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Nature

DOI:

[10.1038/s41586-024-07568-w](https://doi.org/10.1038/s41586-024-07568-w)

E-pub ahead of print: 19/06/2024

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):

Chen, S., Stark, S. C., Nobre, A. D., Cuartas, L. A., Amore, D. D. J., Restrepo-Coupe, N., Smith, M., Chitra-Tarak, R., Ko, H., Nelson, B., & Saleska, S. R. (2024). Amazon forest biogeography predicts resilience and vulnerability to drought. *Nature*. Advance online publication. <https://doi.org/10.1038/s41586-024-07568-w>

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Amazon forest biogeography predicts resilience and vulnerability to drought

Authors: Shuli Chen^{1*}, Scott C Stark², Antonio Donato Nobre³, Luz Adriana Cuartas⁴, Diogo de Jesus Amore⁴, Natalia Restrepo-Coupe^{1,5}, Marielle N. Smith^{2,6}, Rutuja Chitra-Tarak⁷, Hongseok Ko¹, Bruce W Nelson⁸, Scott R Saleska^{1,9*}

Affiliations:

¹Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA

²Department of Forestry, Michigan State University, East Lansing, MI 48824, USA

³National Institute for Space Research (INPE), Avenida dos Astronautas, São José dos Campos, São Paulo 12201-1758 Brazil

⁴Center for Monitoring and Early Warning of Natural Disasters (CEMADEN); São José dos Campos, São Paulo 12247-016, Brazil

⁵Cupoazu LLC, Etobicoke, ON, M9A4L3, Canada

⁶School of Environmental & Natural Sciences, College of Environmental Sciences and Engineering, Bangor University, Bangor LL57 2DG, United Kingdom

⁷Los Alamos National Laboratory, Earth and Environmental Sciences, PO Box 1663, Los Alamos, NM 87545, USA

⁸Brazil's National Institute for Amazon Research (INPA), Manaus, Amazonas, Brazil

⁹Department of Environmental Sciences, University of Arizona, Tucson, AZ 85721, USA

*Corresponding author. Email: slchen@arizona.edu, saleska@arizona.edu

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 droughts¹⁻⁴ threaten to push these forests past a tipping point towards collapse⁵⁻⁸. Forests exhibit complex drought responses, indicating both resilience (photosynthetic “greening”) and vulnerability (browning and tree 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} (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,**

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

44 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}, provoking multiple difficult-to-explain
46 forest responses (**Fig. 1**, Extended Data Fig. 2). For instance, unexpected overall increases
47 ("green-up") in remotely sensed canopy greenness (a proxy for photosynthetic function) during
48 the 2005 drought^{9,10} (**Fig. 1a**, Extended Data Fig. 2a) appear at odds with reports of simultaneous
49 carbon losses from increased tree mortality observed in ground plots¹⁶. Further, the 2005
50 green-up contrasts with a strong decrease in greenness ("browndown") during the 2010 drought¹¹
51 (**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 important¹⁰, are evidently
54 insufficient to predict the complexity of drought responses across heterogeneous landscapes²².
55 Still missing is a general understanding of what drives differences in drought resilience across
56 Amazonian landscapes, a "functional biogeography"²³ of forest drought response that can
57 address the question: why are some forests (or times) resilient (exhibiting green-up, or reduced
58 mortality), while others are vulnerable (exhibiting browndown, or enhanced mortality)?

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

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

63 The first (“other side of drought”²⁴) hypothesis is that shallow water table hydrological
64 environments²⁵ provide trees with greater access to water resources, making them more drought
65 resilient (as observed in forest plots near Manaus^{26,27}), than trees in forests over deep water
66 tables, whose mortality rates typically increase with drought^{2,16}. 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.

70 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.

76 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}, or drought tolerance traits (high wood density or
79 embolism resistant xylem)^{29,34–36} are more drought tolerant, even over deep water tables.

80 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

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

86 We tested these hypotheses using satellite indices of photosynthetic capacity (the
87 Enhanced Vegetation Index, EVI, corrected for view- and illumination-geometry artifacts)³⁷ and
88 of photosynthetic activity (the Global OCO-2 Solar Induced Fluorescence product, GOSIF)³⁸. We
89 focused on drought-affected regions, defined as those whose maximum cumulative water deficit
90 (MCWD, methods §2.3) reached more than one standard deviation below the mean of the remote
91 sensing record (from 2000-2020)³⁹. Vegetation index anomalies during drought were analyzed as
92 a function of water table depth (as captured by “height above nearest drainage”, or 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.
95 5).

96 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
99 associated with resilience at the individual tree scale (lower mortality, greater growth, and
100 greater xylem embolism resistance, see methods §2.4).

101 **Southern Amazon forest drought response**

102 Focusing first on the locale of the 2005 drought (in the Southern Amazon, one of three
103 regions identified in methods §2.2, Extended Data Fig. 6), we found substantial structuring of the
104 2005 greening by water table depth across the drought-impacted region. This is visually evident
105 in the spatial correspondence of 2005 forest green-up/browndown regions (Fig. 1a, ellipse) with

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

In order to rigorously quantify the sensitivity of forest response across multiple droughts, we implemented two separate statistical approaches in sequence: non-linear multiple regression (using Generalized Additive Modeling, GAM), to test hypotheses and predict basin-wide drought anomalies, using AIC selection to identify the best predictive models (methods §2.6.1)⁴⁰, and Structural Causal Modeling (SCM) (using Directed Acyclic Graphs, DAGs) to more systematically evaluate the causal relations suggested by the GAM analysis (methods §2.6.2)⁴¹. Both modeling approaches were conducted on a 0.4 degree grid, the resolution needed to avoid inflation of statistical significance by accounting for spatial autocorrelation among nearby pixels (methods §2.5, Extended Data Fig. 7). We focus on the multiple regression GAM results below, and report comparisons with SCM results in methods §2.6.3.

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 large differences observed in responses among the years (Fig. 1: a vs b vs c), the overall other-side-of-drought (hypothesis 1) prediction of a negative relationship between remotely

sensed vegetation anomalies and deepening water tables observed in 2005 was consistently confirmed across all three droughts in this region (**Fig. 3a**). Notably, though there was an almost universal browning response to the 2010 drought (Fig. 1b), vegetation anomalies remained 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 respond positively to excess sunlight (possibly including relief from anoxia²⁴) was a key general (multi-drought) mechanism of southern Amazon forest drought response (**Fig. 3b** colored curves). Inter-drought differences in climate drivers — not differences in water-table depth distribution of impacted areas (Fig. 3a, distributions did not differ much) — accounted for much of the inter-drought differences in forest response (in Fig. 3a, the observed points correspond 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 Fig. 5a, g), promoting green-up, but decreased during the 2010 drought (due in part to excess smoke aerosols from high fire rates⁴², Fig. 3b distribution; Extended Data Fig. 5d). Anomalously high VPD across the droughted region in 2010 (Extended Data Fig. 5e vs Extended Data Fig. 5b, H), may also have contributed to reduced green-up/increased browning in 2010.

Importantly, inter-drought differences in Southern Amazon forest responses were mediated by drought length (**Fig. 3c**) (as hypothesized in Costa et al²⁴). Despite the even greater 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 (Fig. 3c distribution). Initial green-up in shallow-water-table-forests (blue lines in Fig. 3c) reversed to browning in regions experiencing drought longer than three months, with

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.

153 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} (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 average¹⁶ (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} 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) partially offsetting the more negative effect of drought seen on forest mortality
170 and carbon balance in deeper water table forests^{2,16}.

171 **Basin-wide forest drought response**

172 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

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 cations⁴³). 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.

183 When gridded ecotope factors (soil fertility and texture^{43,44} and vegetation properties
184 such as canopy height^{34,45}) 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 1²⁴), soil
187 fertility (hypothesis 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}).

190 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} that as soil nutrients become more
196 limiting, trees invest in drought resistance traits (e.g. high xylem embolism resistance), and with

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

200 The effect of water-table depth on drought response also depended on forest height (Fig.
201 4b), with the tallest forests, expected to have deeper rooting zones, enabling green-up even in
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.
207 Deep water tables may promote deep-rooted tall trees with resilience to seasonal atmospheric
208 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.

211 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
213 (Extended Data Fig. 3), was able to consistently predict the different kinds of drought responses
214 observed in different regions of the basin (Fig. 4e).

