

Slow-down of the greening trend in natural vegetation with further rise in atmospheric CO₂

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Key Points:

- Satellite observations since the early 1980s show that Earth's greening trend is slowing down and that browning clusters are emerging.
- A collection of model simulations in conjunction with causal theory points at climatic changes as principal driver of vegetation changes.
- Most models underestimate the observed vegetation browning, which could be due to an excessive CO₂ fertilization effect in the models.

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Abstract

Satellite data reveal widespread changes of Earth's vegetation cover. Regions intensively attended to by humans are mostly greening due to land management. Natural vegetation, on the other hand, is exhibiting patterns of both greening and browning in all continents. Factors linked to anthropogenic carbon emissions, such as CO₂ fertilization, climate change and consequent disturbances, such as fires and droughts, are hypothesized to be key drivers of changes in natural vegetation. A rigorous regional attribution at biome-level that can be scaled into a global picture of what is behind the observed changes is currently lacking. Here we analyze the longest available satellite record of global leaf area index (LAI, 1981-2017) and identify several clusters of significant long-term changes. Using process-based model simulations (Earth system and land surface models), we disentangle the effects of anthropogenic carbon emissions on LAI in a probabilistic setting applying Causal Counterfactual Theory. The analysis prominently indicates the effects of climate change on many biomes – warming in northern ecosystems (greening) and rainfall anomalies in tropical biomes (browning). Our results do not support previously published accounts of dominant global-scale effects of CO₂ fertilization. Altogether, our analysis reveals a slowing down of greening and strengthening of browning trends, particularly in the last two decades. Most models substantially underestimate the emerging vegetation browning, especially in the tropical rainforests. Leaf area loss in these productive ecosystems could be an early indicator of a slow-down in the terrestrial carbon sink. Models need to account for this effect to realize plausible climate projections of the 21st century.

PLAIN LANGUAGE SUMMARY

The satellite-observed greening trend of Earth's land surface is a well documented phenomenon. Our analysis of almost four decades of global leaf area observations reveal a weakening of the greening trend and an expansion of browning regions. Leaf area gain is seen mostly in low

28 density vegetation and the loss in high density tropical forests. These opposing trends imbue
29 a distinct signature of texture loss in green coverage of natural vegetation. A collection of
30 factorial model simulations and causal theory identify biome-unique drivers of change linked
31 to anthropogenic carbon emissions. The effects of climate change are prominently seen in
32 many biomes, for example, warming in northern ecosystems and rainfall decline/anomalies in
33 tropical biomes. However, most models do not reproduce the observed vegetation browning,
34 especially in tropical rainforests. The leaf area loss in these highly productive ecosystems could
35 be an early indicator of a slow-down in the terrestrial carbon sink.

36 1 INTRODUCTION

37 Satellite observations reveal widespread changes in terrestrial vegetation across the entire
38 globe. The greening and browning trends reflect changes in the abundance of green leaves,
39 and thus, the rate and amount of photosynthesis. Plants modulate pivotal land-atmosphere
40 interactions through the process of photosynthesis. Hence, changes in photosynthetic activity
41 have immediate effects on the land-atmosphere exchange of energy (Forzieri et al., 2017), water
42 (McPherson, 2007; Ukkola et al., 2016) and carbon (Poulter et al., 2014; Thomas et al., 2016;
43 Winkler et al., 2019). Several studies have reported that many biomes are largely greening,
44 from Arctic tundra to subtropical drylands (Myneni et al., 1997; Nemani et al., 2003; Mao et al.,
45 2016; Zhu et al., 2016; Chen et al., 2019; Winkler et al., 2019). Others have identified regions of
46 declining trends in leaf area (Goetz et al., 2005; Verbyla, 2011). The drivers underlying these
47 long-term vegetation changes, however, remain under debate. In the light of nearly forty years
48 of continuous satellite observations, we reassess the driver attribution of natural vegetation
49 changes in a new framework of cause-and-effect and challenge previous findings (Zhu et al.,
50 2016).

51 Anthropogenic vegetation, *i.e.* actively cultivated vegetation, and natural vegetation should
52 be considered separately due to their distinct origins and properties. A recent study by Chen
53 et al. (2019) reported that anthropogenic vegetation (35% of the global vegetated area) is
54 greening due to human land management. The authors identified irrigation, multiple cropping,
55 and the application of fertilizers and pesticides as the main drivers of leaf area enhancement
56 (direct drivers). These results challenge the conclusions of a previous study by Zhu et al. (2016)
57 that attributed the global greening trend mostly to indirect drivers induced by CO₂ emissions,
58 in particular, the CO₂ fertilization effect (70%).

59 Indirect drivers of vegetation changes usually include CO₂ fertilization and climate change
60 in the literature, both of which are consequences of rising atmospheric CO₂ concentration.
61 The term "CO₂ fertilization" includes two effects of increased ambient CO₂ on the physiology
62 of plants. First, elevated CO₂ in the interior of leaves stimulates carbon assimilation, which
63 enhances plant productivity and biomass (Leakey et al., 2009; Fatichi et al., 2016). Second,

64 in time leaves adapt to CO₂-enriched atmosphere by lowering their stomatal conductance.
65 As a consequence, water loss through transpiration decreases, resulting in increased water-
66 use efficiency (ratio of carbon assimilation to transpiration rate; Ukkola et al., 2016; Fatichi
67 et al., 2016). In theory, both effects should result in an expansion of leaf area, especially in
68 environments where plant growth is constrained by water availability (Ukkola et al., 2016;
69 Donohue et al., 2009; Donohue et al., 2013).

70 The radiative effect of CO₂ induces climatic changes that can have both harmful or beneficial
71 effects on the functioning of ecosystems. Temperature-limited biomes are expected to green due
72 to warming and associated prolongation of the growing season (Park et al., 2016; Winkler et al.,
73 2019). But long-term drying (Zhou et al., 2014), as well as increased intensity and frequency of
74 disturbances (Seidl et al., 2017) such as droughts (Bonal et al., 2016) and wildfires (Goetz et al.,
75 2005; Verbyla, 2011), can induce regional vegetation browning trends. Regional greening and
76 browning patterns can also be associated with insect outbreaks, local deforestation practices,
77 regrowing or degrading forests, or nitrogen deposition; however, these drivers are considered
78 to be of minor importance at the global scale (Zhu et al., 2016).

79 Indirect drivers affect both natural and anthropogenic vegetation unlike direct drivers which
80 affect anthropogenic vegetation only. Chen et al. (2019) demonstrated that indirect drivers have
81 either opposing or minor enhancing effects on the leaf area of anthropogenic vegetation. In
82 general, the greening of anthropogenic vegetation has a negligible effect on the carbon cycle,
83 because carbon absorbed by agricultural plants almost immediately reenters the atmosphere
84 due to harvest and consumption. Natural terrestrial ecosystems, however, act as a strong
85 carbon sink by absorbing about 30% of the anthropogenic CO₂ emissions (3.8 ± 0.8 Pg C yr⁻¹;
86 Quéré et al., 2018) and mitigate man-made climate change (Bonan, 2008; Sitch et al., 2015;
87 Winkler et al., 2019). Thus, a mechanistic understanding of natural vegetation dynamics under
88 rising CO₂ is critical and helps to answer one of the key question in current climate research:
89 *Where does the anthropogenic carbon go* (Marotzke et al., 2017)?

90 This study focuses on the response of natural vegetation under the influence of the two key
91 indirect drivers, the physiological and radiative effect of rising CO₂. Throughout this paper
92 and in accordance with literature, the terms "CO₂ fertilization" and "physiological effect of

93 CO₂" are used interchangeably, as are "climate change" and "radiative effect of CO₂". To assess
94 observed changes in vegetation over climatic time scales, we make use of a 37-year record of
95 leaf area index (LAI) satellite observations (1982–2017, LAI3g, Section 2.1). The LAI3g product
96 is based on the Advanced Very High Resolution Radiometer (AVHRR) sensors, for which there
97 are a number of shortcomings (no on-board calibration, no correction of orbit loss, minimal
98 correction for atmospheric contamination and limited cloud screening; Section 2.1; Zhu et al.,
99 2013; Chen et al., 2019). Despite these limitations, the AVHRR record is unique in terms of its
100 temporal coverage and offers an opportunity to study the evolution of Earth's vegetation while
101 atmospheric CO₂ concentration increased by 65 ppm (341 to 406 ppm). We define greening
102 and browning as statistically significant increasing and decreasing trends in LAI, respectively
103 (Section 2.6). Based on a detailed biome map (Figure S1, Table S1, Section 2.2), we identify
104 spatial clusters of significant vegetation greening and browning in different natural vegetation
105 types.

106 We make use of the latest version of the fully-coupled Max Planck Institute Earth system
107 model in ensemble-mode (MPI-ESM, Section 2.3) and a collection of 13 land surface models
108 (LSMs) driven with observed climatic conditions (TRENDYv7 ensemble; Section 2.4; Quéré
109 et al., 2018). As a first step, we analyze historical simulations to examine whether these models
110 capture the observed behavior of natural vegetation under rising CO₂. Next, we analyze
111 factorial simulations to disentangle and quantify the effects of rising CO₂ on LAI changes.
112 Each factorial experiment consists of all historical forcings except one, which is set to its
113 pre-industrial level (similar approach in TRENDYv7 simulations, Section 2.4 and 2.6).

114 The conventional approach to detection and attribution in climate science is the method of
115 optimal fingerprinting, for example as in Zhu et al. (2016). This framework which considers the
116 observed change to be a linear combination of individual forced signals, is prone to overfitting,
117 and assumes that linear correlation reflects causation (Hannart and Naveau, 2018). To overcome
118 these limitations, we propose to use the Causal Counterfactual Theory which has recently been
119 introduced to climate science (Pearl, 2009; Hannart et al., 2016; Hannart and Naveau, 2018).
120 The method allows us to test if long-term greening/browning trends can be attributed to the
121 effects of rising CO₂ in a probabilistic setting combining necessary and sufficient causation
122 (Section 2.7).

123 This is the first study that addresses vegetation browning as well as greening patterns
124 across all major biomes, integrated into a global picture. Greening is dominant in terms of
125 areal fraction, but browning clusters are intensifying, primarily in the tropical forests that are
126 biodiversity-rich and highly productive. We find that CO₂ fertilization is an important driver
127 of greening in some biomes, but not dominant globally as suggested previously (Zhu et al.,
128 2016). The strengthening browning trend identified in our study is most likely linked to the
129 long-term drying and recurring droughts. Overall, our findings suggest that the emerging
130 browning clusters in the highly productive ecosystems might be a precursor of a weakening
131 land carbon sink, which is not yet captured by the current land components of Earth system
132 models.

