

Enhanced Carbon Uptake by Terrestrial Ecosystems

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28 **Abstract**

29 **Climate change has been largely mitigated by an increasing carbon sink on land.**
30 **Understanding the causes of enhanced carbon uptake is essential for protecting, managing,**
31 **and projecting this important ecosystem service. In this Review, we critically examine**
32 **evidence of enhanced land uptake and attribute the observed response to drivers and**
33 **processes. We conclude that this enhanced carbon uptake results largely from the combined**
34 **effects of increased photosynthesis due to CO₂ fertilization, particularly in tropical forest**
35 **regions, and reduced cold-limitation due to elevated temperatures, primarily at higher**
36 **latitudes. Continued land carbon sequestration is projected through the end of this century**
37 **under various emissions scenarios. Therefore, appropriately managing ecosystems that can**
38 **mitigate climate change is essential to addressing the climate problem. We propose strategies**
39 **to improve understanding of future carbon uptake potential, calling for a new generation of**
40 **field experiments distributed globally to study belowground carbon release, CO₂**
41 **enrichment, and long-term shifts in ecosystem functionality to better predict and manage the**
42 **land sink.**

43

44 ***Keywords:*** carbon sequestration; terrestrial biosphere; ecosystem dynamics; global carbon cycle;
45 CO₂ fertilization

46 **1. Introduction**

47 The terrestrial biosphere absorbs roughly 15% of the carbon in the atmosphere each year through
48 primary productivity but then returns nearly all of it via respiration and to a lesser degree biomass
49 combustion (Keenan and Williams 2018, Friedlingstein et al. 2022, Crisp et al. 2022). These gross
50 fluxes of photosynthesis and respiration approach a long-term balance if forced by steady climatic,
51 atmospheric, edaphic, and disturbance conditions. However, since the Industrial Revolution, the
52 biosphere has exhibited a growing imbalance between these gross fluxes due to increasing carbon
53 dioxide (CO₂) emissions from the combustion of fossil fuels (Canadell et al. 2007), amongst other
54 factors such as deforestation and land use change.

55
56 To date, the imbalance between gross fluxes has caused a net gain in the terrestrial carbon sink.
57 Indeed, 25-33% of the CO₂ emitted annually by human activities is offset, with land ecosystems
58 removing about 215 PgC from the atmosphere between 1750 and 2020 (Friedlingstein et al. 2022).
59 As a result, atmospheric CO₂ concentration [Glossary Term I] remains 100 ppm lower than would
60 otherwise be expected given historic anthropogenic emissions. The rate of net carbon uptake has
61 also increased, doubling since the 1960s (Ballantyne et al. 2012, Graven et al. 2013, Keenan et al.
62 2016, Friedlingstein et al. 2022). However, future projections of the terrestrial carbon sink are
63 widely divergent, ranging from an expected acceleration in carbon dioxide uptake to a saturating
64 or even a net release of carbon over time (Friedlingstein et al. 2014, Huntzinger et al. 2017).

65
66 Understanding historic and future changes in the land carbon sink is paramount to addressing the
67 climate problem. The proportion of carbon emissions that is taken up by land and ocean carbon
68 sinks determines allowable anthropogenic emissions for specific global warming targets.
69 Knowledge of the terrestrial carbon sink can help guide climate change mitigation efforts,
70 specifically through the use of natural climate solutions such as reforestation, agroforestry, and
71 sustainable land management practices (Walker et al. 2022). More broadly, accurate estimates of
72 land-atmosphere feedbacks and their effects on atmospheric CO₂ concentrations are needed for
73 reliable predictions of the Earth System.

74
75 Human activities influence terrestrial ecosystem carbon uptake in multiple ways. Historically, land
76 use change has resulted in a direct decrease of the natural land sink [Glossary Term II] and reduces

77 the net land sink [Glossary Term III] (Guo and Gifford 2002, Smith 2008, Shevliakova et al. 2009
78 p. 300). Other indirect human influences include stimulation of plant photosynthesis and water use
79 efficiency from elevated atmospheric CO₂ concentrations (Walker et al. 2021) and changes in
80 nitrogen availability (Wang et al. 2017), air quality (Talhelm et al. 2014), temperature (Richardson
81 et al. 2013, Keenan and Williams 2018) and precipitation patterns (Nemani et al. 2002, Gherardi
82 and Sala 2019). Climate change-induced regional droughts, changes in fire frequency and
83 intensity, and more frequent climate extremes may also reduce the terrestrial carbon sink
84 (Reichstein et al. 2013). The combined effects of these direct and indirect human influences
85 determine how much atmospheric carbon is sequestered by global lands.

86

87 In this Review, we examine the evidence for and implications of an enhanced terrestrial carbon
88 sink. First, we explore the evidence of land sink enhancement from various observations and
89 methodologies. We then outline the key processes driving this change, before discussing projected
90 changes in terrestrial carbon uptake and associated implications for natural climate solutions and
91 society. We end by outlining future research priorities to better understand and manage dynamic
92 terrestrial carbon stocks and sinks.

93 **2. Evidence for an Enhanced Land Sink**

94 Various methods are available to estimate the strength of the terrestrial carbon sink, and each
95 provides insight into different aspects of land carbon sink changes, from global to regional uptake
96 (Table 1). Taken together, there is clear evidence of an enhanced land sink, although regional
97 trends are more difficult to identify. Descriptions of these methods are provided in Table 2. In this
98 section we review evidence of long term sink enhancement across spatial scales, along with
99 insights provided by terrestrial biosphere models.

100

101 **2.1 Global**

102 Atmospheric observations provide the clearest evidence of enhanced carbon uptake by natural
103 sinks globally (Ciais et al. 1995). Measurements over the past six decades show that only about
104 44% of anthropogenic CO₂ emissions remains in the atmosphere each year (the airborne fraction
105 [Glossary Term IV]) (Raupach et al. 2008, Ciais et al. 2019, Canadell et al. 2021b). Of the rest,
106 about one half is absorbed by the world's oceans (Tans et al. 1990, Hauck et al. 2020), and the

107 other half is taken up by ecosystems on land (Ballantyne et al. 2012, Schimel et al. 2015b, Keenan
108 et al. 2016, Friedlingstein et al. 2022). The land sink from the carbon budget is estimated to be 3.1
109 ± 0.6 PgC yr⁻¹ in the 2010s (Friedlingstein et al. 2022). Additional constraints on the global land
110 sink can be explored via atmospheric inversions (Peylin et al. 2013, Peiro et al. 2021). These
111 suggest a total land CO₂ sink with a range of 1.3-2.0 PgC yr⁻¹ and a long-term increase in the land
112 sink of about 0.1 PgC yr⁻¹ since the 1960s (Peylin et al. 2013), in accordance with terrestrial
113 biosphere model simulations (Figure 1). Atmospheric measurements of CO₂, O₂ and $\delta^{13}\text{C}_{\text{CO}_2}$ also
114 unequivocally point to a strong land sink (Tans et al. 1990, Keeling et al. 2005, Ciais et al. 2019).
115

116 The airborne fraction has not increased with increasing anthropogenic emissions (Rayner et al.
117 2015, Canadell et al. 2021b). The relatively constant airborne fraction since the 1950's implies
118 that the terrestrial and oceanic sinks have been increasing over time, even doubling (Ballantyne et
119 al. 2012, Huang et al. 2018, Tharammal et al. 2019). Without increasing carbon land sinks,
120 atmospheric CO₂ concentration would have reached >500 ppm by 2020 (Figure 1). However, the
121 airborne fraction is highly variable from year to year and exhibits decadal periods of increases,
122 such as an 1.8% growth per year in the 1960s-1990s with a subsequent declining trend of -2.2%
123 per year (Keenan et al. 2016), associated with macroclimatic or land-use changes (van Marle et al.
124 2022).

125
126 A growing constellation of Earth-observing satellites provides information on ecosystem function
127 and carbon storage since the 1980's (Schimel and Schneider 2019, Smith et al. 2020b). A
128 widespread greening of the Earth has been observed via satellites (Zhu et al. 2016, Mao et al. 2016,
129 Chen et al. 2019a, Piao et al. 2020) (Figure 2), with enhanced seasonality and an extension of the
130 growing season in high latitudes (Keenan et al. 2014, Park et al. 2016, Huang et al. 2018). About
131 12% of the increased global terrestrial carbon sink over the satellite era (1981-present) has been
132 attributed to increased leaf area index (LAI) (Keenan et al. 2016, Chen et al. 2019b). Trends in
133 global plant biomass from satellite passive microwave observations are positive and consistent in
134 magnitude with the global carbon budget and forest inventory estimates. Global estimates of land
135 cover change in combination with space-based lidar from ICESat and ground plots from 2001-
136 2019 suggest a natural carbon sink in the world's forests of 4.35 PgC yr⁻¹, offset by 2.2 PgC yr⁻¹
137 due to emissions from deforestation and other disturbances (Harris et al. 2021). For example,

138 boreal and temperate biomass increased by 0.13 PgC yr^{-1} in from 1993 to 2012 (Liu et al. 2015).
139 Despite widespread greening (Piao et al. 2020), increases in leaf area do not necessarily translate
140 to increases in the net land sink. For example, Europe's carbon uptake has reportedly not benefited
141 from long-term vegetation greening due to offsetting increases in ecosystem respiration (Liu et al.
142 2021) and enhanced evapotranspiration, which increased summer drought (Lian et al. 2020).
143 Furthermore, the intensity and extent of greening trends differs across satellite products (Zhu et al.
144 2016, Jiang et al. 2017a) and depends on the methods used to detect trends (de Jong et al. 2012,
145 Cortés et al. 2021). Divergences between LAI products are more pronounced in highly vegetated
146 regions with dense canopies, resulting in larger uncertainty in areas with greater aboveground
147 biomass (Figure 2).

148

149 **2.2 Regional and in situ**

150 Despite unequivocal global evidence of an enhanced land sink, regional trends are more
151 challenging to identify. Long-term atmospheric CO_2 measurements show a strong increase in the
152 seasonal cycle of atmospheric CO_2 at northern latitudes, suggesting stronger summer uptake offset
153 by larger winter release (Keeling et al. 1996, Randerson et al. 1999, Graven et al. 2013, Thomas
154 et al. 2016, Piao et al. 2018, Tagesson et al. 2020). Land CO_2 uptake during summer increased in
155 the northern latitudes by $0.6 \pm 0.5 \text{ PgC yr}^{-1}$ during the 2000s (Ciais et al. 2019), but with a
156 corresponding larger release during winter (Commane et al. 2017). A 30-50% increase in the
157 seasonal cycle amplitude has been observed since the 1960s in surface and airborne measurements
158 north of 45°N , also suggesting enhanced summer uptake and larger releases in the winter (He et
159 al. 2022). =

160

161 Satellite products also suggest diverging regional trends. A 10% increase in vegetation over semi-
162 arid regions has been observed globally (Donohue et al. 2013), corresponding to widespread
163 greening in semi-arid regions of Australia (Ukkola et al. 2015). However, regional browning trends
164 are also evident (Zhou et al. 2014), though to a much lesser extent. Greening may also be slowing
165 down or reversing in some regions, especially in tropical rainforests (Winkler et al. 2021).

