale, adding confidence that 1166 the key factor of water table depth indeed structures Southern Amazon drought response (as in 1167 Fig. 3a) across different scales. We note that this analysis suggests a need for future investigation 1168 of how the actual magnitudes of greenness anomalies at the ecological neighborhood scale (1 ha) 1169 of operation of community and ecophysiological mechanisms translate to magnitudes at larger 1170 scales. 1153 1158

H2. That different aspects of drought dynamics (e.g. severity interacting with duration) may 1172 confound the reported interpretation of drought duration (as in Fig. 3). Drought severity and 1173 duration are known to have distinct effects on different species in other biomes, raising the 1174 question of whether these dimensions of drought have distinct effects in the Amazon. We tested the interacting effects of severity (as defined as in section 2.3, by the MCWD 1176 anomaly) and drought duration by further analyzing the model of Extended Data Table 1a. This 1177 analysis (not shown) confirms that droughts that are both deep and long have the most negative 1178 effects on photosynthesis. This also confirmed the hump-shaped response to drought duration 1179 reported in Fig. 3c (with a primary hump occurring earlier but persisting longer through a 1180 secondary hump for less severe droughts). 1171 1175

H3: That drought impacts during dry seasons are different than during wet seasons, 1182 complicating interpretation of PAR anomaly and drought length effects (Fig. 3). If light 1183 limitation (and hence PAR sensitivity) is stronger in the wet season (because light is already 1184 more limiting in the wet season due to greater cloud cover), longer droughts will not just be 1185 longer, but (because seasons are of finite length) they will also be more likely to encompass, in 1186 varying fractions, the differing light sensitivities of dry and wet seasons. 1181

In order to test whether the proportion of the drought that occurs in the wet versus dry 1188 season affects reported forest responses, we constructed "DryDrought" as a predictor variable, 1189 representing the proportion of a given pixel's drought that occurred in the dry season. We, added 1190 DryDrought to the GAM for the Southern Amazon (Extended Data Table 1a), comprising 1191 HAND, climate factors and the error terms. Specifically: 1187

 $+ s(DL) + ti$ (pairwise interactions of every two variables except for DryDrought)

 $1192 + ti(DryDrought, \Delta PAR) + ti(DryDrought, DL)$

1193 This analysis (Extended Data Fig. 13) showed that the longest drought (2015) also had the 1194 broadest distribution of occurrences across dry and wet seasons, with about equal parts of the 1195 drought occurring in the dry versus the wet season (median fraction in the dry season = 0.51 ,

(14)

Extended Data Fig. 13a). By contrast, the 2005 and 2010 droughts were primarily dry season 1196 1197 droughts (median dry season fractions $= 0.83$ and 0.77, respectively). This analysis confirms our 1198 finding of a generally positive sensitivity of droughted forests to sunlight reported in the main 1199 narrative (Fig. 3b), but further shows that the greater the proportion of the drought that occurs in 1200 the wet season, the greater the positive sensitivity to sunlight anomalies (in Extended Data Fig. 13b, the blue line representing pixels experiencing predominantly wet season drought is steeper 1201 1202 than the red line representing pixels predominantly experiencing dry season drought). This 1203 analysis also confirms (Extended Data Fig. 13c) that the hump shaped response to drought 1204 duration (as in Fig. 3c, especially the peak of vegetation response at three month's duration) is 1205 general across both dry and wet season droughts. A consistent result of both analyses is that (with the exception of PAR anomalies greater than +2 standard deviations, Extended Data Fig. 1206 1207 13b), forests experiencing wet season droughts are generally more negatively affected by drought 1208 than are forests experiencing dry season droughts, consistent with the idea that although trees are 1209 adapted to the dry conditions of annually recurring dry seasons, they are especially vulnerable 1210 when droughts hit in the wet (recovery) season.