215 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 §3). These include the question of whether coarse-scale patterns (like those
218 deriving from the 1-40 km pixels used here) may emerge from such mechanisms as access to
219 water tables, which vary across landscapes, from forest plateaus to adjacent valleys, at fine scales

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

A functional biogeography of Amazon drought

We used the GAM predictions (Fig. 4) of different drought responses across different 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 §2.4, are those in which ecotope factors promote relative green-up) and vulnerability (pixels in which ecotope factors promote browndown) across the Amazon basin (**Fig. 5a**), including the ecotope factor combinations conducive (or not) to resilience (**Fig. 5b, c**).

This functional biogeography reveals the importance of ecotopes in structuring forest drought response: first, simply because the GAM models which accounted for forest ecotopes (via the variables HAND, SoilFertility, SoilTexture, and ForestHeight; Extended Data Fig. 3) along with climate had significantly more predictive power (higher R^2 while selected by lower AIC) 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 the shallow water table forests of the Rio Negro basin and in deep water table forests of Amapa state (“RN” and “AP” regions, respectively, highlighted in Figs. 1c, 4b and 5a). The biogeography (Fig. 5b) and GAM prediction (Fig. 4b) show both regions sharing infertile soils,

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
245 AP (coded orange in Fig. 5b, c), whereas the RN forests (coded green in Fig. 5b,c), though short,
246 had access to shallow water tables.

247 This new analysis goes beyond previous climate-based explanations of Amazon forest
248 drought response, and importantly complements the recent map of *external* anthropogenic
249 tipping-point threats (due to combined stresses of droughts, deforestation, fire, roads, etc.)⁷ with
250 a biogeography of *intrinsic* ecological resilience/vulnerability (due to characteristics of forests in
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 drought²⁴, but only relatively, especially in regions where high fertility stimulates the fast
256 growth of hydraulically more vulnerable trees²⁸ (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).

261 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

the ground (methods §1.6), 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 anomalies negatively correlated to mortality, and positively to recruitment, as expected if more negative anomalies are associated with increased plant stress. Notably, our GAM-derived remote sensing resilience map also independently predicted observations in forest plots of tree xylem hydraulic safety margins to mortality-inducing embolism⁵⁰, a widely-cited physiological drought tolerance trait (Fig. 5a inset).

Implications of a new Biogeography

This work has important implications for understanding forest responses to climatic 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 neglected by most previous studies of forest drought sensitivity (Fig. 3e histograms), southern Amazon forests are likely more resilient to drought than common estimates of climate sensitivity imply¹⁶, and large-scale plot-based estimates of a drought-induced decline in the Amazon forest carbon sink² may need to be adjusted to account for these more drought resilient but neglected forests.

However, this analysis also warns that climate change is likely simultaneously 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 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 lost to drought²⁸) is likely limited under growing climate change. The buffering effect of shallow water tables appears limited to short duration droughts (< 3 months, Fig. 3c) that do not last long

289 enough to deplete water tables. And the benefits of re-growing trees quickly that are lost to
290 once-in-a-century droughts (whether or not protected by shallow water tables) are much reduced
291 when those drought frequencies increase to become 5 or 10-year droughts (as seen recently and
292 as predicted to continue in the near future^{51,52}). Importantly, these fertility results imply
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.

296 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
299 (substantially overlapping with the “arc of deforestation,” Extended Data Fig. 18). More
300 importantly, because they are predominantly situated under prevailing winds that bring moist
301 Amazonian air to the south (Extended Data Fig. 18) they are critical to maintaining the
302 evapotranspiration that feeds (and likely amplifies⁵³) 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 Brazil⁵⁴.

305 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.

309 FIGURE CAPTIONS

310 **Fig. 1. Amazon forest remotely-sensed responses to the droughts of (a) 2005, (b) 2010, and**
311 **(c) 2015/2016, expressed as** standardized anomalies of Enhanced Vegetation Index (EVI, a
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 ($\overline{\Delta EVI} =$
317 $+0.14$, $p < 0.001$, $df = 916$, (b) 2010 ($\overline{\Delta EVI} = -1.06$, $p < 0.001$, $df = 1057$) and (c) 2015 ($\overline{\Delta EVI} =$
318 -0.57 , $p < 0.001$, $df = 2218$) droughts. Statistics are from student's t-test, where, following the
319 variogram analysis (Methods §2.5) 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.

322 **Fig. 2. Amazon forest response to 2005 drought is structured by water-table depth: (a)**
323 Water-table depth map (indexed by Height Above Nearest Drainage, HAND, in meters, Andes
324 excluded²⁵) with ellipse highlighting shallow and deep water tables that correspond to green-up
325 and browndown patterns in Fig. 1a. **(b)** Observed EVI anomalies (solid symbols \pm SE, from Fig.
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 (>22 m,
330 orange band). **(c)** Observed EVI anomalies (solid symbols \pm SE, from Fig. 1a) bin-averaged by
331 PAR anomalies and by different water-table depths (HAND values) (upper panel); histograms of
332 PAR anomaly (lower panels) according to drought severity.

Fig. 3. Southern Amazon forest responses to multiple droughts: (a-c) GAM (Extended Data Table 1a) predictions: (a) Climate-adjusted EVI responses vs. water-table depths (indexed 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 m^{-1}), 2010 (purple, slope= -0.020 ± 0.002 SD m^{-1}), and 2015 (blue, slope= -0.028 ± 0.002 SD m^{-1}) droughts (shading and dashed regression lines), paired with HAND distributions in each drought region (bottom graphs, right axis); (b) PAR sensitivity, by HAND class, of (climate-adjusted) EVI drought responses, paired with drought-specific area distributions of PAR anomalies (right axis), show greater PAR sensitivity for shallower water tables. (c) Drought-length sensitivity, by HAND class, of (climate-adjusted) EVI drought response, paired with drought-specific area distributions of duration (in months) (bottom graphs, right axis) show that shallow-water-table protection is diminished for long droughts. ‘Climate-adjusted’ responses use southern Amazon drought-specific average climate to predict responses or adjust observations. Each drought’s distribution occupies equal area across the three panels. (d) Above-ground biomass (AGB) mortality drought responses (mortality-associated carbon flux, in percent change relative to long-term $\text{MgC ha}^{-1} \text{ y}^{-1}$ in RAINFOR plots²) vs. water-table depth (HAND) (points $\pm 95\%$ CI, regression line for depths less than 30 meters) support hypothesis 1 (with consistent positive slopes) for the 2005 (green, slope= $1.4 \% \text{ m}^{-1}$, $p=0.051$) and 2010 (purple, slope= $1.8 \% \text{ m}^{-1}$, $p=0.015$) droughts, paired with (e) cumulative distributions of HAND area across basin (gray bars, left axis), and distribution of plot-based sampling efforts (fractional effort, RAINFOR plot area \times years monitored, per HAND bin, divided by fractional basin area per HAND bin, blue bars, right axis). This shows that plot sampling efforts underrepresent prevalent shallow water-table forests that greened up (green band, $\sim 55\%$ of the basin, but 16% of the effort) and over-represent deep water-table forests that browned down (orange band, $\sim 20\%$ of the basin but 55% of the effort).

Fig. 4. Basin-wide Amazon forest responses to the 2015 drought, structured by ecotopes and predicted by whole-basin GAM analysis (Extended Data Table 1d): GAM partial predictions of EVI anomalies (color scale) for (a) soil fertility⁴³ (vertical axis) and HAND²⁵ (horizontal axis) terms only, and for (b) forest height⁴⁵ and HAND²⁵ terms only. Ecotope 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. 1c (RN, in Rio Negro catchment, and AP in Amapa state) illustrate differing mechanisms of 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 HAND with increasing (c) fertility (blue to green, corresponding to colored areas in fertility 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 observations (symbols) to adjusted GAM predictions (lines and 95% confidence shaded area). Note: ‘adjusted’ EVI anomalies indicate that climate and ecotope factors not displayed in the 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 relatively more resilient (likely to exhibit EVI green-up) (green) or more vulnerable (red) to drought, based on standardized GAM drought response predictions of EVI anomaly from ecotope factors only (from Fig. 4, Extended Data Table 1d) (removing effects of climate variability by setting climate equal to its basin-wide average) (see methods §2.8). Crosses are validation sites where remote sensing-derived resilience predicts plot-based physiological 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 mapped in (a), as promoted by presence of resilience factors: shallow water tables ($HAND < 10m$, blue), low-fertility soils (cation concentrations $< 10^{-0.35} \text{ cmol}^+/\text{kg}$, yellow), or tall deep-rooted trees (heights $> 32.5 \text{ m}$, red), with overlap indicated by the primary color mixing rules 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 of relatively vulnerable, resilient, or neutral forest associated with each (left axis) and mean relative resilience (blue horizontal lines, right axis), ordered from most vulnerable to most resilient.