166

167 Additional carbon taken up by the land carbon sink is primarily sequestered in the live biomass
168 and soils, making repeated measures of plot level biomass a useful test of the growth enhancement

169 hypothesis. Reports indicate widespread increased tree growth (Lewis et al. 2009b, Salzer et al.
170 2009, McMahon et al. 2010, Pan et al. 2011), with an average annual gain in woody carbon stocks
171 of $0.23 \pm 0.09 \text{ PgC yr}^{-1}$ from 2000 to 2019 (Xu et al. 2021). In the tropics, analyses of standardized
172 inventory data from forest plot networks such as RAINFOR, AfriTRON and CTFS suggest an
173 overall increase of $0.5 \text{ MgC ha}^{-1} \text{ yr}^{-1}$ in tropical forest plots globally (Lewis et al. 2009b, Qie et
174 al. 2017, Hubau et al. 2020). This is broadly consistent with a global review of biomass inventories
175 suggesting that intact tropical forests contribute up to 50% of the global land sink (Pan et al. 2011)
176 and also consistent with evidence of enhanced growth from temperate and boreal forests (Salzer
177 et al. 2009, McMahon et al. 2010). In addition to intact forests, rapidly regrowing secondary forests
178 following anthropogenic (e.g., agriculture land abandonment, slash and burn agriculture) or natural
179 disturbances (e.g., fire) account for half of the remaining land sink (Pan et al. 2011, Pugh et al.
180 2019b). Temperate forests in the United States have experienced significant increases in wood
181 volume since the 1990s (Davis et al. 2022).

182

183 Despite these gains, there is some suggestion that tropical forest biomass carbon sinks peaked in
184 the 1990s. Amazon forest above-ground biomass increases declined by one-third in the 2000s
185 (Brienen et al. 2015), with positive gains in biomass outweighed by deforestation (Hubau et al.
186 2020). African forests have remained stable at $0.66 \pm 0.13 \text{ tonnes C hectare}^{-1} \text{ yr}^{-1}$ (Hubau et al.
187 2020). Tree mortality in the Amazon has also increased due to stand dynamics, rising atmospheric
188 water stress and drought (Bauman et al. 2022), while global tree mortality since the 1970s is
189 associated with hot and dry climate anomaly events, expected to increase nonlinearly under climate
190 change (Hammond et al. 2022).

191

192 Tree ring characteristics provide some evidence of an enhanced sink. Unprecedented growth has
193 been observed (Salzer et al. 2009); for example, aspen trees in Wisconsin showed up to $0.7\% \text{ yr}^{-1}$
194 increases in growth, after accounting for effects of age, water stress and other variables (Cole et
195 al. 2010). However, a lack of growth enhancement (Peñuelas et al. 2011, van der Sleen et al. 2015,
196 Hararuk et al. 2019), only a limited response (Gedalof and Berg 2010), unexplained divergence in
197 the relationship between ring width, temperature (D'Arrigo et al. 2008, Stine and Huybers 2014)
198 and nutrient limitation (Guerrieri et al. 2020) have also been reported. New approaches are
199 emerging, combining theory with statistical models or satellite observations (Schippers et al. 2015,

200 Levesque et al. 2019, Anderegg et al. 2020), that promise more accurate and insightful
201 quantification of tree growth enhancement.

202

203 The eddy-covariance technique directly measures the net exchange of carbon dioxide between
204 ecosystems and the atmosphere (Baldocchi 2020). Of the over two thousand sites around the world
205 (Burba 2019), many have now been in operation for three decades or more, allowing estimates of
206 annual net carbon uptake or release by ecosystems over multiple years (Novick et al. 2018,
207 Pastorello et al. 2020). Despite high background variability, long-term trends have emerged from
208 many sites with records long enough to allow separation of signal from noise. Enhanced uptake
209 has been observed at US and European sites (Dragoni et al. 2011, Pilegaard et al. 2011, Keenan et
210 al. 2013, Fernández-Martínez et al. 2017). Synthesis across the global network of observation sites
211 indicates an increase of $0.46 \pm 0.09 \text{ PgC yr}^{-1}$ from 1982 to 2016 (Cai and Prentice 2020, Chen et
212 al. 2022). When combined with empirical (Joiner et al. 2018) or process-based (Chen et al. 2022)
213 scaling approaches, eddy-covariance observations suggest an enhancement of global
214 photosynthesis.

215

216 **2.3 Model output**

217 State of the art models of the Earth system represent our best-guess approximations of terrestrial
218 carbon uptake. These models incorporate the known physiological and biological mechanisms
219 responsible for ecosystem function and carbon cycling and are compared to atmospheric and
220 ground observations to assess performance. There is strong theoretical and observational support
221 for a large stimulation of terrestrial uptake by increased CO_2 growth rates. Indeed, a more
222 productive land surface is essential to explain the enhanced net terrestrial carbon uptake inferred
223 from the global carbon budget, with a land sink that has seen an increase from $1.2 \pm 0.5 \text{ GtC yr}^{-1}$
224 in the 1960s to $3.1 \pm 0.6 \text{ GtC yr}^{-1}$ in the 2010s (Friedlingstein et al. 2022). Regional models also
225 suggest an increasing terrestrial carbon sink, even when land use change is incorporated. For
226 example, ecosystem models estimate that rapid forest expansion (by a total of 58 Mha) from 1900
227 to 2019 made up 44% of the increase in China's land sink of $8.9 \pm 0.8 \text{ PgC}$ (Yu et al. 2022).

228 **2.4 Uncertainties**

229 Atmospheric, satellite, and in situ observations, along with model output, all provide ample
230 evidence of an enhancement in the land carbon sink. However, each of these methodologies is
231 subject to uncertainty. At the global scale, atmospheric inversion model estimates of the land sink
232 depend on modeling assumptions and design, including processes that are not represented in
233 models and uncertainty in datasets used to drive models. Detecting long-term changes in biomass
234 from satellite observations is complicated by the lack of high-quality long-term instruments
235 capable of providing accurate biomass estimates (Smith et al. 2020b). Satellite records can
236 generate spurious trends that may be incorrectly attributed (Forkel et al. 2013). Issues such as
237 sensor degradation can lead to large differences between satellite products (Piao et al. 2020).
238 Assumptions regarding the incorporation of physiology needed to translate satellite observables,
239 such as reflectance or vegetation optical depth, to quantities of interest, such as photosynthesis or
240 plant biomass (Konings et al. 2019)

241
242 In-situ evidence of enhanced uptake is widespread but highly dependent on the region and scale
243 of investigation. Tree ring responses are highly variable and depend on the regional climate and
244 background stress conditions. Methods of analysis are also important, with results from traditional
245 trend-detection methods being sensitive to the choice of technique (Peters et al. 2015) and subject
246 to biases if demographic trends are not properly accounted for (Brienen et al. 2012, 2017,
247 Nehrbass-Ahles et al. 2014). Furthermore, changes in growth and carbon stocks for individual
248 trees do not necessarily apply to all trees in a stand and thus may not be relevant at the ecosystem
249 level. Conversely, higher stand density could lead to higher biomass even without a change in
250 individual growth rates. Ecological observatory network sites, such as eddy-covariance flux
251 towers, are far from optimally distributed around the globe and under-sample important regions,
252 particularly in the tropics (Villarreal and Vargas 2021), which may prevent these networks from
253 capturing extreme climate and disturbance events (Mahecha et al. 2017). Thus, empirical upscaling
254 products typically struggle to capture long-term trends and overestimate the magnitude of the
255 global land sink (Jung et al. 2020). Assessing the global significance of observed local and regional
256 processes remains challenging.

257

258 **3. Key Processes and Regions**

259 Multiple drivers contribute to changes in the land sink at global and regional scales, including CO₂
260 fertilization, warming effects on growth and growing season length, N or P fertilization and
261 changes in precipitation or light (Figure 3). Warming, longer growing seasons and elevated CO₂
262 have been identified as large contributors to enhanced uptake, while temperature and moisture
263 stress are thought to have led to increased mortality in tropical regions (Bauman et al. 2022). The
264 rate of change in stand-level biomass and predictors such as mean climate, tree species, initial C
265 stocks, and N deposition suggest a long-term increase in vegetation water use efficiency (Adams
266 et al. 2021), increased growth of temperate deciduous forests (Thomas et al. 2009, Li et al. 2020),
267 and increase in soil carbon storage in tropical systems (Lu et al. 2021) (Figure 4). What follows is
268 a detailed discussion of the mechanisms involved in long-term changes in the land sink.

269 **3.1 CO₂ fertilization**

270 It is very likely that CO₂ fertilization [Glossary Term V] is the leading mechanism behind
271 enhanced global land uptake (Schimel et al. 2015b, Keenan et al. 2016, Fernández-Martínez et al.
272 2019, Tagesson et al. 2020, Walker et al. 2021, Chen et al. 2022). Ecosystem-scale experiments
273 provide the most direct observation of the CO₂ fertilization effect and indicate increased
274 photosynthesis, leaf area index, net primary productivity, water use efficiency and biomass growth
275 for plants grown in elevated CO₂ conditions (Battipaglia et al. 2013, Baig et al. 2015, Walker et
276 al. 2019, 2021, Liu et al. 2019). Free air CO₂ enrichment (FACE), though expensive, remains the
277 best approach to observe the response of production and allocation patterns in natural ecosystems
278 to elevated CO₂. Early FACE experiments have provided invaluable insights into these processes.
279 However, even those that were a decade long still leave questions about the persistence of
280 measured responses (Reich et al. 2018). Some suggest a sustained enhancement of carbon uptake
281 by 20-30% (McCarthy et al. 2010) while others show a diminishing or negligible response over
282 time, particularly in grassland or arid sites (Dukes et al. 2005, Adair et al. 2009, Reich et al. 2014).
283 Large differences in the responses of different ecosystems to experimental increases in CO₂ are a
284 function of primarily nutrient availability (Terrer et al. 2019), along with mycorrhizal association
285 (Terrer et al., 2016) and potentially differences in below-ground allocation (Terrer et al., 2022),
286 which are often unmeasured. The magnitude of the CO₂ fertilization effect varies across species,

287 age, climate, and nutrient and water availability (Norby et al. 2010, Newingham et al. 2013,
288 Sigurdsson et al. 2013, Jiang et al. 2020).

