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## Global trends in carbon sinks and their relationships with CO<sub>2</sub> and temperature

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1 **Global trends in carbon sinks and their relationships with CO<sub>2</sub> and**  
2 **temperature**

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24 Elevated CO<sub>2</sub> increases photosynthesis and, potentially, net ecosystem production  
25 (NEP) meaning greater CO<sub>2</sub> uptake. Climate, nutrients, and ecosystem structure,  
26 however, influence the effect of increasing CO<sub>2</sub>. Here, we analysed global NEP from  
27 MACC-II and Jena CarboScope atmospheric-inversions and 10 dynamic global  
28 vegetation models (TRENDY), using statistical models to attribute the trends in NEP to  
29 its potential drivers: CO<sub>2</sub>, climatic variables and land-use change. We find that  
30 increasing CO<sub>2</sub> was consistently associated with increased NEP (1995-2014).  
31 Conversely, increasing temperatures were negatively associated with NEP. Using the  
32 two atmospheric inversions and TRENDY, the estimated global sensitivities for CO<sub>2</sub>  
33 were  $6.0 \pm 0.1$ ,  $8.1 \pm 0.3$  and  $3.1 \pm 0.1$  Pg C per 100 ppm ( $\sim 1$  °C increase), and  $-0.5 \pm$   
34  $0.2$ ,  $-0.9 \pm 0.4$  and  $-1.1 \pm 0.1$  Pg C °C<sup>-1</sup> for temperature. These results indicate a  
35 positive CO<sub>2</sub> effect on terrestrial C sinks that is constrained by climate warming.

36

37 In recent decades, terrestrial ecosystems have been absorbing 15–30% of all  
38 anthropogenic CO<sub>2</sub> emissions<sup>1,2</sup>. Direct and indirect anthropogenic impacts on the  
39 biosphere, however, can alter terrestrial sinks in the short and long terms<sup>3–6</sup>. Identifying  
40 the factors that affect the capacity of the biosphere to absorb carbon (C) and  
41 quantifying the magnitude of the sensitivity of this C sink to its driving factors helps to  
42 increase confidence in future projections of the coupled C cycle/climate system.

43 Increasing plant growth is a robust response to increasing CO<sub>2</sub> concentrations under  
44 experimental conditions (CO<sub>2</sub> fertilization effect)<sup>7,8</sup>. The extent to which increases in  
45 CO<sub>2</sub> can enhance large-scale photosynthesis and ultimately net ecosystem production  
46 (NEP) remains uncertain<sup>5,7</sup>. Detecting this effect in the real world is much more difficult  
47 than under controlled experiments. However, recent efforts using eddy-covariance-  
48 based data and statistical models have been successful in detecting positive effects of  
49 CO<sub>2</sub> on water-use efficiency (WUE)<sup>9</sup>, photosynthesis, and NEP<sup>5</sup>.

50 The potential positive effect of elevated CO<sub>2</sub> on productivity could be influenced by  
51 global warming<sup>6</sup> and altered precipitation patterns<sup>10</sup> since both water availability and  
52 temperature are strong drivers of photosynthesis and respiration worldwide<sup>11–13</sup>. Land-  
53 use change also alters the capacity of the biosphere to sequester C because land use  
54 causes a drastic change in C turnover and productivity. Atmospheric deposition of  
55 nitrogen (N) and sulphur (S) from the use of fossil fuels and fertilisers may also alter  
56 ecosystem biodiversity, function, productivity and NEP<sup>5,14–17</sup>. N deposition is usually  
57 positively correlated with ecosystem productivity and NEP<sup>17–19</sup>. Conversely, S  
58 deposition may reduce ecosystem carbon sinks, this has rarely been investigated in  
59 field studies<sup>20,21</sup> and absent from global models. Soil acidification, caused by acid  
60 deposition, of N and S, often decreases the availability of soil nutrients<sup>22</sup> and potentially  
61 reduces NEP<sup>23</sup>.

62 The observations underlying the driver analysis of NEP described above were largely  
63 limited to temperate and boreal study sites, making it difficult to assess global  
64 scalability. Additionally, until recently, the only way to assess terrestrial C sink was from  
65 ensembles of dynamic global vegetation models (DGVMs) or as a residual sink, by  
66 subtracting atmospheric and ocean sinks to the estimates of CO<sub>2</sub> emissions. Currently,  
67 inversion models, as well as long-term remotely sensed data<sup>24</sup>, can be used to test the  
68 generality of the patterns derived from ground-based measurements. Inversion models  
69 provide continuous gridded estimates for the net flux of land-atmosphere CO<sub>2</sub>  
70 exchange (i.e. NEP) with global coverage<sup>25,26</sup>. The gridded NEP results from  
71 inversions, combined with CO<sub>2</sub>-concentration records, gridded fields for climate, land-

72 use change, and atmospheric deposition, are arguably the best observation-based data  
73 to attempt a first empirical study of the combined effects of CO<sub>2</sub>, changes in climate  
74 and land use, and atmospheric N and S deposition on terrestrial NEP patterns at the  
75 global scale. Given that previous site level studies revealed that increasing CO<sub>2</sub> is a  
76 dominant driver of trends in NEP, we expect that it will also be the dominant driver at  
77 larger spatial scales and across the globe.

78 Here we investigate if the trends of NEP from the two most widely used multi-decadal  
79 inversion models (MACC-II and Jena CarboScope) and DGVMs (TRENDY) from 1995  
80 to 2014 are related to increasing atmospheric CO<sub>2</sub> and changing climate (temperature,  
81 precipitation, and drought). Additionally, the effect of land-use on NEP at the global  
82 scale was investigated using statistical models to assess the sensitivity of NEP to the  
83 abovementioned predictors. We also analysed the effect of changing rates of  
84 atmospheric deposition of oxidised and reduced N and S on NEP, combined with  
85 increasing CO<sub>2</sub> and changing climate and land use, over Europe and the USA.