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506 Methods

507 In this study, we applied a hypothesis-testing framework^{55,56}, 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
511 Enhanced Vegetation Index, EVI, and Solar Induced Fluorescence, SIF) (section 1.1, including
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 RAINFOR² and from Sousa et al.²⁶) and of physiological drought tolerance
517 (Tavares et. al⁵⁰) (section 1.5) to test remote sensing skill at capturing ground-measured metrics
518 for forest drought response (section 1.6).

519 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
523 2.3), defined forest drought resilience in terms of anomalies in vegetation function (section 2.4),
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
530 Acyclic Graphs, DAG, section 2.6.2). We tested GAM predictions by comparison to adjusted
531 observations (section 2.7) and then used the basin-wide GAM predictive model (from section
532 2.6.1) to derive a functional biogeography of drought response (section 2.8).

533 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.
536 These provided evidence in support of our interpretation, but also pointed to future research
537 needs.

538 1. Datasets

539 1.1. Remote sensing indices of photosynthesis

540 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
544 Terra/Aqua satellites; and the global OCO-2 Solar-induced Fluorescence (GOSIF) product
545 derived from observations by the Orbiting Carbon Observatory 2 satellite. EVI, derived from the
546 spectra of light reflected from surface vegetation, is designed as an index of the *photosynthetic*
547 *capacity*⁵⁷. GOSIF is designed to represent the active light emission from fluorescing chlorophyll
548 molecules during photosynthesis, which is often well-correlated with canopy-scale instantaneous
549 *photosynthetic activity*⁵⁷. This distinction (between reflected light used to construct EVI as a

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.

We chose these indices because they aim to capture different end-members of a spectrum of canopy responses: from transient physiological changes in photosynthesizing/fluorescing leaves (which might be due, for example, to stomatal regulation in response to changing atmospheric VPD) which affect photosynthetic activity for a given capacity⁵⁸, versus more structural responses associated with leaf turnover such as leaf flushing or shedding which also change canopy photosynthetic capacity⁵⁹. We primarily focus here on EVI responses, which have been shown to remotely capture seasonal canopy greenup dynamics that are consistent with underlying mechanisms of leaf development and demography⁶⁰. However, GOSIF corroboration 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 of remotely observed drought responses.

MAIAC EVI: The Multi-Angle Implementation of Atmospheric Correction (MAIAC) algorithm rigorously accounts for sun-sensor geometry, as represented in a bidirectional reflectance distribution function (BRDF), estimating reflectance at a nadir view and 45° solar zenith angle, with strict atmosphere, aerosol, and cloud corrections⁶¹. We used the 8-day MCD19A3 (MAIAC) 1-km product from MODIS collection six, a level 3 product composited from cloud-free and low aerosol conditions. We applied the coefficients (weights) of the RossThick/Li-Sparse (RTLS) Bidirectional Reflectance Distribution Function (BRDF) model (available at <https://e4ftl01.cr.usgs.gov/MOTA/MCD19A3.006/>). We calculated the 8-day EVI from the MAIAC surface reflectances of red, blue, and near-infrared bands as in Huete et al.⁵⁷ 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 that have been excited by absorption of sunlight, provides a direct index of the current physiological state of a photosynthesizing canopy⁶². The OCO-2 satellite observes SIF at coarse resolutions⁶³, and these are used to create the modeled GOSIF data product⁶⁴ available at http://data.globalecology.unh.edu/data/GOSIF_v2), which simulates higher resolution SIF dynamics over longer time periods by interpolating among discrete OCO-2 SIF soundings using the MODIS surface reflectance product MCD43C4 (BRDF-corrected to nadir view and to the solar zenith angle at local noon), and meteorological reanalysis data⁶⁴. We used the monthly 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 land cover types⁶⁵.

1.2. Climate variables

To explore climate effects on forest drought responses, we used monthly precipitation, Maximum Cumulative Water Deficit (MCWD), surface downwelling shortwave radiation and 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) (https://disc2.gesdisc.eosdis.nasa.gov/data/TRMM_L3/TRMM_3B43.7/)⁶⁶.

MCWD measures local drought intensity, defined as the maximum deficit reached in the last month of a string of dry months for each grid cell within the year³⁹, treating forest water deficit as analogous to a bucket whose deficit is zero when the bucket is full. To avoid splitting a

string of dry months between two years, we used a 12-month ‘hydrological year’ running from 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 Modern-Era Retrospective analysis for Research and Applications version 2 (MERRA-2 Reanalysis) for 2000 to 2019 as a proxy for PAR at spatial resolution of $0.5^\circ \times 0.625^\circ$ (https://goldsmr4.gesdisc.eosdis.nasa.gov/data/MERRA2_MONTHLY/M2TMNXRAD.5.12.4/)⁶⁷. Vapor Pressure Deficit (VPD) was calculated based on surface air temperature and relative humidity (L3 Standard Monthly Product, AIRS3STM) from version 6 of the Atmospheric Infrared Sounder (AIRS) at the spatial resolution of 1 degree for 2003-2017 (~100 km, <https://airs.jpl.nasa.gov/data/get-data/standard-data/>)⁶⁸⁻⁷¹.

1.3. Ecotope variables

We follow the ecosystem ecology approach^{18,19} of characterizing different ecosystem types (in this case, forest ecosystems) by their “ecotopes”, that is, by the combination of biotic characteristics and abiotic environments that define them, here including their hydrological environment (water table depth), soil types (fertility and texture), vegetation characteristics, and other factors⁷².

We used the Height Above the Nearest Drainage (HAND) normalized terrain model^{25,73} as a proxy of water table depth and for plant access to groundwater, rederived at 100m resolution from digital elevation model-Shuttle Radar Topography Mission (SRTM) data for this study^{26,74}. The HAND normalization is relative to the local drainage height, using the flow paths to connect all cells (pixels) with the cells of the nearest drainage. The HAND model has been validated over an area of 18,000 km² in the lower Rio Negro catchment²⁵ and used for a wide range of ecohydrological studies^{27,75,76}. HAND is comparable to the water table depth (WTD) model-based product of Fan & Miguez-Macho⁷⁷, which gave broadly similar results to those reported here with HAND. For this study the HAND normalized terrain model was derived from SRTM-DEM at 100 m resolution.

For soil fertility, we used a map (0.1° spatial resolution) of exchangeable base cations (Ca⁺ + Mg⁺ + K⁺ measured in cmol(+)/kg) for the Amazon basin⁴³, the most extensive empirically-validated gridded soil fertility product currently available. Soil cation concentrations estimated from this product achieved good agreement with an independent dataset of field-measured values (correlation of $r = 0.71$ ⁴³).

Our analysis does not include phosphorus, generally considered to be limiting to tropical forest productivity^{78,79}, but not currently available as a high-quality validated gridded data product. We expect base cations to be a partial index of phosphorus availability, as both cations and phosphorus become available through weathering of young soils arising from Andean parent material or runoff sediment, but are eventually leached, leaving older highly weathered soils in the Guiana Shields depleted of both. Cation concentration should also be directly relevant to drought tolerance, as high concentrations should improve osmotic regulation of stomatal conductance, an important regulator of drought response⁸⁰.

For soil texture, we used soil sand/clay fractions from “SoilGrids” system released by ISRIC (International Soil Reference Information Centre) World Soil Information⁴⁴.