289

290 Regionally in semi-arid lands, a 10% increase in vegetation cover was directly attributable to the
291 influence of elevated CO₂ on plant water use efficiency (Donohue et al. 2013), and a 100-ppm
292 increase in CO₂ increased aboveground biomass by 8.2% (Song et al. 2019a). Widespread global
293 greening has also been attributed to increases in atmospheric CO₂ and changes in climate (Los
294 2013, Zhu et al. 2016). However, the estimated impact of elevated CO₂ ranges from 40% (Los
295 2013) to 70% (Zhu et al. 2016) of the observed greening trend. In Australia, only 2.4% of greening
296 was attributable to elevated atmospheric CO₂ (Ukkola et al. 2015).

297

298 Isotopic evidence from tree rings consistently indicates an increase in water use efficiency
299 (Bellassen et al. 2011, Frank et al. 2015, Guerrieri et al. 2019), with a global 40% increase driven
300 by rising CO₂ (Mathias and Thomas 2021). This could be expected to result in increased growth
301 (van der Sleen et al. 2015, Hararuk et al. 2019, Guerrieri et al. 2020). Tree rings confirm the almost
302 universal increase in the WUE in response to increasing atmospheric CO₂, but the result of the
303 water savings in terms of carbon sequestration remains under question. Tree ring development and
304 biomass accumulation can be decoupled from carbon source dynamics, however (Cabon et al.
305 2022a, Green and Keenan 2022), and thus may have lower sensitivity to rising CO₂ than that of
306 photosynthesis. Furthermore, tree ring growth is complicated by other factors (temperature,
307 precipitation, light), which could lead to regional differences in trends. For example, temperate
308 forest biomass plots in the United States increased in wood volume by 1.15% from increasing CO₂,
309 but other factors enhanced or reduced overall growth (Davis et al. 2022).

310

311 Global terrestrial biosphere models attribute the stimulation of plant productivity and reduced
312 transpiration to elevated CO₂ (Schimel et al. 2015b, Keenan et al. 2016, Haverd et al. 2020,
313 Tagesson et al. 2020). Models constrained by field experiments indicate that CO₂ fertilization
314 alone explains most of the observed increase in global land carbon sink since the 1960s (Liu et al.
315 2019). The simulated land sink is very sensitive to CO₂ fertilization: a terrestrial ecosystem model
316 predicted that even a 20 ppm increase in CO₂ resulted in a detectable increase in carbon
317 assimilation rates (Zhan et al. 2022). However, estimates vary considerably among models. Sixty

318 (Schimel et al. 2015b) to 85% (Keenan et al. 2016) of the increase in the terrestrial carbon sink
319 over recent decades could be due to atmospheric CO₂. The largest absolute response is expected
320 in forests because trees allocate carbon to long-lived carbon pools such as wood. Tropical forests
321 are particularly sensitive because of a) their high theoretical expectations of an absolute response
322 to elevated CO₂ proportional to average productivity (Hickler et al. 2008) and b) the stronger effect
323 of CO₂ fertilization at high temperatures, which correspond to higher rates of photorespiration.
324 This pattern is consistent with results from dynamic global vegetation models (DGVM), which
325 indicate the strongest sink enhancement in the tropics (Figure 5), albeit with wide scatter across
326 models. DGVMs attribute a 2.53 ± 0.46 PgC yr⁻¹ increase in the global land sink to CO₂
327 fertilization alone over the 21st century, which is partially offset by negative effects of land use
328 and climate change (Figure 4).

329

330 The stimulation of ecosystem productivity by elevated CO₂ can be reduced by various limiting
331 factors. Elevated CO₂ is likely to increase turnover rates of recently-assimilated soil carbon
332 (Groenigen et al. 2017, Meeran et al. 2021). Negative impacts of climate change, such as drought
333 (see below), substantially offset the sink enhancement resulting from CO₂ fertilization (Wu et al.
334 2020) particularly in the eastern Amazon, south Africa, and western Australia (Figure 5). Low
335 nutrient (N and P) supply may represent another limiting factor (Luo et al. 2004, Reich et al. 2006,
336 Wang et al. 2010, Norby et al. 2010, Fleischer et al. 2019, Terrer et al. 2019, Fleischer and Terrer
337 2022) due to stoichiometric requirements of tissue formation and function. However, nutrient
338 limitation does not necessarily outweigh the effects of CO₂ fertilization, and the effects of P
339 limitation on CO₂ fertilization remain uncertain in key areas such as the Amazon. Increased uptake
340 can however alleviate nutrient constraints, even in low-nutrient environments. Evidence suggests
341 a proactive belowground allocation under elevated CO₂ that stimulates nutrient uptake (Drake et
342 al. 2011, Song et al. 2019b). Mycorrhizal association can play a strong role (Terrer et al. 2016,
343 Soudzilovskaia et al. 2019), with an ectomycorrhizal-associated plant uptake of 24% more N under
344 elevated CO₂ (Terrer et al. 2018). Finally, tradeoffs between above and belowground carbon
345 storage under elevated CO₂ could result in stable biomass even with CO₂ fertilization (Terrer et al.
346 2021). Unfortunately, the majority of these mechanisms are not represented in the current
347 generation of DGVMs.

348 **3.2 Increasing temperature**

349 Climate change-induced increases in temperature have divergent effects across the globe. Longer
350 growing seasons in cold, wet climates may result in an enhanced sink. These regions are most
351 sensitive to increasing temperatures, consistent with experimental results (Zhou et al. 2021),
352 greening trends, and model predictions. High-latitude systems are thought to be greening due to
353 temperature increases (Figure 5), with 16.4% of high-latitude lands released from temperature
354 limitation during 1982-2012 (Keenan and Riley 2018), although seasonal water deficits might limit
355 some of these gains (Buermann et al. 2018, Lian et al. 2020). Increasing carbon sinks offset carbon
356 releases by 60% in springtime (Keenan et al. 2014). However, effects on carbon uptake vary in
357 magnitude (Piao et al. 2008, Dragoni et al. 2011, Keenan et al. 2014, Zhang et al. 2020a). Earlier
358 leaf-out dates might dampen summer (Xu et al. 2019, Lian et al. 2020) and autumn photosynthesis
359 (Zhang et al. 2020b, Zani et al. 2020) (but see Lu and Keenan (2022)), so that growing seasons
360 might not be as productive as previously projected, with fall respiration offsetting up to 90% of
361 spring carbon uptake (Piao et al. 2008, Zhang et al. 2020b).

362

363 In warm regions, higher productivity is partially or wholly offset by increased respiration due to
364 higher temperatures (Jung et al. 2020). Tropical forests may already be at optimal temperatures for
365 photosynthesis, which would indicate strong declines in canopy photosynthesis with further
366 increases in temperature (Huang et al. 2019). Increased temperatures in tropical regions also may
367 result in large releases of CO₂ from soil carbon stocks (Nottingham et al. 2020). Globally, DGVM
368 model output suggests climate change alone reduced the land sink by 0.45 ± 0.39 GtC yr⁻¹ from
369 2011 to 2020 (Friedlingstein et al. 2022).

370

371 **3.3 Water availability**

372 Changes in water availability have the potential to contribute to enhanced uptake. Water
373 availability is also a well-documented limit to plant productivity, net carbon uptake, and ecosystem
374 carbon stocks (Schoor 2003, Beer et al. 2010, Jung et al. 2011, Humphrey et al. 2018, Lian et al.
375 2021) in many regions, though not all (Wang et al. 2022). Strong regional wetting or drying trends
376 have been detected (Sheffield and Wood 2008, Jung et al. 2010, Yuan et al. 2019), driving carbon
377 uptake or releases (Scheff et al. 2021a) on the order of 2 PgC yr⁻¹, which at times counteract the

378 mean background sink (Schwalm et al. 2011). Significant drying trends have been detected in
379 western United States, mid-altitude regions, European peatland, and global islands (Cook et al.
380 2015, Karnauskas et al. 2016, Mankin et al. 2019, Swindles et al. 2019).

381
382 Semi-arid regions have been greening (Milly and Dunne 2016), which has been predicted (Lian et
383 al. 2021) and is already evident in the satellite record (Piao et al. 2020). This trend is likely due to
384 releases from water limitation with elevated CO₂ (Ukkola et al. 2015). Approaches that account
385 for the effect of CO₂ on plant water dynamics, including the majority of earth system models,
386 highlight a ‘drying but greening’ scenario, due to the dynamic role of vegetation responses to CO₂
387 (Trenberth et al. 2014, Milly and Dunne 2016, Mankin et al. 2019, Yang et al. 2019, Berg and
388 McColl 2021). Many ecosystems are becoming more sensitive to water availability (Jiao et al.
389 2021, Denissen et al. 2022, Li et al. 2022), and therefore the magnitude of enhanced sink due to
390 water availability changes may be large in certain regions, especially drylands.

391 **3.4 Nutrient availability**

392 Nitrogen deposition is an important but regionally-specific potential driver of an enhanced sink
393 (Fernández-Martínez et al. 2019). N is well known to stimulate plant growth and carbon uptake in
394 some regions of the world. These regions have seen drastic increases in N fertility due to industrial
395 production of N-fertilizers applied to agro-ecosystems, as well as emissions of NO_x from fossil
396 fuel combustion reaching ecosystems via atmospheric deposition (Gruber and Galloway 2008).
397 Belowground carbon allocation is a substantial component of the land sink (Gherardi and Sala
398 2020); coarse woody debris transfers carbon from aboveground stocks with relatively short
399 turnover times to long-lived below-ground pools (Luyssaert et al. 2008). If realized into long-lived
400 carbon pools such as wood or slow-turnover soil carbon, N fertilization has the potential to
401 generate sizeable and lasting carbon sinks in ecosystems (Rastetter et al. 1991, Zaehle et al. 2010).
402 However, models suggest a fairly modest N-driven global-scale stimulation of C sequestration,
403 reaching only about 0.3 PgC y⁻¹ in recent decades (Figure 4) (Thornton et al. 2007, Zaehle et al.
404 2010, Wang et al. 2017, Terrer et al. 2019). A meta-analysis of 138 experiments found that the
405 best predictor of carbon fertilization effects was soil C:N ratio (Terrer et al. 2019). P-limitation
406 can also play an important role in below-ground biomass (Hou et al. 2020), especially in tropical
407 regions, where gains via CO₂ fertilization may be substantially offset by nutrient limitation

408 (Fleischer et al. 2019, Fleischer and Terrer 2022). However, this effect is still poorly constrained
409 due to few studies conducted in P-poor soils, and the limited number of models that incorporate
410 the P cycle.