#### 86 *CO<sub>2</sub> and climate effects on global NEP*

87 Global land (excluding Antarctica) mean annual NEP was  $2.3 \pm 0.9$ ,  $2.3 \pm 1.5$  and  $1.6 \pm$   
88  $0.5 \text{ Pg C y}^{-1}$  (mean  $\pm 1\sigma$ ), respectively, for MACC-II, Jena CarboScope and the  
89 TRENDY ensemble during the period 1995–2014, similar in magnitude to the recent  
90 global carbon budget<sup>2</sup>. Both inversions and the TRENDY ensemble showed an overall  
91 positive trend in NEP from 1995 to 2014. The estimated NEP increased by (mean  $\pm$   
92  $1\text{SE}$ )  $116.9 \pm 6.1 \text{ Tg C y}^{-1}$  for the MACC-II dataset, by  $178.0 \pm 8.1 \text{ Tg C y}^{-1}$  for the Jena  
93 CarboScope dataset, and by  $22.5 \pm 3.1 \text{ Tg C y}^{-1}$  for the TRENDY ensemble (**Figure 1**).  
94 This supports the increases in the global carbon budget<sup>2</sup>, with a lower increase of the  
95 DGVMs than those shown by the inversion models. The large differences between  
96 inversion models and DGVMs may arise because of the lack of information on river  
97 fluxes, inadequate parameterisations concerning land management and degradation in  
98 the process models or because of potential biases in inversion models. Both inversion  
99 model datasets produced similar trends for many parts of the world, an increasing NEP  
100 for Siberia, Asia, Oceania, and South America, and a decreasing NEP for the southern  
101 latitudes of Africa. Differences between inversions emerged for Europe and North  
102 America, possibly because Jena CarboScope inversion uses a larger spatial error  
103 correlation of prior fluxes than MACC-II or because of other inversion settings<sup>2</sup>.  
104 However, their different flux priors did not drive differences in the trends between both  
105 datasets, given that priors did not change over the studied period. Jena CarboScope  
106 showed largely positive trends for Europe and largely negative trends for North

107 America; MACC II showed more variation in the trends for both continents. The trends  
108 identified by the TRENDY ensemble agreed with atmospheric inversions for the  
109 northernmost latitudes, indicating an increase in C-sink capacity, but differed from  
110 those in many other regions.

111 Our analyses on temporal contributions, using the temporal anomalies of our  
112 predictors, attributed the increases in global NEP to increasing CO<sub>2</sub> but found a  
113 consistent negative impact of temperature on NEP, which limited the positive effect of  
114 increasing CO<sub>2</sub> (**Figure 1**). These results were consistent for both datasets and most of  
115 the DGVMs of the TRENDY ensemble. The predictors used in this study explained a  
116 modest proportion of the variance in NEP, in contrast to the variance explained by  
117 spatial variability (i.e., the pixel), which was rather high (**Supplementary Information**  
118 **(SI), Section 2**). Unknown contributions to trends in NEP, the difference between all  
119 contributions and the observed trend, were very close to zero for the analyses on  
120 inverse models and the TRENDY ensemble (**Figure 1**). This result suggests that trends  
121 were very well captured by our analyses, indicating that the methodology was able to  
122 disentangle spatial from temporal variability. The sensitivity of NEP to increasing CO<sub>2</sub>  
123 averaged  $0.45 \pm 0.01$ ,  $0.61 \pm 0.03$  and  $0.23 \pm 0.01$  g C m<sup>-2</sup> ppm<sup>-1</sup> for MACC-II, Jena  
124 CarboScope and TRENDY, respectively (**Table 1**), representing sensitivities over the  
125 entire terrestrial surface of  $60.4 \pm 1.2$ ,  $81.4 \pm 3.4$  and  $30.7 \pm 1.2$  Tg C ppm<sup>-1</sup>,  
126 respectively. Despite lower temporal attributions for temperature than CO<sub>2</sub>, the  
127 sensitivity of NEP to temperature was high, at  $-3.8 \pm 1.1$ ,  $-6.4 \pm 2.9$  and  $-8.1 \pm 0.9$  g C  
128 m<sup>-2</sup> y<sup>-1</sup> °C<sup>-1</sup> for the MACC-II, Jena CarboScope and TRENDY models, respectively,  
129 equivalent to global sensitivities of  $-515.7 \pm 152.4$ ,  $-859.2 \pm 386.3$  and  $-1088.0 \pm 118.1$   
130 Tg C °C<sup>-1</sup>, respectively. Trends in NEP and the effect of CO<sub>2</sub> and temperature on NEP  
131 significantly differed in magnitude amongst the datasets used, however, they all point  
132 towards the same conclusion: global NEP has increased during the study period and  
133 increasing CO<sub>2</sub> has been the most likely driving factor despite increasing temperatures  
134 constraining this positive effect. The exact magnitude of the effect of increasing CO<sub>2</sub>  
135 and temperatures on global carbon cycle remains to be established

#### 136 *Spatial variability on CO<sub>2</sub> and climate change effects on NEP*

137 Our statistical models for the MACC-II and Jena CarboScope datasets indicated that  
138 the positive effect of CO<sub>2</sub> on NEP was higher in regions with higher annual precipitation  
139 and that this positive effect increased with increasing temperatures (**Figure 2, SI**  
140 **Section 1.1**). In contrast, our analyses using the TRENDY ensemble did not show a  
141 significant interaction between CO<sub>2</sub> and precipitation or with temperature, highlighting

142 the different behaviour in the DGVMs compared to inversion models. We also found a  
143 significant positive interaction between mean annual temperature and CO<sub>2</sub> for Jena  
144 CarboScope and TRENDY. However, the same interaction was negative for MACC-II.  
145 On the other hand, increasing temperatures reduced NEP in warm regions but  
146 increased NEP in cold regions (**Figure 2**).

147 The analyses on temporal contributions performed for inversion and TRENDY NEP  
148 averaged over latitudinal bands (boreal, >55°; temperate, 35-55°; subtropical, 15-35°;  
149 and tropical, 15°N-15°S), further supported previous results obtained at the global  
150 scale (**Table 2, SI Sections 2.2–2.7**). Increasing CO<sub>2</sub> was the main factor accounting  
151 for increasing trends in NEP, with a consistent positive temporal contribution for almost  
152 all latitudinal bands considered and for all three datasets. However, contributions  
153 estimated from the TRENDY ensemble were generally lower than those of the  
154 inversion models. Proportionally, increasing CO<sub>2</sub> accounted for more than 90% of the  
155 trends in NEP in MACC-II and Jena CarboScope datasets. For the TRENDY ensemble,  
156 the estimated contribution of CO<sub>2</sub> to the trends in global NEP was more than 2.7 times  
157 higher than the estimated trends. Increasing temperatures had a negative effect for all  
158 latitudinal bands for the inversion models, but most effects were not statistically  
159 significant and need to be interpreted as such. Instead, our analyses for the TRENDY  
160 ensemble indicated a significant negative effect for all latitudinal bands, except for the  
161 temperate southern hemisphere. Similarly, the proportional contribution of temperature  
162 to the trends in NEP was less than 10% for the inversion models, but accounted for  
163 almost 95% of the trends estimated using the TRENDY ensemble. These results  
164 suggest that the parameterisation of temperature in the DGVMs does not accurately  
165 reproduce the estimation of the inverse models.

