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# 1 **Diagnosing destabilisation risk in global land carbon sinks**

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34

35 **Summary**

36 Global net land carbon uptake, or net biome production (NBP), has increased during recent  
37 decades<sup>1</sup>. Whether its temporal variability and autocorrelation have changed during this period,  
38 however, remains elusive, even though an increase in both could indicate an increased  
39 potential for a destabilised carbon sink<sup>2,3</sup>. Here we investigate the trends and controls of net  
40 terrestrial carbon uptake and its temporal variability and autocorrelation from 1981 to 2018  
41 using two atmospheric inversion models, the amplitude of the seasonal cycle of atmospheric  
42 CO<sub>2</sub> concentration derived from nine monitoring stations distributed across the Pacific Ocean  
43 and dynamic global vegetation models. We find that annual NBP and its interdecadal variability  
44 increased globally while temporal autocorrelation decreased. We observe a separation of  
45 regions characterized by increasingly variable NBP, associated with warm regions and  
46 increasingly variable temperatures, lower and weaker trends in NBP, and regions where NBP  
47 became stronger and less variable. Plant species richness presented a concave-down  
48 parabolic spatial relationship with NBP and its variability at the global scale while nitrogen  
49 deposition generally increased NBP. Increasing temperature and its increasing variability  
50 appears as the most important drivers of declining and increasingly variable NBP. Our results  
51 show increasing variability of NBP regionally that can be mostly attributed to climate change,  
52 and that may point to destabilisation of the coupled carbon-climate system.

53 **Keywords:** carbon cycle, variability, biodiversity, climate, land-use change, early warnings

54

55 **Main**

56 Positive carbon-climate feedbacks have the potential to accelerate climate change and might  
57 compromise the attainability of ambitious climate targets such as those set by the Paris  
58 agreement<sup>4</sup>. Terrestrial ecosystems are key to the functioning of the global carbon (C) cycle  
59 and have increased their productivity and net C uptake during recent decades primarily due to  
60 CO<sub>2</sub> fertilisation and forest regrowth<sup>1,5-7</sup>. However, land-use change, nutrient limitations and  
61 increasing droughts and fires are constraining this potential to sequester C<sup>8-11</sup>. Identifying  
62 processes that might destabilise net land C uptake (or net biome production, NBP) is of  
63 paramount importance for understanding and managing the global C cycle.

64 Destabilisation is the process of losing stability: that is, when a system loses its ability to return  
65 to equilibrium following a disturbance. A symptom of this may be increased variability, as the  
66 system spirals away from its current equilibrium point towards a new one. Destabilisation of a  
67 dynamical system is usually accompanied by concomitant increases in temporal variability and  
68 autocorrelation (i.e., the correlation between consecutive time steps [AR1] also related to  
69 reduced resilience<sup>2</sup>) when AR1 is already positive, because anomalous states of the system  
70 create ripples that can get amplified through time rather than compensated as when AR1 is  
71 negative. Consequently, increasing temporal variability and autocorrelation have been shown  
72 to be potential early-warning signals for abrupt shifts in ecosystems<sup>2,3,12,13</sup>. To date, changes  
73 in NBP temporal variability and autocorrelation have not yet been investigated even though  
74 increased stress and changes in the frequency and intensity of extreme weather events are  
75 likely to alter the temporal patterns of NBP<sup>14-16</sup> due to *i*) a cumulative negative effect of extreme  
76 events on ecosystem functioning, *ii*) increasing climate variability and, *iii*) decreasing  
77 ecosystem resilience due to increased stress. We, thus, hypothesised that regions  
78 experiencing increasing trends in climate variability will also experience increasing variability  
79 in their NBP, and that increase in variability may indicate that a destabilisation of the net land  
80 C uptake is occurring. This finding could serve as an early warning signal for abrupt shifts in  
81 ecosystem's functions<sup>2</sup> that might lead to regime shifts in the Earth's biosphere<sup>17,18</sup>. Even if  
82 these changes do not occur at the global scale, increasing temporal variability and  
83 autocorrelation in several regions of the globe (e.g. Amazon basin, boreal ecosystems with  
84 permafrost) could have a profound impact on the global C balance and a knock-on effect on  
85 other ecosystem functions.

86 Climate is the primary control on NBP in terrestrial ecosystems worldwide in space and  
87 time<sup>19,20</sup>, together with soil nutrient availability<sup>10,21</sup>, atmospheric nitrogen (N) deposition, land  
88 use and management, and increasing atmospheric CO<sub>2</sub><sup>1</sup>. Generally, gross C fluxes (such as  
89 photosynthesis and respiration) are larger in the tropics where high temperature coincides with

90 sufficient precipitation to enable long growing seasons. However, net C uptake tends to be  
91 higher in temperate regions due to higher nutrient availability<sup>19,21–23</sup>. Nutrient availability and N  
92 deposition have indeed been shown to increase net land C uptake<sup>21,22</sup>. Another factor believed  
93 to be important in determining ecosystem functioning is plant biodiversity<sup>24</sup>. A large body of  
94 evidence indicates its role in promoting ecosystem productivity and stability<sup>25,26</sup>. Plant  
95 biodiversity, however, has been included far less in studies of ecosystem C cycling,  
96 presumably due to the difficulty of acquiring good data on species diversity. The few studies  
97 that included biodiversity, however, showed relatively modest correlations with C fluxes<sup>27–29</sup>.  
98 The role of biodiversity in the global terrestrial NBP has not yet been explored even though the  
99 Earth's biosphere is losing biodiversity at an unprecedented speed<sup>30</sup> and those changes are  
100 expected to alter ecosystem functioning.

101 The aim of this study was to quantify the trends in global NBP and its intradecadal temporal  
102 variability (quantified by the proportional variability index, PV<sup>31,32</sup>) and autocorrelation (AR1) to  
103 see whether changes in these variables suggest that NBP at global or regional scales is being  
104 destabilised. We further tested whether regions with increasing variability and AR1 in NBP  
105 showed differential trends in annual NBP. We additionally investigated the spatial correlation  
106 between NBP metrics and plant biodiversity (derived from a global map of plant species  
107 richness<sup>33</sup>), atmospheric total N deposition<sup>34</sup>, climate<sup>35</sup>, and land use (land-use harmonisation<sup>2</sup>  
108 maps). To realise these objectives, we used estimates of NBP derived from the two longest  
109 CO<sub>2</sub> atmospheric inversions (CAM5, CarboScope) and the amplitude of the seasonal cycle of  
110 atmospheric CO<sub>2</sub> derived from nine monitoring stations distributed from south to north of the  
111 Pacific Ocean for 1981 to 2018. We additionally compared these results with the output from  
112 an ensemble of 12 dynamic global vegetation models (TRENDY) to explore how well these  
113 state-of-the-art models predict the spatial and temporal patterns in NBP simulated by  
114 atmospheric inversion models.

