



Integrating the evidence for a terrestrial carbon sink caused by increasing atmospheric CO₂

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Manuscripts

Integrating the evidence for a terrestrial carbon sink caused by increasing atmospheric CO₂

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108 **Summary**

109 Atmospheric carbon dioxide concentration ([CO₂]) is increasing, which increases leaf-scale
110 photosynthesis and intrinsic water-use efficiency. These direct responses have the potential to
111 increase plant growth, vegetation biomass, and soil organic matter; transferring carbon from the
112 atmosphere into terrestrial ecosystems (a carbon sink). A substantial global terrestrial carbon
113 sink would slow the rate of [CO₂] increase and thus climate change. However, ecosystem CO₂-
114 responses are complex or confounded by concurrent changes in multiple agents of global
115 change and evidence for a [CO₂]-driven terrestrial carbon sink can appear contradictory. Here
116 we synthesise theory and broad, multi-disciplinary evidence for the effects of increasing [CO₂]
117 (iCO₂) on the global terrestrial carbon sink. Evidence suggests a substantial increase in global
118 photosynthesis since pre-industry. Established theory, supported by experiments, indicates that
119 iCO₂ is likely responsible for about half of the increase. Global carbon budgeting, atmospheric
120 data, and forest inventories indicate a historical carbon sink, and these apparent iCO₂-
121 responses are high in comparison with experiments and theory. Plant mortality and soil carbon
122 iCO₂-responses are highly uncertain. In conclusion, a range of evidence supports a positive
123 terrestrial carbon sink in response to iCO₂, albeit with uncertain magnitude and strong
124 suggestion of a role for additional agents of global change.

125
126 **Key words:** global carbon-cycle, land-atmosphere feedback, carbon dioxide, terrestrial
127 ecosystems, free-air CO₂ enrichment (FACE), CO₂-fertilisation hypothesis, CO₂-fertilization,
128 beta factor

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141 Acronyms and abbreviations

142	A_{net}	- Net photosynthetic carbon assimilation
143	fAPAR	- Fraction absorbed photosynthetically active radiation
144	BAI	- Basal area increment
145	BP	- Biomass production, the sum of all tissue production over a given time, typically a year
146	CO ₂	- Carbon dioxide
147	[CO ₂]	- Atmospheric CO ₂ concentration
148	eCO ₂	- Elevated CO ₂ from experiments and CO ₂ springs
149	FACE	- Free air CO ₂ enrichment
150	GPP	- Gross primary production
151	g_s	- Stomatal conductance
152	iCO ₂	- Increasing CO ₂ from fossil fuel emissions and land-use change
153	iWUE	- Intrinsic WUE (A_{net}/g_s)
154	LAI	- Leaf area index
155	NBP	- Net biome production, net land atmosphere exchange
156	NEP	- Net ecosystem production
157	OCS	- Carbonyl sulphide
158	UE	- Use efficiency
159	VPD	- Vapour pressure deficit
160	WUE	- Water use efficiency (transpiration/BP)
161		

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1. Introduction

Photosynthesis uses the energy in sunlight to bind CO₂ to a five-carbon sugar, transferring CO₂ from the atmosphere to plants (Calvin & Benson, 1948; Farquhar *et al.*, 1980). Sugars produced by photosynthesis provide the building blocks and the primary fuel for much of life on Earth. Plant tissues, many microbes, animals, and dead organic matter are all composed of carbon-rich compounds formed from these photosynthetic sugars. In many environments, an increase in atmospheric CO₂ concentration [CO₂] increases photosynthesis. Thus an increase in [CO₂] leads to greater plant sugar availability with the potential to increase the total amount of carbon stored in the live and dead organic matter in an ecosystem. These observations have led to the CO₂-fertilisation hypothesis (Box 1): that plant responses to increasing atmospheric [CO₂] drive increases in terrestrial-ecosystem carbon storage creating negative feedback on atmospheric [CO₂] growth.

Since the industrial revolution human activities have increased [CO₂] by 48 % (1760-2019, 277-411 ppm), an increase in atmospheric CO₂-carbon of 277 Pg C (Friedlingstein *et al.*, 2019). However, global-scale carbon accounting quantifies anthropogenic emissions to the atmosphere at 645 Pg C and suggests a substantial 'natural' terrestrial carbon sink (a net flux of carbon from the atmosphere to intact terrestrial ecosystems) which currently removes the equivalent of 33±9 % of anthropogenic atmospheric CO₂ (2009-2018 (Friedlingstein *et al.*, 2019). Along with the ocean carbon sink, this terrestrial carbon sink is mitigating the rate of climate change.