H4: That deforested or degraded forests may be driving or contaminating results that are 1212 reported as for "intact" forests. Deforested regions are excluded from the analysis, but the mask 1213 may still include forests in proximity to deforested regions that, though not deforested, may be 1214 experiencing degradation. We conducted a sensitivity test to address the question of whether 1215 different drought responses in degraded forests could be contaminating our findings, using a 1216 recent classification^{[86](https://paperpile.com/c/gDKLkA/fMhzl)} that identifies partially degraded forests as distinct from both deforested 1217 and intact forests, now updated through 2022. We repeated the GAM analysis reported in Fig. 4, 1218 but here excluded pixels representing degraded forests. The results (Extended Data Fig. 14, 1219 styled after Fig. 4 in the main text) suggest that partially degraded forests likely are indeed more 1220 vulnerable: the curves in panels C and D of Extended Data Fig. 14 (for purely intact forests) 1221 reach a slightly greater EVI anomaly value than the corresponding curves of Fig. 4c, d (including 1222 mainly intact and but also some degraded forests). This suggests that a functional biogeography 1223 approach may be fruitful for future investigations of the effect of forest degradation on drought 1224 sensitivity at the local scale. However, the differences are slight at the basin scale, and the overall 1225 patterns in Fig. 4 and Fig. 5 results do not depend much on whether these forests "in between" 1226 deforested and intact regions are included or excluded. 1211

H5: That relatively taller individual trees are more vulnerable to drought, even as 1228 tall-canopy deep water table forests are on average more resilient to drought. We found that 1229 greater forest canopy height promoted resilience for deep water table forests, but increased 1230 vulnerability for shallow water table forests (Fig. 4d, Extended Data Fig. 11d). Observations of 1231 drought responses in the RAINFOR network^{[49](https://paperpile.com/c/gDKLkA/ld6M0)} and drought experiments^{[47,48](https://paperpile.com/c/gDKLkA/dqt9C+74BPM)} report that tall trees 1232 were more vulnerable to drought. One of the drought experiments was above a moderately 1233 shallow water table (7-10m) and the vulnerability of tall trees there could be explained by our 1234 result^{[47](https://paperpile.com/c/gDKLkA/74BPM)}, but the forest of the Nepstad et al drought experiment^{[48](https://paperpile.com/c/gDKLkA/dqt9C)}, and many of the plots in the RAINFOR network, are over deep water tables, raising the question as to whether the results 1235 1236 reported here might be inconsistent with those. 1227

Recalling that the satellite-derived canopy heights are not individual tree heights but overall 1238 mean heights of forest canopies over a 1km pixel, we hypothesize that both results are true: that 1239 deep water table forests that are tall on average (and presumed to have on average deeper roots 1237

1240 that bring greater collective access to deep water resources) are more resilient than forests that 1241 are on average shorter, but that individual tall trees, subject to greater atmospheric drought stress 1242 from higher VPD, may be individually more vulnerable than their average-height neighbors. 1243 Hydraulic redistribution by roots, observed as part of the Nepstad et al^{[48](https://paperpile.com/c/gDKLkA/dqt9C)} Amazon drought 1244 experiment^{[130](https://paperpile.com/c/gDKLkA/YMJ0C)} and by other studies, is a mechanism that could further enhance forest benefit from 1245 redistributing deep waters upward in the soil profile.

This is a more challenging hypothesis to test, and in contrast to the hypotheses above, it is 1247 beyond the scope of our current study to test here. However, this could be tested by extensive 1248 plot data or higher resolution LIDAR data (e.g. Smith et al. 100 ; Nunes et al. 131) that could resolve 1249 individual tall trees in the canopy, and compare their drought induced mortality rates across 1250 forests of different average heights. 1246

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1453 Author contributions: S.C. and S.R.S. designed the analysis, based on early conception by 1454 A.D.N. and S.R.S., and on funded proposals to investigate "the other side of tropical forest 1455 drought" led by S.C.S., M.N.S. and S.R.S. (from NSF) and by S.C. and S.R.S. (from NASA). 1456 A.D.N., L.A.C and D.d.J.A updated their HAND data product and interpreted it for this analysis. B.W.N. and N.R.C. contributed remote sensing expertise and analysis, R.C.T. contributed 1457 1458 statistical modeling expertise and analysis, and H.K. contributed code, especially for the 1459 variogram analysis. S.C. organized the datasets (with assistance from N.R.C.), conducted the 1460 analysis and wrote the initial draft. S.C., S.R.S. and S.C.S. revised the draft. All authors 1461 contributed to writing the final version.