133 2 MATERIALS AND METHODS

134 2.1 *Satellite observations of LAI: AVHRR LAI3g product*

135 We used an updated version (V₁) of the leaf area index dataset (LAI_{3g}; Chen et al., 2019) based
136 on the methodology developed by Zhu et al. (2013). The data provides global year-round LAI
137 observations at 15-day (bi-monthly) temporal resolution and 1/12 degree spatial resolution.
138 It spans from July 1981 to December 2017 and is currently the only available record of such
139 length. The full time series of LAI_{3g}V₁ was generated using an artificial neural network and
140 the latest version (third generation) of the Global Inventory Modeling and Mapping Studies
141 group (GIMMS) Advanced Very High Resolution Radiometer (AVHRR) normalized difference
142 vegetation index (NDVI) data (NDVI_{3g}). The latter have been corrected for sensor degradation,
143 inter-sensor differences, cloud cover, observational geometry effects due to satellite drift,
144 Rayleigh scattering and stratospheric volcanic aerosols (Pinzon and Tucker, 2014).

145 The LAI_{3g} datasets prior to 2000 were not evaluated due to a lack of required field data
146 (Zhu et al., 2013; Chen et al., 2019). After 2000, the quality of the LAI_{3g} dataset was assessed
147 through direct comparisons with ground measurements of LAI and indirectly with other
148 satellite-data based LAI products, and also through statistical analysis with climatic variables
149 such as temperature and precipitation variability (Zhu et al., 2013). Various studies used
150 the predecessor LAI_{3g}V₀ and the related dataset of fraction of absorbed photosynthetically
151 active radiation (fapar; Anav et al., 2013; Forkel et al., 2016; Zhu et al., 2016; Mao et al., 2016;
152 Mahowald et al., 2016; Piao et al., 2014; Poulter et al., 2014; Keenan et al., 2016) and its successor
153 LAI_{3g}V₁ (Winkler et al., 2019; Chen et al., 2019).

154 Leaf area index is defined as the one-sided green leaf area per unit ground area in broadleaf
155 canopies and as one-half the green needle surface area in needleleaf canopies in both satellite
156 observations and models (ESMs and LSMs). It is expressed in units of m² green leaf area per
157 m² ground area. Missing values in the LAI_{3g}V₁ dataset are filled using the climatology of
158 each 16-day composite during 1982-2017. We use the annual averaged LAI of each pixel in this
159 study.

160 2.2 *Characterization of biomes & clusters of significant change*

161 The land cover product of the MODIS sensors (MCD12C1; MODIS/Terra and Aqua Com-
 162 bined Land Cover Type Climate Modeling Grid (CMG) Yearly Global 0.05 Deg V006, https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mcd12c1_v006) is the
 163 primary source underlying the land cover map used in this study (hereafter MODIS land
 164 cover). The classes from the International Geosphere–Biosphere Programme (IGBP) in the
 165 MODIS land cover product are aggregated as follows: Tropical Forests include Evergreen
 166 Broadleaf Forest (EBF), Temperate Forests include Deciduous Broadleaf Forest (DBF) and
 167 Mixed Forest, and Boreal Forests include Evergreen Needleleaf Forest (ENF) and Deciduous
 168 Needleleaf Forest (DNF). Savannas include Woody Savannas and Savannas. Shrublands include
 169 Closed Shrublands and Open Shrublands. Croplands include Croplands and Croplands /
 170 Natural Vegetation Mosaic. The class Others includes Permanent Wetlands, Urban and Built-up
 171 Lands, Permanent Snow and Ice, and Barren. The classes Grasslands and Water Bodies remain
 172 unchanged. The MODIS land cover product provides estimates for the time period from 2001
 173 to 2017 for each pixel. In this study we define a representative biome map based on the most
 174 frequently occurring land cover type throughout the period of 17 years.

176 The MODIS land cover classification does not contain the biome tundra, which is why we
 177 use in addition the land cover product GLDAS2 / Noah version 3.3 that uses a modified IGBP
 178 classification scheme providing the classes Wooded, Mixed or Bare Ground Tundra (<https://ldas.gsfc.nasa.gov/gldas/GLDASvegetation.php>, hereafter GLDAS land cover) (Rodell et
 179 al., 2004). Accordingly, pixels originally of the classes Shrublands, Grasslands, Permanent
 180 Wetlands, or Barren, are converted to Tundra, if classified as Wooded, Mixed or Bare Ground
 181 Tundra in the GLDAS land cover product. The classes Woody Savannas and Savannas span vast
 182 areas across the globe in the MODIS land cover product. We use the GLDAS classification for
 183 these pixels, but only for regions where the MODIS and GLDAS land cover products disagree.
 184 In doing so, we obtain a more accurate global land cover classification. Table S1 describes in
 185 detail how the fusion of the MODIS and GLDAS land cover products is realized.

187 As a last step, we integrate the MODIS tree cover product MOD44B (MODIS/Terra Vegetation
 188 Continuous Fields Yearly L3 Global 250 m SIN Grid V006, https://lpdaac.usgs.gov/dataset_

189 discovery/modis/modis_products_table/mod44b_v006) to account for the underestimation of
190 forested area in the MODIS land cover product. Areas with tree cover exceeding 10% are
191 formally defined as forests (MacDicken et al., 2015). Thus, we set non-forest pixels in the
192 MODIS land cover product above 10% tree cover to Boreal Forest in the high latitudes 50°
193 N/S. For tropical forest (25° S – 25° N), we increase the threshold to 20% tree cover to allow
194 for a realistic areal extent of savannas. The pixels in the bands 25° N/S – 50° N/S remain
195 unchanged, because the MODIS land cover product already realistically represents the forested
196 area in these latitudes.

197 Table S1 provides a detailed overview on the conflation of MODIS land cover product,
198 GLDAS land cover product and the MODIS Tree cover product. The final biome map (originally
199 resolved at 0.05°) is regridded to the different resolutions of the AVHRR sensor and the models
200 simulations (MPI-ESM and TRENDYv7) applying a largest area fraction remapping scheme.

201 Based on the observational LAI dataset we define various clusters for greening or browning
202 in most biomes: North American Tundra (NAm Tundra), Eurasian Tundra (EA Tundra), North
203 American Boreal Forests (NAm Brl F), Eurasian Boreal Forests (EA Brl F), Temperate Forests
204 (Tmp F), Tropical Forests (Trp F), Central African Tropical Forests (CAf Trp F), Northern African
205 Savannas and Grasslands (NAf Sv Gl), Southern African Savannas and Grasslands (SAf Sv
206 Gl), Cool Grasslands (Cool Gl), and Australian Shrublands (Aus Sl). Some clusters require a
207 more detailed definition of their geographical location and extent: Southern (Northern) African
208 Savannas and Grasslands represent these vegetation type south (north) of the equator including
209 Madagascar. Central African Tropical Forests represent all tropical forests in Africa. Cool
210 Grasslands refer to grasslands above 30° N.

211 2.3 *Max-Planck-Institute Earth System Model*

212 MPI-ESM1.2 is the latest version of the state-of-the-art Max Planck Institute Earth System
213 Model, which participates in the upcoming sixth phase of the Coupled Model Intercomparison
214 Project (CMIP6; Eyring et al., 2016). Mauritsen et al. (2019) describes thoroughly the model
215 developments and advancements with respect to its predecessor, the CMIP5 version (Giorgetta
216 et al., 2013). Here, we use the low resolution (LR) fully coupled carbon/climate configuration

217 (MPI-ESM1.2-LR), which consists of the atmospheric component ECHAM6.3 with 47 vertical
218 levels and a horizontal resolution of 200 km grid spacing (spectral truncation at T63). The
219 ocean dynamical model MPIOM is set up on a bi-polar grid with an approximate grid-spacing
220 of 150 km (GR1.5) and 40 vertical levels. MPI-ESM1.2-LR includes the latest versions of the land
221 and ocean carbon cycle modules, comprising the ocean biogeochemistry model HAMOCC6
222 and the land surface scheme JSBACH3.2 (Mauritsen et al., 2019).

223 As opposed to the high-resolution configuration, the LR variant of the MPI-ESM includes all
224 the important processes relevant for longer time-scale changes of the land surface, such as a
225 thoroughly equilibrated global carbon cycle, dynamical vegetation changes, interactive nitrogen
226 cycle, land-use transitions, a process-based fire model (SPITFIRE), and an interactive coupling
227 of all sub-models. Furthermore, it is possible to run this model configuration to generate 45-85
228 model years per real-time day with a modern supercomputer (Mauritsen et al., 2019). This
229 opens up the possibility of conducting a larger number of realizations for each experiment.

230 Specifically, we used the initial CMIP6 release of the MPI-ESM version 1.2.01 (mpiesm-
231 1.2.01-release, revision number 9234). The final CMIP6 version will include further bug fixes,
232 which are expected to only slightly influence long-term sensitivities of simulated land surface
233 processes.

234 We conducted historical simulations (all forcings) and three factorial experiments (all forcings
235 except one): (a) all historical forcings except the physiological effect of CO₂ (No PE; increasing
236 CO₂ does not affect the biogeochemical processes), (b) all historical forcings except the radiative
237 effect of CO₂ (No RE; increasing CO₂ does not affect climate), and (c) all historical forcings
238 except anthropogenic forcings (No CO₂). All experiments were performed in ensemble-mode
239 (6 realizations per experiment) using the latest CMIP6 forcing data (1850–2013). Individual
240 realizations were initialized from different points in time of a prolongation run of the official
241 MPI-ESM1.2-LR pre-industrial control simulation. In doing so, we account for the influence
242 of climatic modes (e.g. El Niño Southern Oscillation) as a source of uncertainty in simulating
243 long-term changes.

244 The simulated time series were shifted by four years to maximize the overlap with the
245 observational record of 1982–2017.

246 2.4 *Land surface models: TRENDYv7*

247 Land-surface models (LSMs) or dynamic global vegetation models (DGVMs) simulate key
248 physical and biological key processes of the land system in interaction with the atmosphere.
249 LSMs provide a deeper insight into the mechanisms controlling terrestrial energy, hydrological
250 and carbon cycles, as well as the drivers of phenomena ranging from short-term anomalies
251 to long-term changes (Sitch et al., 2015; Bastos et al., 2018). Here, we analyze the most
252 recent TRENDY ensemble (version 7) comprising 13 state-of-the-art LSMs which vary in
253 their representation of ecosystem processes. All models simulate vegetation growth and
254 mortality, deforestation and regrowth, vegetation and soil carbon responses to increasing
255 atmospheric CO₂ levels, climate change and natural variability (Quéré et al., 2018). Some
256 models simulate an explicit nitrogen cycle (allowing for potential nitrogen limitation) and
257 account for atmospheric N deposition (Table A1 in Quéré et al., 2018). Most LSMs include
258 the most important components of land-use and land-use changes, but they are far from
259 representing all processes resulting from direct human land management (Table A1 in Quéré
260 et al., 2018). A more detailed description of the TRENDYv7 ensemble, model-specific simulation
261 setups and references can be found in Quéré et al. (2018, Table A4).

262 We use output from five simulations: all forcings (S₃), physiological effect of CO₂ only (S₁),
263 radiative plus physiological effect of CO₂ (S₂), land-use changes only (S₄), and the control run
264 (S₀; no forcings: fixed CO₂ concentration of 276.59 ppm and fixed land-use map, loop of mean
265 climate and variability from 1901–1920). The forcing data consist of observed atmospheric
266 CO₂ concentrations, observed temporal patterns of temperature, precipitation, and incoming
267 surface radiation from the CRU-JRA-55 reanalysis (Quéré et al., 2018; Harris et al., 2014), and
268 human-induced land-cover changes and management from an extensions of the most recent
269 Land-Use Harmonization (LUH2) dataset (Hurtt et al., 2011; Quéré et al., 2018).