For forest height, we used a canopy height metric derived from spaceborne lidar measurements⁴⁵ (https://webmap.ornl.gov/ogc/dataset.jsp?dg_id=10023_1) and validated by field measurements, with an increased accuracy in the Amazon compared to previous metrics³³). This wall-to-wall global map of canopy height is at 1-km spatial resolution, interpolated from lidar observations by the Geoscience Laser Altimeter System (GLAS) aboard ICESat (Ice, Cloud, and

Land Elevation Satellite). We take forest canopy height as a proxy of rooting depth, based on standard allometries backed by observations in Brazilian tree plantations^{31,32,46}, in a central Amazon forest^{31,32,46} and across biomes^{31,32,46} that show they are correlated^{31,32,46}. However, observations of the tree height-rooting depth allometry are limited, especially in tropical forests (although one study cited here³¹ is directly relevant, as it is from central-eastern Amazon upland forest, conducted during the 2015 drought); this limitation remains a key uncertainty in our 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 shallow WTD limits rooting depth such that canopy height correlations to rooting depth in these forests may be diminished⁸¹.

We also applied community-weighted mean wood density and the abundance of Fabaceae (legumes)³⁴. Fabaceae refers to a large, nearly cosmopolitan family that relates woody plants with nitrogen-fixing nodulation, usually assumed adaptations to low-fertility soils⁸².

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 forest map at 1 km spatial resolution (MOD12Q1.006) to identify evergreen forest pixels within the Amazon basin⁸³, excluding open water, deforested forests, and non-forest vegetation types. A floodplain map was also used in order to identify targeted non-flooded forests, and exclude floodplain forests⁸⁴. We used the map of Gomez et al.⁸⁵ to define the boundary of the Amazon 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 forest cover classification that now includes a category for “degraded” forests at 30 meter spatial resolution (Vancutsem et al.⁸⁶, updated to 2022), to test drought sensitivity (methods 3).

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 Amazon basin-wide carbon balance (most, but not all, of these were from the RAINFOR network)², 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 respect to the distribution of water table depths (HAND) across the Amazon basin (Fig. 3e); (2) to test whether forest mortality anomalies (% deviation from long term mean) in 247 plots subject to the 2005 and 2010 droughts were associated with water table depth (Fig. 3d); and (3) to validate EVI remote sensing with spatial variations in long term (2000-2011) average 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, likely including a greater range of environments⁸⁷, but published results representing drought response of “the Amazon rainforest”¹⁶ and “the Amazon carbon sink”² are the ones whose sample plot distributions are analyzed here for their representivity.

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 road in the southern Amazon between Manaus and Porto Velho (from 62.5°W, 5.9°S to 60.9°W, 4.4°S) as analyzed in Sousa et al.²⁶ These are shallow water table sites (2.81 m ± 2.38 deep [M ± SD]) intended to complement the on average deeper water table sites of the RAINFOR network

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

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 a species in the field and the water potentials leading to hydraulic failure, with narrower margins indicating greater mortality risk)⁵⁰, including 108 species distributed across 9 forest sites across western, central eastern and southern Amazon, to validate our derived resilience map (Fig. 5). These sites belong to old-growth lowland forests, little disturbed by human activities, spanning the Amazonian precipitation gradient and encompassing the principal axes of species composition in the Amazon⁵⁰. The HSM was calculated with respect to P50/88 (HSM50/88) at species level, and then basal-area weighted averaged occurring at sites⁵⁰.

1.6. Remote sensing validation and consistency

1.6.1 Validation by ecosystem flux measurements (eddy flux towers)

MAIAC EVI: EVI has been extensively validated against measurements of ecosystem photosynthesis (Gross Primary Productivity, GPP) from eddy flux towers across land types world-wide⁸⁸, including temperate^{89–91} and tropical biomes^{92–94}. Earlier versions of MODIS EVI were criticized as influenced by aerosol or sun-sensor geometry artifacts when detecting tropical forest greening^{95,96}, but such effects are largely eliminated in the current MAIAC EVI product used here (which corrects artifacts from aerosol contamination and sun-sensor geometry)⁶¹. Particularly relevant for this study, MAIAC EVI well-detected Amazon forest seasonal green-up dynamics across a network of eddy flux tower sites in the Brazilian Amazon^{97,98}, with patterns shown to be consistent with understandings of leaf development and demography derived from flux towers and phenocam studies on the ground⁶⁰.

EVI or EVI-based models predict independent tower measurements of monthly GPP with $R^2 \sim 0.5$ – 0.7 for tropical^{92–94,97}, and $R^2 \sim 0.7$ – 0.8 for temperate biomes^{89–91}.

GOSIF: Despite non-linear and sometimes decoupled relationships between chlorophyll fluorescence and photosynthesis at leaf scales⁹⁹, satellite observations of SIF from OCO-2 have been shown to be linearly related to canopy scale GPP⁶³, suggesting that canopy scale processes can effectively average over leafscale complexities. GOSIF modeled datasets built from SIF observations have been multiply validated by tower-based CO₂ flux estimates of GPP, achieving good correlation ($R^2 = 0.73$ globally) with the 91 sites of global Fluxnet GPP (2015 Tier 1 dataset)⁶⁴, with somewhat lower correlations ($R^2 = 0.51$, comparable to EVI in the tropics) for the evergreen broadleaf forest biome, including sites in the Amazon⁶⁵.

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

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 forest demographic effects (growth, recruitment, and mortality, section 1.5). We should expect remote sensing skill in predicting demography to be weaker than for predicting photosynthetic

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

We nevertheless found validation at multiple scales: MAIAC EVI significantly predicted 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 also confirmed consistent detection by EVI and GOSIF of short-term demographic drought-response metrics during the 2015/2016 drought (mortality, recruitment, and the mortality:recruitment ratio, Extended Data Fig. 16), as expected if excess mortality (or a decline 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 expectation that they should be about half of the remote detection R^2 for GPP (0.5 to 0.6, discussed in 1.6.1), since GPP is about one-half the determinant of the NPP driver of demography.

With respect to remote detection of the physiological drought tolerance of trees, we 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 drought, hydraulic safety margins (HSM) for xylem embolism. Individual tree HSM -- the difference between observed stem water potentials and the stem water potentials at which trees become vulnerable to xylem embolism -- are widely regarded as predictors of tree mortality risk under drought⁵⁰, with narrower HSMs indicating greater mortality risk³⁶. We found that our remote sensing-derived estimates of forest resilience (Fig. 5a) could significantly predict basal-area weighted tree HSM measured on the ground at forest plots across the Amazon basin (Fig. 5a inset) (reported in Tavares et al.⁵⁰, as summarized in section 1.5). (Note that forest resilience was estimated as in methods section 2.8, but using canopy height mapped at 0.1 degree resolution--instead of the baseline model resolution of 0.4 degrees--in order to avoid mixing the height signal of intact HSM plot forests with that of occasionally nearby deforested areas.) This validation strongly supports the validity of using remotely sensed photosynthetic indices to derive a definition of photosynthetic resilience to drought.

1.6.3. Consistency between EVI and GOSIF

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

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. stomatal adjustment) as well as slower structural effects due to changes in capacity (e.g. biochemical inhibition, leaf growth or shedding)^{58,100}. We indeed see this expectation reflected in observed drought response, with the range of GOSIF (activity) anomalies (from -9.6 to +4.8 standard deviations, excluding 0.1% of the distribution in each tail) 30% greater than the range 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 hypotheses that are the focus of this analysis -- for example, whether the “other side of drought” prediction that drought response anomalies should decline with water table depth, and here we

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

Within the broadscale consistency, there is also substantial finescale differences in spatial 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 study of these finer-scale differences could reveal additional insights into the biogeography of forest drought response¹⁰¹.

2. Mapping and Statistical Analysis

2.1. Spatial Grid resolutions

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

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

For statistical modeling we interpolated different datasets to common grid resolutions, according to the resolution of the model. For this we initially downscaled all maps to the native resolution of the EVI product (1km), then aggregated to the desired coarser resolution, typically 0.4°, that was needed to avoid inflation of statistical significance of drought responses in models by accounting for spatial autocorrelation among nearby pixels using variogram analysis (section 2.5, Extended Data Fig. 7). Grid cells in the drought-affected domain that included no intact 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 aggregated all intact forest pixels at the smaller (1km) subgrid scale to accurately represent intact vegetation properties (EVI, canopy height, etc), and represented the coarser model grid cell by those intact forest properties.