## 115 **Results**

### 116 *Temporal patterns of net land C uptake*

117 Global NBP derived from atmospheric inversions increased from  $5.6 \pm 2.0 \text{ gC m}^{-2} \text{ y}^{-1}$  during  
118 1981 – 1990 (mean  $\pm$  standard error) to  $13.8 \pm 1.4 \text{ gC m}^{-2} \text{ y}^{-1}$  during 2009 – 2018 over the  
119 global land area excluding Antarctica (**Figure 1**). This represents an overall increase of 145%  
120 and an annual linear increase of  $0.24 \pm 0.08 \text{ gC m}^{-2} \text{ y}^{-2}$  ( $P < 0.001$ ). Both atmospheric inversions  
121 used (CAM5 and CarboScope) identified annual increases in NBP (**Supplementary Figure 1**  
122 and **Supplementary Figure 2**,  $0.32 \pm 0.09$ , and  $0.18 \pm 0.09 \text{ gC m}^{-2} \text{ y}^{-2}$  respectively,  $P < 0.001$ ,  
123  $N = 38$ ). The positive trend in NBP shown by inversions is similar in magnitude to the trend  
124 identified by the TRENDY ensemble ( $0.10 \pm 0.07 \text{ gC m}^{-2} \text{ y}^{-2}$ ,  $P < 0.001$ ; 147% when comparing

125 the periods 1981 – 1990 and 2009 – 2018). Both observations and models, however, showed  
126 a flattening trend during the last decade (**Figure 1c**). In parallel with the increased NBP  
127 throughout the entire study period and in agreement with previous literature<sup>36,37</sup>, the amplitude  
128 of the seasonal atmospheric CO<sub>2</sub> concentration increased by  $0.027 \pm 0.004$  ppm y<sup>-1</sup> ( $P < 0.001$ ,  
129 16.6% during the study period) (**Supplementary Figure 3a**).

130 Interannual NBP variability (NBP<sub>PV</sub>) derived from the combination of atmospheric inversions  
131 increased globally by 7.2% over the entire period ( $P < 0.001$ ) (**Figure 1f**) (CAMS 14.9%,  
132  $P < 0.001$ ; CarboScope: -1.3%,  $P < 0.001$ ). The origin of the discrepancy between the inversions  
133 remains unclear. Though the inversions differ in whether they use a growing number of  
134 measurement stations (CAMS) or a constant station set (CarboScope), the discrepancy is  
135 unlikely to be related to this because a test inversion with a growing station set in the  
136 CarboScope inversion did not yield an increase in NBP<sub>PV</sub>. Temporal variability in the amplitude  
137 of the seasonal atmospheric CO<sub>2</sub> concentration also increased (by 35%,  $P < 0.001$ ) during the  
138 study period (**Supplementary Figure 3b**). TRENDY NBP did not simulate this increase in  
139 variability, showing a negative trend of -1.7% in NBP<sub>PV</sub> similar to that from the CarboScope  
140 inversion.

141 Global NBP<sub>AR1</sub> significantly decreased over time for NBP derived from atmospheric inversions  
142 (**Figure 1i**) and for the average monthly CO<sub>2</sub> concentrations across the Pacific Ocean  
143 (**Supplementary Figure 3c**). TRENDY NBP<sub>AR1</sub>, also showed a significant negative trend  
144 representing a reduction of 2.9% over the study period. Trends of contrasting sign, however,  
145 were significant amongst atmospheric measurement stations and atmospheric inversions  
146 (CAMS: -10.0%,  $P < 0.001$ ; CarboScope: 4.7%,  $P < 0.001$ ). Several regions showed increases  
147 in the temporal autocorrelation between consecutive months (NBP<sub>AR1</sub>) derived from  
148 atmospheric inversions that are of a similar magnitude (ca. 0.2 over three decades) to those  
149 previously suggested to precede abrupt shifts in climate datasets and simulations<sup>2,3</sup>. Additional  
150 information on how changes in NBP<sub>PV</sub> and NBP<sub>AR1</sub> may affect annual NBP and their limitations  
151 can be found in Supplementary text, Section 1.

152 Our analyses identified several regions of potential concern given their concomitant increase  
153 in NBP<sub>PV</sub> and NBP<sub>AR1</sub> (**Figure 2a**), such as eastern Africa, the Mediterranean region, the west  
154 coasts of North and Central America, India, and southeast Asia. Regions with increasing  
155 NBP<sub>PV</sub> and NBP<sub>AR1</sub> had statistically lower NBP and experienced a much less pronounced  
156 increase in NBP over time ( $0.15 \pm 0.06$  gC m<sup>-2</sup> y<sup>-1</sup>,  $P < 0.001$ ) compared to regions where NBP<sub>PV</sub>  
157 and NBP<sub>AR1</sub> decreased ( $0.73 \pm 0.12$  gC m<sup>-2</sup> y<sup>-1</sup>,  $P < 0.001$ ) (**Figure 2b-d, Supplementary**  
158 **Figure 4**). Stronger increases in NBP over regions with decreasing NBP<sub>PV</sub> and NBP<sub>AR1</sub>,

159 compared to those where they increased, were also evident from both atmospheric inversions  
160 when analysed separately (**Supplementary Figure 5**).

161 Global temperature and precipitation increased during the study period (**Supplementary**  
162 **Figure 6a and d**) even though there was considerable spatial variability in those trends  
163 (**Supplementary Figure 7a and d**). Temperature and precipitation interannual variability,  
164 however, decreased significantly at the global scale, despite the reported increase in extreme  
165 weather<sup>14</sup>. Temporal autocorrelation of monthly temperature and precipitation, instead,  
166 increased slightly, albeit only significantly for temperature. A concomitant increase in temporal  
167 variability and autocorrelation of temperature was evident in several regions (e.g., Eurasia,  
168 Australia, Central America) but those were not so obvious for precipitation (**Supplementary**  
169 **Figure 8**).

#### 170 *Controls of NBP, variability and autocorrelation*

171 NBP, derived from atmospheric inversions, had a concave-down parabolic relationship with  
172 biodiversity (**Figure 3**), increasing from low to intermediate values of biodiversity and  
173 decreasing at high biodiversity (**Supplementary Figure 9a**). Our analyses also identified a  
174 significant positive interaction between biodiversity and N deposition accounting for NBP. The  
175 concave-down relationship between biodiversity and NBP included mainly positive NBP values  
176 across regions with high atmospheric N deposition ( $850 \text{ mg N m}^{-2} \text{ y}^{-1}$ ) and mainly negative  
177 NBP values at low atmospheric N deposition ( $100 \text{ mg N m}^{-2} \text{ y}^{-1}$ ) (**Supplementary Figure 9a**).  
178 Similarly, the positive correlation between N deposition and NBP was stronger in regions with  
179 higher plant biodiversity (**Supplementary Figure 9b**). Opposite relationships emerged when  
180 analysing TRENDY NBP.