270 In this study, we only analyze output for the period 1982–2017 (matching the observational
271 record) from models providing spatially gridded data for all five simulations. A few models
272 provide LAI at the level of plant functional types (PFTs). We calculate the average value of
273 all LAI values on PFT level multiplied by their land cover fraction for each grid cell. All

274 model outputs were spatially regridded to a common resolution of 1° based on a first-order
275 conservative remapping scheme (Jones, 1999).

276 The design of factorial simulations in TRENDYv7 and by the MPI-ESM are conceptually
277 different. The MPI-ESM simulations were conducted using the counterfactual approach, *i.e.*
278 all forcings are present except the driver of interest. TRENDYv7 provides simulations with
279 different combinations of drivers as described above. To obtain comparability, we have to make
280 the assumption that the absence of a specific driver has the same effect, in absolute values, as
281 its sole presence. Thus, we process the output of the simulations S₁, S₂, S₃ and S₄ to obtain the
282 counterfactual setup as described above for MPI-ESM. This approach neglects possible synergy
283 effects from simultaneously acting forcings. Also, it has to be noted that these simulations are
284 only to some extent comparable between the two ensembles. For instance, in the MPI-ESM we
285 can specifically determine the impact of the radiative effect of CO₂, whereas TRENDYv7 uses
286 observed atmospheric fields including changes induced from other drivers, such as non-CO₂
287 greenhouse gases.

288 For certain clusters, some models show unreasonable LAI changes and/or extreme inter-
289 annual variability. To reduce the influence of these extreme models on the overall analysis,
290 we apply a two-step filtering method for each cluster beforehand. Models are excluded from
291 the analysis, if they exceed three times the inter-annual variability of observations and/or
292 show a drastic change (of either sign) of more than 250% between the start and end of the
293 observational period. Further, we apply a weighting scheme based on the performance of the
294 all-forcings run for each cluster. We calculate quartic weights based on the distance between
295 the simulated and observational estimate. These weights are applied when calculating the
296 multi-model average and standard deviations for the factual and counterfactual runs.

297 2.5 *Atmospheric CO₂ concentration*

298 Global monthly means of atmospheric CO₂ concentration are taken from the GLOBALVIEW-
299 CO₂ product (for details see <http://dx.doi.org/10.3334/OBSPACK/1002>) provided by the Na-
300 tional Oceanic and Atmospheric Administration/Earth System Research Laboratory (NOAA/ESRL).

301 2.6 *Processing of the gridded data*

302 Areas of significant change in LAI are estimated using the non-parametric Mann-Kendall
 303 test, which detects monotonic trends in time series. In this study, we set the significance level
 304 to $p \leq 0.1$. An alternative statistical test for trend detection (Cox-Stuart test; Sachs, 1997) yields
 305 approximately the same results. The trends are either calculated for time series on the pixel
 306 level or for area-weighted large-scale aggregated time series (e.g. biome level).

307 We define greening (browning) either as a positive (negative) temporal trend, or for better
 308 comparison among models and observations as well as for a better global comparison across
 309 diverse biomes, we express these trends relative to the initial LAI level at the beginning of the
 310 observational record (average state from 1982-1984), denoted as Λ (% decade⁻¹).

311 The calculation of yearly net changes in leaf area balances the effects from both statistically
 312 significant browning and greening grid cells. For each cell, we multiply the estimated trends by
 313 the respective grid area. The net change is the sum of all grid cells, where areas of insignificant
 314 change are set to zero.

315 Models fairly accurately reproduce global patterns of vegetation greening, however, the
 316 fraction of browning is considerably underrepresented. Yet, we can only consider pixels with
 317 significant negative trends in LAI, in observations and models alike, and test models with
 318 respect to driver attribution of browning trends. Thus, the attribution of browning trends in
 319 this paper exclusively refers to browning pixels only.

320 Models reveal biases in comparison to observations. To obtain informative results in the
 321 attribution analysis, we process the simulations to match the mean and variance of the
 322 observational time-series. Assuming additive and multiplicative biases in simulations, we
 323 apply the following corrections:

$$b = \frac{\sigma_o}{\sigma_{af}}, \quad (1)$$

$$a = \bar{x}_o + b \times \bar{x}_{af} , \text{ and} \quad (2)$$

$$y_i = a + b * x_i , \quad (3)$$

324

325 where \bar{x}_o represents the mean value and σ_o the standard deviation of the observational times
 326 series. \bar{x}_{af} and σ_{af} are analogous to the all-forcings simulations. All simulated time series x_i are
 327 scaled using equation 3, where $i \in \Omega = \{\text{factual runs, counterfactual runs}\}$. This processing
 328 step does not affect the nature of simulated trends.

329 2.7 Causal Counterfactual Theory

330 The causal counterfactual approach is anchored in a formal theory of event causation
 331 developed in computer science (Pearl, 2009; Marotzke, 2019). Recently, a framework for driver
 332 attribution of long-term trends in the context of climate change has been introduced (Hannart
 333 et al., 2016; Hannart and Naveau, 2018), and increasingly gains popularity (Marotzke, 2019).
 334 Through the use of this method we can ascertain the likelihood that a certain external forcing
 335 has caused an observed change in the Earth system. More precisely, we address the question of
 336 interest in a probabilistic setting, *i.e.* what is the probability that a given forcing (e.g. radiative
 337 effect of CO₂) has caused an observed long-term change in the system (e.g. greening of the
 338 Arctic).

339 In the following, we highlight the key ideas and relevant concepts of causal theory. A detailed
 340 description and formal derivations can be found in (Pearl, 2009; Hannart et al., 2016; Hannart
 341 and Naveau, 2018). We define the cause event (C) as "presence of a given forcing" (*i.e.* the
 342 factual world that occurred) and the complementary event (\bar{C}) as "absence of a given forcing"
 343 (*i.e.* the counterfactual world that would have existed in the absence of a given forcing; Hannart
 344 and Naveau, 2018). Further, we define the effect event (E) as the occurrence of a long-term
 345 change (here, greening or browning) and the complementary event (\bar{E}) as the non-occurrence
 346 of a long-term change (*i.e.* no persistent vegetation changes). In making use of numerical

347 models, we can conduct factual runs comprising all forcings (*i.e.* historical simulations) as well
 348 as simulate counterfactual worlds by switching off a forcing of interest (*i.e.* all forcings except
 349 one). Based on an ensemble of simulations, either in a multi-model and/or multi-realizations
 350 setup, we derive the so-called factual (p_1) and counterfactual probability (p_0), which read
 351 $p_1 = P\{E|\text{do}(C)\}$ and $p_0 = P\{E|\text{do}(\bar{C})\}$, respectively (Hannart and Naveau, 2018). More
 352 precisely, p_1 describes the probability of the event E in the real world where forcing C was
 353 present, whereas p_0 refers to the probability of the event E in a hypothetical world where
 354 forcing C was absent. The notation $\text{do}(\cdot)$ means that an *experimental intervention* is applied to
 355 the system to obtain the probabilities (Hannart and Naveau, 2018).

The three distinct facets of causality can be established based on the probabilities p_1 and p_0 :

$$\text{PN} = \max \left\{ 1 - \frac{p_0}{p_1}, 0 \right\} , \quad (4)$$

$$\text{PS} = \max \left\{ 1 - \frac{1 - p_1}{1 - p_0}, 0 \right\} , \text{ and} \quad (5)$$

$$\text{PNS} = \max \{ p_1 - p_0, 0 \} . \quad (6)$$

356 PN refers to the probability of necessary causation, where the occurrence of E requires that of
 357 C but may also require other forcings. PS refers to the probability of sufficient causation, where
 358 the occurrence of C drives that of E but may not be required for E to occur. PNS describes
 359 the probability of necessary and sufficient causation, where PN and PS both hold (Hannart
 360 and Naveau, 2018). In other words, PNS may be considered as the probability that combines
 361 necessity and sufficiency. Thus, the main goal is to establish a high PNS that reflects and
 362 communicates evidence for the existence of a causal relationship in a simple manner (Hannart
 363 and Naveau, 2018).

364

365 To obtain PNS, we follow the methodology described in detail in Hannart and Naveau
366 (Hannart and Naveau, 2018) and derive cumulative distribution functions (CDF) for the factual
367 and counterfactual worlds, denoted D_0 and D_1 , respectively. Assuming a Gaussian distribution,
368 PNS follows as

$$\text{PNS} = \max\{D_1(\mu_1, \Sigma) - D_0(\mu_0, \Sigma)\}, \quad (7)$$

369 where μ_1 and μ_0 refer to the mean response of all factual and all counterfactual runs,
370 respectively. Σ denotes the overall uncertainty and is estimated based on all simulations,
371 comprising factual, counterfactual, and centuries-long unforced (pre-industrial) model runs
372 (for details see Hannart and Naveau, 2018). Finally, the maximum of PNS determines the
373 sought probability of causation (Hannart and Naveau, 2018). We express probabilities using
374 the terminology and framework defined by the IPCC (Mastrandrea et al., 2011; Hannart and
375 Naveau, 2018).

376 3 RESULTS AND DISCUSSION

377 3.1 *Natural vegetation exhibits a net gain of leaf area over the last decades, but the number of browning*
378 *regions is increasing*

379 More than three and half decades of satellite observations (1982–2017, Section 2.1) reveal
380 that 40% of the Earth’s natural vegetation shows statistically significant positive trends in LAI
381 (Mann-Kendall test, $p < 0.1$; Table 1), concurrent with a 65 ppm increase in atmospheric CO₂.
382 However, more and more browning clusters are beginning to emerge in all continents (14%;
383 Table 1). Analyzing earlier versions of three shorter duration (1982–2009) LAI datasets, Zhu
384 et al. (2016) reported a considerably smaller browning fraction of less than 4% and greening
385 percentages ranging from 25% to 50% for all vegetation (*i.e.* including agriculturally dominated
386 regions). The higher browning proportion in the extended record analyzed in this study
387 indicates an intensification of leaf area loss in recent years.

388 3.2 *Earth’s forests respond diversely throughout the satellite era*

389 A global map of statistically significant trends in LAI (denoted Λ , Section 2.6) for natural
390 vegetation reveals greening ($\Lambda > 0$) and browning ($\Lambda < 0$) clusters across the globe (Figure 1).
391 Temperate forests ($\Lambda > 0$: 56%) and Eurasian boreal forests ($\Lambda > 0$: 53%) exhibit extensive
392 regions of increasing LAI, and thereby, contribute the largest fraction to the enhancement of
393 leaf area on the planet (Table 2). The global belt of tropical forests, on the other hand, while
394 showing a net greening ($\Lambda > 0$: 28%), also feature widespread browning areas ($\Lambda < 0$: 16%).
395 In particular, the Central African tropical forests contain large areas of pronounced negative
396 trends ($\Lambda < 0$: 25%). North American boreal forests exhibit the largest fraction of browning
397 vegetation ($\Lambda < 0$: 31%) resulting in an annual net loss of leaf area (Table 1 and 2). The
398 picture of Earth’s forests is generally in line with results based on other data sources. For
399 instance, Song et al. (2018) reported a net gain of global forested area, with net loss in the
400 tropics compensated by a net gain in the extra-tropics.