411 **3.5 Light availability**

412 Changes in light intensity and quality might have also contributed to enhanced land uptake. Light
413 quality appears to be the most relevant factor (Zhang et al. 2021). A global ‘dimming’ trend was
414 observed through the mid-20th century, with less but more diffuse light, due to aerosol loading and
415 increased cloudiness (Roderick et al. 2001). Including a diffuse light effect in a land surface model
416 caused a net enhancement of land carbon uptake of $\sim 0.4 \text{ PgC yr}^{-1}$ in recent decades (Figure 4)
417 (Mercado et al. 2009, O’Sullivan et al. 2021). Aerosol-induced cooling effects can also reduce
418 respiration, especially in the tropics, enhancing the global land sink (Zhang et al. 2019). Over the
419 longer term, anthropogenic aerosols have been reported to have induced a global land sink increase
420 of 0.14 PgC yr^{-1} , or cumulatively 22.6 PgC since 1850 (Zhang et al. 2021).

421 **3.6 Land use**

422 The effects of land use and land cover change on the terrestrial carbon sink are largely uncertain,
423 undermining efforts to constrain the land sink and its trends. Disturbance events, for example, can
424 both increase and decrease the land carbon sink. Initial declines in aboveground biomass following
425 a disturbance, such as fire (Bowman et al. 2020), forest pathogen outbreaks (Lesk et al. 2017), or
426 land clearing (Pugh et al. 2019b), may lead to long term gains in carbon uptake as systems
427 regenerate. These disturbances could also reverse the historic sink enhancement trend and result
428 in net carbon releases to the atmosphere (Reichstein et al. 2013).

429
430 Over the 21st century, global land use change is estimated to have decreased the land sink by 1.2
431 PgC yr^{-1} (Figure 4). However, estimates of recent land use change emissions vary considerably.
432 Land use change emissions may have remained relatively flat, declined (van Marle et al. 2022) or
433 increased (Xu et al. 2021) since 2000. The role of agricultural intensification has been shown to
434 dominate greening trends in many parts of the world, particularly in India and China, which alone
435 accounts for 25% of the global increase in leaf area (Chen et al. 2019a). Agricultural expansion
436 and intensification at the expense of forests has also been linked in part to a global decline in fire
437 (Andela et al. 2017).

438

439 Fire activity reportedly declined since the start of the century (Doerr and Santín 2016, Andela et
440 al. 2017), with a decline in forest fires from 0.5 to 0.1 PgC yr⁻¹ from 2000 to 2019 and an average
441 2.2 PgC yr⁻¹ total global fire emissions from 1997-2016 (Xu et al. 2021). Fires decreased
442 particularly in grasslands, though with a slight increase in forest burned area (Zheng et al. 2021).
443 Large-scale and long-term fire dynamics are particularly sensitive to the remote sensing product
444 used, however, and there are difficulties in separating climate and direct anthropogenic effects
445 (Forkel et al. 2019). Fire suppression in the United States has resulted in an increased carbon sink
446 (Houghton et al. 1999, Abram et al. 2021). In the northern boreal forests, increased fire activity
447 has reportedly led to increased carbon uptake, based on evidence from burn sites (Mack et al. 2021)
448 and is expected to continue to do so as fire increases in the future (Mekonnen et al. 2019).
449 However, fire also releases carbon to the atmosphere. Australia has experienced a 30% increase in
450 fire risk from 1920 to 2019 (van Oldenborgh et al. 2021), and the unprecedented bushfires there
451 in 2019-2020 (van der Velde et al. 2021) released an estimated 0.715 PgC to the atmosphere.
452 Recent increases in Australian megafires (Canadell et al. 2021a) are part of a multi-decadal upward
453 trend in burned area and frequency of fires, driven by long-term warming (Jones et al. 2022).

454

455 **3.7 Complex, Coupled responses**

456 CO₂ stimulation and warming-induced elongation of growing seasons are likely to be the leading
457 factors driving an enhanced land uptake. However, ecosystem responses to all the above factors
458 are mediated by a host of plant and stand level adjustments. Changes to carbon allocation,
459 acclimation, tissue turnover rates, demographics and species composition strongly influence long-
460 term behavior and are poorly known. For example, plants are genetically constrained to approach
461 a certain morphology and size regardless of environment (i.e. CO₂, or N availability) over the
462 course of a life cycle. Tree mortality depends on size: wind throw events (Seidl et al. 2011),
463 drought (Rowland et al. 2015), and stand-replacing disturbances vary between forest types (Pugh
464 et al. 2019a). Thus, it remains debated whether enhanced plant growth will result in larger live
465 carbon pools of similar longevity or whether plants will approach a maximum size faster and die
466 sooner. For example, trees across the globe experienced a 50% increase in early growth, which
467 was associated with a concurrent 23% decrease in lifespan (Brienen et al. 2020). If enhanced

468 growth results in shorter life spans and faster turn over, these gains will not translate into an
469 enhanced carbon sink in the long term, except for the relatively small portion that may become
470 incorporated into stable soil carbon. Furthermore, observed enhancement of carbon fixation is
471 potentially unrelated to carbon sink rates (Cabon et al. 2022b), suggesting a mismatch between
472 carbon fixation and long term storage in woody tissue. Causes of enhanced growth, including CO₂
473 fertilization or changes in disturbance dynamics, continue to be debated (Wright 2005, Clark 2007,
474 Lewis et al. 2009a, Muller-Landau 2009).

475
476 Complex regional interplays of global change drivers and other factors influence ecosystem
477 behavior. Detecting such expected responses can be challenging as many changes occur
478 concurrently. For example, increased growth due to nitrogen deposition (Thomas et al. 2009)
479 occurs in tandem with increased mortality due to warming-induced drought. Woody encroachment
480 in semi-arid systems is expected given increased water use efficiency from elevated CO₂ (Donohue
481 et al. 2013, Stevens et al. 2017) but is also dependent on regional water availability. The enhanced
482 seasonal cycle of atmospheric CO₂ at northern latitudes has been attributed to climate and CO₂
483 (Piao et al. 2018, Bastos et al. 2019, Liu et al. 2020), a greening of northern high-latitude vegetation
484 (Forkel et al. 2016, Park et al. 2016), an increase in vegetation light-use efficiency due to rising
485 CO₂ (Thomas et al. 2016), and the intensification of North American agriculture (Gray et al. 2014,
486 Zeng et al. 2014).

487
488 Some processes can be counterintuitive, such as the estimated increase in carbon uptake due to
489 increasing fire regimes in boreal ecosystems, caused by compositional changes during recovery
490 (Mekonnen et al. 2019, Mack et al. 2021). The same process can even generate opposite net effects
491 on the carbon cycle depending on the role of other limiting factors. For example, an extension of
492 the growing season in autumn leads to a net release of carbon during autumn in high latitude
493 ecosystems (Piao et al. 2018), but a net increase in carbon uptake during autumn for mid-latitude
494 ecosystems (Dragoni et al. 2011, Keenan et al. 2014), due largely to variation in the extent of
495 temperature limitations on respiration in autumn. Positive impacts of warming on plant growth are
496 expected in temperature-limited regions, but negative impacts are expected where water is limiting
497 (Song et al. 2019b). Coupled responses and confounding factors (such as the uncertainty regarding

498 land use change emissions) make attribution and detection of an enhanced sink challenging,
499 especially on regional scales.

500

501 **4. Future projections**

502 Across the current generation of models, terrestrial carbon sequestration is predicted to continue
503 to increase in the future. The Coupled Climate Intercomparison Project (CMIP6) predicts an
504 increasing sink under various emissions scenarios, albeit at a slower pace and with an approach to
505 saturation at high CO₂ levels (Figure 6). This suggests that sink enhancement will persist despite
506 the increasing pressures of climate change on ecosystem resilience and health.

507

508 However, predictions of the biosphere remain uncertain (Luo et al. 2015). Models predict a wide
509 range of land sink projections, ranging from negative to positive trends in uptake (Friedlingstein
510 et al. 2014, Huntzinger et al. 2017). Modeling studies often exclude important processes, such as
511 land cover change and disturbance, especially from fire (Sanderson and Fisher 2020, Canadell et
512 al. 2021a), and misrepresent carbon allocation (Terrer et al. 2021), all of which would likely
513 dampen the positive gains from the CO₂ fertilization effect. Models also exclude complex
514 interactions between meteorological drivers, management, demography and mortality (Pugh et al.
515 2019a). For example, including nitrogen cycling in models suggests a 50% smaller land carbon
516 sink (Huntzinger et al. 2017), though the processes controlling nutrient mineralization,
517 immobilization, fixation, and leaching are incompletely understood, and the degree to which
518 progressive nutrient limitation has limited the land sink enhancement remains debated. Together,
519 these omissions lead to a divergence in predictive performance between simulations of the historic
520 period and future projections (Fatichi et al. 2019).

521

522 Process knowledge remains insufficient to determine with confidence the true sensitivity of the
523 terrestrial carbon sink to CO₂ (Walker et al. 2021), and whether the enhanced CO₂ sink will
524 continue into the future (Friedlingstein et al. 2014). The longevity of current carbon sinks may be
525 threatened by demographic or climate trends that increase the frequency or intensity of extreme
526 events and associated ecosystem disturbances (Reichstein et al., 2013; Anderegg et al. 2022). The
527 likelihood of a sustained sink into the future thus remains uncertain, and reports suggest near term

528 saturation in important regions, such as in the Amazonian and African tropical forests (Hubau et
529 al. 2020).

530

531 Increasing temperature may continue to enhance the land carbon sink in cold climates, but this
532 effect is still uncertain and may be largely offset by concurrent carbon release. Warming of soils
533 and permafrost will likely result in sizeable carbon releases over the next century (He et al. 2016,
534 Soong et al. 2021), with an observed 34-37% increase in soil respiration concurrent in response to
535 4°C warming (Hicks Pries et al. 2017). However, concurrent increases in carbon inputs from plants
536 may offset some or all of these releases (van Gestel et al. 2018). Even if warming enhances net
537 land carbon uptake in cold regions, the response may tip toward net releases both locally, in
538 historically cold-limited regions, and more broadly at the global scale, with continued warming
539 also resulting in higher vapor pressure deficits, drier soil, and more frequent extreme events and
540 disturbances (Peñuelas et al. 2017, Yuan et al. 2019, Scheff et al. 2021b). In tropical ecosystems,
541 warming temperatures may exceed the optimum for and therefore decrease photosynthesis (Huang
542 et al. 2019), though resilience to future warming in tropical ecosystems has also been predicted
543 (Sakschewski et al. 2016, Mercado et al. 2018, Ciemer et al. 2019, Sullivan et al. 2020, Smith et
544 al. 2020a).