Competing interests: The authors declare that they have no competing interests. 1462

Data and materials availability: All remote sensing data and products are publicly available at 1463 1464 the website locations cited in the supplementary methods. The ground-based demographic 1465 validation data is publicly available in the supplement to Sousa et al $(^{26})$ $(^{26})$ $(^{26})$ and Brienen et al $(^{2})$ $(^{2})$ $(^{2})$. Code for reproducing the modeling analysis and figures is posted on Code Ocean at 1466 1467 https://codeocean.com/capsule/2432086/tree.

Extended Data Figs. 1 to 18 1468

Extended Data Table 1 to 2 1469

Supplementary Information is available for this paper. 1470

1471 Supplementary Materials

References (*55*–*134*) 1472

Extended Data Fig. 1 Maximum cumulative water deficit (MCWD) standardized anomalies (relative 1473 1474 to the long term mean MCWD across years, blue=positive, orange=negative) during drought for (a) 2005, **(b)** 2010, and **(c)** 2015 droughts. MCWD is calculated (methods section 1.2) as the maximum water 1475 1476 deficit reached for each hydrologic year (from May of the nominal year to the following April). The 1477 "drought region" is defined as pixels whose MCWD anomaly is more than one SD below the mean (light 1478 orange to red).

Extended Data Fig. 2. GOSIF-based forest response to droughts. GOSIF anomalies during drought, 1479 1480 relative to the long term mean GOSIF (green=positive, orange=negative) in drought regions for the (a) 2005, (**b**) 2010 and (**c**) 2015 droughts, respectively. (**d**) Photosynthetic index anomalies in the 2005 1481 1482 drought elliptical region: EVI and GOSIF (left and right vertical axes) versus HAND (elliptical region is 1483 depicted in Fig. 1a and Extended Data Fig. 2a); (e) GOSIF responses (anomalies) vs. HAND for 1484 observations (solid points $+/-95\%$ CI and regression line) for the 2005 (green, slope= -0.016 ± 0.006 SD 1485 m⁻¹), 2010 (purple, slope=-0.012±0.003 SD m⁻¹), and 2015 (blue, slope=-0.010±0.003 SD m⁻¹) droughts, 1486 paired with area distributions of drought-affected HAND values for each drought (right axis).

Extended Data Fig. 3. Ecotope factors of the Amazon basin. (**a**) Height Above Nearest Drainage 1487 1488 (HAND), a proxy for water-table depth^{[25](https://paperpile.com/c/gDKLkA/465Cp)}; (b) Soil fertility, as exchangeable base cation concentrations^{[43](https://paperpile.com/c/gDKLkA/x1zXd)}; 1489 (c) Average forest heights as acquired by lidar^{[45](https://paperpile.com/c/gDKLkA/pbgPo)}; (d) Community-weighted wood density^{[34](https://paperpile.com/c/gDKLkA/bb7bO)}; (e) Proportion 1490 of trees belonging to the Fabaceae family^{[34](https://paperpile.com/c/gDKLkA/bb7bO)}; (f) MCWD variability (see methods section 2.3), in terms of 1491 the standard deviation of the long-term MCWD timeseries. High variance in climate and low soil fertility 1492 in Guiana shield might contribute to the greatest proportion of trees belonging to the family Fabaceae 1493 with the very high wood density; (g) Averaged minimum monthly precipitation (low=green, 1494 high=orange). The north-west everwet Amazon is distinguished by lacking a dry season (precipitation 1495 exceeds evapotranspiration). (h) Soil sand content^{[44](https://paperpile.com/c/gDKLkA/8CpZL)}. The first row of factors are used as ecotope 1496 predictors in the GAM analysis of Extended Data Table 1.

Extended Data Fig. 4. Pixel-based drought duration. Panels **a**, **d**, and **g** show dates of the onset of the 1497 2005, 2010 and 2015 droughts, respectively. Panels **b**, **e**, and **h** show dates of the end of the 2005, 2010 1498 and 2015 droughts. Panels **c**, **f**, and **i** show the duration (end date minus start date, in number of months) 1499 1500 of the 2005, 2010 and 2015 droughts. Pixel-by-pixel drought responses (EVI in Figs. 1-3, 4; or GOSIF in 1501 Extended Data Figs. 6 & 11) are taken as the vegetation index standardized anomalies that occur during 1502 the pixel-specific drought period defined here.