401 3.3 *As in forests, other biomes also indicate divergent vegetation responses to rising CO₂*

402 Tundra in North America is primarily greening ($\Lambda > 0$: 46% versus $\Lambda < 0$: 7%), whereas
 403 in Eurasia, browning is intensifying ($\Lambda > 0$: 35% versus $\Lambda < 0$: 20%), especially in northern
 404 Scandinavia and on the Taymar Peninsula in Northern Russia. Grasslands in cool arid climates,
 405 mainly comprising the Mongolian and Kazakh Steppe, as well as the Australian shrublands,
 406 stand out as prominent greening clusters ($\Lambda > 0$: 40% and 49%, respectively). Although these
 407 biomes show strong positive trends, they are characterized by a low level of LAI. The African
 408 continent, which is still dominated by natural vegetation, reveals a distinct change in leaf area.
 409 A greening band of savannas and grasslands in the northern regions of Sub-Saharan Africa
 410 and a greening cluster in Southern Africa border the browning regions of equatorial Africa
 411 (Figure 1). Overall, the response of LAI to rising CO₂ is somewhat homogeneous for some
 412 biomes (widespread browning of the tropical forests and dominant greening of the temperate
 413 forests), but divergent for others (tundra and boreal forests show a 'North America – Eurasia'
 414 asymmetry, interestingly, in that they show changes of reversed sign; Figure 1).

415 3.4 *Net annual gain of leaf area is declining in natural vegetation*

416 Leaf area loss occurs primarily in densely vegetated biomes (*i.e.* forests), which outweighs
 417 leaf area gain in rather sparsely vegetated regions (e.g. grasslands). For instance, vigorously
 418 greening areas of circumpolar tundra result in a leaf area gain of $8.74 \times 10^3 \text{ km}^2 \text{ yr}^{-1}$, which
 419 is almost outbalanced fourfold by a leaf area loss of $34.31 \times 10^3 \text{ km}^2 \text{ yr}^{-1}$ in the browning
 420 regions of the tropical forests (Table 2). To assess the responses of different biomes to rising
 421 CO₂ in more detail, we iteratively calculate statistically significant LAI trends for different
 422 time windows with advancing initial year (*i.e.* 1982, 1983, ..., 2000), but fixed final year (2017).
 423 Although the estimated trends become less robust with shorter time series, this analysis allows
 424 us to test for weakening or strengthening responses to further rising CO₂. We see that the
 425 fraction of significantly browning regions is increasing over time, reaching a maximum for
 426 a time window starting in 1995. The greening fraction evolves in the opposite manner. The
 427 estimates are represented as fractions of the total area of significant change, because the latter
 428 inherently decreases as a result of the Mann-Kendall test for shorter time windows. Thus,

429 the average annual net leaf area gain of $150.51 \times 10^3 \text{ km}^2 \text{ yr}^{-1}$ for the entire observational
 430 period (1982–2017) decreases with advancing initial year, approaching zero for the period
 431 1995 to 2017, and rebounding to $\sim 40 \times 10^3 \text{ km}^2 \text{ yr}^{-1}$ for the period 2000 to 2017 (black
 432 line in Figure 1 inset). To obtain comparability between different time windows, the net leaf
 433 area gain estimates were scaled to the total area of significant change derived for 1982–2017
 434 (unprocessed estimates for period 2000–2017 are listed in Table S2). Chen et al. (2019) reported
 435 a global greening proportion of $\sim 33\%$ (AVHRR: 21%; Table S2) and a browning proportion
 436 of only 5% (AVHRR: 13%; Table S2) analyzing the MODIS record including anthropogenic
 437 vegetation (2000–2017). On a global scale, LAI trends from MODIS and AVHRR agree over
 438 61% of the vegetated area (Chen et al., 2019). Disagreement arises primarily in the tropical
 439 regions (absence of browning in the Central African tropical forests in the MODIS record) and
 440 in the northern high latitudes (Chen et al., 2019). In a recent study, Yuan et al. (2019) presented
 441 results comparing various remote sensing datasets of vegetation greenness which are in line
 442 with AVHRR-based estimates.

443 3.5 *High LAI regions are browning and low LAI regions are greening*

444 The intensification of browning during the second half of the AVHRR observational period
 445 (2000–2017) results in a reversal of the sign in terms of net leaf area change in some biomes
 446 (e.g. tropical forests, North American boreal forests, and Eurasian tundra; Table S3). Critically,
 447 the tropical forests display the sharpest transition from a substantial net gain of 24.11×10^3
 448 $\text{km}^2 \text{ yr}^{-1}$ (Table 2) to a comparably strong net loss of leaf area ($-18.42 \times 10^3 \text{ km}^2 \text{ yr}^{-1}$; Table
 449 S3). To address the temporal development of positive and negative changes in leaf area in
 450 more detail, we calculate time series of area-weighted averages of LAI (Figure 2a). We find that
 451 browning of natural vegetation occurs at a considerably higher level of LAI (on average ~ 1.85)
 452 than greening (on average ~ 1.32). Throughout the observational period, these two time series
 453 of opposite trends converge towards a LAI of 1.6 (Figure 2a). This convergence of greening and
 454 browning is not only evident in terms of their LAI level (Figure 2a), but also in their proportions
 455 (inset in Figure 1). The time series of anthropogenic vegetation on the other hand, aggregated
 456 for positive and negative Δ separately, are both confined to a comparable low LAI level (on
 457 average between 1 and 1.25). We next investigate the global LAI distributions of negative

458 and positive changes and their development over time. Comparing distributions of the earlier
459 (1982–1984) with those of the more recent years (2015–2017) reveals that browning primarily
460 occurs at a high (5–6) and a medium level of LAI (1–2.5; Figure 2b). Greening, however, is
461 occurring almost entirely at low levels of LAI between 0–1.5. As a consequence, the global
462 area-weighted averages of the browning and greening regions are approaching one another
463 (dashed versus solid vertical lines in Figure 2b), as also depicted by the time series (Figure
464 2a). Overall, these results suggest a homogenization of Earth’s natural vegetation in terms of
465 LAI texture with rising CO₂. This homogenization becomes prominent when we compare the
466 distributions of negative and positive Δ over time using a Q-Q plot (quantile-quantile; Figure
467 2c). The relationship between the quantiles is skewed to the left at higher LAI (positive Δ on
468 x -axis, negative Δ on y -axis), because browning is prevalent in high LAI regions. Over time, the
469 quantiles of the greening and browning distributions are approaching the 1-1 line (representing
470 identical distributions), emphasizing their convergence.

471 3.6 *The majority of models reproduce the observed convergence of greening and browning trends*

472 Thus far, we have described the diverse long-term changes of natural vegetation across all
473 continents and throughout the satellite era. We next investigate the underlying mechanisms
474 driving these greening and browning trends and use the fully-coupled MPI-ESM and the
475 TRENDYv7 ensemble of observation-driven LSMs (Section 2.3 and 2.4). First, we ask if
476 these models capture the observed behavior of natural vegetation under rising CO₂. MPI-
477 ESM reproduces the observed browning of high LAI and the greening of low LAI regions,
478 however, the levels of LAI do not match the observations (Figure S2). Historical simulations of
479 TRENDYv7 (here 13 models) also show pronounced changes in vegetation, but exhibit a diverse
480 behavior among the models (results not shown for brevity). Seven LSMs reproduce observed
481 converging trends of greening and browning, whereas the other six models show divergent
482 trends. All TRENDYv7 models are driven with identical atmospheric forcing fields, hence, these
483 six models most likely lack or incorrectly represent key processes of ecosystem functioning. In
484 general, simulated greening patterns are comparable to observations (Murray-Tortarolo et al.,
485 2013; Sitch et al., 2015; Mahowald et al., 2016), but browning, especially in the North American
486 boreal forests, is underestimated (Sitch et al., 2015).

487 3.7 Models point to the physiological effect of CO₂ as the main driver of greening at the global scale

488 Hereafter, we use changes in annual average LAI relative to the baseline period 1982–1984
 489 (Section 2.6) for better comparability between biomes, various simulations and the observed
 490 signal. Time series of relative LAI changes from historical simulations (multi-model average for
 491 TRENDYv7 and multi-realizations average for MPI-ESM) are comparable to observations at the
 492 global scale (Figure 3a and 3b; temporal correlations are low due to high internal variability of
 493 the signal).

494 We use the framework of Counterfactual Causal Theory to attribute changes in LAI to a given
 495 driver in a probabilistic setting (Pearl, 2009; Hannart et al., 2016; Hannart and Naveau, 2018).
 496 Based on the all-forcings (also termed factual) and factorial runs (also termed counterfactual),
 497 we derive Probabilities of causation that combines Necessity and Sufficiency of each factor
 498 (PNS). At the global scale, the observed estimate (~ 1.08 % decade⁻¹) and the factual MPI-
 499 ESM estimate (~ 1.14 % decade⁻¹) are comparable, whereas the multi-model average of the
 500 TRENDYv7 ensemble is an overestimate (~ 1.79 % decade⁻¹; Figure 3c). Omitting CO₂-induced
 501 climate change (no radiative effect of CO₂, No RE) does not have a strong effect in the MPI-ESM
 502 (~ 1.04 % decade⁻¹), *i.e.* the estimate does not differ considerably from the factual run. The
 503 TRENDYv7 models indicate that the positive trend in LAI can be explained by climate change
 504 to some extent (~ 1.21 % decade⁻¹). However, PNS values are low for the radiative effect of
 505 CO₂ (Figure 3d). The opposite is the case, when the physiological effect of CO₂ (No PE) is
 506 excluded. Both model setups agree that almost no positive trend in LAI is present in a world
 507 without CO₂ fertilization (MPI-ESM: ~ 0.18 % decade⁻¹, TRENDYv7: ~ 0.08 % decade⁻¹; both
 508 estimates are lower than internal variability of ~ 0.49 % decade⁻¹). As a consequence, high
 509 PNS can be established: The physiological effect of CO₂ has in the case of MPI-ESM *likely*
 510 (68%) and in the case of TRENDYv7 *very likely* (91%) caused the positive trend of global LAI in
 511 recent decades (Figure 3d). This result is in line with Zhu et al. (2016) who reported that 70%
 512 of global greening is attributable to CO₂ fertilization. Removing both effects of CO₂ results in
 513 slight negative trends, probably due to land use practices (deforestation; Figure 3c).