545

546 Future water availability remains uncertain globally (Sheffield et al. 2009, 2012, Schwalm et al.
547 2011, Dai 2013, Kannenberg et al. 2020, Gampe et al. 2021). A drier global future is expected in
548 many regions (Trenberth et al. 2014, Cook et al. 2020, 2022). However, other evidence suggests
549 there will not be substantial decreases in water availability in the future (Milly and Dunne 2017,
550 Yang et al. 2019). The disagreement stems in part from alternate ways of quantifying drought
551 severity (Swann et al. 2016, Yang et al. 2019), as well as different methods for incorporating
552 warming-induced elevation of atmospheric vapor pressure deficit and its effects on plant stress and
553 mortality (Park Williams et al. 2013, Novick et al. 2016, Yuan et al. 2019, Bauman et al. 2022).
554 In particular, the degree to which plant stomata close in response to elevated CO₂, and thereby
555 reduce evapotranspiration, is uncertain (Lian et al. 2021, Zhou et al. 2022), which may lead to an
556 overestimation of ecosystem water demand (Milly and Dunne 2016).

557

558 **5. Implications for natural climate solutions**

559 Management and policy implications of enhanced growth are large (Cook-Patton et al. 2020),
560 particularly in light of the Paris Agreement, where two-thirds of the signatories indicated they
561 would use the land sink of natural and managed lands to offset emissions (Grassi et al. 2017,
562 Roelfsema et al. 2020). Effectively tackling climate change requires urgent action to reduce
563 anthropogenic emissions while simultaneously removing carbon dioxide from the atmosphere. The
564 challenge is vast and requires the removal of billions of tons of carbon dioxide from the atmosphere
565 to limit global warming to < 2 °C by 2100 (the Paris climate target). NbCS represent a growing
566 suite of strategies to increase land carbon storage and avoid greenhouse gas emissions through
567 natural ecosystem management (Griscom et al. 2017). NbCS represent low-cost methods to reduce
568 the atmospheric CO₂ burden and can be designed to provide multiple co-benefits (Novick et al.
569 2022) such as improved soil health, nutrient retention, biodiversity and drought resilience.
570 Examples include ecological restoration, climate-smart commodity certification, and agricultural
571 land management. Estimates suggest NbCS could technically enhance the land sink by up to 30.6
572 Gt CO₂ equivalents yr⁻¹, or 8.3 PgC yr⁻¹, globally (Roe et al. 2021). This value may even be
573 underestimated if CO₂ and climate effects continue to increase the land sink (e.g., Walker et al.,
574 2022). Reducing deforestation, reforestation, and agroforestry account for the majority of
575 mitigation potential (20 Gt CO₂ equivalents yr⁻¹) (Figure 7).

576
577 Enhanced growth and carbon sequestration has implications for consideration of carbon credits
578 available from forest management that avoids degradation and deforestation (i.e. REDD+) or
579 promotes reforestation (Walker et al. 2022). Existing forests, even if old, continue to act as net
580 carbon sinks, as has been shown by numerous studies (Lewis et al. 2009b, Pan et al. 2011). On the
581 other hand, serious consideration must be given to the biogeochemical and biogeophysical impacts
582 of reforestation and afforestation for carbon sequestration (Winckler et al. 2019, Williams et al.
583 2021, Meier et al. 2021, Windisch et al. 2021). There is also ambiguity about the persistence of
584 growth-enhancement sinks given that some disturbance processes have a return time controlled in
585 part by the size of carbon pools (wind throw, fuel-limited fire regimes). These issues
586 notwithstanding, evidence of growth enhancement is good news for those concerned about rising
587 atmospheric CO₂ and attendant climate changes. Biological responses to longer growing seasons

588 or CO₂ fertilization, for example, offer a natural mitigation mechanism, though still modest
589 compared to current anthropogenic emissions of fossil carbon.

590

591 Despite high expectations, where, when, and how NbCS strategies could be most effective remains
592 unclear. Three challenges limit the feasibility of many potential NbCS projects. First, current
593 measurement, reporting and verification (MRV) methods rely on antiquated inventory techniques
594 and fail to leverage the wealth of ecological observations available (Novick et al. 2022). Second,
595 the models used for projecting the impact of NbCS strategies (Griscom et al. 2017) are highly
596 empirical, do not represent the risks posed by climate change, and therefore do not extrapolate well
597 to the future. Whether NbCS will continue enhancing carbon sinks or reducing emissions is
598 challenging to assess and predict, with initial gains potentially saturating or even reversing over
599 long time scales (Figure 7). Third, major technical advances are needed to reduce project costs in
600 order to reach the large implementation scales needed to effectively meet climate and conservation
601 goals. These challenges call for a deeper integration of the wealth of ecological observations with
602 process-based understanding that incorporates known biophysics and biochemistry, to project
603 ecosystem responses to management and climate change.

604

605 **6. Summary and Future Perspectives**

606 **6.1 Summary**

607 The land biosphere sequesters roughly one third of the CO₂ emitted annually by human activities,
608 with a rate that has doubled from 1.2 ± 0.5 GtC yr⁻¹ in the 1960s to 3.1 ± 0.6 GtC yr⁻¹ in the 2010s.
609 Understanding the causes of the enhanced carbon uptake is essential for evaluating the longevity
610 of this important ecosystem service. With this review, we critically examine evidence of enhanced
611 land uptake and attribute the observed response to drivers and processes. We conclude that there
612 is strong support for an enhanced terrestrial CO₂ uptake globally. Indeed, a more productive land
613 biosphere is an essential requirement to explain the enhanced net terrestrial carbon uptake
614 independently inferred in the global carbon budget (Friedlingstein et al. 2022). Synthesis of the
615 diverse lines of evidence presented here offers compelling, collective support for the existence of
616 an enhanced land sink driven substantially by CO₂ fertilization and, at high latitudes, reduced cold-
617 limitation due to elevated temperatures. However, uncertainties in monitoring and predicting the

618 terrestrial carbon sink persist. Long term ecosystem responses to changing climate regimes, land
619 use change, and nutrient cycling, for example, are still largely uncertain at the global scale.

620 **6.2 Future perspectives**

621 Large opportunities exist to advance understanding of whether the historic enhancement of the
622 land sink will continue into the future or whether limiting factors will begin to play a stronger role
623 (Peñuelas et al. 2017, Yuan et al. 2019). Research should be targeted to address these key
624 questions.

625
626 First and foremost, research is needed to determine the fate of the extra carbon being taken up by
627 photosynthesis (Jiang et al. 2020). Therefore, we advocate for a new generation of large-scale
628 model-guided ecosystem manipulation experiments, where fundamental questions guide
629 experimental design, focused on long-term ecosystem responses, such as FACE experiments.
630 These may be complemented by less expensive, simpler experiments regarding leaf-level
631 photosynthesis and plant-level carbon allocation in controlled environments. Carbon cycle
632 responses to changes in growing season length, as well as the resilience of whole plant and whole
633 ecosystem carbon dynamics subject to climate extremes (Bahn et al. 2014, Kannenberg et al.
634 2020), is of high importance in predicting the future land sink.

635
636 The role of nutrient limitations in constraining ecosystem responses to elevated CO₂ is another
637 area in critical need of investigation, particularly in the tropics (e.g., NGEE-Tropics and Amazon-
638 FACE) (Fleischer et al. 2019, Fleischer and Terrer 2022). The ability of plants to actively stimulate
639 nutrient uptake through interactions with microbial communities and fungal associations (Drake
640 et al. 2011, Terrer et al. 2016) as well as flexibility in stoichiometry in phosphorus cycling
641 (Fleischer et al. 2019) and the ability to alleviate phosphorous limitations (Chen et al. 2020) remain
642 key unknowns. New experiments examining how the response to elevated CO₂ varies with
643 mycorrhizal association and microbial community composition along nutrient gradients are needed
644 (Terrer et al. 2016, 2019).

645
646 Research must address known terrestrial biosphere model deficiencies, in particular in relation to
647 altered competitive and successional dynamics driven by global environmental changes.

648 Demographic models, such as the Functionally Assembled Terrestrial Ecosystem Simulator, are
649 being developed to replicate competitive interactions of individuals at a global scale (Koven et al.
650 2020). These promise a step change in predictive ability, though information with which to
651 constrain important processes such as competition for light (Weng et al. 2015), recruitment, and
652 mortality, is lacking at a global scale, undermining the reliability of their projections (Prentice et
653 al. 2015). Initiatives focused on model benchmarking and functional response analyses, such as
654 the ILAMB project (Collier et al. 2018, Seiler et al. 2022) provide a rigorous system for assessing
655 model efficacy, but efforts that use observations to directly inform predictive models within a data-
656 assimilation framework (Peylin et al. 2016) are still needed. Such efforts would benefit from
657 broader integration of the growing suite of satellite remote sensing observations relevant to the
658 carbon cycle (Schimel et al. 2015a, Schimel and Schneider 2019).

659

660 Sustained, in-situ and remote observation networks (FLUXNET, Earth Observing Satellites,
661 biometric inventories, global CO₂ station networks) are essential for detecting and attributing
662 changes in the biosphere's carbon metabolism and carbon stocks, with new insights coming from
663 each additional year and decade of observations. Improving the representativeness of in situ
664 networks, with attention to increased monitoring of disturbance events and underrepresented
665 regions, is essential in addressing remaining uncertainties of the land carbon sink. While it can be
666 difficult to secure funding for these long-term investments, many of the most valuable insights
667 have come from expensive, large-scale, coordinated activities. Comprehensive data integrations
668 present fruitful opportunities (Schimel et al. 2015b), as do combinations of observations and
669 models to interrogate hypotheses and develop holistic, predictive understanding (Medlyn et al.
670 2015, Norby et al. 2016, Song et al. 2019b). Research using recent remote sensing advances,
671 including in solar-induced fluorescence and vegetation optical depth, and increased temporal and
672 spatial resolution, will also advance understanding of the carbon cycle at the global scale (Schimel
673 and Schneider 2019).