181  $\text{NBP}_{\text{PV}}$  derived from inversions also showed a concave-down parabolic relationship with plant  
182 biodiversity, peaking at intermediate to high values of biodiversity (**Supplementary Figure**  
183 **9d**). We also found an interaction between plant biodiversity and N deposition in their  
184 relationship with  $\text{NBP}_{\text{PV}}$ : the relationship between  $\text{NBP}_{\text{PV}}$  and biodiversity differed between  
185 areas receiving low N deposition and areas receiving high N deposition (**Supplementary**  
186 **Figure 9d**). No relationship between N deposition and  $\text{NBP}_{\text{PV}}$  was found in regions with high  
187 biodiversity, whereas a positive relationship occurred in regions with low biodiversity  
188 (**Supplementary Figure 9e**). Interannual variability in temperature and precipitation were  
189 positively correlated with  $\text{NBP}_{\text{PV}}$  (**Figure 3**). In this case, the patterns for the TRENDY  
190 ensemble and the inversion models matched very well. Again,  $\text{NBP}_{\text{AR1}}$  derived from inversions  
191 had a concave-down parabolic relationship with biodiversity (**Supplementary Figure 9g**), but  
192 here no interaction occurred between the effects of biodiversity and N deposition, which was  
193 negatively correlated with  $\text{NBP}_{\text{AR1}}$ .  $\text{NBP}_{\text{AR1}}$  was also positively correlated with temperature



194 AR1, the only result that match those from TRENDY  $NBP_{AR1}$  (**Supplementary Figure 9i**).  
195 Results emerging from individual atmospheric inversions (CAM5 and CarboScope) mostly  
196 coincided with those reported above (**Supplementary Figure 10**).

197 Spatial variability in the trends of NBP,  $NBP_{PV}$  and  $NBP_{AR1}$  derived from atmospheric inversions  
198 were all correlated with N deposition, climate, and land use (**Figure 3** and **Supplementary**  
199 **Figure 11**). The estimated effects of land use and land use change, however, were generally  
200 lower than those from N deposition and climate, hence accounting for a smaller proportion of  
201 the change at the global scale. N deposition was positively correlated with the trends in NBP  
202 and negatively with trends in  $NBP_{PV}$  and  $NBP_{AR1}$  (**Supplementary Figure 11**). Warmer regions  
203 were more likely than colder regions to have decreasing trends in NBP, and increasing  
204 temperatures contributed to decreasing NBP (**Supplementary Figure 11b and c**). Regions  
205 with the strongest increases in  $NBP_{PV}$  were spatially associated with low increases in annual  
206 temperature (**Supplementary Figure 11e**). Increases in  $NBP_{PV}$  were also found to be more  
207 likely in regions showing increases in temperature temporal variability (**Supplementary Figure**  
208 **11f**). Increasing  $NBP_{AR1}$  was more likely in regions with increasing temperatures  
209 (**Supplementary Figure 11h**) and mildly with increasing temporal autocorrelation of  
210 precipitation (**Figure 3**). Our analyses using TRENDY reproduced the abovementioned  
211 findings well for trends in NBP and  $NBP_{AR1}$ , but not for  $NBP_{PV}$ . Again, results from individual  
212 atmospheric inversions were very similar to those reported here (**Supplementary Figure 10**).  
213 Warm regions presenting a concomitant increase in temperature temporal variability and  
214 autocorrelation (symptoms of destabilisation) were more likely to be correlated with similar  
215 changes in NBP variability and AR1, and those results were well supported by both  
216 atmospheric inversions and their combination (**Supplementary Figure 12**). Additionally,  
217 regions with higher N deposition, larger proportions of forested areas and lower crops were  
218 related to concomitantly decreasing  $NBP_{PV}$  and  $NBP_{AR1}$ .

### 219 *Biodiversity, N deposition and net C uptake*

220 NBP derived from atmospheric inversions provided correlational evidence indicating that plant  
221 biodiversity may be playing an important role in regulating regional variation in the land C  
222 balance and in its temporal variability. TRENDY models, instead, do not include biodiversity in  
223 their parameterisation and, hence, any spurious relationship is necessarily driven by factors  
224 other than biodiversity. The spatial relationship between biodiversity and NBP clearly differed  
225 between atmospheric inversions and TRENDY (**Supplementary Figure 9a**), hence  
226 suggesting that the reported effect of biodiversity when analysing atmospheric inversions may  
227 emerge due to a mechanistic effect. The emerging relationship between biodiversity and  
228  $NBP_{PV}$  derived from atmospheric inversions, however, was very similar to the one emerging

229 from TRENDY, which suggests that factors other than biodiversity may be driving this  
230 relationship. The positive relationship between biodiversity and  $\text{NBP}_{\text{AR1}}$  found here has never  
231 been reported before and further research is needed to understand the mechanisms behind  
232 this relationship.

233 The concave-down parabolic relationships of biodiversity with NBP and  $\text{NBP}_{\text{PV}}$  differ from the  
234 majority of biodiversity-productivity and stability relationships reported in the literature: positive  
235 asymptotic for productivity and negative for variability<sup>38,39</sup>. This difference in the biodiversity-  
236 NBP relationship may result from two opposing ecosystem processes, photosynthesis and  
237 respiration, because both are likely to be enhanced by biodiversity<sup>27,40,41</sup>. The concave-down  
238 relationship would then suggest that the positive effect of biodiversity on respiration  
239 overshadows the positive effect of photosynthesis in regions with high biodiversity. However,  
240 our biodiversity data, like in similar studies<sup>39</sup>, was restricted to species richness and did not  
241 include information on species abundance, their individual contribution to NBP, or traits to allow  
242 the calculation of actual species diversity or functional diversity, often better indicators of  
243 ecosystem functioning than species richness<sup>42</sup>. Unfortunately, this information is not available  
244 at the global scale. Including actual diversity in future analyses could lead to different results  
245 to those reported here. Additionally, future efforts are needed to understand how biodiversity  
246 loss, not included here, will impact global carbon balance.

247 Interestingly, our analyses indicated that the effect of biodiversity on NBP depended on  
248 atmospheric N deposition, and vice versa (**Figure 3**). The effect of atmospheric N deposition  
249 on NBP was mainly positive but was stronger in regions with higher biodiversity, further  
250 supporting the premise that biodiversity promotes ecosystem functions such as N uptake<sup>43</sup>.  
251 Regions with higher N deposition also had larger increases in NBP over time (**Supplementary**  
252 **Figure 11a**), supporting previous findings suggesting a stronger  $\text{CO}_2$  fertilisation effect in  
253 regions with higher N deposition<sup>1</sup>. On the other hand, N deposition was negatively related to  
254 trends in  $\text{NBP}_{\text{PV}}$ ,  $\text{NBP}_{\text{AR1}}$  and the aggregated trend of  $\text{NBP}_{\text{PV-AR1}}$  (**Supplementary Figure 12**),  
255 which suggests that N addition may ameliorate nutrient imbalances derived from increasing  
256 atmospheric  $\text{CO}_2$  concentrations<sup>8</sup> and prevent ecosystem functioning from becoming more  
257 variable.

### 258 *Climate and changing land C uptake*

259 Our results clearly indicate that NBP decreased in regions with warm climates and where  
260 warming has been most pronounced (**Supplementary Figure 11**). These findings support  
261 results from previous studies<sup>1</sup> and further suggests that increasing droughts and heat waves  
262 limit C sequestration by terrestrial ecosystems<sup>44</sup>. Our analyses revealed that higher  $\text{NBP}_{\text{PV}}$ ,  
263  $\text{NBP}_{\text{AR1}}$  and their trends were associated, respectively, with climates showing higher and

264 increasing temporal variability and autocorrelation (**Supplementary Figure 9**). We also found  
265 that concomitantly increasing trends in  $\text{NBP}_{\text{PV-AR1}}$  were positively related to increasing  
266 temperature variability and autocorrelation (**Supplementary Figure 12**). These results support  
267 our initial hypothesis stating that climate change may be the main contributing factor for  
268 changing the temporal behaviour of land C sinks.