514 3.8 *The global signal switches to a minor negative trend in the second half of the observational period*

515 Natural vegetation shows a slight negative trend for the period 2000–2017 (~ -0.4 % decade⁻¹;
 516 Figure 3e). This estimate is within the range of internal variability, and thus, should be
 517 interpreted with caution. Note, that the net change in leaf area is still positive when considering
 518 only significantly changing pixels (inset in Figure 1). Models reproduce this reversal in the
 519 sign when the physiological effect of CO₂ is excluded or with a complete absence of CO₂
 520 forcing (Figure 3e). Overall, driver attribution at the global scale, as described above, and also
 521 in Zhu et al. (2016), neglects the heterogeneity of natural vegetation and the possibility that
 522 divergent responses of different natural biomes might cancel out. To account for this omission,
 523 we identify eleven clusters of significant change and derive probabilities of causation for each
 524 driver across different vegetation types (Figure 4).

525 3.9 *Temperate forests prosper with rising CO₂ while tropical forests are increasingly under stress*

526 Forests in temperate climates exhibit a strong positive trend in LAI (~ 2.53 % decade⁻¹),
 527 which is also seen in the models, albeit slightly overestimated (MPI-ESM: ~ 3.18 % decade⁻¹,
 528 TRENDYv7: ~ 2.69 % decade⁻¹; Figure S3). The physiological effect of CO₂ is the main driver
 529 with high PNS (85% for MPI-ESM, 80% for TRENDYv7; Figure 4). The trends are slightly
 530 weaken when only analyzing the second half of the observational period, but the overall
 531 result does not change. Observed warming might have additionally contributed to enhanced
 532 vegetation growth (e.g. growing season extension; Piao et al., 2011; Park et al., 2016), however,
 533 it is not identified as an important driver by models. Most temperate forests are in developed
 534 countries, and thus, have been managed in a sustainable manner for several decades (Currie
 535 and Bergen, 2008). It is conceivable, that some of the positive trends in LAI could be attributed
 536 to forest management or regrowing forests (Pugh et al., 2019), however, this is not captured by
 537 the models (*i.e.* trends are negative when complete CO₂ forcing is absent; Figure S3).

538 The response of tropical forests to rising CO₂ is more complex. The signal over the entire
 539 observational period is slightly positive (~ 0.3 % decade⁻¹), however, it is within the range of
 540 internal variability. Therefore, no robust driver attribution is possible (Figure 4 and Figure S4).
 541 TRENDYv7 models show strongly opposing responses of LAI to the different effects of CO₂:

542 LAI decreases when the physiological effect is omitted, but increases when the radiative effect
543 is omitted. MPI-ESM shows qualitatively the same responses, but less pronounced (Figure S4).
544 For the second half of the satellite record, the observed trend switches sign to a strong negative
545 trend ($\sim -1.4\%$ decade⁻¹). The models reproduce this tendency, but the multi-model average of
546 the TRENDYv7 ensemble is still positive. During the same time period, the opposing reactions
547 to CO₂ in the factorial runs are more strongly marked (Figure S4). These results suggest that
548 browning caused by CO₂-induced climate change is compensated by greening affiliated with
549 the CO₂ fertilization effect at the biome level. Based on these findings, we hypothesize that the
550 physiological effect of CO₂ is strong in models and outbalances the negative effect of climate
551 change in the tropical forests (Kolby Smith et al., 2016). As a consequence, the all-forcings
552 simulations fail to reproduce the observed patterns of strengthening vegetation browning in
553 the tropics (Zhou et al., 2014; Song et al., 2018), for reasons discussed below.

554 3.10 *Droughts and intensification of the dry season in the Amazon basin*

555 The Amazonian tropical forests are being frequently afflicted by severe droughts. During
556 the satellite era most of these droughts were strongly modulated by the El Niño Southern
557 Oscillation (ENSO). For example, the droughts of 1982-83, 1987 and 1991-92 (Asner and Alencar,
558 2010; Anderson et al., 2018), 1997 (Williamson et al., 2000), and 2015-16 (Jiménez-Muñoz et al.,
559 2016). The causes of the droughts in 2005 and 2010, however, were not related to ENSO, but
560 rather to a warm anomaly in sea surface temperatures in the tropical North Atlantic (Marengo
561 et al., 2008; Marengo et al., 2011; Xu et al., 2011). Whereas the ENSO-driven droughts peak in
562 northern hemispheric winter, thus during the wet season, the non-ENSO droughts happened
563 during the dry season (July – September), when tropical ecosystems are more vulnerable to
564 negative rainfall anomalies.

565 These intense and frequent droughts have diverse impacts on tropical ecosystems (Bonal
566 et al., 2016), the most prominent being an increase in wildfires and tree mortality. Recently,
567 perennial legacy effects have been identified which lead to persistent biomass loss in the
568 aftermath of severe droughts (Saatchi et al., 2013; Yang et al., 2018). For instance, some regions
569 were still recovering from the impact of the megadrought of 2005 when the next major drought
570 began in 2010 (Saatchi et al., 2013). Maeda et al. (2015) found that these extreme events are also

571 capable of disrupting hydrological mechanisms, which can lead to long-lasting changes in the
572 structure of Amazonian ecosystems. Such droughts and associated wildfires are predicted to
573 increase in frequency (Cai et al., 2014) and intensity (Fasullo et al., 2018) as a consequence of
574 the ENSO-related amplification of heat waves, but also due to the projected warming of the
575 tropical North Atlantic (Munday and Washington, 2019).

576 In addition to these episodic disturbances, long-term changes in climate also affected the
577 tropical forests in the Amazon region. Rising surface air temperatures have considerably
578 increased atmospheric water vapor pressure deficit (VPD), which has a negative effect on
579 vegetation growth (Yuan et al., 2019). Moreover, we find that precipitation has steadily
580 decreased during the dry season (July – September, Figure S5 and S6) based on the latest
581 version of the ECMWF reanalysis for the last forty years (ERA5; Dee et al., 2011). This rainfall
582 deficit and the identified lengthening of the dry season (Fu et al., 2013) exacerbate vegetation
583 water stress during dry seasons and favor conditions for wildfires. The slight increasing trend
584 in wet season precipitation (February – April) most likely cannot compensate for the water loss
585 and its impact during the dry season (Figure S5). Overall, the intensification of the dry season
586 and the recurring droughts cause long-term browning trends (Xu et al., 2011), in line with our
587 results of intensified browning of Amazonian forests (Figure S6).

588 3.11 *Drying trend in central African humid forests*

589 African tropical forests have been experiencing a long-term drying trend since the 1970s
590 (Malhi and Wright, 2004; Asefi-Najafabady and Saatchi, 2013; Zhou et al., 2014). In contrast to
591 South America, the steady decline in rainfall is seen during both dry and wet seasons (Figure
592 S5). The origin of this decreasing trend in year-round rainfall is still under debate. Precipitation
593 in equatorial Africa is expected to increase under climate change (Weber et al., 2018), so
594 it is hypothesized that this trend is associated with the Atlantic Multidecadal Oscillation
595 and/or changes in the West African Monsoon system (Asefi-Najafabady and Saatchi, 2013).
596 Long-term drying in rainforests could also be connected to the physiological effect of rising
597 CO₂. Recently, it has been demonstrated that the reduction in stomatal conductance and
598 transpiration induces a drier, warmer, and deeper boundary layer, resulting in a decline in local
599 rainfall (Langenbrunner et al., 2019). Regardless of what the causes may be, this long-term

600 water deficiency most likely has led to the most pronounced cluster of vegetation browning in
601 Earth's tropical forests ($\sim 174 \times 10^3 \text{ km}^2$ net loss of leaf area in the time period of 2000–2017).
602 No robust attribution is possible with the set of models analyzed in this study, since they
603 fail to capture this substantial decrease in leaf area in the all forcing runs (Figure S7). In the
604 case of the TRENDYv7 models, this finding is particularly noteworthy as they are driven with
605 observed precipitation estimates: The spatial patterns of negative trends in LAI and dry season
606 precipitation in the Central African tropical forests coincide to a large extent (Figure S5).

607 Interestingly, the MODIS record does not exhibit this browning cluster (Chen et al., 2019),
608 though it has been reported in other independent observational datasets (Zhou et al., 2014).
609 Also, atmospheric CO_2 inversion studies have identified negative trends in carbon uptake for
610 this region (Fernández-Martínez et al., 2019), which corroborates our results based on the
611 LAI3g dataset.

612 3.12 *Tropical forests in Oceania are afflicted by deforestation*

613 Although we exclude anthropogenic land cover changes (Figure S1, Table S1) as well as
614 abrupt changes (Mann-Kendall test for monotonic trends, Section 2.6), the LAI trend maps
615 nevertheless show characteristic deforestation patterns, e.g. the so-called "arc of deforestation"
616 in the Amazon region (Figure S6; Aldrich et al., 2012). Hence, deforestation practices may
617 explain some part of the observed gradual browning of the Amazon (Song et al., 2015) and
618 African tropical forests (Mayaux et al., 2013; Tyukavina et al., 2018).

619 In Oceania, however, deforestation appears to be a crucial driver of the observed browning in
620 the pristine tropical forests. Significant negative trends align strongly with patterns of drastic
621 deforestation during recent decades, described in detail by Stibig et al. (2014, in comparison to
622 Figure 1). As opposed to Central Africa and the Amazon region, climate changes are unlikely
623 to be the key driver of browning regions in Oceania. There, precipitation, although highly
624 variable in the dry season, appears to increase (Figure S5) and the increase in VPD is rather
625 minor (Yuan et al., 2019) in tropical forests.

626 3.13 *Climate change drives an asymmetrical development of North American and Eurasian ecosystems*

627 The boreal forests show strong positive trends in Eurasia (Observations: ~ 2.69 % decade⁻¹,
628 MPI-ESM: ~ 3.48 % decade⁻¹, and TRENDYv7: ~ 2.08 % decade⁻¹), which can mostly be
629 attributed to amplified warming of the temperature-limited northern high latitudes (PNS =
630 71% for TRENDYv7, PNS = 44% for MPI-ESM; Figure S8). North American boreal forests
631 exhibit a negative response to rising CO₂, which has amplified over the last two decades
632 (~ -0.95 % decade⁻¹, 2000–2017). Models do not reproduce the dominant browning pattern
633 (Figure S9), which is most likely connected to inadequate representation of disturbances (Sitch
634 et al., 2015). Several studies have proposed that browning has occurred as consequence of
635 droughts, wildfire, and insect outbreaks in the North American boreal forests (Goetz et al., 2005;
636 Sitch et al., 2015; Beck and Goetz, 2011; Kurz et al., 2008). Macias Fauria and Johnson (2008)
637 showed that the frequency of wildfires is strongly related to the dynamics of large-scale climatic
638 patterns (Pacific Decadal Oscillation, El Niño Southern Oscillation, and Arctic Oscillation) and
639 thus, cannot be tied conclusively to anthropogenic climate change. However, there is also
640 evidence that the residing tree species suffer from drought stress induced by higher evaporative
641 demand as the temperature rises (Verbyla, 2011). Moreover, models lack a representation of
642 the asymmetry in tree species distribution between North America and Eurasia, which could
643 explain their divergent reactions to changes in key environmental variables (Abis and Brovkin,
644 2017). Further observational evidence for the browning of North American boreal forests and
645 the associated decline in net ecosystem productivity can also be inferred from CO₂ inversion
646 products (Fernández-Martínez et al., 2019; Bastos et al., 2019).