2.2. Classification of forest regions according to ecotopes

We investigated whether the distribution of factors defining forest types (ecotopes) across Amazonia could lead to a coherent clustering of different forest ecotopes into different regions, each with different broadscale forest drought responses. To this end, we conducted a supervised forest classification, using factors identified in previous studies as important:^{17,34,102,103} two climate variables (average minimum monthly precipitation and MCWD variability), soil fertility

(concentration of exchangeable base cations⁴³) and three tree functional characteristics (forest 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 their mean and SD, were mapped, with each grid cell considered to occupy a point in a six dimensional space, and each dimension indexed in comparable units of standard deviations. *Second*, a principal component analysis (PCA)¹⁰⁴ (“FactoMineR” package in R, Extended Data Fig. 6a) identified three complementary dimensions of forests in this space: a dimension defined by *vegetation* characteristics (wood density, and proportions of the family Fabaceae), nearly coincident with the first principal component (horizontal axis, Extended Data Fig. 6a); a dimension defined by water availability (minimum monthly precipitation and MCWD 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 these initial PCA results suggesting three relatively distinct dimensions, we chose to cluster Amazon basin pixels into three classes. Given their diversity, Amazon forests could likely be classified into more than three, but we judged that three would be sufficient to capture substantial functional variation, without being so complex as to prevent intuitive understanding.

Third, an automatic procedure extracted endmember characteristics based on percentile thresholds¹⁰⁵ from the PCA space¹⁰⁶. Pixels with low climate variability had high minimum precipitation and long wet seasons (in the 90th percentile), and were identified as a water availability spectrum end-member. Grid cells with the highest proportion of Fabaceae, overlaying with tall, dense-wooded trees (in the 90th percentile) and low-fertility soils, were identified as another endmember. A third endmember was defined by a combination of high variability climates and moderately high (67th percentile) soil fertility. *Finally*, supervised classification via the Minimum Distance method was used in ENVI 5.3 software¹⁰⁷ to cluster 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 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 in the northeast, and *the southern Amazon*. The standardized values within each cluster, of each of the characteristics defining the regional clustering (ordered by water availability, soil fertility, and tree traits), exhibit the distinct niches of each region (Extended Data Fig. 6c). The ever-wet Amazon is differentiated by lack of dry seasons (periods with months < 100 mm rainfall, Extended Data Fig. 3a). Forests in this region might be composed of species that do not well-tolerate climate conditions (such as droughts), compared to tree assemblies (in other regions) adapted to regular droughts or dry seasons. The Guiana shield region is distinct in having old, highly weathered, low-fertility soils, with tree communities containing the largest proportion of trees in the family Fabaceae, with dense wood and high seed mass (Extended Data Fig. 3c-e)³⁴. The southern Amazon is then differentiated further from the Guiana shield as 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 text figures) is independent of the results (Figs. 3-4) of the basin-wide modeling investigation (described in sections 2.6-2.7 below) because model predictions depend on pixel-pixel variations of environmental factors regardless of what region they are in. However, the three region Amazon is useful for presenting model results because it illustrates how different functional responses emerge from different ecotope regions (as shown in Fig. 4e).

2.3. Climate anomalies for Drought definition and Mapping

866 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
 868 (Extended Data Fig. 1). MCWD anomaly for each grid cell is calculated by Eqn. (1):

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

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

874 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).

878 Drought duration (for each of the three droughts separately for each grid cell) was measured
 879 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:

$$\begin{aligned} & \text{if} \quad CWD_{d,i-1} \geq \overline{MCWD}, \\ & \quad CWD_{d,i} < \overline{MCWD}, \\ & \text{and} \quad CWD_{d,i+1} < \overline{MCWD}, \\ & \text{then} \quad Onset_d = i \end{aligned} \quad (2)$$

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

$$\begin{aligned} & \text{if} \quad CWD_{d,j} < \overline{MCWD}, \\ & \quad CWD_{d,j+1} \geq \overline{MCWD}, \\ & \text{and} \quad End_d \geq Onset_d, \\ & \text{then} \quad End_d = j \end{aligned} \quad (3)$$

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

889 2.4. Drought resilience and Vegetation Anomalies

890 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}, and our definition (which can also be characterized as
 894 "resistance" or ability to resist changes in function with perturbation¹⁰⁸) is nominally distinct for
 895 example, from another common definition, the capacity of a system to return to its equilibrium
 896 state following a disturbance¹¹⁰. 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

strategies (likely including system capacity to return to equilibrium following disturbance), making it a logical general metric of resilience. Practically, greening has been widely cited and discussed in the literature, and, notably, is predictive of outcomes on the ground commonly associated with resilience at the individual tree and plot scale (lower mortality, greater growth, 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 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 non-drought-year means) across a 9-year window centered on each drought (for example, 2001-2009 for the 2005 drought and 2011-2019 for the 2015 drought):

$$Anomaly_{d,du} = \frac{X_{d,du} - \overline{X}_{du}}{\sigma_{du}} \quad (4)$$

where $X_{d,du}$ is the value of the index in a grid cell during drought d , averaged over the duration du (extracted by Eqn. (2) and (3)) – and \overline{X}_{du} and σ_{du} are the average and standard deviation, 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 realism in drought response metrics by capturing pixel-pixel variability in drought response due 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 pixels)^{9,10,111}.

Correspondingly, we also calculated the field-based demographic mortality anomalies for drought years 2005 and 2010 from RAINFOR plots,² as above-ground biomass (AGB) mortality drought responses (mortality carbon flux following drought, in percent change relative to long-term mean MgC ha⁻¹ y⁻¹).

2.5. Variogram analysis for removal of spatial autocorrelation

Observations from spatial samples are not independent, due to spatial autocorrelation among grid cells that are near to each other¹¹². To obtain independent observations for general additive models (GAM) and for statistical quantification of average drought response (Fig. 1), we resampled grid cells at increasingly coarse resolutions, until response differences (between forests with different water table depths) were no longer spatially autocorrelated -- that is, a sill (plateau) was reached in the variogram (Extended Data Fig. 7) at around 40 km, indicating a scale at which samples could be treated as statistically independent. The variogram was calculated from the covariance of the difference between drought responses in shallow and deep water table grid cells:

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

$$z_m = Anomaly_{EVI, SWTD_m} \quad (6)$$

$$z_n = Anomaly_{EVI, DWTd_n} \quad (7)$$

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

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

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

944 For this, we implemented two sequential statistical approaches: First (§2.6.1), we used
945 GAM statistical regression¹¹⁰, 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}. 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
950 moderate-sized models within a hypothesis-testing framework, where causal hypotheses are
951 specified based on ecological considerations and the selected regression fits test the predictions
952 made by those hypotheses. Second (§2.6.2), we also employed structural causal modeling
953 (SCM)^{40,113} an approach which formalizes hypothesis testing as part of the model structure (e.g.,
954 using Directed Acyclic Graphs, DAG^{114,115}). 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.

959 Finally, we compare the two approaches (§2.6.3), 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.

962 2.6.1. AIC-selected General Additive Models (GAM) for hypothesis testing and prediction

963 We developed GAM regression models of forest drought response as a function of climate
964 variables and ecotope factors^{10,18,37} to represent our three core hypotheses of water table depth²⁸,
965 soil fertility^{32,33}, and tree characteristics^{34–36,49}. 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}. 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.

971 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 response¹⁰; 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).

978 (i) Effect of local hydrological environment and climate on drought response (**regional GAMs**).

979 GAMs were fit separately for the southern Amazon, Guiana shield, and ever-wet Amazon
980 regions, and for all three droughts together, as:

$$\begin{aligned} \Delta EVI = & s(HAND) + s(\Delta PAR) + s(\Delta VPD) + s(\Delta P) + s(\Delta MCWD) + s(DL) \\ & + ti(\text{pairwise interactions of every two predictors}) + \varepsilon \end{aligned} \quad (8)$$

where ΔEVI is the vegetation response anomaly, ΔPAR , ΔVPD , ΔP and $\Delta MCWD$ are the radiation, VPD, precipitation, and MCWD anomalies, respectively; DL denotes the drought length; ε is the normally distributed residual; $s()$ and $ti()$ are the smoothing functions of predictor variables, obtained using a scatterplot smoothing algorithm with a back-fitting procedure for the appropriate smoothing function for each predictor. The degree of freedom (df) for the smoothers is determined with “REML” with gaussian distribution implemented by Wood’s R package “mgcv”¹¹³. Models were implemented with gam.check function by R package “mgcv”¹¹³ for 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).