### 269 *Implications of altered land C sinks*

270 Compelling evidence from atmospheric inversions (**Figure 1**) and the annual amplitude of the  
271 seasonal  $\text{CO}_2$  cycle (**Supplementary Figure 3**) suggests that global net land C uptake is now  
272 larger and, most likely, more variable than three decades ago, while its temporal  
273 autocorrelation ( $\text{NBP}_{\text{AR1}}$ ), instead, has significantly decreased. The increase in global NBP and  
274 the reduction in  $\text{NBP}_{\text{AR1}}$  were well identified by TRENDY NBP, including the evidence of a  
275 flattening trend in NBP during the last two decades. Our results for the increase in global NBP  
276 and a potential recent saturation are consistent with previous findings of increases in global  
277 productivity and NBP and a recent decline of the  $\text{CO}_2$  fertilisation effect<sup>1,5,8,20</sup>. Even though the  
278 main emerging spatial controls for CAMS and CarboScope atmospheric inversions in NBP  
279 were in agreement (**Figures S8 and S10**), trends at the global scale for  $\text{NBP}_{\text{PV}}$  and  $\text{NBP}_{\text{AR1}}$   
280 were significantly different (**Supplementary Figure 13**), which calls for caution in the  
281 interpretation of these results due to their uncertainty.

282 We observed a bifurcation of regions characterised by concomitant increases and decreases  
283 in  $\text{NBP}_{\text{PV}}$  and  $\text{NBP}_{\text{AR1}}$  (**Figure 2**). This bifurcation relates to differences in their mean annual  
284 temperature, their increase in annual temperature, their average N deposition loads and their  
285 percentage of forests and crops (**Supplementary Figure 12**). The observed increase in the  
286 variability and autocorrelation of net C uptake in several regions of the planet (**Figure 2a**) is  
287 concerning because of the implications it can have on the stability of their ecosystems. First,  
288 increasing  $\text{NBP}_{\text{PV}}$  and  $\text{NBP}_{\text{AR1}}$  is indicative of increasing variability and reducing resilience<sup>3,45</sup>  
289 potentially in many ecosystem processes: from photosynthesis and respiration<sup>27</sup> to cascading  
290 effects on animals and decomposers<sup>46</sup>. Second, an increase in variability in NBP implies that  
291 ecosystem C balance is less predictable over time, which is troublesome for projections of  
292 future climate change. Third, regions showing a combined increase in  $\text{NBP}_{\text{PV}}$  and  $\text{NBP}_{\text{AR1}}$  had  
293 a consistently lower NBP and lower increases in NBP than regions where  $\text{NBP}_{\text{PV}}$  and  $\text{NBP}_{\text{AR1}}$   
294 decreased (**Figure 2b-d**), suggesting that these increases  $\text{NBP}_{\text{PV}}$  and  $\text{NBP}_{\text{AR1}}$  reflect  
295 dynamical instability in the carbon system rather than some other cause (such as changes in  
296 the external forcing of the system). This destabilization may jeopardise future C sequestration.  
297 Our analyses, however, could not determine the mechanisms driving the observed changes in  
298  $\text{NBP}_{\text{PV}}$  and  $\text{NBP}_{\text{AR1}}$ . More importantly, we could not determine whether the observed increases

299 NBP<sub>PV</sub> and NBP<sub>AR1</sub> truly reflect dynamical instability in the carbon system, as opposed to some  
300 other cause, such as changes in the external forcing of the system (e.g., increasing CO<sub>2</sub>  
301 emissions, N deposition). Hence, regions showing increased variability and autocorrelation  
302 should be monitored in detail to properly understand the mechanisms and consequences  
303 behind these changes given that increasing variability and autocorrelation have been shown  
304 to act as early warning signals preceding abrupt phase transitions in simulations of ecosystem  
305 functioning<sup>2,3</sup>. The increase of NBP<sub>PV</sub> and NBP<sub>AR1</sub> in several regions should serve as an early  
306 warning signal of potential future changes that the Earth's biosphere may be facing. Given the  
307 main role of climate change as a driver of these changes in their temporal behaviour, mitigating  
308 climate change is needed to prevent further unforeseen changes in land C sinks.

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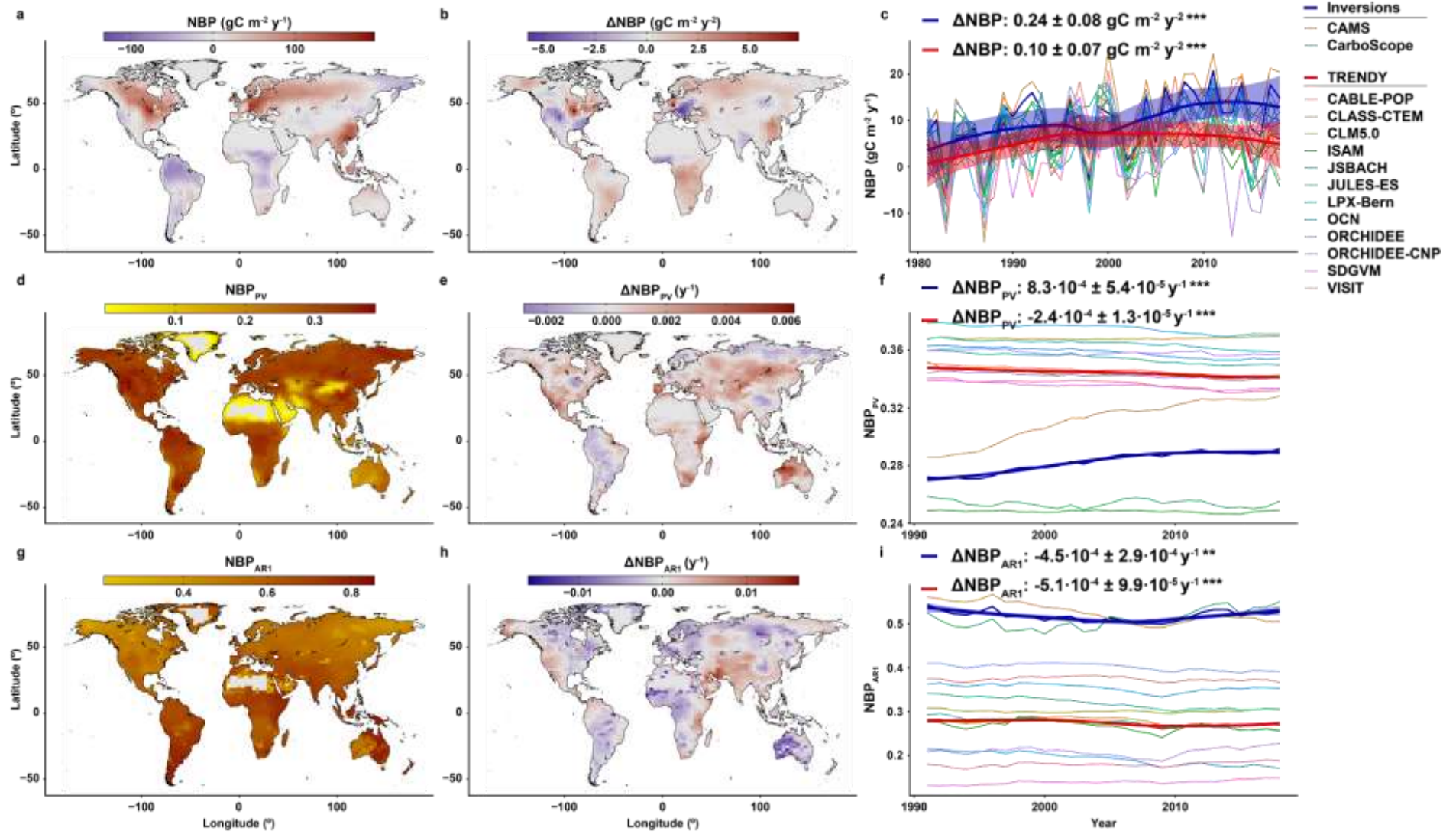
413