Process-based carbon-cycle models attribute increasing [CO₂] (iCO₂) as the primary driver of the terrestrial carbon sink, albeit with substantial uncertainty (Huntzinger *et al.*, 2017; Arora *et al.*, 2019). However, iCO₂ is not the only global-change factor that can influence terrestrial carbon stocks. Anthropogenic land-use and land-cover change (hereafter land-use change) and recovery (Pugh *et al.* 2019), nitrogen cycle changes (Fowler *et al.*, 2013), and climate change all affect ecosystem carbon stocks (Keenan & Williams, 2018). A vast and overwhelming literature often disagrees on the size and duration of CO₂-driven increases in terrestrial carbon storage and predictive understanding of this process is a long-standing and unresolved scientific goal.

Predictive understanding of how terrestrial ecosystems respond to iCO₂ requires knowledge of a range of processes, their interactions, and how these processes scale. For example, terrestrial ecosystem responses begin with photosynthesis inside the leaf, yet scale to have long-term global impacts. All the relevant processes must be understood across scales, and ultimately at the global scale because iCO₂ and climate change are global-scale phenomena with decadal to centennial dynamics.

Given that around 50 % of plant biomass is carbon acquired via photosynthesis, it is reasonable to assume that increased photosynthesis increases plant biomass production (BP) and experimentally elevated $[\text{CO}_2]$ (eCO₂) commonly increases BP (e.g. Baig *et al.*, 2015). However, in natural ecosystems iCO₂ may not always increase BP, primarily because plant tissues require nutrients, and BP responses to iCO₂ will interact with soil nutrient availability and other limiting factors (Strain & Bazzaz, 1983; Rastetter *et al.*, 1997). A related argument is that present day $[\text{CO}_2]$ is likely to supply plants with unprecedented carbon availability that may be surplus to BP requirements (Körner, 2003a). This is because for at least one million years prior to the industrial revolution $[\text{CO}_2]$ was much lower (170-300 ppm) (Bereiter *et al.*, 2015).

Ecosystem carbon stocks are the result of both inputs (BP for plants or litter production for soils) and outputs. Thus for the CO₂-fertilisation hypothesis to hold true, the residence time of carbon in an ecosystem must not be reduced by an amount that would negate effects of increased BP on terrestrial carbon pools. However, it has been suggested that both vegetation and soil carbon residence times may be reduced by iCO₂ (van Groenigen *et al.*, 2014; Körner, 2017).

Drawing from multiple disciplines, vast quantities of diverse data have been collected on the $[\text{CO}_2]$ -responses of many processes. Often this evidence can appear conflicting. For example, many Free Air CO₂ Enrichment (FACE) experiments show BP gains (Walker *et al.*, 2019), while others show none (Bader *et al.*, 2013; Ellsworth *et al.*, 2017). Many tree-ring studies indicate historical increases in intrinsic water-use efficiency (iWUE) but no detectable change in BP (Peñuelas *et al.*, 2011; van der Sleen *et al.*, 2015), while the majority of forest-inventory analyses suggest biomass gains (Brienen *et al.*, 2015; Hubau *et al.*, 2020). Flux-tower data, global CO₂-flask networks, and remote-sensing data are now of sufficient timescales (decades) to study CO₂ responses against background variability, but have led to different inferences (Kolby Smith *et al.*, 2016; Fernández-Martínez *et al.*, 2017).

This literature represents a wealth of information and inference that can appear fragmented, posing an opportunity for integration. Thus our overall goal is to provide a synthetic review of key lines of evidence related to the CO₂-fertilisation hypothesis, specifically:

1. overview of theory and potential mechanisms within the CO₂-fertilisation hypothesis;
2. quantitative evaluation of the evidence, identifying agreement and major conflicts;
3. resolution of apparent conflicts and, where not possible, identification of key knowledge gaps to guide future studies.

We structure this multi-disciplinary review within the mechanistic theory of the five broad processes that are key to the CO₂-fertilisation hypothesis (Box 1, Fig. 1a): gross primary

production (GPP), plant biomass production (BP), vegetation mortality rate (k_{veg}), soil organic matter decomposition rate (k_{soil}), and terrestrial carbon storage (C_{eco}). Within each of these high-level processes, numerous inter-related mechanisms and sub-processes shape terrestrial ecosystem CO_2 responses (Fig. 1b, Section 2).