674

675 By improving on previous experimental designs and using advances in model-experiment
676 integration, we expect major advances will narrow the gap between theory and observations. These
677 steps are crucial for understanding the magnitude and causes of the biosphere's trend of increasing
678 carbon uptake and critical for projecting the future evolution of the Earth System.

679 **Glossary**

CO ₂ atmospheric growth rate [I]	The difference in atmospheric CO ₂ concentration between the start and end of each year, representing the sum of all CO ₂ fluxes into and out of the atmosphere by both natural and human processes
Natural land sink [II]	Net carbon sequestered by terrestrial ecosystems independent of direct anthropogenic interventions such as land use and land use change (or net primary productivity minus heterotrophic respiration and other natural C losses to the atmosphere like fire, VOCs etc.)
Net land sink [III]	The balance between terrestrial ecosystem CO ₂ exchange with the atmosphere ecosystem carbon and land use change emissions
Airborne fraction [IV]	The long-term fate of anthropogenic CO ₂ emissions that remain in the atmosphere (not taken up by the land or oceanic sinks)
CO ₂ fertilization [V]	The stimulation of both photosynthetic light and water use efficiency by rising atmospheric CO ₂ concentrations, the response to which can be an increase in photosynthesis and/or a decrease in leaf level water use

680

681 **Table 1: Evidence of an enhanced sink**

Method	Spatial scale	Time scale	Observations	Estimate	Certainty (1-10)	Citations
Yearly atmospheric observations	Global	1960s-present	Enhancing	44% of anthropogenic CO ₂ emissions	10	(Raupach et al. 2008, Ciais et al. 2019, Canadell et al. 2021b)
Atmospheric inversions	Global	1990s-present	Enhancing	0.1 PgC yr ⁻¹ increase*	9	(Peylin et al. 2013)
DGVM output	Global	1800s-present	Enhancing	1.2 ± 0.5 GtC yr ⁻¹ (1960s) to 3.1 ± 0.6 GtC yr ⁻¹ (2010s)*	5	(Friedlingstein et al. 2022)
Satellite observations	Global-regional	1981-present	Widespread greening	Global 0.8% mean LAI increase yr ⁻¹	6	(Jiang et al. 2017a)
Seasonal atmospheric observations	Regional	1960s-present	Enhancing seasonal cycle in northern hemisphere	30-50% increase in the seasonal cycle since 1960s, with a 0.6 ± 0.5 PgC yr ⁻¹ (2000s) summer uptake	8	(Commane et al. 2017, Ciais et al. 2019, He et al. 2022)
Biomass plots	Ecosystem	1960s-present	Increased growth and mortality	0.5 MgC ha ⁻¹ yr ⁻¹ in the tropics	9	(Lewis et al. 2009b, Qie et al. 2017, Hubau et al. 2020)
Eddy covariance flux towers	Ecosystem	1990-present	Enhanced C uptake	0.46 ± 0.09 PgC yr ⁻¹ (1982-2016)	7	(Cai and Prentice 2020, Chen et al. 2022)
Tree rings	Individual	1600s-present	Increased growth rates	Up to 0.7% yr ⁻¹ increase	8	(Cole et al. 2010)

682

683

684

*Atmospheric inversion models include fire and land use change in estimating the land carbon sink, while DGVM output does not consider fire and land use change.

685 **Table 2: Methods of sink enhancement detection and attribution**

Method	Description
Atmospheric observations	Calculating the residual land sink from the global carbon budget based on atmospheric observations of CO ₂ concentrations.
Atmospheric inversion modeling	Combining available atmospheric CO ₂ measurements (both surface observations and satellite-based information on the atmospheric column) with inverted atmospheric transport models to infer optimized land-atmosphere fluxes.
Climate models (CMIP)	Multi-model predictions of historic and future climate changes from natural variability or radiative forcing.
Dynamic Global Vegetation Models (DGVMs)	Models that simulate shifts in vegetation and resulting change in biogeochemical and hydrological cycles in response to climate change.
Satellite observations	The current generation of satellites allows for spatially and temporally explicit estimation of key aspects such as rates of photosynthesis, gross carbon uptake, leaf area, biomass, canopy water content, evapotranspiration, biomass and biomass burning. Despite the plethora of observations, few are available over a long enough period to quantify trends in ecosystem function.
Eddy covariance flux towers	The eddy-covariance technique can directly measure the net exchange of carbon dioxide between ecosystems and the atmosphere. Of the over 2,000 sites around the world, many are now over three decades in operation, supporting estimates of annual net carbon uptake or release by ecosystems over multiple years.
Free atmospheric carbon experiments (FACE)	Artificially enhancing the concentration of CO ₂ around a natural system to observe effects on ecosystem function.

686

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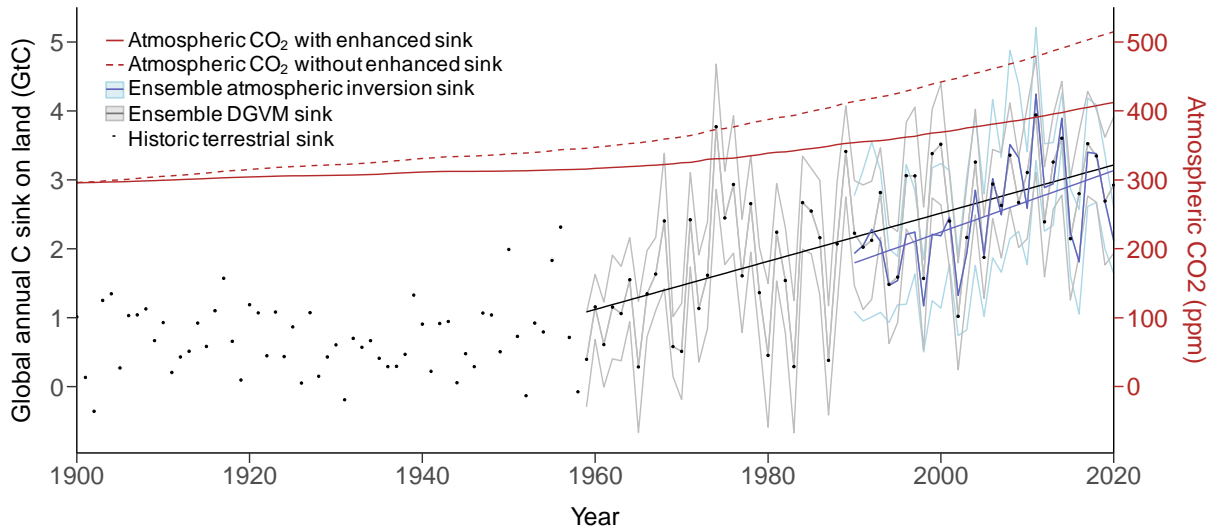
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689 contributed figure data. All authors contributed to writing and made substantial contributions to
690 the discussion of content.

691

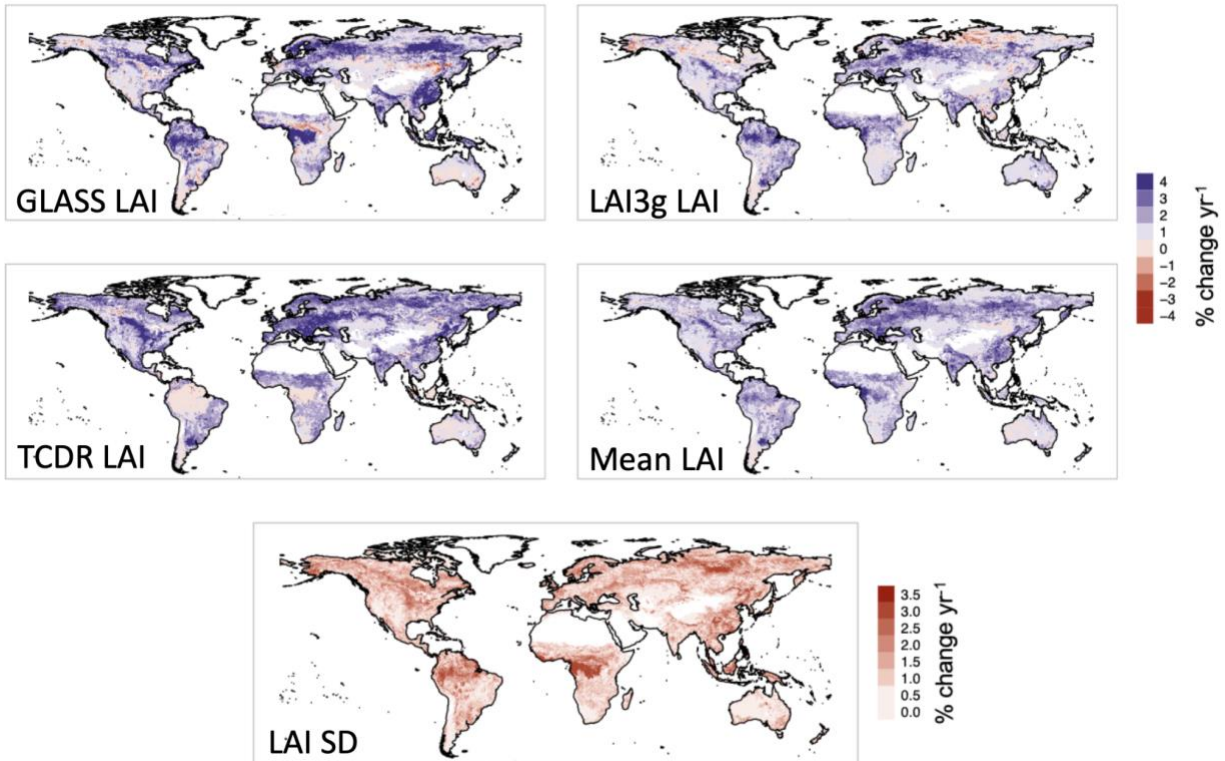
692 **Author Information:** All requests for reprints and permissions should be addressed to the
693 corresponding authors. The authors declare no competing interests.