Extended Data Fig. 5. Spatial distributions of climate variations' anomalies across 2005, 2010 and 1503 **2015 droughts.** Panels **a**, **d**, and **g** show photosynthetic active radiation (PAR) anomaly distributions 1504 (blue=negative, red=positive) in the drought regions of the 2005, 2010 and 2015 droughts, respectively. **b**, 1505 1506 e, and h show the vapor pressure deficit (VPD) anomaly distributions (blue=negative, red=positive) in the 1507 drought regions of the 2005, 2010 and 2015 droughts. Panels **c**, **f**, and **i** show the precipitation anomaly 1508 distributions (red=negative, blue=positive) in the drought regions of the 2005, 2010 and 2015 droughts.

Extended Data Fig. 6. Regions in the Amazon basin that emerge from a principal components analysis 1509 (PCA) followed by classification: (**a**) PCA of the Amazon basin pixel data (colored according to a 1510 1511 supervised classification into three classes identified by variance minimization), projected onto their first 1512 two principal components, which are composed mainly of three dimensions, one defined by wood density 1513 and proportions of the family Fabaceae (first principal component, horizontal axis), one defined by 1514 minimum monthly precipitation and MCWD variability (second principal component, vertical axis), and a 1515 third defined mainly by soil fertility; the classes are significantly separated in PCA space (F=950, df=2, 1516 3805, $p \sim 0$, permanova test); (b) Th Amazon pixels colored according to their class (corresponding to the 1517 colors in a), showing that the classification of (a) maps pixels into distinct, mostly contiguous spatial 1518 regions.) (c) Standardized values, for each region, of each group of characteristics (ordered by water 1519 availability, soil fertility, and tree traits/characteristics), illustrate distinct regional niches: the Everwet

1520 Amazon is highest in minimum precipitation and lowest (highest negative) in MCWD variability; the 1521 Southern Amazon is moderately high in mean fertility, and the Guiana shield has the tallest mean forest 1522 height and greatest wood density. (d) scree plot of the eigenvalues of PCA shown in (a), plotted in rank 1523 order.

Extended Data Fig. 7. Variograms of spatial autocorrelation effect across three droughts. The 1524

1525 variance of the difference of MAIAC EVI anomalies between shallow and deep water tables against distance between pairs of pixels from shallow and deep water tables for the whole basin (**a**, **e**, and **h**), 1526 southern Amazon (**b**, **f**, and **i**), everwet Amazon (**c**, **g**, and **j**) and Guiana shield (**d** and **k**), 1527 1528 respectively. Variance was lower (indicating spatial autocorrelation) for pairs formed from nearby pixels, 1529 but tended to reach a sill (plateau) at around 40 km, indicating a scale at which spatial autocorrelation 1530 weakened, and samples could be treated as independent for purposes of statistical analysis.

Extended Data Fig. 8. Amazon forest EVI and GOSIF responses to multiple droughts in (a, c) 1531 **ever-wet northwest and (b, d) in northeast Guiana shield regions show consistently positive slopes** 1532 **with HAND, in contrast to responses in the Southern Amazon (Fig. 3a)**: **(a), (b)** Enhanced vegetation 1533 1534 index (EVI) anomalies versus water table depth (i.e., HAND) for observations (solid points with standard 1535 error bars, with linear regression solid line) and for unified multi-drought GAM predictions (Extended 1536 Data Table 1b, c) (with climate fixed to region-wide average drought conditions for each drought, smooth 1537 lines with shaded uncertainty regions, and associated linear regression dashed line) for the 2005 (green), 2010 (purple), and 2015/2016 (blue) droughts in drought regions of Guiana shield (a) and ever-wet 1538 Amazon (b). The 2010 drought did not significantly affect the Guiana shield. **(c), (d)** GOSIF anomalies 1539 1540 versus water table depth (HAND), following the same analysis as in (a, b) for EVI.