Within these processes we integrate four primary evidence themes (Box 2). eCO₂ studies in evidence theme 1 provide the only direct evidence for CO_2 responses but are restricted in space and time. Observation studies (evidence themes 2-4) span a broader range of evidence types covering larger spatial-scales and longer temporal-scales but provide only indirect evidence for the effect of iCO₂ on terrestrial ecosystems.

To quantify and standardise CO_2 effects across variables and varying ranges of $[\text{CO}_2]$ we report data as a relativised β -factor:

$$\beta = \ln(y_e/y_a) / \ln(\text{CO}_{2,e}/\text{CO}_{2,a}) \quad (\text{Eq. 1})$$

where y_a and y_e are the value of any response variable at lower $[\text{CO}_2]$ ($\text{CO}_{2,a}$) and higher $[\text{CO}_2]$ ($\text{CO}_{2,e}$). Other methods to calculate the β -factor have been proposed (e.g. Friedlingstein *et al.*, 1995) but we use Eq. 1 for ease of interpretation that results from scale-independence (Supporting Information). A β of 1 represents direct proportionality between a variable's CO_2 response and the change in CO_2 . Where possible (i.e. when reported at source) we report uncertainties as 95 % confidence intervals.

As described above, attributing iCO₂ as the cause of trends is confounded by covarying factors which also drive variability in the terrestrial carbon sink. We discuss these other global-change factors in the context of attribution, but do not cover them in depth. The difference between direct evidence from eCO₂ experiments and indirect evidence from historical data (concurrent with a suite of global-change factors) motivates our use of two abbreviations: eCO₂ and iCO₂. As with eCO₂ and iCO₂, we distinguish direct CO_2 responses (β_{dir}) from indirect apparent CO_2 'responses' (β_{app}).

2. Theory—a hierarchy of mechanism

2.1 Direct plant physiological responses to CO_2

Photosynthesis is limited by CO_2 or light (Farquhar *et al.*, 1980). When CO_2 is limiting, theory predicts that eCO₂ increases leaf-scale net carbon assimilation (A_{net}) ($\beta_{\text{dir,hist}} = 0.86$, Table S1). The enzyme that fixes CO_2 (RuBisCO) also catalyses an oxygenation reaction, which results in

CO₂ loss (photorespiration; Farquhar *et al.*, 1980). eCO₂ also suppresses photorespiration (Fig. 2a). Given that photorespiration always occurs during C3 photosynthesis, the suppression of photorespiration by eCO₂ increases A_{net} also when light is limiting, but with a lower response ($\beta_{\text{dir,hist}} = 0.31$). Canopy-scale A_{net} results from a mixture of CO₂ and light-limited photosynthesis, thus has an intermediate eCO₂ response that depends on the fraction of light-saturated leaves in the canopy ($\beta_{\text{dir,hist}} = 0.60 \pm 0.3$, c. 280 to 400 ppm; Fig 2c). As [CO₂] increases, the fraction of light-saturated leaves in the canopy is expected to decrease and therefore historical eCO₂ response of GPP is expected to be higher than the future response ($\beta_{\text{dir,fut}} = 0.46 \pm 0.2$, c. 400 to 550 ppm; Fig 2c).

C4 plants have evolved to concentrate carbon, thus saturating photosynthesis and suppressing photorespiration at low [CO₂] (Ehleringer & Björkman, 1977). Therefore A_{net} in C4 plants is not directly influenced by [CO₂] above c. 200 ppm (Fig. 2a), though water savings from reduced g_s may stimulate A_{net} indirectly (Leahey *et al.*, 2004).

Photosynthesis requires the acquisition of other resources and iCO₂-stimulation of A_{net} increases A_{net} per unit resource consumption, i.e. increases resource use-efficiencies (UE) of: water (WUE), light (LUE), and leaf nitrogen (Cowan, 1982; Drake *et al.*, 1997). Increased use-efficiencies imply a shift in a plant's resource-use economy (Bloom *et al.*, 1985) which is commonly studied using optimisation theory.