166 Despite all regions presented, on average, positive trends, the tropical regions clearly  
167 had the highest contribution, across all three datasets, to global NEP trends accounting  
168 for almost half of the increase (**Table 2**). Similarly, the tropical regions had the highest  
169 sensitivity to CO<sub>2</sub> increase, accounting for more than half of the total global sensitivity  
170 (**Table 1**). A similar pattern was found for temperature, although the sign of the  
171 contribution was positive for MACC-II but negative for Jena CarboScope and TRENDY.  
172 The contribution of the southern hemisphere to the global trends was very modest  
173 compared to the contribution of the northern hemisphere using all datasets. Our results  
174 using the MACC-II dataset showed that subtropical, temperate and boreal regions of  
175 the northern hemisphere accounted for 44.2% of the global trends in NEP, while only  
176 9.5% was attributed to subtropical and temperate regions of the southern hemisphere.  
177 Using the Jena CarboScope dataset these regions accounted for 63.3% and 6.1%,

178 respectively. Differences on the regional attributions between inversion models may  
179 emerge from the different interhemispheric transport models or other inversion  
180 settings<sup>2</sup>. Results from the TRENDY ensemble were more extreme, because they  
181 indicated a negative contribution of the subtropical and temperate regions to the global  
182 trends in NEP. Differences between the global estimates (trends and contributions of  
183 CO<sub>2</sub> and temperature) and the sum of every region were low for all datasets.  
184 Contribution of other variables to the trends in NEP (precipitation, drought, land-use  
185 change, and unknown variables) were on average also low for most of the latitudinal  
186 bands, despite the variability amongst datasets (**Table 2**).

### 187 *Atmospheric deposition*

188 The MACC-II and Jena CarboScope datasets showed that NEP increased over Europe  
189 and the USA by  $0.45 \pm 0.13$  and  $0.68 \pm 0.16$  g C m<sup>-2</sup> y<sup>-1</sup>, respectively (**Figure S1**). Our  
190 temporal contribution analyses suggested that increasing atmospheric CO<sub>2</sub> in both  
191 datasets contributed significantly to increasing NEP. NEP sensitivity to CO<sub>2</sub> was more  
192 than two-fold higher in the Jena CarboScope than the MACC-II dataset (**Table S1**),  
193 similar to the temporal contributions, at  $0.22 \pm 0.06$  and  $0.46 \pm 0.07$  g C m<sup>-2</sup> y<sup>-1</sup> ppm<sup>-1</sup>  
194 for the MACC-II and Jena CarboScope models, respectively. The temporal contribution  
195 of decreasing N<sub>ox</sub> deposition to NEP differed between the two datasets; the  
196 contribution was positive for MACC-II and negative for Jena CarboScope. Our analyses  
197 consequently estimated a negative sensitivity of NEP to N<sub>ox</sub> for the MACC-II dataset  
198 but a positive sensitivity for the Jena CarboScope dataset. Additionally, neither MACC-  
199 II, nor Jena CarboScope indicated a strong impact of land use change.

200 These statistical models indicated that, in both datasets, the positive effect of CO<sub>2</sub> on  
201 NEP was higher in regions with higher N<sub>RED</sub> deposition but lower in regions with high S  
202 deposition (means for MACC-II and annual anomalies for Jena CarboScope; see **SI**  
203 **section 2.8**). The results for N<sub>ox</sub> deposition, however, differed between the models.  
204 The positive effect of CO<sub>2</sub> on NEP for the MACC-II dataset was constrained by the  
205 annual anomalies of N<sub>ox</sub> but was higher for the Jena CarboScope dataset. We also  
206 estimated an overall negative but not significant sensitivity of NEP to S deposition for  
207 both inversion models.

### 208 *CO<sub>2</sub> fertilisation and global NEP*

209 The positive effect of atmospheric CO<sub>2</sub> on NEP must originate from a stronger positive  
210 effect on photosynthesis than on the sum of all respiratory processes. Increasing  
211 atmospheric CO<sub>2</sub> concentrations have been widely reported to increase ecosystem



212 photosynthesis, mainly by two mechanisms: i) increasing carboxylation rates and  
213 decreasing photorespiration<sup>27</sup>, and ii) decreasing stomatal conductance and therefore  
214 increasing WUE<sup>9,28</sup>, which would theoretically increase photosynthesis under water  
215 limitation. An increase in GPP by either mechanism may thus account for the higher  
216 NEP due to increasing atmospheric CO<sub>2</sub>. A recent global analysis suggested that most  
217 of the GPP gains from CO<sub>2</sub> fertilization are associated with ecosystem WUE<sup>29</sup>. The  
218 positive interaction between CO<sub>2</sub> and annual precipitation that we found may not  
219 support this hypothesis (**Figure 2**), given that plants living under wet conditions are  
220 usually less efficient in water use. However, plants having higher water availability may  
221 benefit from increasing CO<sub>2</sub> more than those suffering drought because photosynthesis  
222 would not be water-limited.

223 Our estimates of global NEP sensitivity to CO<sub>2</sub> were  $0.45 \pm 0.01$ ,  $0.61 \pm 0.03$  and  $0.23$   
224  $\pm 0.01$  g C m<sup>-2</sup> ppm<sup>-1</sup> (globally  $60.4 \pm 1.2$ ,  $81.4 \pm 3.4$  and  $30.7 \pm 3.4$  Tg C ppm<sup>-1</sup>) for the  
225 MACC-II, Jena CarboScope and TRENDY datasets, respectively, but these estimates  
226 varied amongst the latitudinal bands and were inconsistent between datasets (**Table**  
227 **1**). These estimates were similar to those reported in CO<sub>2</sub>-enrichment FACE  
228 experiments<sup>30</sup>, despite the fact that FACE values were calculated for a much higher  
229 CO<sub>2</sub> range for which the effect of CO<sub>2</sub> may saturate<sup>31</sup>. However, they were much lower  
230 than the  $4.81 \pm 0.52$  g C m<sup>-2</sup> ppm<sup>-1</sup> reported in a study using eddy-covariance flux  
231 towers for a similar period<sup>5</sup>. The much larger areas analysed by the inverse models  
232 than the footprints covered by the eddy-covariance flux towers, and FACE  
233 experiments, may explain these differences between the estimates. Flux towers are  
234 usually located in relatively homogenous, undisturbed ecosystems, while each pixel in  
235 the inverse model aggregates information from several ecosystems (and even biomes),  
236 often including non-productive land such as bare soil or cities.

237 Our results indicated that the variability of the estimates of NEP sensitivity to CO<sub>2</sub>  
238 amongst the latitudinal bands might be associated with differences in climate and  
239 atmospheric N and S deposition. The two atmospheric inversion models indicated that  
240 the effect of CO<sub>2</sub> fertilisation was stronger in wet climates (high annual precipitation)  
241 (**Figure 2**), supporting the estimates provided by the latitudinal bands, with the highest  
242 sensitivity estimates for the tropical band (**Table 1**). However, analyses based on the  
243 TRENDY ensemble did not show the same results. The positive effect of CO<sub>2</sub> tended to  
244 increase with temperature anomalies in both inversion models, but, again, the DGVMs  
245 did not show the same behaviour. These differences between inversion models and  
246 process-based models suggest that DGVMs still fail to capture some of the interactions  
247 occurring in nature. The MACC-II and Jena CarboScope datasets further agreed on a

248 stronger positive effect of increasing CO<sub>2</sub> in regions with higher N<sub>RED</sub> deposition, which  
249 confirms previous studies suggesting that the effect of CO<sub>2</sub> fertilisation is stronger in  
250 nitrogen-rich sites<sup>32–34</sup>.