414 **Figure 1: Global distribution of net biome production (NBP), its interannual variability**  
415 **( $NBP_{PV}$ ) and temporal autocorrelation ( $NBP_{AR1}$ ), and their trends from 1981 to 2018.** Panel  
416 a shows the average global distribution of NBP (positive values indicate C sinks) derived from  
417 CAMS and CarboScope atmospheric inversions. Panel b shows the temporal trends in NBP  
418 ( $\Delta NBP$ ), and panel c shows the temporal change in NBP derived from atmospheric inversions  
419 and 12 DGVMs (TRENDY). Panels d, e, and f, and g, h, and i mimic panels a, b, and c,  
420 respectively, for interannual variability of NBP ( $NBP_{PV}$ ) and temporal autocorrelation ( $NBP_{AR1}$ )  
421 calculated over an 11-year moving window. Thick lines in panels c, f, and i represent smooth  
422 trends estimated with a local regression (shaded areas show the standard error of the trend),  
423 and the coefficients at the top of the panels indicate robust Theil-Sen's slopes ( $\pm$  standard error  
424 of the slope) with their corresponding p-values, estimated using the non-parametric Wilcoxon  
425 Mann-Whitney rank sum test. Values in panels c, f and i, represent spatially-weighted global  
426 means. \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ . Data to reproduce this figure can be found in Source Data  
427 1.

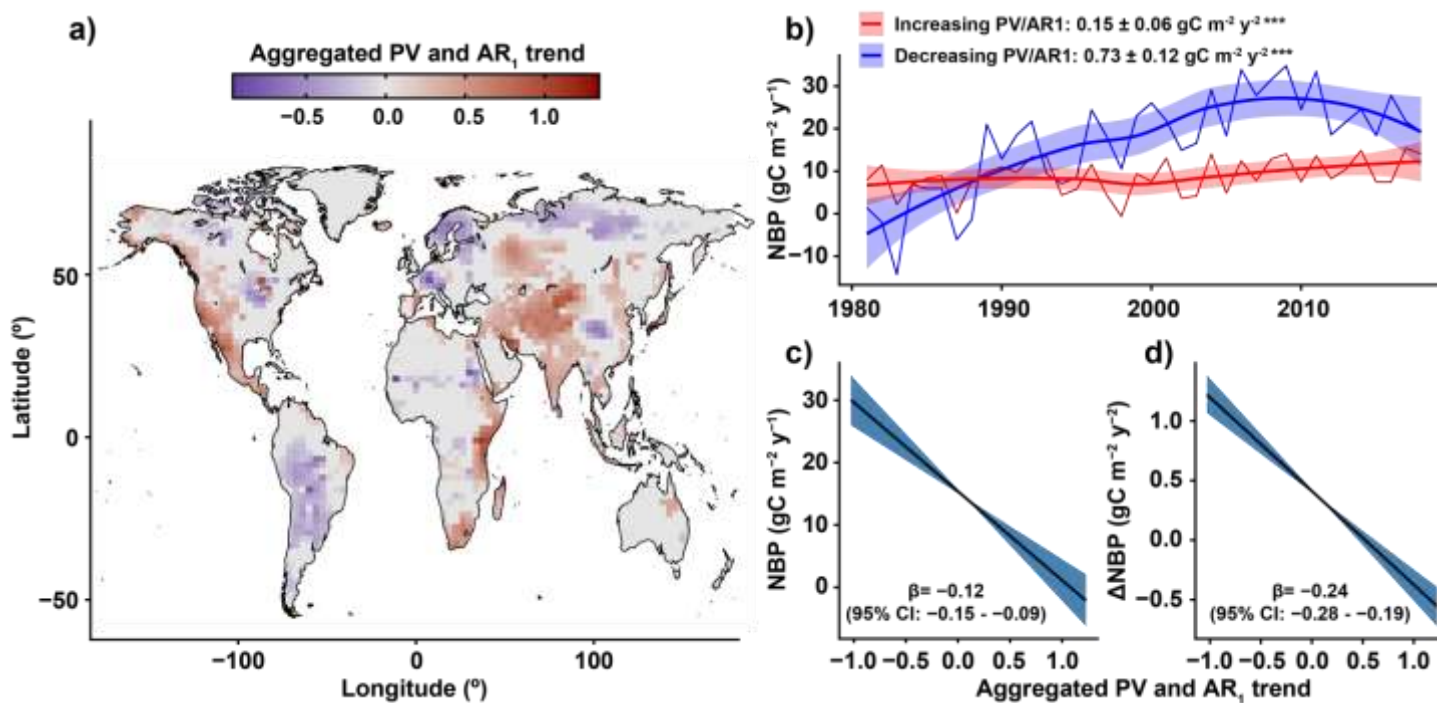
428 (See **Figure 1** on the following page)