Optimisation theory predicts that a change in the ratio of A_{net} to g_s (intrinsic WUE, iWUE) in proportion to the change in [CO₂] (β_{dir} c. 1; Fig 2d) maximises the benefit of carbon gain while minimising the cost of water lost for C3 (Medlyn *et al.*, 2011) and C4 plants (Lin *et al.*, 2015). Canopy-scaling theory predicts that the increase in iWUE is preserved at the canopy scale (Fig 2e). Where the response of A_{net} to eCO₂ is less than proportional ($\beta_{\text{dir}} < 1$) the increase in iWUE (i.e. A_{net}/g_s) implies a reduction in g_s (canopy-scale iWUE $\beta_{\text{dir,hist}} = 1.1 \pm 0.1$, $A_{\text{net}} \beta_{\text{dir,hist}} = 0.60 \pm 0.3$, thus $g_s \beta_{\text{dir,hist}} = -0.53 \pm 0.2$; Fig. 2f,i). Due to the lower predicted A_{net} in the future, the predicted decrease in g_s is greater ($\beta_{\text{dir,fut}} = -0.62 \pm 0.1$).

Optimisation theory also predicts reduction in photosynthetic carboxylation capacity (V_{cmax}), reducing nitrogen demand (Bowes, 1991; Drake *et al.*, 1997). A reduction in leaf nitrogen may also occur due to limited plant-available soil nitrogen (Section 2.2) or physiological competition for the products of electron transport (Bloom *et al.*, 2012).

2.2 Plant biomass production

BP of leaf, wood, and root tissues is controlled by the interplay of source (resource acquisition),

sink (metabolic tissue production) (Muller *et al.*, 2011; Fatichi *et al.*, 2019), and regulatory processes (phenology, hormones) (Schwartz, 2013; Bahuguna & Jagadish, 2015). Within this framework eCO₂ can increase BP when BP is either carbon-source limited or when eCO₂ can alleviate other limitations. Plant BP is carbon-source limited when in competition with respiration for available carbon and when light limits BP (Lloyd & Farquhar, 2008). Sustained periods of high growth may also reduce carbon stores (Würth *et al.*, 2005), potentially leading to carbon-source limitation.

BP is also carbon-sink limited by stoichiometric nutrient requirements (Elser *et al.*, 2010). Thus increased BP requires either increased nutrient acquisition or increased stoichiometric carbon-to-nutrient ratios. Increased plant-available carbon may be able to “pay” for increased nutrient acquisition via a number of mechanisms (e.g. increased fine-root BP, mycorrhizal investment, exudation, atmospheric N fixation) (Luxmoore, 1981; Hungate *et al.*, 1999; Fleischer *et al.*, 2019). Changing stoichiometry may result in feedbacks that compound nutrient limitations by reducing decomposition rates and nutrient availability (Comins & McMurtrie, 1993), known as progressive nitrogen limitation (Luo *et al.*, 2004).

In environments where BP is primarily sink-limited, e.g. tree-lines (temperature-limitation), arid and semi-arid (water-limitation), increased carbon availability may have little effect on BP (Kramer, 1981; Körner, 2003b). However, in water-limited environments, increased iWUE could increase BP (Mooney *et al.*, 1991; Wullschleger *et al.*, 2002). Leaf area index (LAI) may also be limited by water availability (Woodward, 1987; Yang *et al.*, 2018) and increased WUE may increase LAI and light absorption leading to indirect positive feedback on GPP and transpiration (Fatichi *et al.*, 2016; Trancoso *et al.*, 2017).

If BP is restricted by sink limitation, biomass production efficiency (BP per unit GPP) would decrease and the labile products of photosynthesis would accumulate. If BP is stimulated this may be as short-lived, primary tissues (leaves and fine-roots) or long-lived, secondary tissues (wood) (De Kauwe *et al.*, 2014). Division of carbon among these tissues determines residence time of carbon in plant biomass. Wood has greater residence time and thus greater potential to increase C_{veg} accumulation over multiple years. Greater production of short-lived tissues (i.e. leaves and fine-roots) may increase resource capture and will increase litter carbon inputs to the soil.

2.3 Plant mortality

Increases in mortality rates reduce vegetation residence times and have the potential to offset

any biomass gains resulting from increased BP (Eq. B3) (Bugmann & Bigler, 2011; Körner, 2017). Hydraulic failure, and less-so, carbon starvation are thought to be interrelated mechanisms of plant death (McDowell *et al.*, 2008). By easing the carbon and hydraulic impacts of abiotic and biotic stressors such as drought, or pest and pathogen attack, eCO₂ could potentially *decrease* mortality. Greater carbon resources could supply greater maintenance respiration, stored carbon reserves, or synthesis of defense compounds (McDowell *et al.*, 2008). More efficient water use (Section 2.1) could delay the onset or the intensity of drought, which could reduce the risk of xylem-conductivity losses.