#### 251 *Climate, land-use and C sinks*

252 Climatic warming clearly had a secondary effect on the trends in NEP from 1995 to  
253 2014. The MACC-II, Jena CarboScope and TRENDY datasets estimated that NEP  
254 decreased globally by around  $-0.5 \pm 0.2$ ,  $-0.9 \pm 0.4$  and  $-1.1 \pm 0.1$  Pg C for every  
255 degree of increase in the Earth's temperature. Assuming that a CO<sub>2</sub> increase of 100  
256 ppm is equivalent to an increase of global temperature of 1 °C, the effect of the  
257 increasing CO<sub>2</sub> concentrations largely outweighs the negative effect of increasing  
258 temperature on NEP (global estimates:  $6.0 \pm 0.1$ ,  $8.1 \pm 0.3$  and  $3.1 \pm 0.1$  Pg C for a  
259 100 ppm of CO<sub>2</sub> increase according to MACC-II, Jena CarboScope and TRENDY). The  
260 difference, though, is much lower for TRENDY than for the inversion models, having a  
261 higher negative impact of temperature and a lower positive effect of CO<sub>2</sub>. This  
262 difference in the effects of temperature and CO<sub>2</sub> may explain the lower trends observed  
263 in TRENDY datasets compared to MACC-II and Jena CarboScope. It also suggests  
264 that a different parameterisation of temperature, CO<sub>2</sub> and their interaction may be  
265 needed on DGVMs to capture the observed trends in the inversion models.

266 The quasi monotonically increasing atmospheric CO<sub>2</sub> concentrations have been more  
267 important than temperature in driving NEP trends. Increasing temperature, however,  
268 did not have the same effect on NEP around the world. The analyses of both inverse  
269 models indicated that increasing temperatures had a positive effect on NEP only in cold  
270 regions (when MAT  $\leq 1.5$ , 9 and  $-5.9$  °C for MACC-II and Jena CarboScope and  
271 TRENDY respectively, when CO<sub>2</sub> = 400 ppm, see **SI section 2.1**, and **Figure 2**).  
272 These findings support previous literature reporting a positive effect between  
273 temperature increase and NEP in temperate and boreal forests<sup>35</sup>. Instead, the general  
274 negative effect of temperature on NEP could be due to a greater stimulation of Re than  
275 photosynthesis by higher temperatures<sup>36,37</sup>. The potential benefit to C sequestration of  
276 increased photosynthesis would then be negated by a greater increase in Re.  
277 Increasing temperatures can also be linked to heat waves and drier conditions, which  
278 may decrease GPP more than Re<sup>38</sup>.

279 The effects of land-use change on NEP trends differed greatly amongst the datasets,  
280 both at the global scale and when using latitudinal bands. Our statistical models  
281 identified several significant relationships between NEP and land-use change, but the  
282 large differences in effects (direction and magnitude) amongst the datasets preclude

283 drawing firm conclusions. The coarse resolution of analysis likely blurred the effects of  
284 land-use change on the NEP trends.

285 Our study highlights the dominant role of rising atmospheric CO<sub>2</sub> concentrations  
286 triggering an increase in land C sinks over the entire planet from 1995 to 2014, with the  
287 tropics accounting for around half of this increase in NEP despite being only around  
288 22% of the global land (excluding Antarctica, **Table 2**). Therefore, preserving tropical  
289 ecosystems should be a global priority in order to mitigate anthropogenic CO<sub>2</sub>  
290 emissions. Temperature has diminished the capacity of terrestrial ecosystems to  
291 sequester C, which jeopardises future C sink capacity in light of global warming. So far,  
292 our results suggest that the benefit of increasing atmospheric concentrations of CO<sub>2</sub>  
293 are still compensating the negative ones of temperature rise, in terms of C  
294 sequestration. However, if it has not started to change already<sup>6</sup>, this pattern may  
295 eventually reverse with saturation of land C sinks<sup>5,31</sup> or because warm ecosystems tend  
296 to decrease NEP as temperature rises (**Figure 2**). Additionally, the comparison  
297 between model results indicated that the DGVMs were unable to reproduce several  
298 features of the global land C sinks observed in inversion models. Process-based earth  
299 system models will need to improve their parameterisation to capture these features in  
300 order to better predict the future of land C sinks.

301

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432

#### 433 **Author Contributions**

434 M.F-M., J.S., I.A.J., and J.P. conceived, analyzed and wrote the paper. F.C., P.F., and  
435 S.S., provided data. All authors contributed substantially to the writing and discussion  
436 of the paper.

437



438 **Figure captions**

439 **Figure 1: Global trends in NEP and their contributing factors.** Global temporal  
440 contributions of CO<sub>2</sub>, climate and land-use change to the trends in NEP (annual  
441 change) are shown on the right side of each panel. The difference between the  
442 modelled temporal contributions and the trends (shaded) has been treated as an  
443 unknown contribution to the temporal variation in NEP. Statistically significant ( $P <$   
444 0.01) temporal variations of the predictors are shown in square brackets. Error bars  
445 indicate 95% confidence intervals. The boxplots in panel c indicate the estimated  
446 contributions of the 10 DVGMs used in the TRENDY ensemble. Units are ppm y<sup>-1</sup> for  
447 CO<sub>2</sub>, °C y<sup>-1</sup> for temperature, mm y<sup>-2</sup> for precipitation, standard deviation for SPEI, and  
448 percentage of land-use cover per pixel for forests, crops, and urban areas. See the  
449 Materials and Methods section for information about the methodology used to calculate  
450 the contributions. Significance levels: \*,  $P < 0.01$ ; \*\*,  $P < 0.005$ ; \*\*\*,  $P < 0.001$ .

451 **Figure 2: Plots showing the estimated effects of the interactions of the statistical**  
452 **models.** The graphs show interactions between CO<sub>2</sub> and climate (mean annual  
453 precipitation [MAP] and temperature [MAT], and annual anomalies in temperature  
454 [MAT.an]) on NEP for the MACC-II and Jena CarboScope inversion models and the  
455 TRENDY ensemble. Shaded bands indicate the 95% confidence intervals of the  
456 slopes. Non-significant interactions are indicated by “n.s.”.

