

38 **Abstract:**

39 **The growth rate of atmospheric CO₂ concentrations since industrialization is**
40 **characterized by large interannual variability, mostly resulting from variability in the**
41 **CO₂ uptake by terrestrial ecosystems. However, the contributions of regional ecosystems**
42 **to that variability are not well known. Using an ensemble of ecosystem and land-surface**
43 **models and an empirical observation-based product of the global gross primary**
44 **production, we show that the mean sink, trend, and interannual variability in CO₂**
45 **uptake by terrestrial ecosystems are dominated by distinct biogeographic regions.**
46 **Whereas the sink strength is dominated by highly productive lands, mainly tropical**
47 **forests, the trend and interannual variability of the sink are dominated by semi-arid**
48 **ecosystems whose carbon balance is strongly associated with circulation-driven**
49 **variations in both precipitation and temperature.**

50 **One Sentence Summary:**

51 **Semi-arid savannas and shrub lands dominate the trend and interannual variability of**
52 **the global land CO₂ sink.**

53 **Main Text:**

54 Since the 1960s, terrestrial ecosystems have acted as a substantial sink for atmospheric CO₂,
55 sequestering about one quarter of anthropogenic emissions in an average year (1). This
56 ecosystem service, which helps mitigate climate change by reducing the rate of increase of
57 atmospheric greenhouse gases, is due to an imbalance between the uptake of CO₂ through
58 gross primary production (GPP, the aggregate photosynthesis of plants) and the release of
59 carbon to the atmosphere by ecosystem respiration (R_{eco}) and other losses, including wildfires
60 (C_{fire}). The net carbon flux (net biome production, NBP = GPP - R_{eco} - C_{fire}) results from the
61 small imbalance between the much larger uptake and release fluxes. Consequently, small
62 fractional variations in either of these fluxes can cause substantial absolute variations in net
63 carbon exchange with the atmosphere. These variations account almost entirely for year-to-
64 year variations around the overall trend in atmospheric concentrations of CO₂ (2, 3).

65 Modelling studies suggest a large uncertainty of the future magnitude and sign of the carbon
66 sink provided by terrestrial ecosystems (4-8). Robust projections are crucial to assess future
67 atmospheric CO₂ burdens and associated climate change, and also for developing effective
68 mitigation policies. Reducing uncertainty requires better knowledge of the regions and
69 processes governing the present sink and its variations. Inventories suggest that the majority
70 of carbon sequestered by the terrestrial biosphere since industrialization has accumulated in
71 forest ecosystems of the tropics and temperate zones (9). However, the relative contributions
72 of ecosystems of different, climatically-distinct, regions to variations in the land sink on
73 interannual to multi-decadal time scales are not well characterized. Here we investigate
74 relative regional contributions to, respectively, the mean sink, its trend over recent decades
75 and the interannual variability (IAV) around the trend.

76 We simulate the geographic pattern and time course of NBP using LPJ-GUESS (10-12), a
77 biogeochemical dynamic global vegetation model (DGVM) that explicitly accounts for the
78 dependency of plant production and downstream ecosystem processes on the demography
79 (size structure) and composition of simulated vegetation. We force the model with historical
80 climate (13) and CO₂ concentrations, accounting for emissions from land use change and
81 carbon uptake due to regrowth following agricultural abandonment (14). We compare the
82 results to an ensemble of nine ecosystem and land surface model simulations from the
83 TRENDY model intercomparison project (12, 15) (hereinafter TRENDY models, Table S1).
84 The TRENDY ensemble is similarly based on historical climate and CO₂, but employs a static
85 1860 land use mask.

86 Global NBP as simulated by LPJ-GUESS shows strong agreement ($r^2=0.62$) with the Global
87 Carbon Project (GCP) estimate of the net land CO₂ flux; an independent, bookkeeping-based
88 estimate derived as the residual of emissions, atmospheric growth and ocean uptake of CO₂
89 (1) (Fig 1A). TRENDY models do not account for land use change. In comparison to the GCP
90 land flux estimate they consequently predict a higher average NBP but similar interannual
91 variation. Moreover, the offset between the TRENDY ensemble mean and the GCP land flux
92 estimate is comparable to the GCP estimate of mean land use change emissions for the period
93 1982-2011 (fLUC).

94 We divide the global land area into six land cover classes following the MODIS MCD12C1
95 land cover classification (12, 16): tropical forests (Fig 1B), extra-tropical forest, grasslands
96 and croplands (here combined), semi-arid ecosystems (Fig 1C), tundra and arctic shrub lands,
97 and sparsely vegetated lands (areas classified as barren) (Fig S1 and S2).