Indirect influences on mortality may emerge from the acceleration of individual size-growth. Increased growth could reduce small-size related mortality by speeding individuals out of the hazards of early life (e.g., browsing) and increasing their ability to acquire resources (Metcalf *et al.*, 2014; Hülsmann *et al.*, 2018). Conversely, increased growth could increase large-size mortality risk, with tall trees being more susceptible to hydraulic stress, windthrow, lightning, and certain pests or pathogens (Bugmann & Bigler, 2011; Bennett *et al.*, 2015; Körner, 2017; Trugman *et al.*, 2018).

At the stand-scale, increased growth may accelerate post-disturbance successional dynamics (McDowell *et al.*, 2020). Intensified competition for light, water, and nutrients could lead to early reorganisation and transition (self-thinning) phases of development (Bormann & Likens, 1979), but also an earlier switch from transition to steady-state phases (Miller *et al.*, 2016).

Acceleration of stand-development by eCO₂ may or may not change self-thinning relationships (tree-size to stem-density) of a forest stand, with no change leading to no change in biomass. However, acceleration of stand-development could increase biomass at the landscape scale by closing forest gaps more quickly. Differential mortality effects on different plant species could alter competitive dynamics, community composition, and associated stand properties, e.g. among fast-growing, ruderal/pioneer species and more conservative, slow-growing species (Ruiz-Benito *et al.* 2017).

2.4 Organic matter decomposition

Residence times of litter and soil organic matter (SOM) vary from minutes to millenia and can respond rapidly to environmental perturbation (Trumbore, 2009; Schmidt *et al.*, 2011; Dwivedi *et al.*, 2019). Increases in SOM decomposition rates reduces SOM residence times and has the potential to offset any eCO₂-related increases in litter inputs. Accelerated decomposition of litter and particulate SOM (i.e. priming) can result from microbial responses to increased labile-carbon availability (Kuzyakov *et al.*, 2000; Blagodatskaya *et al.*, 2014), including at depth

(Fontaine *et al.*, 2007). Organic acids produced by roots can destabilise mineral-associated SOM (Keiluweit *et al.*, 2015). eCO₂ effects on environmental conditions could also affect SOM decomposition. CO₂-related increases in soil water (Section 2.1) would likely stimulate decomposition in water-limited ecosystems (Castanha *et al.*, 2018), but could reduce oxygen availability (slowing decomposition) in energy-limited ecosystems.

Microbial activity has also been linked to the formation of mineral-associated SOM (Cotrufo *et al.*, 2013; Liang *et al.*, 2017), and potentially soil aggregates (Ge *et al.*, 2018), which might slow decomposition by restricting microbial access to SOM (Kögel-Knabner *et al.*, 2008). Changing stoichiometry might slow decomposition (Section 2.2). Roots can distribute carbon deeper in the soil where decomposition is slower and capacity for mineral stabilization is higher (Jackson *et al.*, 2017; Hicks Pries *et al.*, 2018).

Greater decomposition rates might also increase soil nutrient availability, potentially reducing plant nutrient limitation (Treseder, 2004; Dijkstra, 2008) or increasing microbial immobilisation. Over longer timescales, nutrient immobilisation can reduce nutrient losses, leading to accumulation of ecosystem nutrient stocks which may enhance mineralisation and progressively release plants from nutrient limitation (Rastetter *et al.*, 1997; Walker *et al.*, 2015).

2.5 Terrestrial ecosystem carbon responses to CO₂

The response of terrestrial carbon storage to eCO₂ (ΔC_{eco}) is the net result of the above discussed processes. Potential increases in BP and litter production are balanced by potential increases in loss rates (Eqs. B3 and B4). Increased BP of short-lived primary tissues such as leaves and fine-roots could lead to greater biomass of these transient C_{veg} pools and to increased litter inputs to the soil. If wood BP is stimulated by eCO₂, over medium timescales (annual to several decades) ecosystem biomass could increase due to the longer residence time of wood. However, wood BP is tied to tree size-growth rates and the effects of tree size on mortality rates may be either positive or negative (Section 2.3). Greater wood BP or greater wood mortality rates would result in greater coarse woody debris, which may immobilise nutrients (e.g. Zimmerman *et al.*, 1995).