457 **Table 1: Global and latitudinal analyses of sensitivity of NEP to changes in**  
458 **atmospheric CO<sub>2</sub> concentrations and mean annual temperature.** The “%” columns  
459 indicate the contribution of the latitudinal band to the global estimate. Differences are  
460 calculated as the difference between the sum of all latitudinal bands and the global  
461 estimate. Bold coefficients differ significantly from 0 at the 0.01 level. Empty cells  
462 indicate that anomalies in temperature were not a significant predictor in the models  
463 predicting NEP. Units are Tg C y<sup>-1</sup> ppm<sup>-1</sup> for CO<sub>2</sub> and Tg C y<sup>-1</sup> C<sup>-1</sup> for temperature.

464 **Table 2: Global and latitudinal trends and temporal contributions of changes in**  
465 **atmospheric CO<sub>2</sub> concentrations and mean annual temperature to NEP trends.**  
466 The “%” columns indicate the percentage of contribution of each latitudinal band to the  
467 global estimate. Columns “Cont.” show the percentage of contribution of CO<sub>2</sub> and  
468 temperature to the trends in NEP. Column “Other” shows the difference between the  
469 NEP trend and the sum of contributions of CO<sub>2</sub> and temperature. If different from zero,  
470 it indicates that other factors are contributing to the trends in NEP. The “differences”  
471 rows are calculated as the difference between the sum of all latitudinal bands and the

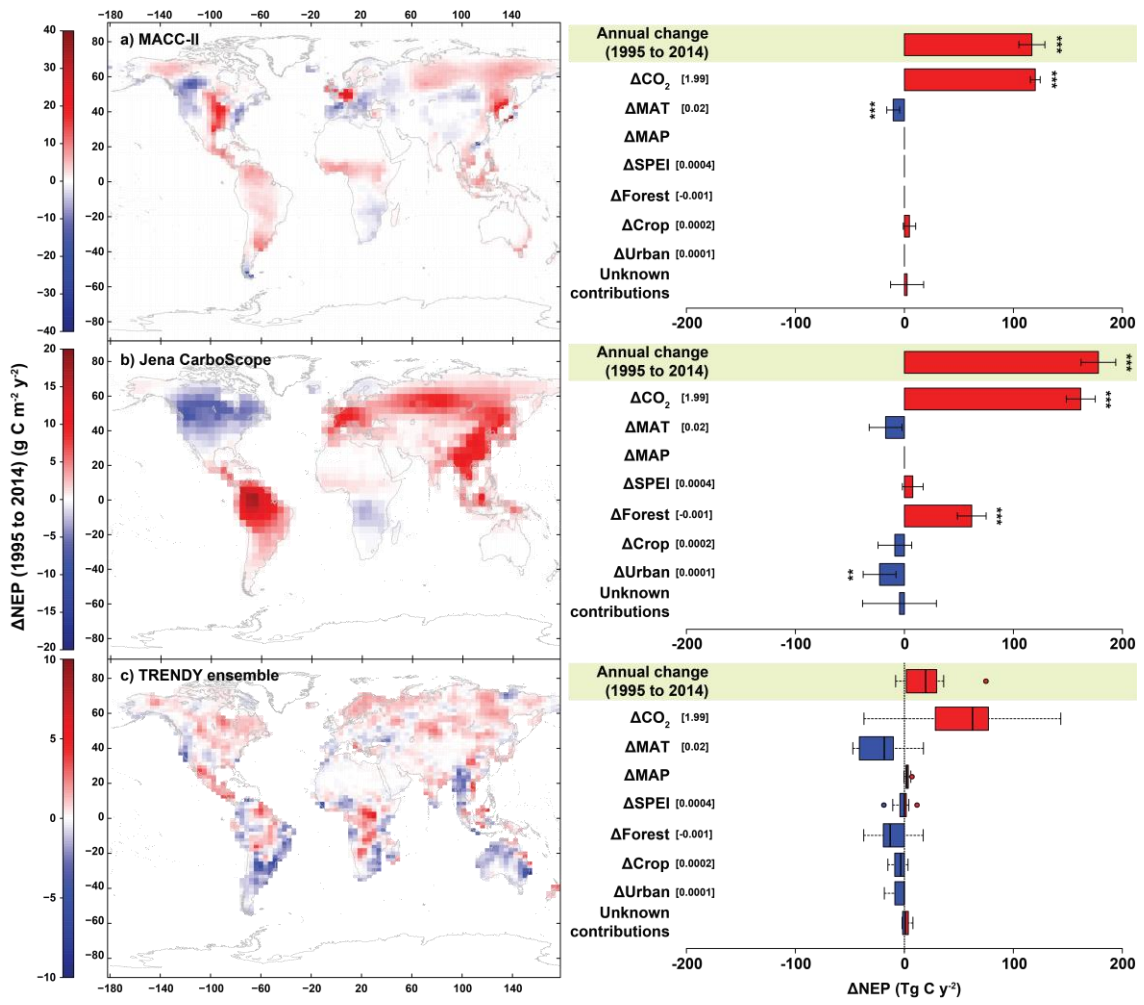
472 global estimate. NH and SH indicate Northern and Southern Hemispheres,  
473 respectively. Bold coefficients differ significantly from 0 at the 0.01 level. Empty cells  
474 indicate that anomalies in temperature were not a significant predictor in the models  
475 predicting NEP. Units are Tg C y<sup>-1</sup> for trends, Tg C y<sup>-1</sup> ppm<sup>-1</sup> for CO<sub>2</sub> and Tg C y<sup>-1</sup> C<sup>-1</sup>  
476 for temperature. Errors were calculated using the error propagation method. See the  
477 Materials and Methods section for information about the methods used to calculate the  
478 contributions.