694

695 **Figures**

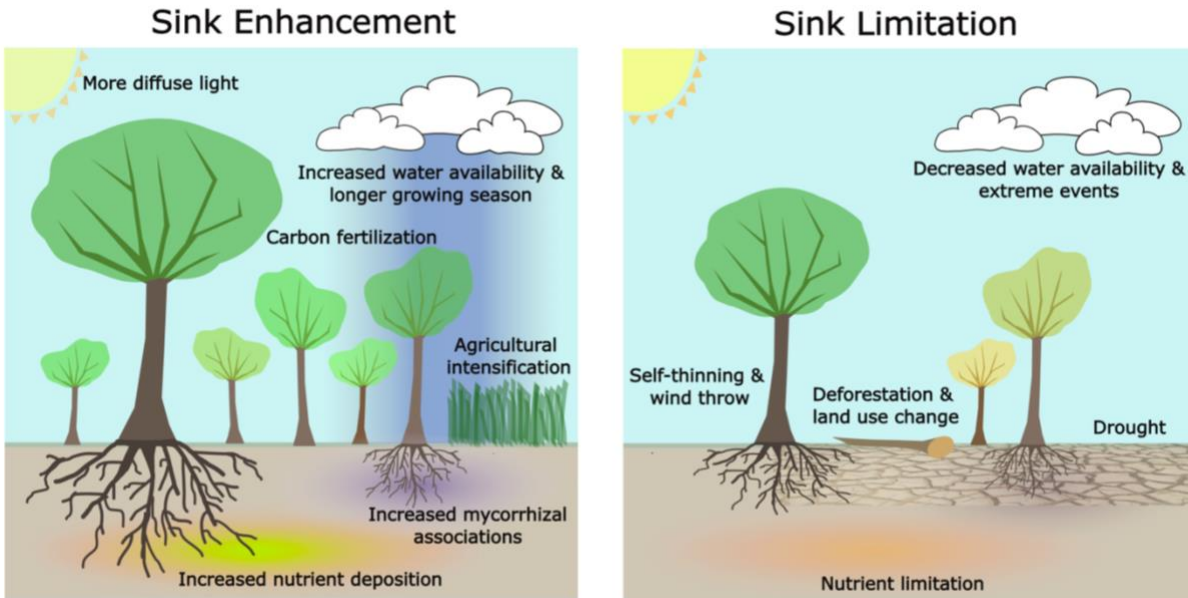


696
 697 **Figure 1 | Historic enhancement of ecosystem carbon sequestration.** Observed atmospheric
 698 CO₂ concentrations (red line) and multiple estimates of the terrestrial carbon sink from 1900 to
 699 2020. Theoretical atmospheric CO₂ concentrations estimated in the absence of an increasing
 700 terrestrial carbon sink (red dashed line) were calculated by detrending the terrestrial sink and
 701 adding the residual carbon to the atmosphere. Historical estimates of the terrestrial sink (dots) and
 702 mean ensemble dynamic global vegetation model (DGVM) projections from 1959 to 2020 (thin
 703 black line) are provided by the Global Carbon Project (Friedlingstein et al. 2022) ± 1 standard
 704 deviation across the 13 models included in the ensemble (gray shading) and linear regression of
 705 the ensemble mean over time (straight black line). Atmospheric inversion mean model estimates
 706 of the land sink from 1990-2020 (thin blue line) ± 1 standard deviation across 6 models (blue
 707 shading) and linear regression line (straight blue line) are from the RECCAP-2 project (Ciais et al.
 708 2022).
 709



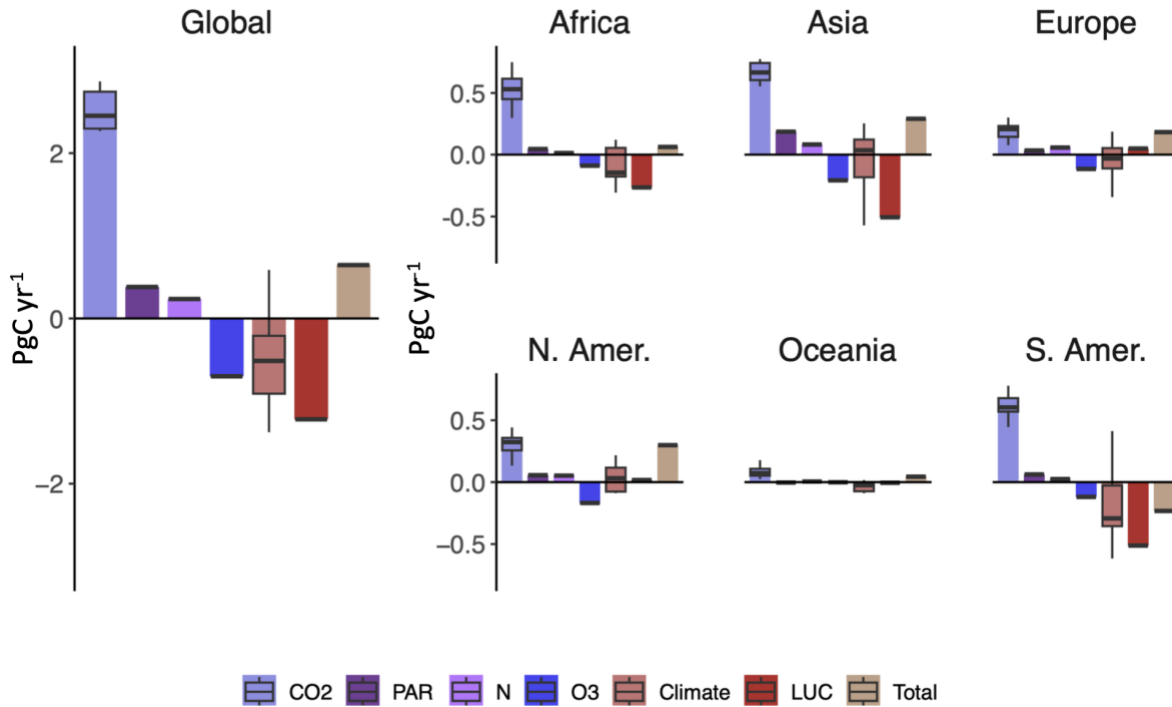
710

711 **Figure 2 | Global changes in vegetation cover.** Long-term trends in maximum leaf area index
712 1982-2016, presented as percent change over time. Changes are estimated as the linear trend of the
713 annual maximum leaf area index (LAI) over vegetated land derived from satellite reflectance
714 observations from GLASS, LAI3g, and TCDR datasets (Jiang et al. 2017b), with mean and
715 standard deviations across the three products.



716

717 **Figure 3 | Changes to the land sink.** The carbon sink on land may be enhanced by several
718 processes, including more diffuse light, release from temperature limitations resulting in a longer
719 growing season, increased water availability, agricultural intensification, increased mycorrhizal
720 associations, increased nutrient deposition, and carbon fertilization. These processes may stimulate
721 enhanced growth including larger and more individuals with increased above and belowground
722 biomass. The carbon sink on land may also be increasingly limited, resulting in less carbon storage
723 or enhanced carbon emissions to the atmosphere. Processes leading to sink limitation include
724 deforestation and other land use change, nutrient limitation, extreme events like drought, and
725 decreased water availability, along with ecosystem responses such as self-thinning. Together, these
726 processes may result in fewer, smaller individuals, with less above and belowground biomass and
727 a smaller carbon land sink. The past, present and future of the land sink is determined by the net
728 result of enhancement and limitation processes.



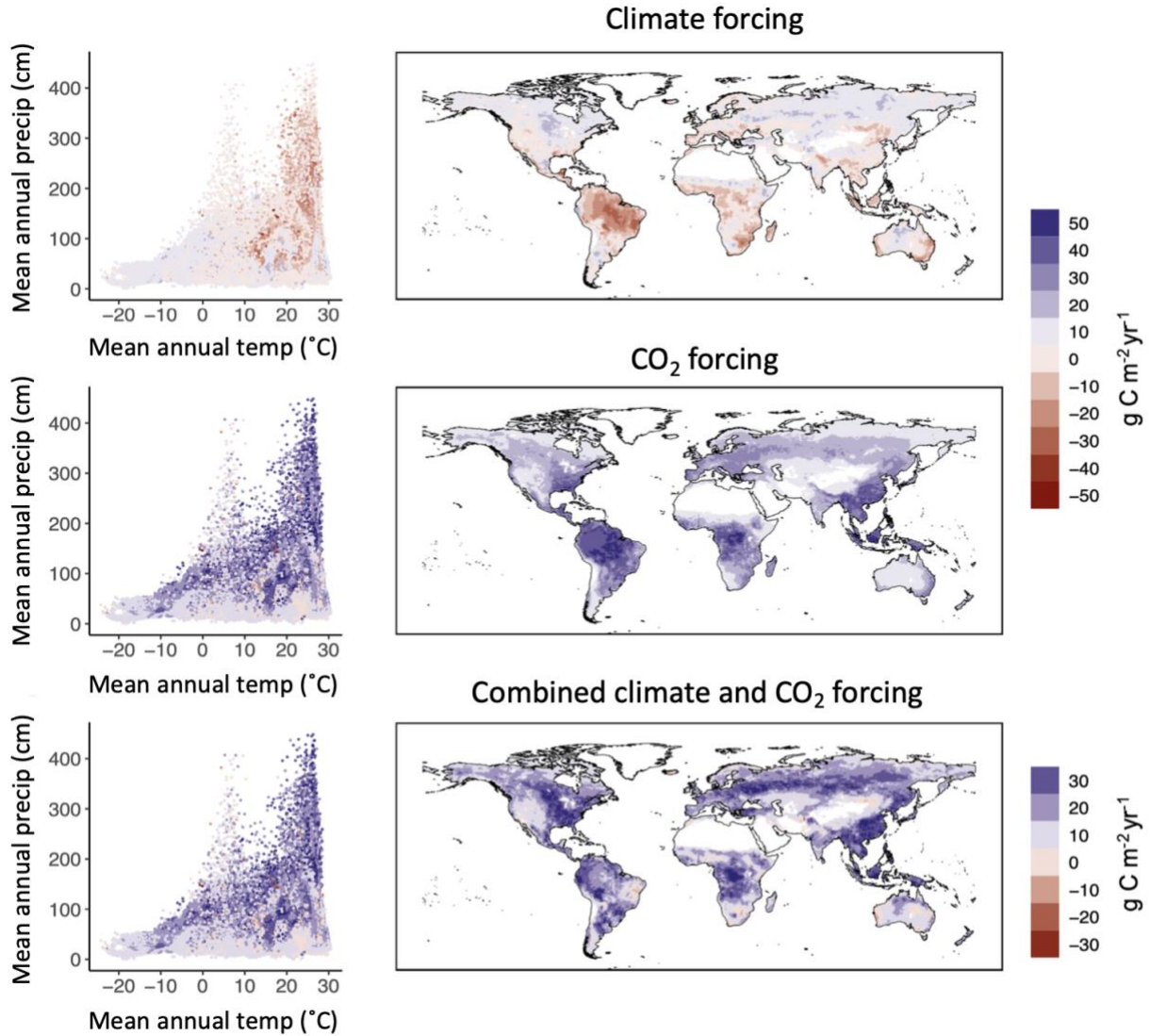
729

730 **Figure 4 | Global and regional carbon flux responses over the 21st century.** Early 21st century
 731 change in net biome carbon exchange reported for individual forcing factors including published
 732 estimates for CO₂ (Sitch et al. 2015), climate (Sitch et al. 2015), ozone (O₃) (Sitch et al. 2007),
 733 light (PAR, photosynthetically active radiation, both diffuse and direct) (Mercado et al. 2009),
 734 nitrogen addition and deposition (N) (Zaehle et al. 2011), land use change (LUC) (Hansis et al.
 735 2015), and their sum (total). Multi-model mean changes are calculated from 1901-1920 to 2001-
 736 2019 for net ecosystem exchange (NEE = ecosystem respiration – gross primary productivity)
 737 based on results from TRENDY-v7 (Sitch et al. 2015).