647 Tundra ecosystems also reveal a dipole-type development between North America and
648 Eurasia, however with a reversed sign. Hence, North American tundra is strongly greening
649 (Observations: ~ 4.23 % decade⁻¹, MPI-ESM: ~ 4 % decade⁻¹, and TRENDYv7: ~ 4.51 %
650 decade⁻¹), which is *virtually certain* (PNS = 99% for TRENDYv7) and *about likely as not* (PNS
651 = 51% for MPI-ESM) caused by warming (Figure S10). The trend decreases for the period
652 2000–2017, which could be linked to the warming hiatus in the years 1998–2012 (Bhatt et al.,
653 2013; Ballantyne et al., 2017; Hedemann et al., 2017). This is in line with the observed slow
654 down in tundra greening due to short-term cooling after volcanic eruptions (Lucht et al., 2002).

655 Eurasian tundra show a positive trend for the years 1982–2017, but a reversal in trend sign for
656 the years 2000–2017 (Figure S11). Models exhibit some evidence of a strengthening browning
657 signal, but fail to capture the full extent of the emerging browning clusters seen in observations.
658 If we only consider the grid cells that show significant browning in observations and models,
659 we are able to conduct a robust driver attribution. According to the TRENDYv7 ensemble,
660 the browning cluster in Eurasian tundra can *very likely* be attributed to CO₂ induced climate
661 change (PNS = 93%, PNS = 47% for MPI-ESM). These results are in line with studies showing
662 that tundra ecosystems are susceptible to warm spells during growing season (Phoenix and
663 Bjerke, 2016) and to frequent droughts (Beck and Goetz, 2011). The asymmetry between Eurasia
664 and North America can be explained by changes in large-scale circulation. Eurasia is cooling
665 through increased summer cloud cover, whereas North America is warming through more
666 cloudless skies (Bhatt et al., 2013; Bhatt et al., 2014). Also linkages between regional Arctic sea
667 ice retreat, subsequent increasing ice-free waters, and regional Arctic vegetation dynamics have
668 been postulated (Bhatt et al., 2014).

669 3.14 *Vegetation in arid climates is greening, except in South America*

670 Non-forested greening clusters beyond the high northern latitudes coincide with semi-arid
671 to arid climates (Park et al., 2018). The Northern Sub-Saharan African savannas and grasslands
672 greened extensively in recent decades (~ 4.63 % decade⁻¹; Figure S12), which is reproduced by
673 the observation-driven TRENDYv7 models (~ 4.55 % decade⁻¹), and is *likely* caused by climatic
674 changes (PNS = 68%). No robust attribution is feasible based on the MPI-ESM simulations.
675 However, it is noteworthy, that the fully-coupled Earth system model points to climate change
676 as having a negative effect in these regions, thus, not reproducing the observed increase in
677 rainfall (Figure S12). This provides evidence for the hypothesis that African precipitation
678 anomalies are not induced by rising CO₂, but rather follow a multidecadal internal climatic
679 mode (Asefi-Najafabady and Saatchi, 2013).

680 Internal variability in LAI changes is strong in the Southern African grasslands and savannas,
681 and thus, no robust long-term change can be identified (Figure S13). It has been shown
682 that shrublands in the more southern regions are greening in response to increased rainfall
683 (Fensholt and Rasmussen, 2011). In general, the literature suggests that greening and browning

684 patterns in arid climates are mainly driven by precipitation anomalies (Fensholt and Rasmussen,
685 2011; Fensholt et al., 2012; Gu et al., 2016; Adler et al., 2017). Close resemblance arises when
686 comparing the spatial patterns of precipitation trends throughout the satellite era (Adler et al.,
687 2017) with significant changes in vegetation in arid environments, especially so in the African
688 continent. Decreased rainfall in arid South America coincides with strong browning clusters
689 (Fensholt et al., 2012). This is in disagreement with the expected strong manifestation of CO₂
690 fertilization in water-limited environments (Ukkola et al., 2016).

691 Australian Shrublands show a persistent positive LAI trend (~ 3.84 % decade⁻¹), intermit-
692 tently perturbed by climatic extreme events (e.g. strong anomalous rainfall with subsequent
693 extensive vegetation greening in 2011, Figure S14; Poulter et al., 2014). Models reproduce
694 the steady greening of Australia, but no robust driver attribution is feasible due to strong
695 internal variability. However, both model setups point to the physiological effect of CO₂ as the
696 dominant driver (Figure S14). These results are congruent with recent studies (Donohue et al.,
697 2009; Ukkola et al., 2016) that show CO₂ fertilization enhanced vegetation growth by lowering
698 the water limitation threshold.

699 Grasslands in the cool arid climates exhibit persistent positive trends (~ 2.03 % decade⁻¹,
700 Figure S15). Simulated estimates are in the range of the observations (MPI-ESM: ~ 2.33
701 % decade⁻¹ and TRENDYv7: ~ 1.81 % decade⁻¹). Our analysis suggests that the positive
702 response of cool arid grasslands to rising CO₂ can be explained by the physiological effect of
703 CO₂ (PNS = 85% for TRENDYv7, PNS = 88% for MPI-ESM). These ecosystems are dominated
704 by C₃-type plants (Still et al., 2003), which are susceptible to CO₂ fertilization (Sage et al.,
705 2012), thus, consistent with our results. In the warm arid areas, C₄-type grasses dominate
706 (Still et al., 2003), which are less sensitive to the physiological effects of CO₂ (Sage et al., 2012).
707 As discussed above, vegetation changes there are mostly driven by precipitation anomalies,
708 although CO₂ fertilization might also contribute to a limited extent (Sage et al., 2012).

709 4 CONCLUSIONS

710 In this paper we examine nearly four decades of global LAI changes under rising atmospheric
711 CO₂ concentration. We find that the Earth's greening trend is weakening and clusters of
712 browning are beginning to emerge, and importantly, expanding during the last two decades.
713 Leaf area is primarily decreasing in the pan-tropical green belt of dense vegetation. Leaf area
714 gain is occurring mostly in sparsely vegetated regions in cold and/or arid climatic zones, and
715 in temperate forests. Thus, vegetation greening is occurring mainly in regions of low LAI,
716 whereas browning is seen primarily in regions of high LAI. Consequently, these opposing
717 trends are decreasing the texture of leaf area distribution in natural vegetation.

718 We identify clusters of greening and browning spread across all continents and conduct
719 a regional, *i.e.* biome-specific, driver attribution based on factorial model simulations. The
720 results suggest that the physiological effect of CO₂ (*i.e.* CO₂ fertilization) is the dominant
721 driver of increasing leaf area only in temperate forests, cool arid grasslands and likely the
722 Australian shrublands. A cause-and-effect relationship between CO₂ fertilization and greening
723 of other biomes could not be established. This finding questions the study by Zhu et al. (2016)
724 that identified CO₂ fertilization as the most dominant driver of the Earth's greening trend.
725 We find that many clusters of greening and browning bear the signature of climatic changes.
726 The greening of Sub-Saharan grasslands and savannas can be explained by increased rainfall.
727 Climatic changes, primarily warming and drying, determine the patterns of vegetation changes
728 in the northern ecosystems, *i.e.* greening of Eurasian boreal forests and North American tundra,
729 but also emerging browning trend in the Eurasian tundra. Models fail to capture the browning
730 of North American boreal forests. Models suggest rising CO₂ has compensatory effects on
731 LAI in the tropical forests. Climatic changes induce browning, which is opposed by greening
732 due to a strong physiological effect in the models. Hence, if the physiological effect of CO₂
733 is "turned-off", models simulate the emerging browning trend in the tropics comparable to
734 observations. Our analysis of changes in rainfall during the satellite age underpins climate
735 changes as the main cause of tropical forest browning: recurrent droughts and decline in dry
736 season precipitation in the Amazon as well as long-term drying trends in Africa.

737 Models represent a simplified view of the real world reduced to its essential processes.
738 Some of these processes are under-represented or lacking in the current generation of land
739 surface models. Whether they are driven with observed climatic conditions or operate in a
740 fully-coupled Earth System model, they fail to capture the full extent of adverse effects of
741 rising CO₂ in natural ecosystems. In particular, the deficiency of reproducing the observed
742 leaf area loss in North American boreal and in pan-tropical forests - biomes which account
743 for a large part of the photosynthetic carbon fixation - has considerable implications for
744 future climate projections. Thus, it is important to focus model development not only on a
745 better representation of disturbances such as droughts and wildfires, but also on revising the
746 implementation of processes associated with the physiological effect of CO₂, which currently
747 offsets browning induced by climatic changes.

748 Another vital issue for future research is the impact of large-scale climatic anomalies on
749 vegetation. All three major clusters of browning are hypothesized to be associated with
750 temperature or precipitation anomalies modulated by climatic modes. Many droughts in
751 the Amazon were attributed to El Niño events (Bonal et al., 2016). The long-term drying
752 trend in tropical Africa is possibly connected to the Atlantic Multidecadal Oscillation (Asefi-
753 Najafabady and Saatchi, 2013). Likewise, disturbances in North American boreal forests
754 are likely controlled by an interplay between large-scale climatic patterns (Pacific Decadal
755 Oscillation, El Niño Southern Oscillation, and Arctic Oscillation; Macias Fauria and Johnson,
756 2008). Little is known about how these large-scale patterns might change in a warming
757 climate. Current Earth system models struggle to simulate these climatic modes and related
758 precipitation patterns, which is likely rooted in their coarse spatial resolution. New tools, such
759 as high-resolution simulations or large ensembles, offer possibilities to study these phenomena.

760 Finally, it is important to note that the impacts of leaf area changes are not comparable
761 between biomes. Regarding biodiversity, the consequences of leaf area loss in tropical forests
762 that harbor the most diverse flora and fauna of the planet are not compensated for by leaf area
763 gain in temperate and arctic ecosystems. A similar caveat is in order with respect to the carbon
764 cycle, e.g. an additional leaf in the tundra does not offset the reduction in primary productivity
765 of a leaf lost in the tropical rainforest. Thus, our results indicating loss of tropical leaf area
766 should be of concern. A recent study suggested that the tropical forests have already switched

767 to being a net source of carbon, also considering land-use emissions (Baccini et al., 2017). The
768 uncertainty in future projections is large, ranging from a stable CO₂ fertilization-driven carbon
769 sink to a collapse of the system at a certain CO₂ concentration (Cox et al., 2000). Concerning leaf
770 area, the models project a steady greening of the tropical forests in the high-end CO₂ emissions
771 scenario (business-as-usual) and a slight browning in the low-end scenario (mitigation) by
772 the end of the century (Piao et al., 2019). Altogether, the tropical forests have the potential to
773 crucially influence the evolution of climate throughout the 21st century and should be a vital
774 issue for future research.

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1044 4.1 *Data availability*

1045 All data used in this study are available from public databases or literature, which can be
1046 found with the references provided in respective Methods section. Processed data and analysis
1047 scripts are available from the corresponding author upon request and will also be published in
1048 public repositories together with this article.