98 When the global terrestrial CO₂ sink (average NBP) and its trend (1982-2011) are partitioned
99 among land cover classes, we find that tropical forests account for the largest fraction (26%,
100 0.33 PgC year⁻¹) of the average sink over this period (1.23 PgC year⁻¹) (Fig. 1D). In contrast,
101 we find that semi-arid ecosystems dominate the positive global CO₂ sink trend (57%, 0.04
102 PgC year⁻², global: 0.07 PgC year⁻²) (Fig. 1E). The TRENDY ensemble shows a consistent
103 pattern, with tropical forests dominating the mean sink (median: 24%) and semi-arid
104 ecosystems dominating the trend (median: 51%). The predominance of semi-arid ecosystems
105 in explaining the global land sink trend is consistent with widespread observations of woody
106 encroachment over semi-arid areas (17) and increased vegetation greenness inferred from
107 satellite remote sensing over recent decades (17-19). Likewise, a recent study attributes the
108 majority of the record land sink anomaly of 2011 to the response of semi-arid ecosystems in
109 the Southern Hemisphere, particularly Australia, to an anomalous wet period; the study
110 further postulates a recent increase in the sensitivity of carbon uptake to precipitation for this
111 region due to vegetation expansion (20).

112 We further partition interannual variability in global NBP among land cover classes based on
113 the contribution of individual grid cells to global NBP IAV (12). To this end, we adopted an
114 index (Eq. S1, Fig S3) that scores individual geographic locations according to the
115 consistency over time (years) with which the local NBP flux resembles the sign and
116 magnitude of global NBP (Fig S4). Regions receiving higher and positive average scores are
117 inferred to have a larger contribution in governing global NBP IAV, as opposed to regions
118 characterized by smaller or negative (counteracting) scores (Fig S3). The index we adopt does
119 not characterize the *variability* of ecosystems of different land cover classes as, for example

120 the standard deviation would do (Fig S5) but rather enables a comparison of their relative
121 importance (contribution) in governing global IAV.

122 Semi-arid ecosystems were found to account for the largest fraction, 39%, of global NBP
123 IAV, exceeding tropical forest (19%), extra-tropical forest (11%; all forest: 30%) and
124 grasslands and croplands (27%) (Fig 1F). The TRENDY ensemble shows a similar
125 partitioning, with semi-arid ecosystems accounting for 47% (median; tropical forests: 28%,
126 extra-tropical forest: 6%, all forest: 35%). The overall contributions per land cover class are
127 the sum of both positive and negative contributions that result from differences in phase
128 between IAV of individual grid cells compared with global IAV (Fig S4). The extent to which
129 negative contributions reduce the overall land cover class contributions is minor for all
130 regions except grasslands and crops (Fig S6) (LPJ-GUESS: -13%, TRENDY median: -13%)
131 the latter being distributed widely across climate zones, both climate variations and the
132 sensitivity of NBP to climate variations differing among regions.

133 To partition the global NBP IAV among component fluxes (GPP, R_{eco} , C_{fire}) and among land
134 cover classes, we applied Eq. S1. We found that global NBP IAV is most strongly associated
135 with variation in GPP; interannual GPP anomalies contribute 56% of the global NBP IAV in
136 LPJ-GUESS, and a median of 90% in the TRENDY model ensemble. Comparing different
137 land cover classes, the GPP anomalies of semi-arid ecosystems alone contribute 39% in LPJ-
138 GUESS and a median of 65% in the TRENDY model ensemble to global NBP IAV (Fig. S7).
139 Semi-arid vegetation productivity thus emerges clearly as the single most important factor
140 governing global NBP IAV.

141 We employed two complementary methods to attribute the variability in GPP—as the inferred
142 primary driver of global NBP IAV—to its environmental drivers. Firstly, we analyzed
143 simulation results from LPJ-GUESS, linking output GPP anomalies to variability in the
144 climatic input data. Secondly we use a time-resolved gridded global GPP product derived
145 from upscaled flux tower measurements (12, 21) (hereinafter empirical GPP product). This
146 product uses an empirical upscaling of flux measurements and is thus entirely independent of
147 the modelled GPP in our study.

148 The three main climatic drivers temperature (T), precipitation (P) and shortwave radiation (S)
149 are interdependent and correlated. To account for combined effects of these drivers we adopt
150 an analysis of GPP variations from an “impact perspective” (22-24): we first identify GPP
151 anomalies and then extract their climatic covariates. The primary challenge of such analysis
152 on annual scale is to target climate indices that adequately characterize the “period of climatic
153 influence”, e.g. growing season average, annual averages, minima or maxima of a given
154 climatic forcing. To overcome this challenge we use semi-annual time series of climate
155 drivers constructed using an optimization procedure that weights monthly anomalies of a
156 given climate variable (T, P or S), accounting for time lags of up to 24 months while making
157 no additional prior assumptions as to the period of influence (12). For each GPP event we
158 extract climatic covariates as z-scores of the semi-annual climatic drivers.