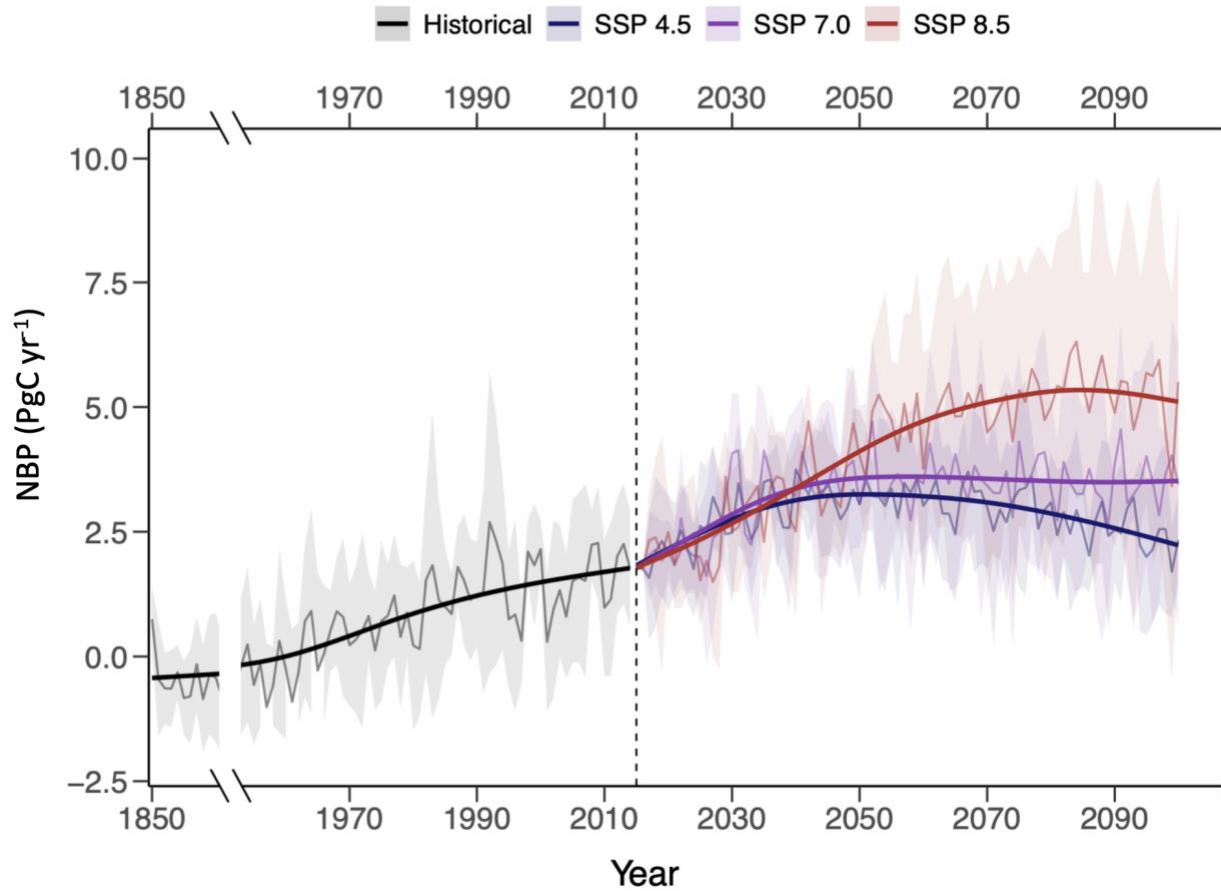
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742 **Figure 5 | Carbon flux responses to CO₂ and climate change over the 20th century.** Multi-
743 model mean changes are calculated from 1901-1920 to 2001-2019 for net ecosystem exchange
744 (NEE = ecosystem respiration – gross primary productivity) based on results from TRENDY-v7
745 (Sitch et al. 2015). Scatter plots denote CO₂ (S2 – (S1 + baseline)) and climate (S1 – (S0 +
746 baseline)) responses based on local temperature and precipitation regimes from the Climatic
747 Research Unit gridded Time Series Version 4 (Harris et al. 2020). Combined (net) effects are the
748 sum of CO₂ and climate responses.

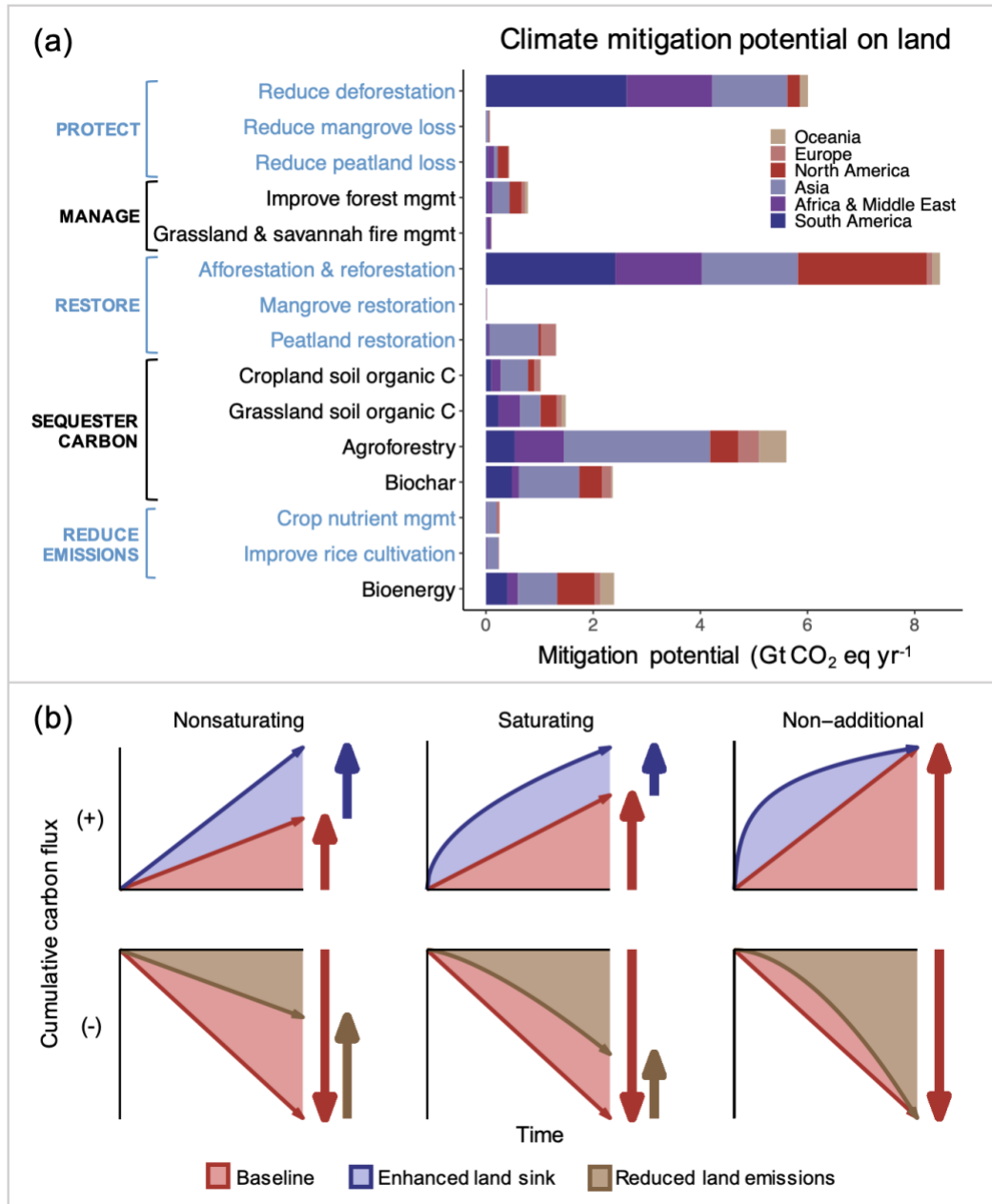


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750 **Figure 6 | Historical and future projections of the natural land sink.** Changes in the net biome
751 production (NBP) of terrestrial ecosystems projected by an ensemble of Earth system models
752 (NorESM2-MM, MPI-ESM1-2-LR, IPSL-CM6A-LR, INM-CM5-0, ESM1-2-LR, CESM2,
753 CanESM5, and MIROC-ES2L) from the Coupled Model Intercomparison Project (CMIP6) for the
754 historical period (1850-2015) (black) and from 2015 to 2100, under different scenarios of future
755 change (SSP 4.5, 7.0 and 8.5 emissions scenarios; blue, purple, and red, respectively). Thin lines
756 show yearly average between all model simulations, with shading representing ± 1 standard
757 deviation across models. Thick lines show loess smooths of mean yearly values.

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762 **Figure 7 | Carbon emission mitigation potential on land.** a) Carbon mitigation potential per year
 763 in Gt CO₂ equivalents for nature-based climate solutions by geographic area. Y-axis labels denote
 764 various strategies, grouped by their method (e.g., protecting existing carbon resources vs. restoring
 765 previously degraded resources) (Roe et al. 2021). b) Theoretical projections of nature-based
 766 climate solutions (NbCS). Enhanced carbon storage relative to baseline situations (red) may
 767 enhance carbon uptake (blue) or reduce carbon emissions (brown) via non-saturating, saturating

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768 or non-additional NbCS. The amount of additional carbon captured (thick blue arrows) or
769 emissions avoided (thick brown arrows) relative to baseline conditions (thick red arrows) by the
770 enhanced land carbon sink varies over time, with non-additional NbCS potentially resulting in
771 little or no long term land carbon sink gains.

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