The smooth functions were determined by thin plate splines^{114,115}. Here, we fitted thin plate regression splines using automatically optimized smoothing parameters using the restricted maximum likelihood, or REML method. Three optimal models were selected for the corresponding three regions, with all three model selection procedures evaluated by delta AIC and R square¹¹⁶ using the “dredge” function in the mgcv package in R¹¹³, with results reported in **Extended Data Table 1** (models a, b, and c).

(ii) Effect of hydrological environment interacting with regional ecotopes (basin-wide GAM).

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

$$\Delta EVI = s(HAND) + s(SF) + s(ST) + s(FH) + s(DSL) + s(\Delta PAR) + s(\Delta VPD) + s(\Delta P) + s(\Delta MCWD) + ti(\text{pairwise interactions of every two climate variables})$$

$$+ ti(\text{pairwise interactions of HAND with other ecotope-based variables and } \Delta PAR) + \varepsilon \quad (9)$$

where DSL denotes dry season length, FH denotes forest height, ST denotes soil texture and SF denotes soil fertility. Considering variable correlations (**Extended Data Table 2**), we avoided choosing highly correlated variables for the same model (which for example excluded wood density when soil fertility was in the model). Considering the complexity of the model and computational cost, the pairwise interactions were included separately among ecotope factors, among climate variables, and between HAND and PAR, but did not traverse interactions among every possible pair of variables. The fitting process was the same as for the regional GAMs of (i): smoother determined with “REML” as implemented by “mgcv”¹¹³, and models evaluated by delta AIC and R square¹¹⁶ coded by the “dredge” function in the “mgcv” package in R, with final results reported in **Extended Data Table 1** (model d). Basin-wide modeled forest response for the 2015/2016 drought is presented in Extended Data Fig. 17 where the GAM well-predicts the pattern of response (Extended Data Fig. 17b), but under-estimates the extremes of the responses (as evident from residuals in Extended Data Fig. 17c showing greening/browning patterns beyond the predictions).

Beyond the three more recent hypotheses discussed in the main text, soil texture was also expected to affect soil hydraulic properties and forest ecosystem response to drought^{102,117}. We found that forests on sandy soils were more resilient (i.e., higher relative green-up) than those on clay soils (which bind water more closely), consistent with findings of process model studies²² of clays that bring soils more quickly to wilting points²³. But again, this depended on water table depth, and deep water table forests also became more vulnerable with increasing sand content (Extended Data Fig. 11), perhaps because in the absence of a shallow water resource, sandy soils drained water too quickly

This final basin-wide GAM model (Extended Data Table 1d) including soil texture (along with WTD, forest height, and soil fertility) suggests a further hypothesis for how soil texture moderates the effects of forest height and water table depth on drought response (Extended Data Fig. 11). The potential counteracting effects of the positively correlated forest height (which increases resilience when water tables are deep) and soil clay fraction (which generally decreases resilience due to binding water more tightly to soil particles) may explain the otherwise puzzling result that the tall forest advantage in deep water table forests does not just disappear but reverses in shallow water table environments (Fig. 4d). As shown in Extended Data Fig. 11, the reversal of the general trend (of decreasing resilience as clay fraction increases = sand fraction decreases) 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 the low sand (=high clay) end of the spectrum, the effect of soil texture depends strongly on WTD: in shallow WTD forests where tall trees are not advantaged, the negative effect of clay depresses forest drought response, but in deep WTD forests drought resilience increases again, even with increasing clay (decreasing sand), possibly because the associated taller tree effect outweighs the negative effect of clay soils. This mechanism could serve to improve models of how soil texture modulates drought response^{118,119}.

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

In order to further test the causal mechanisms proposed by our three core hypotheses, we used a framework for causal inference from SCM^{40,118}, DAG analysis^{119,120}. We proposed and tested hypothesized causal relationships (represented by DAG diagrams, as in Extended Data Fig. 9a).

Implementing DAG analysis with ‘dagitty’ (R package¹²⁰, we first developed a DAG diagram for Amazon forest drought response with relevant climate variables and ecotope factors expected from the literature^{10,17,34}, including our three core hypotheses of water table depth²⁴, soil fertility^{28,29}, and tree characteristics^{30–32,50} (Extended Data Fig. 9a). We assessed ‘DAG-data consistency’, testing to ensure that unconnected nodes are not correlated, applying root mean square error of approximation (RMSEA) (R functions “localTests” and “cis.loess” to allow potential non-linear correlations using loess fits¹²⁰; Extended Data Fig. 9b).

We iteratively tested and revised the DAG by repairing detected independence violations between unconnected nodes (i.e. where RMSEA was greater than 0.30, as in Ankan et al.¹²¹), by adding either a new direct causal link between such nodes (after first verifying an ecological basis for the link), or new links to each of the correlated nodes from a common causal node (again, if they made ecological sense). For example, longer dry season length should promote generally drier conditions, including greater VPD and MCWD; positive precipitation anomalies will cause higher relative humidity and therefore lower VPD anomaly³³; more clayey soils allow taller trees¹²², supporting the addition of links between these nodes. These adjustments gave a final DAG with a greater number of links (Extended Data Fig. 9c) and no independence

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

2.6.3. Comparing inferences from SCM with predictive GAM regressions

We found that both modeling approaches consistently supported the “other side of drought” hypothesis (hypothesis 1) for forest drought response in the southern Amazon across all three droughts (negative dependence on water table depth, Fig. 3a and Extended Data Fig. 10a), with associated consistent climate dependencies (positive dependence on sunlight, Fig. 3b and Extended Data Fig. 10b, and declining overall dependence on drought length, but with a peak at ~3 months duration, Fig. 3c, Extended Data Fig. 10c). Across the basin for the 2015/2016 drought, both modeling approaches supported hypothesis 2, that increasing soil fertility (past a moderate fertility level) would negatively affect drought response (Fig. 4a,c and Extended Data Fig. 10e), and both supported a “hypothesis 1- hypothesis 3” interaction, finding that increasing forest height (and presumed deeper rooting depth) positively affected drought response in deep 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 approaches found similar effects of soil texture on drought response (Extended Data Fig. 10f and Extended Data Fig. 11).

2.7. Comparing adjusted observations to GAM predictions for different predictor variables

The observed vegetation indices (MAIAC EVI, and GOSIF) were graphed in adjusted form (as “climate adjusted” or “ecotope-adjusted” observations) in order to compare observed versus predicted relationships with one predictor variable at a time (e.g. water table depth) while 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 variable plots in conventional regression models¹²⁵. EVI (Figs. 3a, 4e, Extended Data Fig. 8a, b) or GOSIF (Extended Data Fig. 8c, d) observations of anomalies were adjusted by the difference between the full GAM predictions at each pixel and the partial prediction for the median conditions. For example, to plot climate-adjusted EVI/GOSIF versus water table depth (across different HAND bins) as in Fig. 3a and Extended Data Fig. 8, the adjustment (shown for EVI) was:

$$\text{Adjusted } \Delta EVI_i = \Delta EVI_i - \text{Correction}_i$$

$$\text{Correction}_i = f(\text{HAND}_i, \text{Climates}_i) - f(\text{HAND}_i, \overline{\text{Climates}}) \quad (10)$$

where ΔEVI_i is the observed *i*th EVI anomaly, $f(\text{HAND}_i, \text{Climates}_i)$ is the prediction of the *i*th EVI anomaly from GAM (model function for Eqn. 8 denoted as $f()$ here) and

1113 $f\left(HAND_i, \overline{Climates}\right)$ 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).

1115 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

$$1119 \text{Correction}_i = f\left(HAND_i, \overline{Climates}_i, \overline{SF}_i, \overline{ST}_i, \overline{FH}_i\right) - f\left(HAND_i, \overline{Climates}, \overline{SF}, \overline{ST}, \overline{FH}\right) \quad (11)$$

1120 where SF denotes soil fertility, ST denotes soil texture, and FH denotes forest height. The
 1121 domain of the prediction for which median values of ecotop distributions were taken was, in
 1122 this case, each of the three regions, considered separately.

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

1124 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}. Here, following recent ideas in the emerging field of functional biogeography^{23,128},
 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 ecotop 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):

$$1135 \text{Standardized resilience}_i = \frac{\text{Resilience}_i - \overline{\text{Resilience}}}{SD_{\text{resilience}}} \quad (12)$$

$$1136 \text{Resilience}_i = f\left(HAND_i, \overline{SF}_i, \overline{ST}_i, \overline{FH}_i, \overline{Climates}\right) \quad (13)$$

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

1139 We defined thresholds conducive to resilience to define ecotop factor groups associated
 1140 with resilience or vulnerability. Overlapping ecotop 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, low soil fertility: 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).