1049 4.2 *Author Contributions*

1050 A.J.W. performed the research and drafted the manuscript with inputs from R.B.M., V.B.,
1051 S.S., V.H., D.L, V.K.A., J.P., J.E.M.S.N., D.S.G., E.K., H.T., A.A., and P.F.; A.J.W. carried out the
1052 attribution analysis with support from A.H.; R.B.M., A.H. and V.B. contributed ideas and to
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1063 4.4 *Author Information*

1064 The Authors declare no conflict of interests. Correspondence and requests for materials
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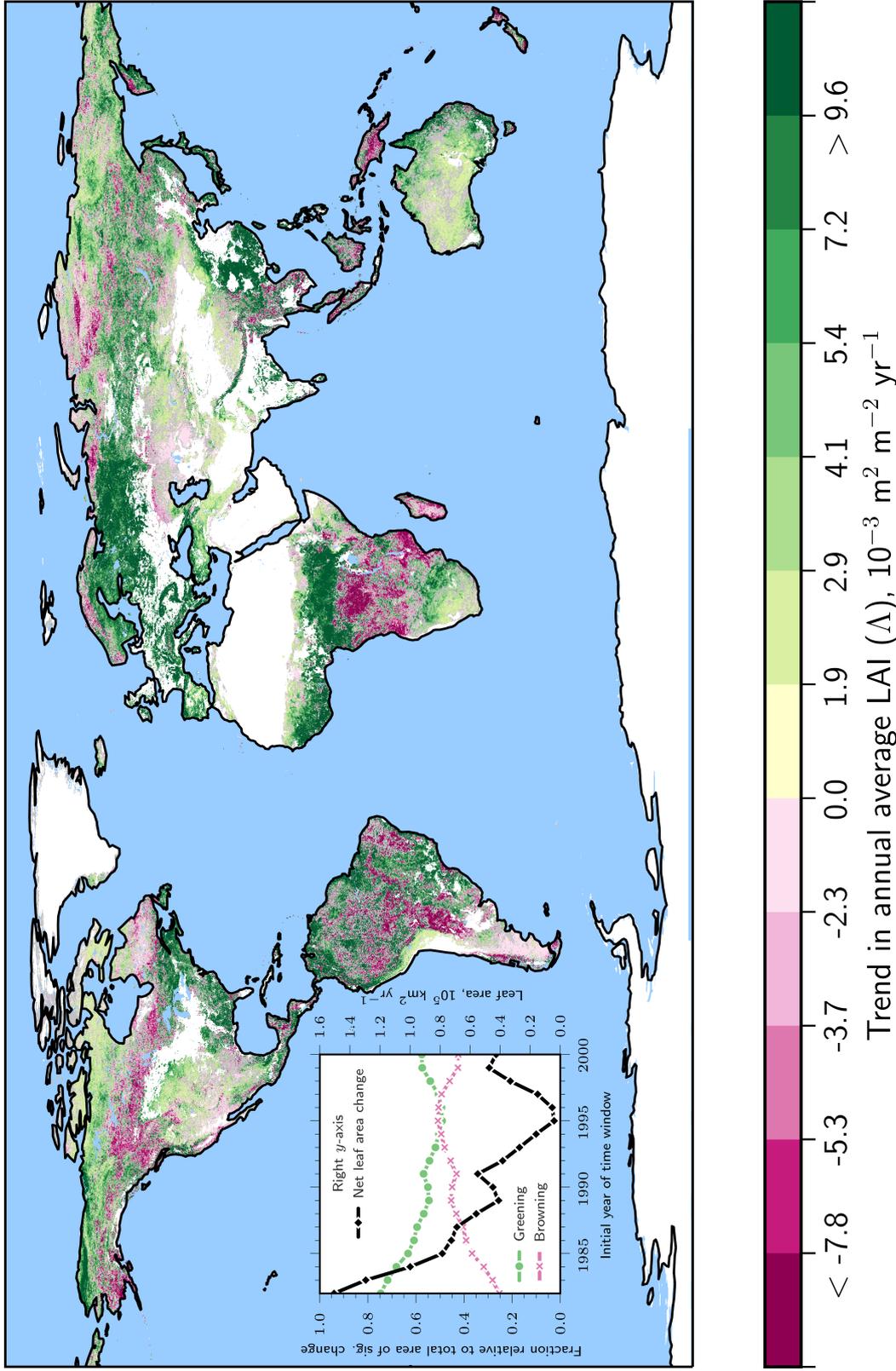


Figure 1 | **Natural vegetation exhibits patterns of opposing long-term LAI trends with rising CO₂.** Global map of statistically significant (Mann-Kendall test, $p < 0.1$) annual average LAI trends (denoted Δ) for the entire period 1982–2017 (AVHRR, color-coded). Areas of non-significant change are shown in gray. Anthropogenic vegetation (defined as croplands, Materials and Methods) is masked in white. Other white areas depict ice sheets or barren land. The inset line plot illustrates the change in fraction of positive (green dots) and negative Δ (red crosses) relative to the total area of significant change, and net leaf area change (black squares; right y -axis) for time windows of moving initial year (final year fixed at 2017). The x -axis shows the advancing initial year of the time window.

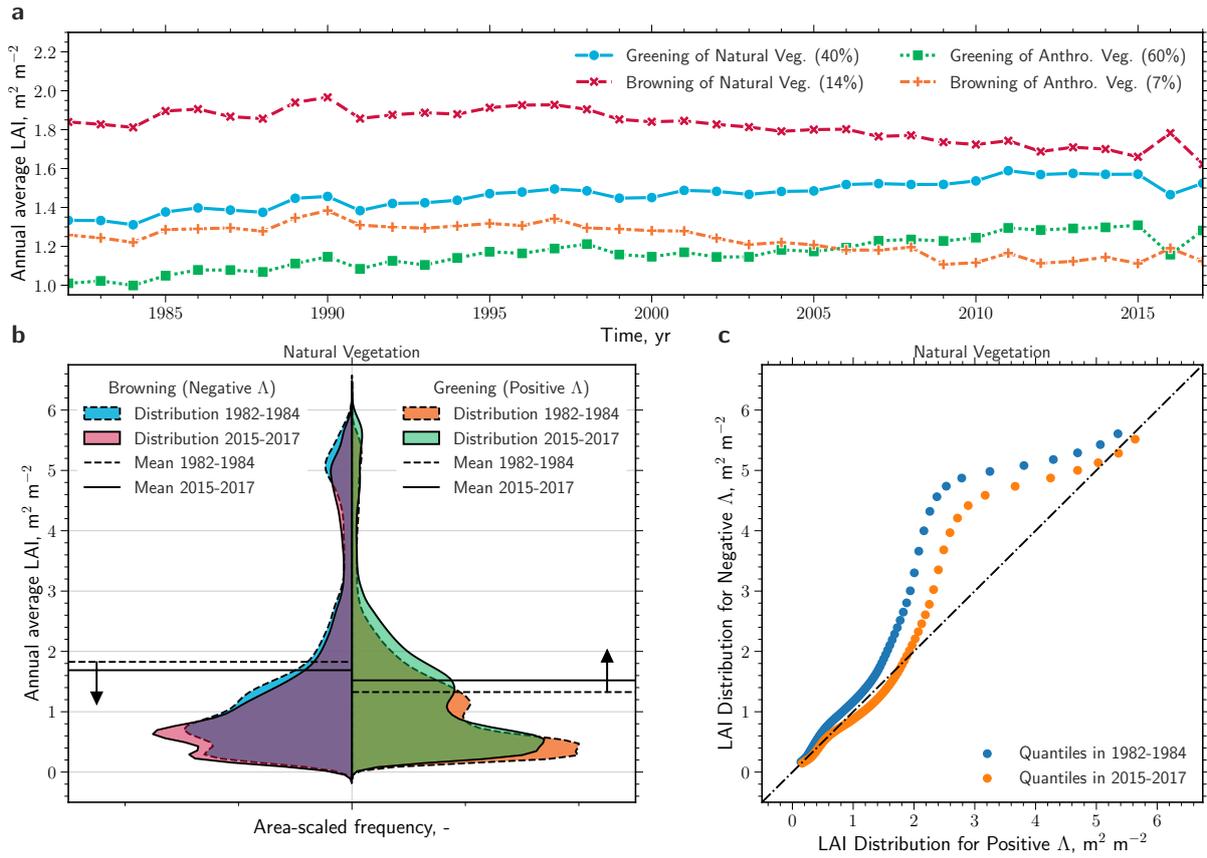


Figure 2 | Observed homogenization of the global natural vegetation. **a** Time series of the area-weighted annual average LAI (AVHRR, 1982-2017) of natural and anthropogenic vegetation for regions of positive (greening) and negative trends (browning). Only regions exhibiting significant trends are considered (Mann-Kendall significance test, $p < 0.1$) and are referred to as Δ . The percentages in brackets in the legend represent the respective proportions with respect to the total area. **b** Violin plot comparison of probability density functions (PDF, Gaussian kernel density estimation; all PDFs scaled to contain the same area) of LAI distributions of natural vegetation for negative (left) and positive Δ (right), and in time, 1982-1984 (dashed) versus 2015-2017 (solid). The horizontal lines represent the mean values for the respective period. **c** Q-Q (quantile-quantile) plot comparing the distributions of LAI for negative (x -axis) and positive Δ (y -axis) and their change over time, 1982-1984 (blue dots) versus 2015-2017 (orange dots).