Extended Data Fig. 9. Development of a Directed acyclic graph (DAG) representing the structure of 1541 **factors influencing tropical forest responses to drought. (a)** Initially hypothesized DAG characterizing 1542 1543 the causal relationships among climatic, environmental, and forest variables (measured variables depicted 1544 as blue nodes, unmeasured rooting depth is depicted in gray) leading to forest drought response (other 1545 color node), with arrows representing the hypothesized causal links. (b) **DAG-data consistency tests for** 1546 initial DAG, with the largest 20 approximated non-linear correlation coefficients (estimated via root mean 1547 square error of approximation, RMSEA) between unlinked variables in (a). (Note: unlinked variables in a 1548 DAG are hypothesized to have zero correlation or zero conditional correlation; thus, the second row of 1549 panel b tests "DR \parallel DSL $|$ DL" -- whether DR is independent of DSL conditioned on DL, by estimating 1550 the non-linear correlation between DR and the residuals of DSL regressed on DL.) Correlations greater 1551 than an acceptability threshold (dashed vertical lines at ± 0.30) fail the test of conditional independence, 1552 addressed by adding to the DAG either a direct causal link (indicated by a green symbol), or links to a 1553 common cause (pink symbol) (such added arrows are included in panel c). (c) **Final DAG** after correcting 1554 for conditional independency inconsistencies of the initial DAG in A, in light of ecological 1555 considerations. Also illustrates use of the backdoor criterion to determine the causal effect of 'drought 1556 length (DL)' (the exposed predictor node and associated forward causal paths, in green) on forest drought 1557 response (corresponding to the model in Extended Data Fig. 10c), while blocking the confounding 1558 variable dry season length, DSL (hypothesized to itself affect DL) and its associated causal backdoor paths (which are considered non-causal paths with respect to the exposed variable DL) (in pink). **(D)** 1560 DAG-Data consistency tests for final DAG (panel c), showing the largest 20 RMSEA values. 1559

Extended Data Fig. 10. Causal effects of different variables derived from DAG employing backdoor 1561 **criterion, for: (a)(b)(c) the Southern Amazon across all three droughts: (a)** of HAND (no backdoor 1562 to be blocked) (**b**) of PAR (adjusting for back door paths through drought length, dry season length) (**c**) of 1563 1564 Drought length (adjusting for back door path through dry season length) on EVI responses (adjusted EVI prediction)**; (d)(e)(f) the Amazon basin during the 2015 drought: (d)** of forest height, categorized by 1565 1566 shallow (blue, HAND=0-10 m) and deep (red, HAND=20-40 m) water tables (adjusting for back door 1567 paths through soil fertility, soil texture and dry season length), (e) of soil fertility (adjusting for back door

1568 path through dry season length) (f) of soil texture (no backdoor path to be blocked). Causal effects are on EVI drought anomalies (adjusted EVI predictions after conditioning confounding variables in causal 1569 1570 GAMs, lines with 95% confidence shaded area).

Extended Data Fig. 11. The sensitivity of forest response to soil texture (sand content) in basin-wide 1571 1572 GAM analysis: GAM-predicted adjusted EVI anomaly (left axis) versus soil sand content (%), with 1573 water table-depth in color (shallow=blue to deep=red), paired with distributions of mean forest height in 1574 each soil texture bin (bottom graph, right axis). 'Adjusted' GAM predictions are made by setting 1575 non-displayed predictors (climate variables, tree-height, soil fertility) to their median values during the 1576 drought.