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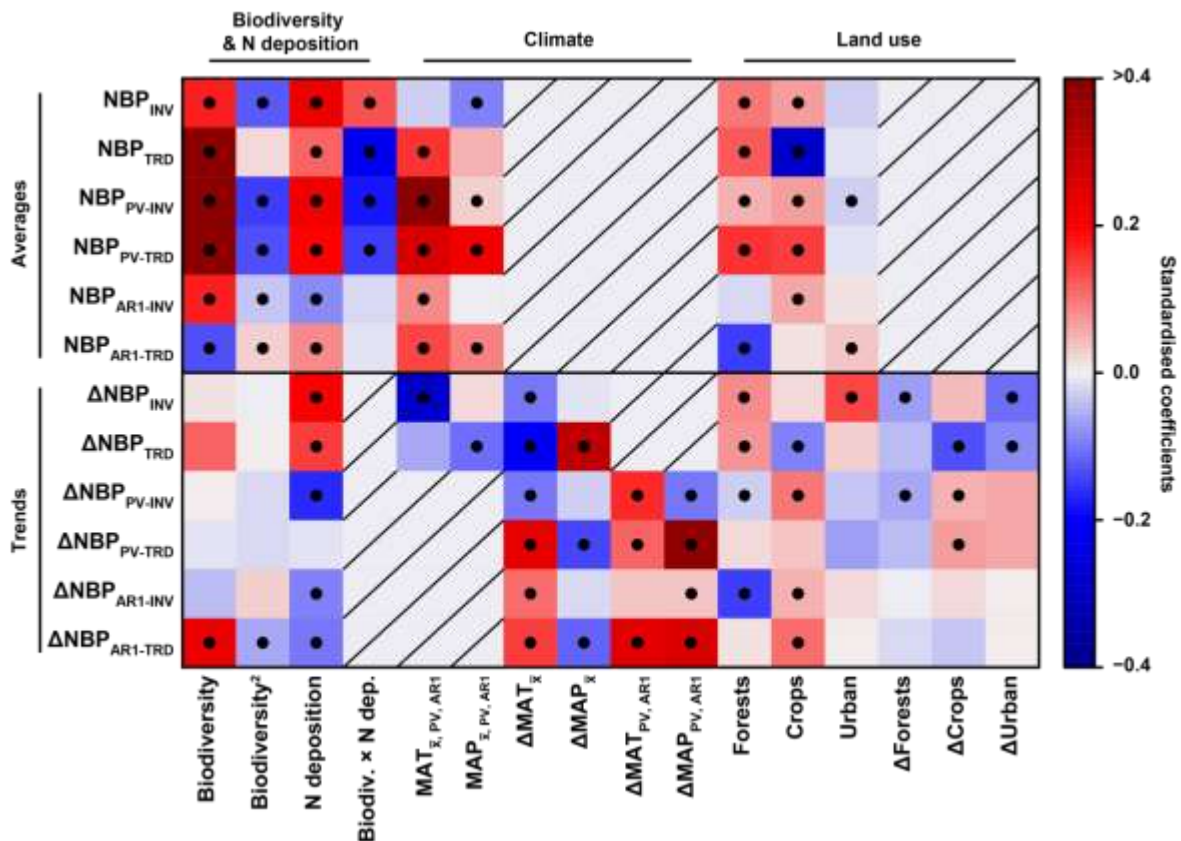




432 **Figure 2: Regions with concomitantly increasing  $\text{NBP}_{\text{PV}}$  and  $\text{NBP}_{\text{AR1}}$  present lower NBP and a lower increase of NBP over time.** Panel a  
 433 shows regions of the world where concomitant increases (red) and decreases (blue) in  $\text{NBP}_{\text{PV}}$  and  $\text{NBP}_{\text{AR1}}$  have occurred during the study period.  
 434 Regions with contrasting trends in  $\text{NBP}_{\text{PV}}$  and  $\text{NBP}_{\text{AR1}}$  appear in grey. Panel b shows the aggregated annual mean NBP of regions with increasing  
 435 (red) and decreasing (blue)  $\text{NBP}_{\text{PV}}$  and  $\text{NBP}_{\text{AR1}}$  (see **Supplementary Figure 4** for information on their global contribution). Smooth trends were  
 436 estimated with a local regression (shaded indicate the standard error of the trend), and the coefficients at the top of the panel indicate robust  
 437 Theil-Sen's slopes ( $\pm$  standard error of the slope) and their associated significance (\*\*\*,  $P < 0.001$ ), estimated using the non-parametric Wilcoxon  
 438 Mann-Whitney rank sum test. Panel c and d show the spatial relationship of NBP and trends in NBP ( $\Delta\text{NBP}$ ) with the aggregated trend of  $\text{NBP}_{\text{PV}}$   
 439 and  $\text{NBP}_{\text{AR1}}$ . Coefficients are standardised and include the 95% credible intervals (CI). See **Methods** for details on how the aggregated trend of  
 440  $\text{NBP}_{\text{PV}}$  and  $\text{NBP}_{\text{AR1}}$  was calculated. Data to reproduce this figure can be found in Source Data 2.



442 **Figure 3: Contribution of biodiversity, N deposition, climate, and land use to the**  
 443 **global terrestrial C balance (NBP), its interannual variability (NBP<sub>PV</sub>), its temporal**  
 444 **autocorrelation (NBP<sub>AR1</sub>), and their trends.** The colour scale indicates the strength of the  
 445 relationship (standardised  $\beta$  coefficients) between each predictor (bottom) and the response  
 446 variable (left). Black dots indicate that 95% of the posterior distributions differed from 0.  
 447 Biodiversity was fitted as a second-order polynomial to account for nonlinearities  
 448 (biodiversity + biodiversity<sup>2</sup>; the second term indicates the change in the slope in biodiversity  
 449 as biodiversity increases). Hashed areas indicate relationships not included in the  
 450 regression models. See **Methods** for further information on model fitting. INV and TRD  
 451 indicate the averages for all atmospheric inversions (2) and DGVMs (12), respectively.  
 452 Predictors MAT $\bar{x}$ , PV, AR1 and MAP $\bar{x}$ , PV, AR1 indicate mean, PV, or AR1 metrics of MAT and  
 453 MAP matching the metric of the response variable (e.g. NBP<sub>INV</sub> ~ MAT $\bar{x}$ ; NBP<sub>PV-INV</sub> ~  
 454 MAT<sub>PV</sub>). The same applies for  $\Delta$ MAT<sub>PV</sub>,  $\Delta$ MAT<sub>AR1</sub>,  $\Delta$ MAP<sub>PV</sub>,  $\Delta$ MAP<sub>AR1</sub>. MAT, mean annual  
 455 temperature; MAP, mean annual precipitation; PV, proportional variability; AR1, temporal  
 456 autocorrelation with previous month;  $\Delta$ , trend in a given variable.



457

458

## 459 **Methods**

### 460 Data sets

#### 461 *NBP and atmospheric CO<sub>2</sub> data*

462 We obtained the global NBP data for 1981–2018 from the two atmospheric-inversion  
463 models that provided the longest time series: i) the CAMS Greenhouse Gases Flux  
464 Inversions ([https://ads.atmosphere.copernicus.eu/cdsapp#!/dataset/cams-global-](https://ads.atmosphere.copernicus.eu/cdsapp#!/dataset/cams-global-greenhouse-gas-inversion)  
465 [greenhouse-gas-inversion](https://ads.atmosphere.copernicus.eu/cdsapp#!/dataset/cams-global-greenhouse-gas-inversion))<sup>47,48</sup> version v18r3, and ii) the Jena CarboScope database  
466 version s81oc\_v2020 using a constant network of measurement stations ([http://www.bgc-](http://www.bgc-jena.mpg.de/CarboScope/)  
467 [jena.mpg.de/CarboScope/](http://www.bgc-jena.mpg.de/CarboScope/))<sup>49,50</sup>. We also used NBP data from an ensemble of 12 dynamic  
468 global vegetation models (DGVMs) run with varying concentrations of atmospheric CO<sub>2</sub> and  
469 changing land uses and climates. Models compiled by the TRENDY project (version 8,  
470 models CABLE-POP, CLASS-CTEM, CLM5.0, ISAM, JSBACH, JULES-ES, LPX-BERN,  
471 OCN, ORCHIDEE, ORCHIDEE-CNP, SDGVM and VISIT) were used to test whether the  
472 DGVMs also identified the patterns from atmospheric inversions<sup>51</sup>. Even though previous  
473 studies indicate that DGVMs explain trends in NBP adequately, we are the first to test  
474 whether their emerging trends in NBP temporal variability and autocorrelation also match  
475 those from local observations or atmospheric inversions. We used model results from the  
476 simulation experiment S3, which was run with changing atmospheric CO<sub>2</sub>, land use and  
477 climate (see <https://blogs.exeter.ac.uk/trendy/protocol/> for more details). We used monthly  
478 NBP estimates as the basis for all calculations in this study. We rescaled all atmospheric  
479 inversions, the TRENDY model outputs, and the predictors to the same spatial resolution  
480 of the coarsest data set for fitting the statistical models (see section below) (i.e. CAMS: 3.75  
481 × 1.875°).