1147 3. Testing alternative interpretations and considering caveats

1148 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
 1152 GAM model:

1153 H1. That spatial scaling artifacts contaminate the results. In particular, it might be that the
 1154 primary spatial scale of our analysis (~40km, 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.

1158 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
 1160 (Fig. 3a, reproduced in Extended Data Fig. 12a) to the native MODIS scale (1km) (Extended
 1161 Data Fig. 12b), and across the finer scales (resolved to 30 meters using Landsat OLI 8 land
 1162 surface reflectance, see Extended Data Fig. 12c) available for a region near Manaus¹²⁹ (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.

1171 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.

1175 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).

1181 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.

1187 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:

$$\Delta EVI = s(HAND) + s(\Delta PAR) + s(DryDrought) + s(\Delta VPD) + s(\Delta P) + s(\Delta MCWD) \\ + s(DL) + ti(\text{pairwise interactions of every two variables except for DryDrought})$$

$$+ ti(DryDrought, \Delta PAR) + ti(DryDrought, DL) \quad (14)$$

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,

Extended Data Fig. 13a). By contrast, the 2005 and 2010 droughts were primarily dry season droughts (median dry season fractions = 0.83 and 0.77, respectively). This analysis confirms our finding of a generally positive sensitivity of droughted forests to sunlight reported in the main narrative (Fig. 3b), but further shows that the greater the proportion of the drought that occurs in 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 than the red line representing pixels predominantly experiencing dry season drought). This analysis also confirms (Extended Data Fig. 13c) that the hump shaped response to drought duration (as in Fig. 3c, especially the peak of vegetation response at three month's duration) is 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. 13b), forests experiencing wet season droughts are generally more negatively affected by drought than are forests experiencing dry season droughts, consistent with the idea that although trees are adapted to the dry conditions of annually recurring dry seasons, they are especially vulnerable when droughts hit in the wet (recovery) season.

H4: That deforested or degraded forests may be driving or contaminating results that are reported as for "intact" forests. Deforested regions are excluded from the analysis, but the mask may still include forests in proximity to deforested regions that, though not deforested, may be experiencing degradation. We conducted a sensitivity test to address the question of whether different drought responses in degraded forests could be contaminating our findings, using a recent classification⁸⁶ that identifies partially degraded forests as distinct from both deforested and intact forests, now updated through 2022. We repeated the GAM analysis reported in Fig. 4, but here excluded pixels representing degraded forests. The results (Extended Data Fig. 14, styled after Fig. 4 in the main text) suggest that partially degraded forests likely are indeed more vulnerable: the curves in panels C and D of Extended Data Fig. 14 (for purely intact forests) reach a slightly greater EVI anomaly value than the corresponding curves of Fig. 4c, d (including mainly intact and but also some degraded forests). This suggests that a functional biogeography approach may be fruitful for future investigations of the effect of forest degradation on drought sensitivity at the local scale. However, the differences are slight at the basin scale, and the overall patterns in Fig. 4 and Fig. 5 results do not depend much on whether these forests "in between" deforested and intact regions are included or excluded.

H5: That relatively taller individual trees are more vulnerable to drought, even as tall-canopy deep water table forests are on average more resilient to drought. We found that greater forest canopy height promoted resilience for deep water table forests, but increased vulnerability for shallow water table forests (Fig. 4d, Extended Data Fig. 11d). Observations of drought responses in the RAINFOR network⁴⁹ and drought experiments^{47,48} report that tall trees were more vulnerable to drought. One of the drought experiments was above a moderately shallow water table (7-10m) and the vulnerability of tall trees there could be explained by our result⁴⁷, but the forest of the Nepstad et al drought experiment⁴⁸, and many of the plots in the RAINFOR network, are over deep water tables, raising the question as to whether the results reported here might be inconsistent with those.

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

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 Amazon drought
1244 experiment¹³⁰ and by other studies, is a mechanism that could further enhance forest benefit from
1245 redistributing deep waters upward in the soil profile.

1246 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.

1251 Methods References

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Acknowledgments: We thank T.R. Sousa for sharing and discussing plot-based forest demographic data (from along the BR-319 road) (now published as Sousa et al.²⁶), we thank G. Zuquim for sharing an early version of mapped basin-wide soil fertility data (now published as Zuquim et al.⁴³), and H. ter Steege for sharing mapped basin-wide tree characteristics data.³⁴ We thank L. Alves for advice on forest demography plots, R. Palacios and D. Bauman for recommending use of, respectively, General Additive Models (GAM) and Structural Causal Modeling, M.N. Garcia for discussion about soil fertility, N. Boers for advice on the South American monsoon system, and T.C. Taylor and V. Ivanov, for helpful discussions. We thank Chris Baraloto, Dave Bauman, James Cronin, and Sean McMahon for detailed advice and comments, and S.C. doctoral dissertation committee members W.K. Smith, J. Hu and B. Enquist for constructive criticism and advice on the direction of this work.

Funding:

U.S. National Aeronautics and Space Administration, fellowship #80NSSC19K1376 (S.C.)
U.S. National Science Foundation, DEB grant #1950080 (S.C.S., M.N.S.)
U.S. National Science Foundation, DEB grant #2015832 (S.R.S.)
U.S. National Science Foundation, DEB grant #1754803 (S.R.S., N.R.C. and S.C.S.)
Brazil National Council for Scientific and Technological Development (CNPq) scholarships
371626/2022-6, 372734/2021-9, 381711/2020-0 (D.d.J.A.)
U.S. Department of Energy's Next Generation Ecosystem Experiments-Tropics (R.C.T.)

Author contributions: S.C. and S.R.S. designed the analysis, based on early conception by A.D.N. and S.R.S., and on funded proposals to investigate “the other side of tropical forest 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). A.D.N., L.A.C and D.d.J.A updated their HAND data product and interpreted it for this analysis.

1457 B.W.N. and N.R.C. contributed remote sensing expertise and analysis, R.C.T. contributed
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.

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

1463 **Data and materials availability:** All remote sensing data and products are publicly available at
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) and Brien et al (²).
1466 Code for reproducing the modeling analysis and figures is posted on Code Ocean at
1467 <https://codeocean.com/capsule/2432086/tree>.

1468 **Extended Data Figs.** 1 to 18

1469 **Extended Data Table** 1 to 2

1470 **Supplementary Information is available for this paper.**

1471 **Supplementary Materials**

1472 **References** (55–134)

Extended Data Fig. 1 Maximum cumulative water deficit (MCWD) standardized anomalies (relative 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 deficit reached for each hydrologic year (from May of the nominal year to the following April). The “drought region” is defined as pixels whose MCWD anomaly is more than one SD below the mean (light orange to red).

Extended Data Fig. 2. GOSIF-based forest response to droughts. GOSIF anomalies during drought, 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 drought elliptical region: EVI and GOSIF (left and right vertical axes) versus HAND (elliptical region is depicted in Fig. 1a and Extended Data Fig. 2a); (e) GOSIF responses (anomalies) vs. HAND for observations (solid points \pm 95% CI and regression line) for the 2005 (green, slope= -0.016 ± 0.006 SD m^{-1}), 2010 (purple, slope= -0.012 ± 0.003 SD m^{-1}), and 2015 (blue, slope= -0.010 ± 0.003 SD m^{-1}) droughts, 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 (HAND), a proxy for water-table depth²⁵; (b) Soil fertility, as exchangeable base cation concentrations⁴³; (c) Average forest heights as acquired by lidar⁴⁵; (d) Community-weighted wood density³⁴; (e) Proportion of trees belonging to the Fabaceae family³⁴; (f) MCWD variability (see methods section 2.3), in terms of the standard deviation of the long-term MCWD timeseries. High variance in climate and low soil fertility in Guiana shield might contribute to the greatest proportion of trees belonging to the family Fabaceae with the very high wood density; (g) Averaged minimum monthly precipitation (low=green, high=orange). The north-west everwet Amazon is distinguished by lacking a dry season (precipitation exceeds evapotranspiration). (h) Soil sand content⁴⁴. The first row of factors are used as ecotope 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 2005, 2010 and 2015 droughts, respectively. Panels b, e, and h show dates of the end of the 2005, 2010 and 2015 droughts. Panels c, f, and i show the duration (end date minus start date, in number of months) of the 2005, 2010 and 2015 droughts. Pixel-by-pixel drought responses (EVI in Figs. 1-3, 4; or GOSIF in Extended Data Figs. 6 & 11) are taken as the vegetation index standardized anomalies that occur during the pixel-specific drought period defined here.