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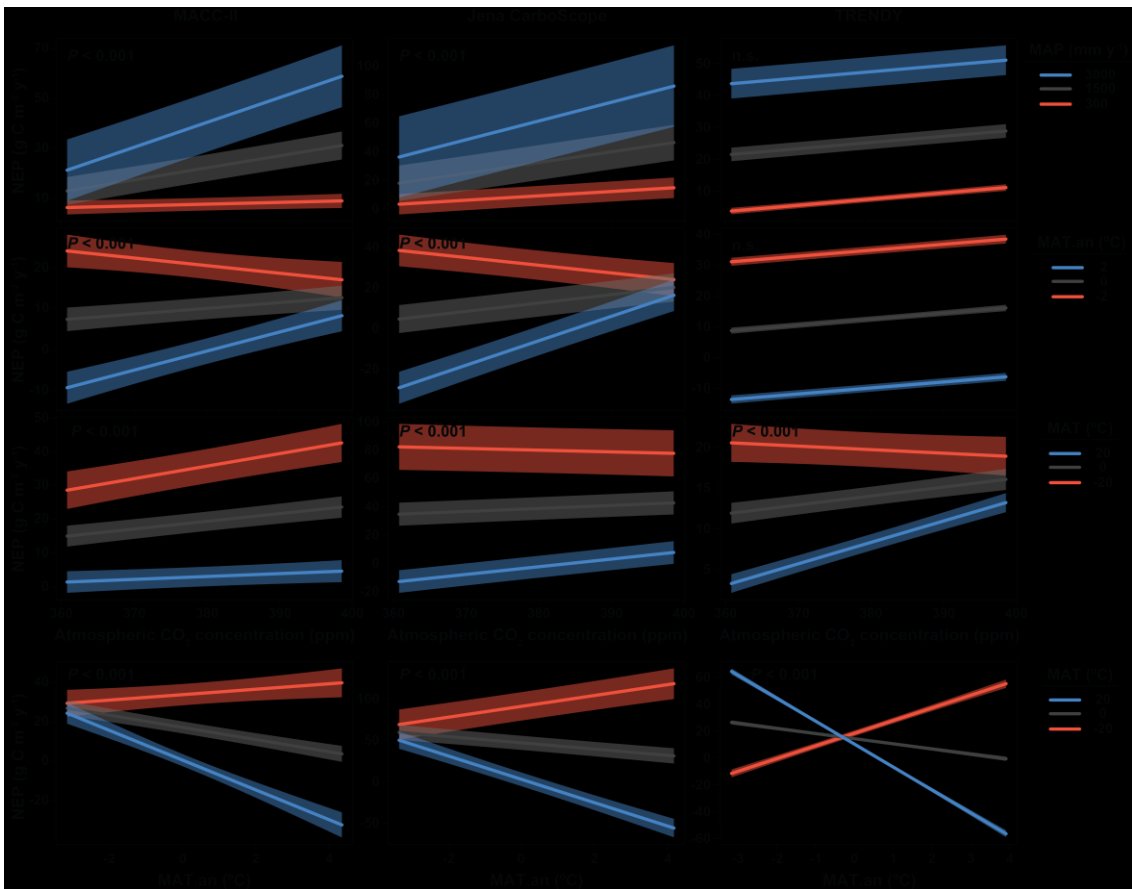
482 **Figure 1**



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485 **Figure 2**



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487

488 **Table 1**

	CO <sub>2</sub>	%	Temperature	%
<i>MACC</i>				
NH >55°	8.5 ± 0.4	14.1	-35.3 ± 24.1	6.8
NH 35-55°	14.7 ± 1.3	24.3	-132.0 ± 259.9	25.6
NH 15-35°	-5.0 ± 1.4	-8.3		
NH 15-SH 15°	31.9 ± 0.7	52.9	101.9 ± 216.6	-19.8
SH 15-35°	2.2 ± 0.9	3.7	-150.2 ± 131.3	29.1
SH 35-55°	0.6 ± 0.3	1.0	-13.4 ± 49.3	2.6
<b>Global</b>	<b>60.4 ± 1.2</b>		<b>-515.7 ± 152.4</b>	
<b>Difference</b>	<b>-7.4 ± 2.6</b>	-12.3	286.6 ± 397.4	-55.6
<i>JENA</i>				
NH >55°	-0.3 ± 1.0	-0.3	-49.8 ± 48.2	5.8
NH 35-55°	11.1 ± 3.9	13.6	-213.6 ± 558.1	24.9
NH 15-35°	26.3 ± 2.7	32.3	-268.7 ± 400.0	31.3
NH 15-SH 15°	54.2 ± 3.6	66.6	-697.6 ± 1136.5	81.2
SH 15-35°	5.4 ± 0.9	6.6	-167.0 ± 133.9	19.4
SH 35-55°	0.2 ± 0.0	0.3		
<b>Global</b>	<b>81.4 ± 3.4</b>		<b>-859.2 ± 386.3</b>	
<b>Difference</b>	15.4 ± 6.9	19.0	-537.4 ± 1390.2	62.5
<i>TRENDY</i>				
NH >55°	2.8 ± 0.1	9.0	17.3 ± 7.3	-1.6
NH 35-55°	5.8 ± 0.5	19.0	-251.1 ± 79.3	23.1
NH 15-35°	5.9 ± 0.6	19.4	-368.8 ± 51.9	33.9
NH 15-SH 15°	16.6 ± 1.1	54.2	-1612.2 ± 213.4	148.2
SH 15-35°	4.6 ± 1.2	14.9	-379.2 ± 141.1	34.9
SH 35-55°	0.3 ± 0.2	1.0	-36.8 ± 18.1	3.4
<b>Global</b>	<b>30.7 ± 1.2</b>		<b>-1088.0 ± 118.1</b>	
<b>Difference</b>	5.4 ± 2.1	17.5	-1542.7 ± 298.0	141.8