159 We evaluate the climatic covariates of GPP anomalies for semi-arid ecosystems from the
160 empirical GPP product and modelled by LPJ-GUESS, focusing on T and P, and find similar
161 responses of GPP to climate with both approaches across all latitude bands (Fig 2 A,B).
162 Negative GPP anomalies in semi-arid ecosystems are mainly driven by warm and dry (low
163 rainfall) climatic events in most latitudes, suggestive of drought. By contrast, positive GPP

164 anomalies are dominated by cool and wet conditions. Averaging the distributions over
165 latitudes (Fig 2 A,B) and extracting the climatic covariates per percentile of the GPP
166 distributions shows that GPP varies with climatic conditions on a straight line in T-P space
167 (Fig S8), with a stronger covariation with P than T. This implies that the full GPP
168 distributions are driven by similar climatic patterns, i.e. anomalies that differ in size and sign
169 covary with corresponding differences in size and sign in the drivers. GPP extremes (the tails
170 of the distribution of GPP among years) covary with ENSO across all latitudes (Fig 2 C,D).
171 Both in the model and the empirical GPP product, GPP anomalies are more strongly
172 associated with the positive phase of ENSO (El Niño) than the negative phase (La Niña),
173 while the sign of the relationship varies with latitude. Positive ENSO tends to coincide with
174 negative GPP anomalies in the tropics (30°S - 20°N), and with positive GPP anomalies north
175 of 20°N.

176 The agreement between climatic covariates of the data-based empirical GPP product and
177 modelled GPP alongside the comparatively robust pattern of the covariation with climate
178 suggests that GPP IAV for semi-arid ecosystems is mediated by climate. Since ENSO
179 covaries with a considerable portion of the GPP distribution, we infer that ENSO is the
180 dominating mode of global circulation variations driving GPP IAV over semi-arid
181 ecosystems. Recent modelling studies have found that extreme El Niño events could become
182 more common under climate change (25), which together with an increased atmospheric
183 demand for water associated with global warming might exacerbate the impact of El Niño
184 events over semi-arid ecosystems and further increase the role of semi-arid regions in driving
185 global NBP IAV (26-28).

186 We repeat the calculation of climatic covariates to simulated NBP for LPJ-GUESS and each
187 of the TRENDY models. The resulting maps of covariates in T-P space are shown as average
188 covariates of negative (low CO₂ uptake or CO₂ release) extremes (Fig 3 A,B) and positive
189 (high CO₂ uptake or low CO₂ release) extremes (Fig 3 C,D). In general, semi-arid ecosystems
190 stand out as regions in which strong CO₂ uptake events are consistently associated with cool
191 and moist conditions, and strong CO₂ release events with warm and dry conditions. In tropical
192 forests NBP covaries with both T and P as in semi-arid regions, but also with T alone. In high
193 latitudes wet or warm and wet conditions lead to negative NBP extremes whereas warm and
194 dry or dry conditions tend to lead to positive extremes, although the spatial heterogeneity of
195 the covariates is large in this region (Fig 3).

196 Our approach offers detailed spatial and temporal disaggregation of drivers and responses
197 which is important when analyzing drivers or covariates of global NBP IAV because of the
198 high temporal and spatial variability in P (Fig S9-11). Using four upscaling levels with
199 increasing spatial and temporal disaggregation (ranging from land surface mean P and T to
200 using semi-annual P and T, averaged based on the spatial origin of each year's global NBP
201 anomaly (Eq S5 and S6)) we show that P and NBP IAV become more correlated at higher
202 levels of disaggregation. At the highest disaggregation level, P is almost as strongly correlated
203 with NBP IAV as T, suggesting a strong influence of soil moisture variations on global NBP
204 IAV (28). This strong increase in P correlations with disaggregation resolves an apparent
205 conflict between the findings of the present study, and those of studies using regionally
206 averaged drivers which emphasize the role of T in governing IAV in atmospheric CO₂ (28-
207 30). For semi-arid ecosystems T correlations are slightly stronger than P correlations with
208 NBP IAV (Fig 4B), partly due to an asymmetric distribution of P and/or an asymmetric
209 response of NBP to P IAV (Fig S12). The correlation of tropical forest P with NBP IAV

210 increases when we use the semi-annual drivers, suggesting large importance of accounting for
211 time lags and “period of climatic influence” of P variations (12), but P-NBP IAV correlations
212 are still weaker than T-NBP IAV correlations (Fig 4C).