482 We calculated average annual NBP per pixel, its temporal variability expressed as the  
483 proportional variability index (NBP<sub>PV</sub>)<sup>31,32</sup>, and its monthly temporal autocorrelation at lag 1  
484 (NBP<sub>AR1</sub>) for all of the abovementioned datasets. All three indices (NBP, NBP<sub>PV</sub> and NBP<sub>AR1</sub>)  
485 were calculated as the average for the entire period. The PV index is calculated as the  
486 mean proportional variability amongst all possible combinations of values in a time series,  
487 following:  $PV = \frac{2 \sum m}{n(n-1)}$ , where “*n*” indicates the length of the variable, where “*m*” is  
488 calculated as:  $m = 1 - \frac{\min(z_i, z_j)}{\max(z_i, z_j)}$ , and where “*z*” represent the individual values from which  
489 to calculate all the pairwise comparisons between the observations of the time series (e.g.,  
490 observation *z<sub>i</sub>* vs observation *z<sub>j</sub>*). When negative values occurred in a time series, we added  
491 a constant to the entire time series equivalent to the minimum absolute value plus one.

492 Unlike other metrics of temporal variability, the PV index provides estimates of temporal  
493 variability that are independent of the mean of the time series and that have been proven  
494 to be robust even when comparing non-normally distributed data sets, thereby overcoming  
495 the mathematical drawbacks of similar variability indices such as the standard deviation or  
496 the coefficient of variation<sup>52</sup>.  $NBP_{PV}$  per pixel was estimated as the average of the  
497 interannual variabilities of all months (e.g.  $NBP_{PV} = \frac{NBP_{PV\ January} + [...] + NBP_{PV\ December}}{12}$ ). By  
498 using this method,  $NBP_{PV}$  reflects not only the interannual variability of the annual NBP, but  
499 also the variation occurring amongst equal months across the years. Using this method, a  
500 year with average NBP yet with anomalously low NBP in one period offset by anomalously  
501 high NBP in another, would thus result in high interannual variability rather than low  
502 interannual variability. AR1 was estimated using the residuals of generalised additive  
503 models (GAM) used to remove the trend and seasonal cycle of the data. In these models  
504 response variable was monthly NBP and the predictors were the month of the year (i.e. a  
505 factor of 12 levels) and the year, the latter included as a spline smoothed term to account  
506 for nonlinear trends over time (**Supplementary Figure 14**). We used the *mgcv* R package  
507 to fit the GAM models<sup>53</sup>. An 11-year moving average from  $NBP_{PV}$  and  $NBP_{AR1}$  per pixel was  
508 then calculated for all data sets to investigate trends in interannual variability and temporal  
509 autocorrelation. Our sensitivity analysis that showed that our results were consistent despite  
510 the selection of different window lengths (7, 11 and 15 years, **Supplementary Figure 13**,  
511 **Supplementary Table 1**). Robust Theil-Sen's trends<sup>54</sup> were then calculated for NBP,  
512  $NBP_{PV}$  and  $NBP_{AR1}$  ( $\Delta NBP$ ,  $\Delta NBP_{PV}$ , and  $\Delta NBP_{AR1}$ ) per pixel using the *mbim* function in R<sup>55</sup>.  
513 Wilcoxon rank sum tests were performed to test the significance of the Theil-Sen's trends.  
514 Even though we present results for both atmospheric inversions (CAM5, CarboScope), we  
515 combined their results into one fusion dataset in order to further highlight those results for  
516 which both inversion models agreed (**Supplementary Figure 10 and Supplementary**  
517 **Figure 12**). The combination was performed by calculating the average value of each of the  
518 abovementioned variables per pixel. We followed the same approach to provide a TRENDY  
519 dataset combining all simulations following similar studies<sup>1</sup>.

520 Trends in average global NBP,  $NBP_{PV}$ , and  $NBP_{AR1}$  (from 1981 to 2018 for NBP, from 1991  
521 to 2018 for  $NBP_{PV}$ , and  $NBP_{AR1}$ ) were also estimated using the Theil-Sen's approach. We  
522 also combined both atmospheric inversions and the TRENDY simulations to provide the  
523 average results derived from atmospheric inversions and process-based models. In this  
524 case, the combination of products was performed by calculating the average between  
525 products per year and then estimating the temporal trends. We additionally calculated an  
526 aggregated metric of trends in  $NBP_{PV}$  and  $NBP_{AR1}$ . To do so, we first calculated the ratio  
527 between each value and the maximum absolute value of each of the variables ( $\Delta NBP_{PV}$  and



528  $\Delta\text{NBP}_{\text{AR1}}$ ) and then we combined them by summing their relative values per pixel. Next, we  
529 selected those pixels in which both,  $\Delta\text{NBP}_{\text{PV}}$  and  $\Delta\text{NBP}_{\text{AR1}}$ , showed a positive trend and  
530 those that showed a negative trend, and investigated their respective trends in NBP in the  
531 same way that we proceeded for global NBP.

532 Results obtained from the atmospheric inversions were compared with those from nine  
533 stations monitoring atmospheric  $\text{CO}_2$  concentrations distributed from north to south of the  
534 Pacific Ocean that comprised the full period of this study. We selected this subset of  
535 monitoring stations to minimise the influence of anthropogenic emissions in the signal of  
536 atmospheric  $\text{CO}_2$  concentration. These data were downloaded from the Scripps  $\text{CO}_2$   
537 programme: [https://scrippsco2.ucsd.edu/data/atmospheric\\_co2/](https://scrippsco2.ucsd.edu/data/atmospheric_co2/)<sup>56</sup>. We calculated the  
538 annual amplitude in  $\text{CO}_2$  concentration (maximum minus minimum) using monthly data  
539 following<sup>20,36</sup> as a proxy of the net global C uptake capacity. An 11-year moving average  
540 was then used to determine whether the annual amplitude of  $\text{CO}_2$  concentrations, its  
541 interannual variability (PV), and the monthly temporal autocorrelation (AR1) of  $\text{CO}_2$   
542 concentrations changed between 1981 and 2018. Theil-Sen slopes were also used to  
543 calculate trends in  $\text{CO}_2$  amplitude, its interannual variability, and their monthly temporal  
544 autocorrelation.