490 **Table 2**

	Trends	%	CO <sub>2</sub>	%	Cont.	Temp	%	Cont.	Other
<i>MACC</i>									
NH >55°	20.1 ± 1.2	17.2	17.0 ± 0.8	14.1	84.4	-1.2 ± 0.8	11.5	-5.9	4.3 ± 1.7
NH 35-55°	17.5 ± 5.0	15.0	29.2 ± 2.7	24.3	166.6	-1.7 ± 3.2	16.1	-9.4	-10.0 ± 6.5
NH 15-35°	14.0 ± 3.1	12.0	-9.9 ± 2.8	-8.3	-71.0			0.0	23.9 ± 4.1
NH 15- SH 15°	55.4 ± 2.7	47.4	63.5 ± 1.5	52.9	114.6	0.9 ± 1.9	-8.9	1.6	-9.0 ± 3.6
SH 15-35°	7.6 ± 1.4	6.5	4.4 ± 1.9	3.7	57.6	-2.3 ± 2.0	22.2	-29.8	5.5 ± 3.1
SH 35-55°	2.3 ± 0.6	2.0	1.2 ± 0.7	1.0	49.9	-0.3 ± 1.0	2.5	-11.2	1.4 ± 1.3
<b>Global</b>	<b>116.9 ± 6.1</b>		<b>120.1 ± 2.3</b>		<b>102.7</b>	<b>-10.3 ± 3.0</b>		<b>-8.8</b>	<b>7.1 ± 7.2</b>
<b>Difference</b>	0.0 ± 9.1	0.0	-14.8 ± 5.2	-12.3		5.8 ± 5.4	-56.6		
<i>JENA</i>									
NH >55°	13.8 ± 2.2	7.7	-0.5 ± 2.1	-0.3	-3.8	-1.7 ± 1.7	9.9	-12.4	16.0 ± 3.5
NH 35-55°	49.8 ± 5.9	28.0	22.0 ± 7.7	13.6	44.1	-2.7 ± 6.9	15.4	-5.3	30.5 ± 11.9
NH 15-35°	49.2 ± 4.0	27.6	52.3 ± 5.3	32.3	106.2	-5.0 ± 7.4	29.0	-10.2	1.9 ± 10.0
NH 15- SH 15°	80.4 ± 5.1	45.2	107.7 ± 7.1	66.6	133.9	-5.7 ± 9.2	32.9	-7.0	-21.6 ± 12.7
SH 15-35°	10.4 ± 1.3	5.8	10.7 ± 1.7	6.6	103.1	-2.8 ± 2.2	16.2	-26.9	2.5 ± 3.1
SH 35-55°	0.5 ± 0.1	0.3	0.4 ± 0.1	0.3	87.2				0.1 ± 0.1
<b>Global</b>	<b>178.0 ± 8.1</b>		<b>161.8 ± 6.8</b>		<b>90.9</b>	<b>-17.2 ± 7.7</b>		<b>-9.7</b>	<b>33.4 ± 13.1</b>
<b>Difference</b>	26.1 ± 12.2	14.7	30.7 ± 13.8	19.0		-0.6 ± 16.0	3.4		
<i>TRENDY</i>									
NH >55°	9.3 ± 0.6	41.4	5.5 ± 0.3	9.0	59.0	0.6 ± 0.2	-2.7	6.1	3.3 ± 0.7
NH 35-55°	9.4 ± 1.3	41.5	11.6 ± 0.9	19.0	124.0	-3.0 ± 0.9	13.9	-31.6	0.7 ± 1.8
NH 15-35°	3.3 ± 1.3	14.9	11.8 ± 1.1	19.4	352.9	-7.9 ± 1.0	36.9	-235.0	-0.6 ± 2.0
NH 15- SH 15°	10.1 ± 2.3	45.0	33.0 ± 2.1	54.2	326.2	-17.2 ± 1.8	80.8	-170.2	-5.7 ± 3.6
SH 15-35°	-13.7 ± 1.8	-60.9	0.5 ± 0.1	0.9	-3.8	-0.3 ± 0.1	1.6	2.5	-13.9 ± 1.8
SH 35-55°	-1.0 ± 0.4	-4.7	0.6 ± 0.5	1.0	-55.4	-0.7 ± 0.4	3.5	70.4	-0.9 ± 0.7
<b>Global</b>	<b>22.5 ± 3.1</b>		<b>61.0 ± 2.5</b>		<b>270.7</b>	<b>-21.3 ± 2.2</b>		<b>-94.7</b>	<b>-17.1 ± 4.5</b>
<b>Difference</b>	-5.2 ± 4.7	-22.9	2.1 ± 3.6	3.4		-7.3 ± 3.2	34.0		

491

492

## 493 **Methods**

### 494 Datasets

#### 495 *NEP data*

496 We used gridded global monthly NEP data for 1995–2014 from two inversion models: i)  
497 the MACC (Monitoring Atmospheric Composition and Climate) CO<sub>2</sub> ([http://www.gmes-  
498 atmosphere.eu/catalogue/](http://www.gmes-atmosphere.eu/catalogue/))<sup>25,39</sup> database, version v14r2 and ii) the Jena CarboScope  
499 database version s93\_v3.7 using a constant network of towers ([http://www.bgc-  
500 jena.mpg.de/CarboScope/](http://www.bgc-jena.mpg.de/CarboScope/))<sup>26</sup>. The MACC CO<sub>2</sub> atmospheric inversion system relies on  
501 the variational formulation of Bayes' theorem to analyse direct measurements of CO<sub>2</sub>  
502 concentrations from 130 sites around the globe for 1979-2014. Optimised fluxes were  
503 calculated at a global horizontal resolution of 3.75 × 1.875° (longitude, latitude) and a  
504 temporal resolution of eight days, separately for daytime and night-time. The underlying  
505 transport model was run with interannually varying meteorological data from the  
506 ECMWF ERA-Interim reanalysis. The Jena inversion model estimates the interannual  
507 variability of CO<sub>2</sub> fluxes based on raw CO<sub>2</sub> concentration data from 50 sites. The model  
508 uses a variational approach with the TM3 transport model (4 × 5°, using interannually  
509 varying winds). Prior terrestrial fluxes were obtained from a modelled mean biospheric  
510 pattern and fossil-fuel emissions from the EDGAR emission database<sup>40</sup>. We also used  
511 NEP data from an ensemble of 10 dynamic global vegetation models (DGVMs)  
512 compiled by the TRENDY project (version 4, models CLM4.5, ISAM, JSBACH, JULES,  
513 LPJG, LPX, OCN, ORCHIDEE, VEGAS, and VISIT) to see if results obtained from  
514 atmospheric inversions data match those obtained with DGVMs simulations<sup>41</sup>. We used  
515 the output from simulation experiment S3, which was run with varying atmospheric CO<sub>2</sub>  
516 and changing land use and climate<sup>41</sup>.

#### 517 *Meteorological, land-use change and atmospheric CO<sub>2</sub> data*

518 We extracted gridded temperature and precipitation time series from the Climatic  
519 Research Unit TS3.23 dataset<sup>42</sup>. We also used the SPEI (Standardised Precipitation-  
520 Evapotranspiration Index) drought index<sup>43</sup> from the global SPEI database  
521 (<http://SPEI.csic.es/database.html>) as a measure of drought intensity (positive values  
522 indicate wetter than average meteorological conditions, negative values indicate drier  
523 than average conditions). We used annual SPEI1 (monthly SPEI averaged over a  
524 year). Mean annual temperature (MAT) and precipitation (MAP) and SPEI were  
525 calculated for each year and pixel. We used land-use change maps from land-use  
526 harmonisation<sup>2</sup> (LUH2, <http://luh.umd.edu/data.shtml>) and calculated the percent

527 coverages of forests, croplands, and urban areas per pixel, so we could further  
528 estimate whether they increased or decreased from 1995 to 2014. We used the data  
529 for atmospheric CO<sub>2</sub> concentration from Mauna Loa Observatory provided by the  
530 Scripps Institution of Oceanography (Scripps CO<sub>2</sub> programme).

#### 531 *Data for N and S deposition*

532 Annual data for N (oxidised N [N<sub>OX</sub>] from NO<sub>3</sub><sup>-</sup> and reduced N [N<sub>RED</sub>] from NH<sub>4</sub><sup>+</sup>) and S  
533 (SO<sub>4</sub><sup>-</sup>) wet deposition were extracted from: i) the European Monitoring and Evaluation  
534 Programme (EMEP) with a spatial resolution of 0.15 × 0.15° for longitude and latitude,  
535 ii) the MSC-W chemical-transport model developed to estimate regional atmospheric  
536 dispersion and deposition of acidifying and eutrophying N and S compounds over  
537 Europe, and iii) the National Atmospheric Deposition Program (NADP) covering the  
538 USA with a spatial resolution of 0.027 × 0.027° for longitude and latitude. We used only  
539 data for wet deposition because the NADP database only contained records for dry  
540 deposition for 2000. Analyses focused on atmospheric deposition and were restricted  
541 to Europe and the USA because temporal gridded maps of atmospheric deposition  
542 were not available for other regions. Maps of atmospheric deposition for the regional  
543 analyses were adjusted to the resolution of the C-flux maps (3.75 × 1.875° for the  
544 MACC-II model and 4 × 5° for the Jena CarboScope model for longitude and latitude).