Extended Data Fig. 12. **Scale-dependence of Southern Amazon forest responses to drought, showing** 1577 **that detected response patterns are largely invariant across different scales of analysis**: (**a**) At 0.4 1578 1579 degree (40-km) scale (across the Southern Amazon. all three droughts): Climate-adjusted EVI responses 1580 (standardized anomalies from MODIS) vs. water-table depths (indexed by HAND) for observations (solid 1581 points ±95% CI and solid regression line) and for unified multi-drought GAM predictions (model of 1582 Extended Data Table 1a, shaded bands and dashed regression line slopes) for the 2005 (green, 1583 slope=-0.019 \pm 0.001 SD m-1), 2010 (purple, slope=-0.020 \pm 0.002 SD m-1), and 2015 (blue, slope=-0.028±0.002 SD m-1) droughts; (**b**) At 1-km scale (across the Southern Amazon, all three 1584 1585 droughts), as in (a): climate-adjusted EVI responses vs. HAND for observations (solid points and 1586 regression line) and corresponding GAM (with the same Extended Data Table 1a model now fit at 1km 1587 scale, revealing autocorrelation in observations causing too-narrow confidence bands, and slight model 1588 underpredictions of the extremes of the 2005 greenup and the 2010 browdown, but maintaining the 1589 similar negative dependence on HAND across all droughts); (c) At 30 to 180 m scales (for a forest region 1590 around Manaus, 2015-2016 drought only): Delta EVI (the fraction change in EVI due to the drought = 1591 (after-drought EVI (July 2016) - pre-drought EVI (August 2015))/pre-drought EVI) (Landsat OLI8, at 1592 30m resolution) vs. water-table depths (indexed by HAND) for Landsat observations (solid points $\pm 95\%$ 1593 CI and solid regression line) at native (30m) and aggregated to 90 and 180-m scales. Also shown in the 1594 bottom of each panel is the distribution of water table depth at each scale. Aggregations to larger 1595 (coarser) scales induce an apparent regression towards the mean in the water table depth distributions (as 1596 more extreme water table depths at finer scales become diluted by averaging to large scales), while 1597 similar dilution of extremes in EVI response (not shown) preserves the overall relation between EVI 1598 responses and water table depth (especially evident in the Landsat analysis where the slopes through data 1599 aggregated at different scales do not detectably differ).

Extended Data Fig. 13. The sensitivity of Amazon forest drought responses to dry versus wet season 1600 **drought periods, across the three-droughts: (a)** distribution of the proportion of drought that was in the 1601 1602 dry season ($0 =$ all in the wet season to $1 =$ all in the dry season) for drought-affected pixels in each of the 1603 three droughts. (b) GAM-predicted EVI anomaly versus PAR, for different proportions of dry season 1604 drought (blue=all wet to red=all dry, corresponding to colored tick marks in the vertical axis of a). (c) 1605 Adjusted EVI anomaly from GAM prediction versus drought length, for different proportions of 1606 dry-season drought (blue to red, as in panel b).

Extended Data Fig. 14. The sensitivity of Amazon intact terra firme forest to drought responses, 1607 **excluding degraded forests.** Basin-wide Amazon intact forest responses to the 2015 drought, structured 1608 1609 by ecotopes and predicted by whole-basin GAM analysis (fit by model of Extended Data Table 1d, but 1610 fully excluding forests categorized as degraded^{[86](https://paperpile.com/c/gDKLkA/fMhzl)} in fitting the model): GAM partial predictions of EVI 1611 anomalies (color scale), displayed identical to the design of Fig. 4 (for intact terra firme forests, but 1612 including some partly degraded forests) for (a) soil fertility^{[43](https://paperpile.com/c/gDKLkA/x1zXd)} and $HAND^{25}$ $HAND^{25}$ $HAND^{25}$, and for (b) forest height^{[45](https://paperpile.com/c/gDKLkA/pbgPo)} and 1613 HAND^{[25](https://paperpile.com/c/gDKLkA/465Cp)} ecotope distributions are in the margins, identical to those shown in Fig. 4. $(c)(d)$ adjusted EVI 1614 anomaly versus HAND with increasing (c) fertility or (d) forest height, each color-coded as in Fig. 4.

1615 Note: 'adjusted' EVI anomalies indicate that climate and ecotope factors not displayed in the graph are 1616 held constant at basin-wide (a-d) or regional average values (e).