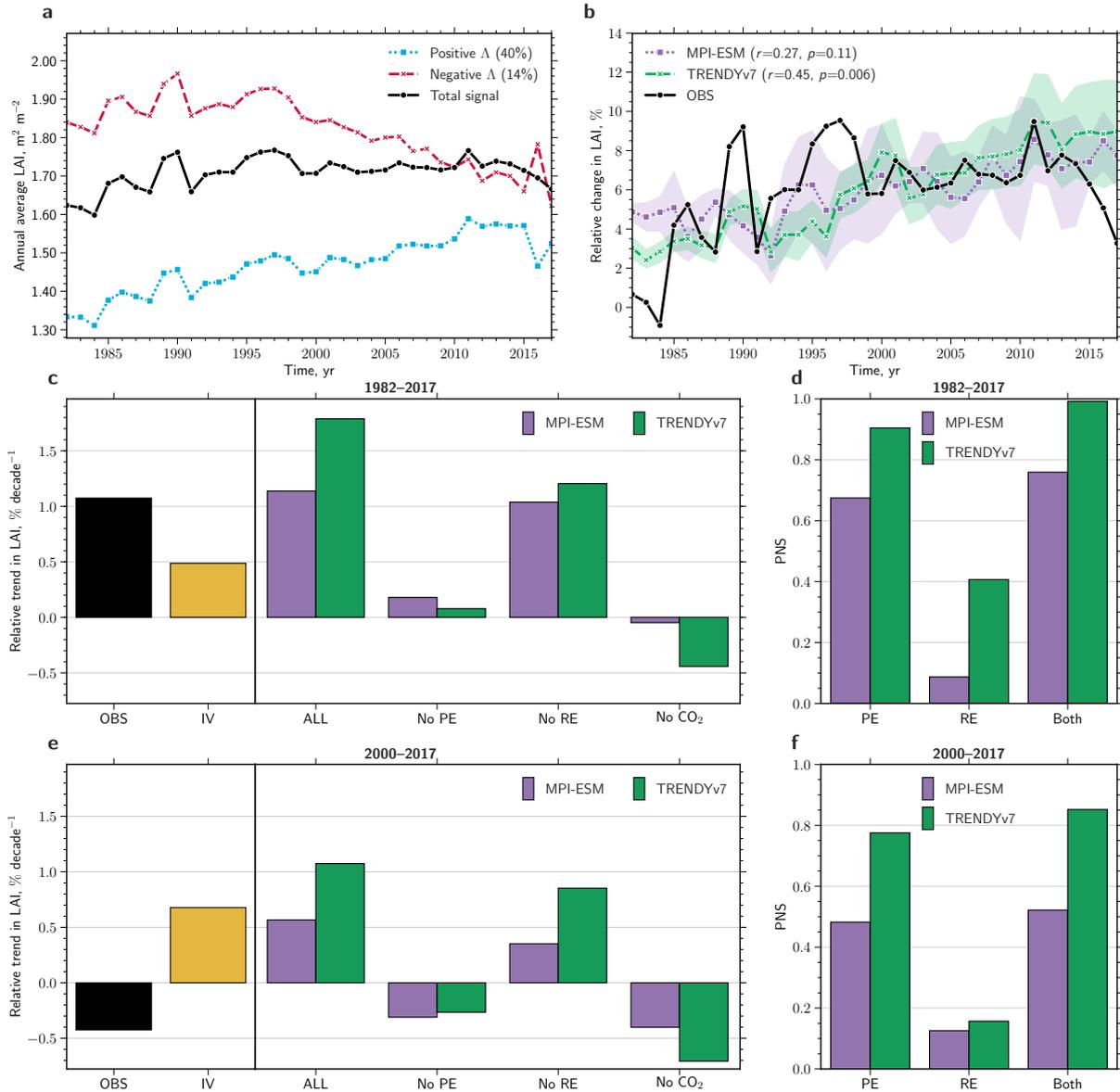


Figure 3 | Global driver attribution of changing natural vegetation for the entire period versus the second half of the observational record. a Time series of the area-weighted annual average LAI (AVHRR, 1982–2017) for regions of positive (blue dotted line) and negative sensitivity (red dashed line) to rising atmospheric CO₂ concentration (Δ) of natural vegetation. Black solid line represents the overall signal of all pixels. The percentages in brackets in the legend represent the greening and browning proportions with respect to the total area. **b** Time series of changes in LAI relative to the average state from 1982–1984, comparing observations (black solid line) with historical simulations, where the green dashed line denotes the ensemble mean of 13 offline-driven land surface models (TRENDYv7, Data and Methods), and the purple dotted line denotes the average of an ensemble of multi-realizations with a fully-coupled Earth system model (MPI-ESM, Data and Methods). The colored shading represents the 95% confidence interval estimated by bootstrapping. The correlation coefficients (including significance level) of the observed and simulated time series are displayed in brackets in the legend. **c** Bar chart showing relative trends in LAI (in % yr⁻¹) of the total observed signal (black) and for factual (all historical forcings; ALL) as well as for counterfactual simulations, i.e. no historical CO₂ forcing (No CO₂), all historical forcings except the physiological effect (No PE) or the radiative effect (No RE) of atmospheric CO₂, as estimated by TRENDYv7 (green) and MPI-ESM (purple). The yellow bar represents internal variability (IV) derived from all simulations (control, factual and counterfactual). **d** Probabilities of necessary and sufficient causation (PNS) of the change in LAI, comparing the physiological (PE) and radiative effect (RE) of CO₂ as well as their combined effect (Both). **e** as in **c** but for the period 2000–2017. **f** as in **d** but for the period 2000–2017.

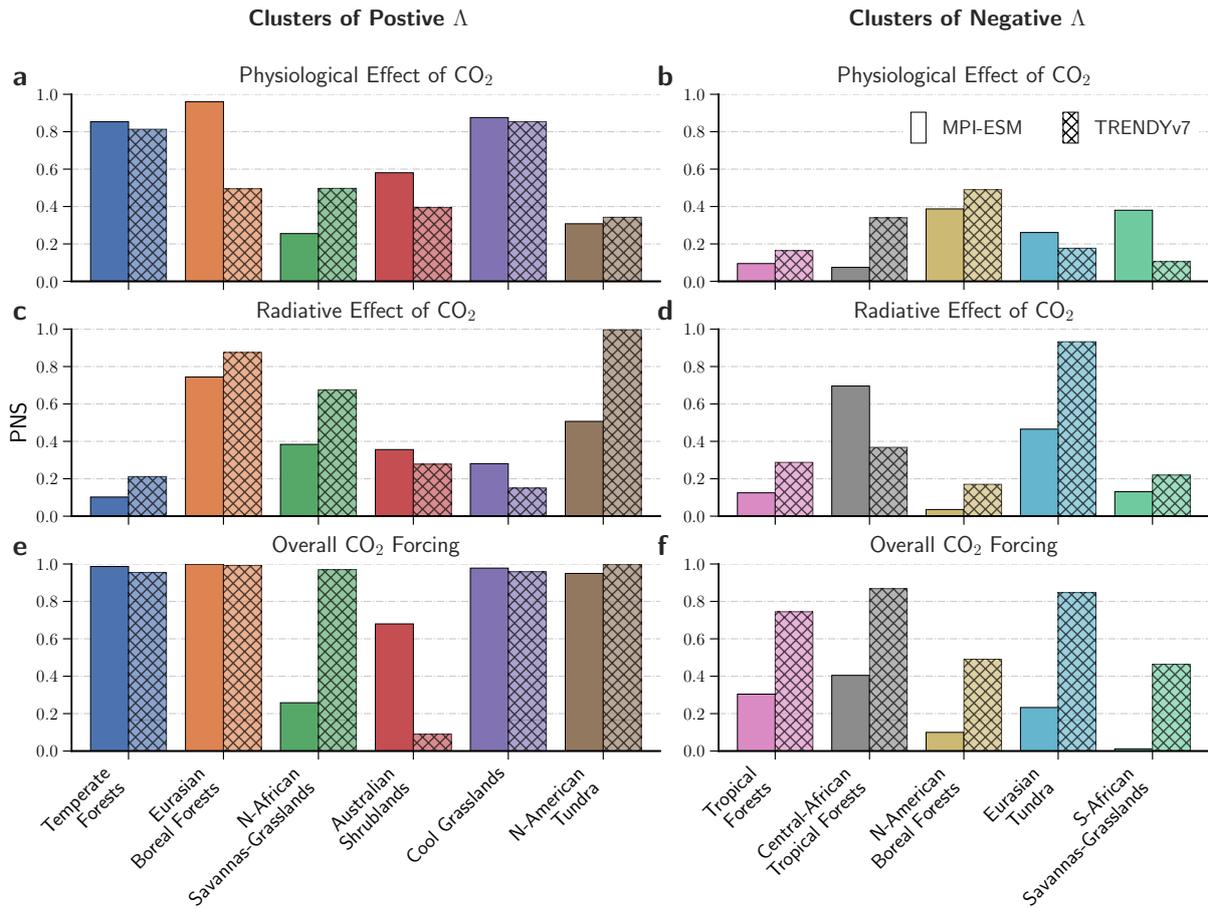


Figure 4 | **Probabilities of sufficient and necessary causation (PNS) of LAI changes in response to CO₂ for eleven clusters.** Bar charts represent PNS of LAI changes in response to the physiological effect (a, b), radiative effect of CO₂ (c, d) and all anthropogenic forcings (e, f). Different colors represent the identified clusters of substantial change in LAI. Panels on the left comprise clusters that show consistent greening, panels on the right represent emerging browning clusters (observed net leaf area loss in the period 2000–2017; attribution is conducted only for significant decreasing trends, Data and Methods). The two types of bar illustrate the two different ensembles of model simulations (left: MPI-ESM, right: TRENDYv7).

Table 1 | Greening (positive Δ), browning (negative Δ) and non-changing fractions of vegetated area for different biomes and prominent clusters of change for the time period 1982–2017. Significant changes are determined by the means of the Mann-Kendall significance test ($p < 0.1$). The abbreviations used to describe the different clusters are explained in Materials and Methods.

Area	Vegetated Area	Positive Δ Fraction	Negative Δ Fraction	No-Change Fraction
<i>Unit</i>	10^6 km^2	-	-	-
All Vegetation	109.42	0.43	0.13	0.45
Anthro. Vegetation	15.37	0.6	0.07	0.32
Natural Vegetation	94.05	0.4	0.14	0.47
Biomes				
Grasslands	26.77	0.4	0.12	0.48
Tropical Forests	20.32	0.28	0.16	0.55
Boreal Forests	13.69	0.4	0.19	0.41
Temperate Forests	11.2	0.56	0.08	0.36
Shrublands	10.37	0.41	0.1	0.49
Tundra	7.03	0.41	0.14	0.45
Savannas	4.22	0.48	0.13	0.38
Clusters				
Cool Gl	12.32	0.4	0.12	0.48
EA Brl F	8.0	0.53	0.1	0.37
NAm Brl F	5.69	0.23	0.31	0.46
NAf Sv Gl	5.6	0.59	0.06	0.35
CAf Trp F	5.35	0.3	0.25	0.45
SAf Sv Gl	4.6	0.24	0.24	0.52
Aus Sl	4.43	0.49	0.03	0.49
EA Tundra	3.57	0.35	0.2	0.44
NAm Tundra	3.46	0.46	0.07	0.47

Table 2 | Leaf area gain, loss, and net change for different biomes and prominent clusters of change for the time period 1982–2017. Significant changes are determined by the means of the Mann-Kendall significance test ($p < 0.1$). The abbreviations used to describe the different clusters are explained in Materials and Methods.

Leaf Area	Leaf Area Gain	Leaf Area Loss	Net Leaf Area Change
<i>Unit</i>	$10^3 \text{ km}^2 \text{ yr}^{-1}$	$10^3 \text{ km}^2 \text{ yr}^{-1}$	$10^3 \text{ km}^2 \text{ yr}^{-1}$
All Vegetation	296.87	-85.71	211.16
Anthro. Vegetation	67.12	-6.47	60.65
Natural Vegetation	229.75	-79.24	150.51
Biomes			
Grasslands	48.01	-12.51	35.50
Tropical Forests	58.42	-34.31	24.11
Boreal Forests	32.11	-14.45	17.66
Temperate Forests	53.32	-7.45	45.87
Shrublands	10.9	-2.4	8.50
Tundra	8.74	-3.69	5.05
Savannas	17.99	-4.21	13.78
Clusters			
Cool Gl	15.06	-3.75	11.31
EA Brl F	25.93	-4.26	21.67
NAm Brl F	6.18	-10.18	-4.00
NAf Sv Gl	23.42	-0.98	22.44
CAf Trp F	16.76	-13.76	3.00
SAf Sv Gl	5.51	-6.76	-1.25
Aus Sl	4.48	-0.16	4.32
EA Tundra	3.96	-3.04	0.92
NAm Tundra	4.78	-0.64	4.14