#### 545 Statistical analyses

##### 546 *Gridded, global and regional trend detection on NEP*

547 To determine how NEP has changed from 1995 to 2014, we first calculated the trends  
548 for each pixel in both inversion models and an average dataset of the TRENDY  
549 ensemble using linear regressions with an autoregressive and moving-average  
550 (ARMA) (autoregressive structure at lag p=1, and no moving average q=0) correlation  
551 structure to account for temporal autocorrelation. Trends over larger areas (e.g. the  
552 entire world, latitudinal bands), either for NEP or the predictor variables, were  
553 calculated using generalised linear mixed models (GLMMs) with random slopes,  
554 including also random intercepts<sup>44</sup> (e.g. NEP ~ year). We used pixel as the random  
555 factor (affecting the intercepts and slopes of the year), and an ARMA (p=1, q=0)  
556 correlation structure. All average trends shown were calculated using this methodology.

##### 557 *Calculation of temporal contributions on trends of NEP*

558 The temporal contributions of increasing CO<sub>2</sub>, climate (MAT, MAP, and SPEI), and  
559 land-use change (forests, croplands, and urban areas) to the observed trends in NEP



560 were assessed for the MACC-II, Jena CarboScope, and TRENDY datasets for the  
561 entire world. We repeated the analysis for five latitudinal bands to determine if the  
562 contributions of CO<sub>2</sub>, climate, and land-use change were globally consistent using  
563 MACC-II, Jena CarboScope, and the mean ensemble of the TRENDY datasets. For the  
564 MACC-II and Jena CarboScope datasets, we also determined the temporal contribution  
565 of atmospheric deposition of N (N<sub>OX</sub> and N<sub>RED</sub>) and S to the trends in NEP in a  
566 combined analysis that also included CO<sub>2</sub>, climatic, and land-use trends. This latter  
567 analysis was restricted to Europe and the USA due to the lack of atmospheric-  
568 deposition time series for the rest of the world.

569 The temporal contributions of the predictor variables were calculated following the  
570 methodology established in references<sup>5,45</sup>, as follows:

571 i) using a GLMM with an autocorrelation structure for lag 1 (AR1) and using the pixel as  
572 the random factor affecting only the intercept, we fitted full models for NEP as a  
573 function of CO<sub>2</sub>, mean MAT per pixel, annual anomaly of MAT, mean MAP per pixel,  
574 annual anomaly of MAP, the annual SPEI, and mean percentage of forested, cropped,  
575 and urban areas per pixel and their annual anomalies. We included the first-order  
576 interaction terms between CO<sub>2</sub> and all predictors and between the mean values and  
577 the anomalies for all predictors (except SPEI, which interacted with mean MAT and  
578 MAP). When the interaction term between the means and the anomalies (e.g. MAT  
579 mean × MAT anomaly) was included, the model estimated the effect of the anomaly as  
580 a function of the average value. This implies a change in the effect of increasing or  
581 decreasing the anomalies, depending on the mean for the site (e.g. increasing  
582 temperature may have a positive effect in cold climates but a negative effect in warmer  
583 climates). For models including atmospheric deposition, we also included the  
584 interaction between climatic variables and CO<sub>2</sub> and the interactions between the means  
585 and the annual anomalies of atmospheric deposition (N<sub>OX</sub>, N<sub>RED</sub>, and S). The models  
586 were fitted using maximum likelihood to allow the comparison of models with different  
587 fixed factors.

588 ii) We used the stepwise backwards-forwards model selection (*stepAIC* function in R<sup>46</sup>)  
589 from the full models, using the lowest Bayesian information criterion (BIC), to obtain the  
590 best model. The amount of the variance explained by the models was assessed using  
591 the *r.squaredGLMM* function in R (MuMIn package: <sup>47</sup>) following the method of  
592 Nakagawa and Schielzeth (2013). Model residuals met the assumptions required in all  
593 analyses (normality and homoscedasticity of residuals).

594 iii) We then used the selected models to predict the changes of the response variables  
595 during the study period (1995–2014). We first extracted the observed trend (mean  $\pm$   
596 SEM, standard error of the mean) in NEP using raw data with GLMMs with an AR1  
597 autocorrelation structure. We then calculated the trend of NEP predicted by the final  
598 model and the trends of NEP predicted by the same model while maintaining the  
599 temporally varying predictors (i.e., anomalies) constant one at a time (e.g. MAT  
600 anomalies were held constant using the median per pixel, while all other predictors  
601 changed based on the observations). The difference between the predictions for the  
602 final model and when one predictor was controlled was assumed to be the contribution  
603 of that predictor variable to the change in NEP. The differences between all individual  
604 contributions and the observed trend in NEP were treated as unknown contributions.

#### 605 *Calculation of sensitivities of NEP to temporal predictors*

606 Finally, we calculated the average sensitivities of NEP to the predictor changes by  
607 dividing the temporal contributions of each predictor of delta NEP by their temporal  
608 trends. Spatial variability on the effects of temporal predictors to NEP were assessed  
609 using the GLMMs fitted to estimate the temporal contributions of the predictors. To  
610 visualise the interactions we used the R package visreg<sup>49</sup>. All errors were calculated  
611 using the error-propagation method using the following two equations, for additions and  
612 subtractions:  $\epsilon C = \sqrt{(\epsilon A)^2 + (\epsilon B)^2}$ ; and for multiplications and divisions:  $\epsilon C =$   
613  $C \sqrt{\left(\frac{\epsilon A}{A}\right)^2 + \left(\frac{\epsilon B}{B}\right)^2}$ ; where  $\epsilon$  indicates the error associated to each value (A, B or C). To  
614 calculate global and regional estimates we multiplied the model outputs, in units of gC  
615 m<sup>-2</sup>, times land area. We considered the land Earth surface area to be 134375000 km<sup>2</sup>  
616 excluding the Antarctic region. Land area for the different latitudinal bands used were:  
617 >55° N, 23818000 km<sup>2</sup>; 35 to 55° N, 31765000 km<sup>2</sup>; 15 to 35° N, 29213000 km<sup>2</sup>; 15° S  
618 to 15° N, 29926000 km<sup>2</sup>; 15 to 35° S, 17308000 km<sup>2</sup>; and 35 to 55° S, 2345600 km<sup>2</sup>.

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#### 620 **Data availability**

621 The authors declare that the data supporting the findings of this study are publically  
622 available in the webpages provided in the article. The TRENDY simulations are  
623 available from the corresponding author upon request.

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