#### 545 *Drivers of NBP*

546 We used temperature and precipitation data from the Climatic Research Unit TS4.03 data  
547 set<sup>35</sup> to calculate mean annual temperature (MAT), mean annual precipitation (MAP), their  
548 temporal variabilities ( $\text{MAT}_{\text{PV}}$  and  $\text{MAP}_{\text{PV}}$ , average of interannual monthly temporal  
549 variability), their monthly temporal autocorrelations ( $\text{MAT}_{\text{AR1}}$  and  $\text{MAP}_{\text{AR1}}$ ), as well as the  
550 temporal trends of all these metrics ( $\Delta\text{MAT}$ ,  $\Delta\text{MAP}$ ,  $\Delta\text{MAT}_{\text{PV}}$ ,  $\Delta\text{MAP}_{\text{PV}}$ ,  $\Delta\text{MAT}_{\text{AR1}}$ , and  
551  $\Delta\text{MAP}_{\text{AR1}}$ ) for each pixel following the same procedure established for NBP (see above). In  
552 order to investigate the controls of the spatial variability in aggregated trends in  $\text{NBP}_{\text{PV-AR1}}$ ,  
553 we also calculated the aggregated indices for  $\Delta\text{MAT}_{\text{PV-AR1}}$  and  $\Delta\text{MAP}_{\text{PV-AR1}}$  following the  
554 same methodology used for NBP (see above). Land-use changes were extracted from land-  
555 use harmonisation<sup>2</sup> maps (LUH2, <http://luh.umd.edu/data.shtml>). We calculated the percent  
556 coverages of forests, croplands, and urban areas per pixel, and the change in these  
557 percentages between 1981 and 2015. We calculated mean total atmospheric N deposition  
558 per pixel derived from<sup>34</sup>, covering the study period. Biodiversity data were extracted from  
559 an interpolated gridded global map of vascular plant biodiversity<sup>33</sup>, providing one datum per  
560 pixel including information on the current number of vascular plant species. We could not  
561 include the effects of biodiversity loss in our analyses because global gridded time series  
562 of plant biodiversity are not available.

563 Statistical analyses

564 We determined how NBP, NBP<sub>PV</sub>, NBP<sub>AR1</sub>, and their trends ( $\Delta$ NBP,  $\Delta$ NBP<sub>PV</sub>,  $\Delta$ NBP<sub>AR1</sub> and  
565 the combined  $\Delta$ NBP<sub>PV-AR1</sub>) were spatially correlated with their drivers using spatial  
566 generalised linear mixed models with a Leroux conditional autoregressive prior<sup>57</sup> and the  
567 *S.CARleroux* function in the *CARBayes* R package<sup>58</sup>. All response variables had one datum  
568 per pixel, representing aggregated information over the entire study period (e.g., NBP  
569 indicates mean annual NBP from 1981 to 2018). Models predicting spatial variability in NBP,  
570 NBP<sub>PV</sub>, and NBP<sub>AR1</sub> included biodiversity as a second-order polynomial function to account  
571 for the nonlinearities usually found between biodiversity and productivity<sup>59</sup> (biodiversity +  
572 biodiversity<sup>2</sup>), mean atmospheric N deposition, the interaction between biodiversity and N  
573 deposition, and the percentages of the area covered by forests and agricultural and urban  
574 areas as predictors. MAT and MAP were also included for NBP models, MAT<sub>PV</sub>, MAP<sub>PV</sub> for  
575 NBP<sub>PV</sub> models, and MAT<sub>AR1</sub>, MAP<sub>AR1</sub> for NBP<sub>AR1</sub> models. We built an additional model  
576 including the interaction between biodiversity and mean and variability in climate  
577 (biodiversity:MAT + biodiversity:MAP + biodiversity:MAT<sub>PV</sub> + biodiversity:MAP<sub>PV</sub>) and the  
578 interactions MAT:MAP and MAT<sub>PV</sub>:MAP<sub>PV</sub> to further test that the relationship between NBP  
579 and biodiversity was not spuriously emerging due to its relationship with climate  
580 (Supplementary information – Model summaries, section 8). As indicated by our results, our  
581 analyses were able to successfully discern the effect of biodiversity from that of climate  
582 (**Figure 3**). The fact that the relationship between mean NBP and biodiversity emerging  
583 from inversions and the TRENDY ensemble (with no parameterisation for biodiversity) were  
584 substantially different increases the likelihood of this relationship not being spurious. Models  
585 predicting  $\Delta$ NBP also included the trends in MAT, MAP and the trends in land-use change  
586 as predictors. Similarly, models predicting  $\Delta$ NBP<sub>PV</sub> and  $\Delta$ NBP<sub>AR1</sub> included trends in  
587 temperature and precipitation ( $\Delta$ MAT and  $\Delta$ MAP) and their temporal variability ( $\Delta$ MAT<sub>PV</sub>,  
588  $\Delta$ MAP<sub>PV</sub>) or autocorrelation ( $\Delta$ MAT<sub>AR1</sub>,  $\Delta$ MAP<sub>AR1</sub>) and trends in land-use changes, but not  
589 average MAT or MAP or their temporal variability or autocorrelation. Models predicting the  
590 combined trends of  $\Delta$ NBP<sub>PV-AR1</sub> included a second-order biodiversity as a second-order  
591 polynomial, N deposition, average and trends in climate, the aggregated trends of MAT<sub>PV-  
592 AR1</sub> and MAP<sub>PV-AR1</sub>, average land-use and its temporal trends. We additionally tested  
593 whether NBP and  $\Delta$ NBP were spatially related to increasing  $\Delta$ NBP<sub>PV-AR1</sub> by fitting two  
594 models in which NBP and  $\Delta$ NBP were the response variables and the aggregated metric of  
595 trends in  $\Delta$ NBP<sub>PV-AR1</sub> (see description above) was their predictor. Models were fitted using  
596 normalised variables (mean=0, sd=1), but effect plots were rescaled to their original units  
597 to facilitate the interpretation of the results. All analyses were performed using R statistical  
598 software v.3.6.3<sup>60</sup>.





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### 638 **Data availability**

639 Data supporting the findings of this study are available in the following open repositories.

640 CAMS: [https://ads.atmosphere.copernicus.eu/cdsapp#!/dataset/cams-global-greenhouse-](https://ads.atmosphere.copernicus.eu/cdsapp#!/dataset/cams-global-greenhouse-gas-inversion)  
641 [gas-inversion](https://ads.atmosphere.copernicus.eu/cdsapp#!/dataset/cams-global-greenhouse-gas-inversion)

642 CarboScope: <http://www.bgc-jena.mpg.de/CarboScope/>

643 Atmospheric CO<sub>2</sub> concentration: [https://scrippsco2.ucsd.edu/data/atmospheric\\_co2/](https://scrippsco2.ucsd.edu/data/atmospheric_co2/)

644 Data from the TRENDY ensembles can be provided upon request from  
645 <http://globalcarbonbudget.data.org/index.html>. Data to reproduce Figures 1 and 2 are  
646 provided as Source Data. Code and data to perform the statistical analyses, calculations  
647 and figures is publicly available at Figshare:  
648 <https://doi.org/10.6084/m9.figshare.17081717.v5>.

### 649 **Code availability**

650 Code and data to perform the statistical analyses, calculations and figures is publicly  
651 available at Figshare: <https://doi.org/10.6084/m9.figshare.17081717.v5>.

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660 **Author contribution statement**

661 MFM, JP, and IAJ planned and designed the research. FC, CR, SS, PF, VA, DG, AKJ, DLL  
662 and PCM provided the data. MFM analysed the data. All authors contributed substantially  
663 to the writing of the manuscript.

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