Extended Data Fig. 15. (a) Remotely sensed map of MAIAC EVI (1-km resolution) (green to blue 1617 **color scale), overlaid with aboveground NPP (ANPP) rates from 321 ground-monitored forest plots** 1618 1619 (red circles, % y^{-1}) as aggregated to 1 degree grid plots (RAINFOR plots in Brienen et al.^{[2](https://paperpile.com/c/gDKLkA/ANsHP)}), with both EVI 1620 and ANPP taken during the 2000-2011 interval. ANPP rate is calculated as Aboveground Biomass (AGB) 1621 gain (Mg/(ha·yr)) (total annual AGB productivity of surviving trees plus recruitment, plus inferred growth 1622 of trees that died between censusing intervals) divided by initial AGB (Mg/ha) (standing above ground biomass at the start of the census interval). **(b) ANPP rates as predicted by EVI** (points from (a) plus 1623 1624 solid regression line with statistics; Dashed line and associated statistics in gray represent linear 1625 regression without the high leverage point, shown in red, with Cook's distances $> 4/n$, where n=number of 1626 points^{[132](https://paperpile.com/c/gDKLkA/JvHud)}.). EVI is the mean extracted from intervals matching the average census interval of the 1627 1627 1627 corresponding plots in Brienen et al.²

Extended Data Fig. 16. Remotely sensed photosynthetic indices versus ground-monitored tree 1628

demography in shallow water table forests during the 2015-2016 drought [26](https://paperpile.com/c/gDKLkA/7LA7D) **: Top row:** MAIAC EVI 1629 1630 standardized drought anomalies:^{[26](https://paperpile.com/c/gDKLkA/7LA7D)}(1-km pixels) versus corresponding ground-monitored (a) mortality, (b) 1631 recruitment, and (c) mortality:recruitment ratios in 1-ha plots. Bottom row: GOSIF standardized drought anomalies (5-km pixels) versus ground-monitored (**d**) mortality, (**e**) recruitment, and (**f**) 1632 1633 mortality: recruitment ratios; Solid lines and statistics (\mathbb{R}^2 and p-values) represent standard linear 1634 regression fits to all data. Red points, if they exist, are high leverage, i.e. with Cook's distances $> 4/n$, 1635 where n=number of points^{[132](https://paperpile.com/c/gDKLkA/JvHud)}, and dotted lines and associated statistics in gray represent standard linear 1636 regressions without such points, showing that remote detection of ground-derived demographic trends is 1637 robust.

Extended Data Fig. 17. Forest response to the 2015 drought in drought-affected pixels: (**a**) Observed 1638 EVI anomalies (resampled at 0.4 degrees to match model resolution which accounts for spatial 1639 1640 autocorrelation (see Extended Data Fig. 7). (b) GAM-predicted EVI anomalies (model of Extended Data Table 1d). (**c**) Residual EVI anomalies (panel a observations minus panel b predictions). The GAM 1641 1642 well-predicts the pattern of response (Panel b), but under-estimates the extremes of the responses (as 1643 evident from residuals in panel c continuing to show greening/browning patterns beyond the predictions).

Extended Data Fig. 18. Map of Amazon forest biogeography of resilience, overlaid with mean winds 1644 **(arrows, at height 650 hPa) and arc of deforestation.** The most productive as well as the most 1645 1646 vulnerable forests (in red) are also the ones most suffering deforestation (the "arc of deforestation" which 1647 is causing local climate affects that are stressing even more our most vulnerable forests. These "arc of 1648 deforestation"/ vulnerable forests are often upwind forests^{[133](https://paperpile.com/c/gDKLkA/ZGil1)} (especially when the Intertropical 1649 convergence zone, ITCZ, swings to the south) so they are the leading edge of hydrological recycling in 1650 the Amazon.

Extended Data Table 1. **Generalized Additive Models (GAM) for**: (**a**) the southern Amazon, (**b**) the 1651 1652 everwet Amazon, (c) the Guiana shield (all droughts combined), and for (d) the whole basin (2015 1653 drought only), all on a 0.4 degree spatial grid. The ∆AIC is the difference from the lowest AIC (selected) 1654 model (ΔAIC=0), relative to a "full model" defined in columns 2-3. For details, see Methods, Section 2.6.1. 1655

Extended Data Table 2. Variable inflation factors (VIF, top row) and pearson correlation coefficients 1656 1657 (matrix) among climate and ecotope variables in drought-affected regions, across all droughts (first 1658 number in each entry) and in the 2015/16 drought only (second number). Variable inflation factors 1659 measure the severity of multicollinearity of a variable with all other independent variables jointly in a 1660 multiple regression, with VIFs of 5 or less often considered acceptable^{[134](https://paperpile.com/c/gDKLkA/ptzxm)}.