213 Our analysis provides evidence that semi-arid ecosystems, largely occupying low latitudes,
214 have dominated the IAV and trend of the global land C sink over recent decades. Semi-arid
215 regions have been the subject of relatively few targeted studies that place their importance in a
216 global context. Our findings indicate that semi-arid regions and their ecosystems merit
217 increased attention as a key to understanding and predicting inter-annual to decadal-scale
218 variations in the global carbon cycle.

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296 **Supplementary Materials**

297 www.sciencemag.com
298 Materials and Methods
299 Figs. S1-S12
300 References (33-57)

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318 research areas MERGE and BECC.

319 **Figure captions:**

320 **Figure 1.** Global and regional NBP mean, trend and variations. (A) Global NBP and GCP
321 land flux time series (1982 – 2011). TRENDY models are plotted on a separate vertical axis
322 with a time-invariant offset corresponding to the time period average GCP fLUC estimate (1.2
323 Pg C). (B) Tropical forest NBP. LPJ-GUESS (red line) includes emissions from land use
324 change. TRENDY models average (blue line) and 1st and 3rd quartiles of the ensemble
325 (shaded blue area) do not include emissions from land use change. (C) NBP of semi-arid
326 ecosystems from LPJ-GUESS (including land use change emissions) and TRENDY models
327 (excluding land use change emissions). (D) Contribution of land cover classes to global mean
328 NBP (1982-2011) (mean NBP of land cover class / mean global NBP). Horizontal lines in
329 boxplots show from top, 95th, 75th, 50th, 25th, and 5th percentiles. (E) Contribution of land
330 cover classes to global NBP trend (land cover class NBP trend / global NBP trend). (F)
331 Contribution of land cover classes to global NBP interannual variations (Eq S1).

332 **Figure 2.** Climatic-covariates of semi-arid ecosystem GPP variations. (A) Distribution by
333 latitude of the empirical GPP product anomalies normalized by average standard deviation of
334 GPP in semi-arid lands. The distribution is colored according to the legend based on average
335 local climatic covariates per latitude zone and distribution bin. (B) LPJ-GUESS GPP
336 distribution calculated and colored as in (A). (C) Covariation of the multivariate ENSO index
337 anomalies (MEI (31, 32)) with the empirical GPP product. (D) Covariation of MEI and
338 modelled GPP anomalies per latitudinal zone. NB: the figure shows the covariates of
339 latitudinal average local GPP anomalies and not the average covariates based on GPP IAV
340 contribution to NBP IAV.

341 **Figure 3.** Climatic covariates of NBP extremes. (A) Climatic covariates of LPJ-GUESS
342 negative NBP extremes ($1-10^{\text{th}}$ percentiles). (B) Mean climatic covariates of TRENDY-
343 models negative NBP extremes ($1-10^{\text{th}}$ percentiles). (C) covariates of LPJ-GUESS positive

344 NBP extremes (90-99th percentiles). (D) Mean climatic covariates of TRENDY-models
345 positive NBP extremes (90-99th percentiles).

346 **Figure 4.** Correlations between annual climatic drivers IAV (P and T) and global NBP IAV
347 (mean of all 10 models). (A) Global P and T correlations to global NBP IAV. From black to
348 white and left to right, bars represent annual P and T IAV correlations to global NBP IAV
349 with increasing spatial and temporal disaggregation of P and T while averaging to global time
350 series: (I) Black bars represent averaged global land surface P and T weighted by grid cell
351 area. (II) Dark grey bars represent P and T weighted by 30-year average contribution to global
352 NBP IAV (Eq S1, Fig S4). (III) Light grey bars represent averaged P and T weighted by each
353 years contributions, thus accounting for the difference in the spatial distribution of
354 contributions between years (Eq S5 and S6). (IV) White bars represent semi-annual climate
355 drivers averaged to global time series using the annual spatial contributions as in (III) thereby
356 accounting for the “period of climatic influence” and time lags of up to 24 months. (B)
357 Correlations between P and T IAV and NBP IAV for semi-arid ecosystems. Weights, where
358 applicable, are based on contributions to global NBP IAV as in (A) but with P and T averaged
359 over semi-arid ecosystems only. (C) Correlations between P and T IAV and global NBP IAV
360 for tropical forest. Weights, where applicable, are based on contributions to global NBP IAV
361 as in (A) but with P and T averaged over tropical forest only.