Extended Data Fig. 5. Spatial distributions of climate variations’ anomalies across 2005, 2010 and 2015 droughts. Panels a, d, and g show photosynthetic active radiation (PAR) anomaly distributions (blue=negative, red=positive) in the drought regions of the 2005, 2010 and 2015 droughts, respectively. b, e, and h show the vapor pressure deficit (VPD) anomaly distributions (blue=negative, red=positive) in the drought regions of the 2005, 2010 and 2015 droughts. Panels c, f, and i show the precipitation anomaly 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 (PCA) followed by classification: (a) PCA of the Amazon basin pixel data (colored according to a supervised classification into three classes identified by variance minimization), projected onto their first two principal components, which are composed mainly of three dimensions, one defined by wood density and proportions of the family Fabaceae (first principal component, horizontal axis), one defined by minimum monthly precipitation and MCWD variability (second principal component, vertical axis), and a third defined mainly by soil fertility; the classes are significantly separated in PCA space ($F=950$, $df=2$, 3805 , $p \sim 0$, permanova test); (b) The Amazon pixels colored according to their class (corresponding to the colors in a), showing that the classification of (a) maps pixels into distinct, mostly contiguous spatial regions. (c) Standardized values, for each region, of each group of characteristics (ordered by water availability, soil fertility, and tree traits/characteristics), illustrate distinct regional niches: the Everwet

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

Extended Data Fig. 7. Variograms of spatial autocorrelation effect across three droughts. The 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)**, southern Amazon **(b, f, and i)**, everwet Amazon **(c, g, and j)** and Guiana shield **(d and k)**, respectively. Variance was lower (indicating spatial autocorrelation) for pairs formed from nearby pixels, but tended to reach a sill (plateau) at around 40 km, indicating a scale at which spatial autocorrelation 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) ever-wet northwest and (b, d) in northeast Guiana shield regions show consistently positive slopes with HAND, in contrast to responses in the Southern Amazon (Fig. 3a): **(a), (b)** Enhanced vegetation index (EVI) anomalies versus water table depth (i.e., HAND) for observations (solid points with standard error bars, with linear regression solid line) and for unified multi-drought GAM predictions (Extended Data Table 1b, c) (with climate fixed to region-wide average drought conditions for each drought, smooth 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 Amazon (b). The 2010 drought did not significantly affect the Guiana shield. **(c), (d)** GOSIF anomalies 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 factors influencing tropical forest responses to drought. **(a)** Initially hypothesized DAG characterizing the causal relationships among climatic, environmental, and forest variables (measured variables depicted as blue nodes, unmeasured rooting depth is depicted in gray) leading to forest drought response (other color node), with arrows representing the hypothesized causal links. **(b)** DAG-data consistency tests for initial DAG, with the largest 20 approximated non-linear correlation coefficients (estimated via root mean square error of approximation, RMSEA) between unlinked variables in (a). (Note: unlinked variables in a DAG are hypothesized to have zero correlation or zero conditional correlation; thus, the second row of panel b tests “ $DR \perp\!\!\!\perp DSL \mid DL$ ” -- whether DR is independent of DSL conditioned on DL, by estimating the non-linear correlation between DR and the residuals of DSL regressed on DL.) Correlations greater than an acceptability threshold (dashed vertical lines at ± 0.30) fail the test of conditional independence, addressed by adding to the DAG either a direct causal link (indicated by a green symbol), or links to a common cause (pink symbol) (such added arrows are included in panel c). **(c)** Final DAG after correcting for conditional independency inconsistencies of the initial DAG in A, in light of ecological considerations. Also illustrates use of the backdoor criterion to determine the causal effect of ‘drought length (DL)’ (the exposed predictor node and associated forward causal paths, in green) on forest drought response (corresponding to the model in Extended Data Fig. 10c), while blocking the confounding 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)** DAG-Data consistency tests for final DAG (panel c), showing the largest 20 RMSEA values.

Extended Data Fig. 10. Causal effects of different variables derived from DAG employing backdoor criterion, for: **(a)(b)(c) the Southern Amazon across all three droughts:** **(a)** of HAND (no backdoor to be blocked) **(b)** of PAR (adjusting for back door paths through drought length, dry season length) **(c)** of 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 shallow (blue, HAND=0-10 m) and deep (red, HAND=20-40 m) water tables (adjusting for back door paths through soil fertility, soil texture and dry season length), **(e)** of soil fertility (adjusting for back door

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 GAMs, lines with 95% confidence shaded area).

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

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

Extended Data Fig. 13. The sensitivity of Amazon forest drought responses to dry versus wet season drought periods, across the three-droughts: (a) distribution of the proportion of drought that was in the dry season (0 = all in the wet season to 1= all in the dry season) for drought-affected pixels in each of the three droughts. (b) GAM-predicted EVI anomaly versus PAR, for different proportions of dry season drought (blue=all wet to red=all dry, corresponding to colored tick marks in the vertical axis of a). (c) Adjusted EVI anomaly from GAM prediction versus drought length, for different proportions of 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, excluding degraded forests. Basin-wide Amazon intact forest responses to the 2015 drought, structured by ecotopes and predicted by whole-basin GAM analysis (fit by model of Extended Data Table 1d, but fully excluding forests categorized as degraded⁸⁶ in fitting the model): GAM partial predictions of EVI anomalies (color scale), displayed identical to the design of Fig. 4 (for intact terra firme forests, but including some partly degraded forests) for (a) soil fertility⁴³ and HAND²⁵, and for (b) forest height⁴⁵ and HAND²⁵. ecotope distributions are in the margins, identical to those shown in Fig. 4. (c)(d) adjusted EVI 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).

1617 **Extended Data Fig. 15. (a) Remotely sensed map of MAIAC EVI (1-km resolution) (green to blue**
1618 **color scale), overlaid with aboveground NPP (ANPP) rates from 321 ground-monitored forest plots**
1619 (red circles, % y^{-1}) as aggregated to 1 degree grid plots (RAINFOR plots in Brien et al.²), 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
1623 biomass at the start of the census interval). **(b) ANPP rates as predicted by EVI** (points from (a) plus
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 points¹³²). EVI is the mean extracted from intervals matching the average census interval of the
1627 corresponding plots in Brien et al.²

1628 **Extended Data Fig. 16. Remotely sensed photosynthetic indices versus ground-monitored tree**
1629 **demography in shallow water table forests during the 2015-2016 drought²⁶: Top row: MAIAC EVI**
1630 **standardized drought anomalies:²⁶(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**
1632 **anomalies (5-km pixels) versus ground-monitored (d) mortality, (e) recruitment, and (f)**
1633 **mortality:recruitment ratios; Solid lines and statistics (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 points¹³², 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.**

1638 **Extended Data Fig. 17. Forest response to the 2015 drought in drought-affected pixels: (a) Observed**
1639 **EVI anomalies (resampled at 0.4 degrees to match model resolution which accounts for spatial**
1640 **autocorrelation (see Extended Data Fig. 7). (b) GAM-predicted EVI anomalies (model of Extended Data**
1641 **Table 1d). (c) Residual EVI anomalies (panel a observations minus panel b predictions). The GAM**
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).**

1644 **Extended Data Fig. 18. Map of Amazon forest biogeography of resilience, overlaid with mean winds**
1645 **(arrows, at height 650 hPa) and arc of deforestation.** The most productive as well as the most
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 forests¹³³ (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.

1651 **Extended Data Table 1. Generalized Additive Models (GAM) for:** (a) the southern Amazon, (b) the
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 ΔAIC is the difference from the lowest AIC (selected)
1654 model ($\Delta AIC=0$), relative to a “full model” defined in columns 2-3. For details, see Methods, Section
1655 2.6.1.

1656 **Extended Data Table 2.** Variable inflation factors (VIF, top row) and pearson correlation coefficients
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 acceptable¹³⁴.