Increased plant inputs to litter and soil (e.g., wood, leaf and root litter, root exudates, and mycorrhizal subsidies) could increase C_{soil} . However, the complex processes that drive the formation and decomposition of SOM make the response of C_{soil} to eCO₂ difficult to predict (Schmidt *et al.*, 2011; Dwivedi *et al.*, 2019; Section 2.4). Increased soil mineralisation rates could lead to greater C_{eco} if nutrients are redistributed from soils to plants, which have higher

carbon:nutrient ratios and hence can store more carbon per unit nutrient (Rastetter *et al.*, 1992; Zaehle *et al.*, 2014).

A one-pool ecosystem carbon model (Box 1, Supporting Information) with simplifying assumptions (BP $\beta_{\text{dir}} = \text{GPP } \beta_{\text{dir}}$; residence time $\beta_{\text{dir}} = 0$) provides baseline expected β_{dir} for carbon storage (Fig. 2j-l). The model indicates that when starting carbon storage is non-zero, β_{dir} depends on the time of measurement (Fig. 2j,k). Based on the observed $[\text{CO}_2]$ trend (Le Quéré *et al.*, 2018), the model indicates that β_{dir} calculations over a 30 year period (typical of forest-inventory analysis) are generally a little smaller ($\beta_{\text{dir,hist}}$ c. 0.5) than steady-state ($\beta_{\text{dir,hist}} = 0.6$; Fig 2. l). Departures from these expected β 's derived from GPP responses alone provide a guide to the magnitude of positive and negative feedbacks in eCO₂ studies and can help to guide iCO₂ attribution in historical studies.

3. The Evidence

3.1 Physiology

Carbon assimilation and GPP

Evidence across FACE experiments (11 sites, 45 species) showed that eCO₂ increased leaf-level, light-saturated photosynthesis ($\beta_{\text{dir}} = 0.73 \pm 0.2$), and supports differences between C₃ ($\beta_{\text{dir}} = 0.79 \pm 0.2$) and C₄ species ($\beta_{\text{dir}} = 0.27 \pm 0.2$) (Ainsworth & Long, 2005; all reported β 's are in Table 1). Evidence suggests that maximum photosynthetic capacity acclimated (reduced) to eCO₂, primarily maximum carboxylation capacity ($\beta_{\text{dir}} = -0.38 \pm 0.1$) (Ainsworth & Long, 2005; Ainsworth & Rogers, 2007). Nevertheless, in many forest eCO₂ experiments photosynthetic stimulation (>5 years) was only minimally affected by acclimation (Crous *et al.*, 2008; Bader *et al.*, 2010; Ellsworth *et al.*, 2017).

Indirect evidence also suggests increased photosynthesis with iCO₂. Deuterium isotopomers of glucose in plant archives indicate that the leaf-level photorespiration:assimilation ratio decreased since pre-industry ($\beta_{\text{app}} = -0.99$) (Ehlers *et al.*, 2015), which translates to an increase in photosynthesis ($\beta_{\text{app}} = 1.0$) (Ehlers *et al.*, 2015). GPP estimates from eddy-covariance (23 sites, c. 20 years) suggest a recent increase ($\beta_{\text{app}} = 1.6 \pm 0.9$), implicating a substantial iCO₂ contribution ($\beta_{\text{dir,hist}} = 1.2 \pm 0.6$) (Fernández-Martínez *et al.*, 2017). Eddy-covariance data used to calibrate a model suggests a lower iCO₂ response ($\beta_{\text{dir,hist}} = 0.5 \pm 0.2$) (Ueyama *et al.*, 2020).

Ice-core measurements of atmospheric carbonyl sulfide (OCS) combined with mass-balance analysis suggests that global GPP has increased since pre-industry ($\beta_{\text{app}} = 0.95 \pm 0.2$) (Campbell

419 *et al.*, 2017). As do ice-core measurements of atmospheric O₂ isotopes combined with models
 420 ($\beta_{\text{app}} = 1.3 \pm 2.3$) (Ciais *et al.*, 2012). Satellite-based evapotranspiration combined with an
 421 ecosystem WUE model estimated increased GPP during recent decades ($\beta_{\text{app}} = 1.1 \pm 0.5$)
 422 (Cheng *et al.*, 2017). 14 methods to estimate GPP from satellite-based fAPAR resulted in wide-
 423 ranging iCO₂ sensitivities (β_{dir} range = -0.39 ± 0.34 to 1.6 ± 1 , mean = 0.52 ± 0.3 ; 2000-2014) (Sun
 424 *et al.*, 2019).

425 Water use efficiency, stomatal conductance, and transpiration

426 Experimental evidence also supports increased iWUE in response to eCO₂ ($\beta_{\text{dir}} = 1.2 \pm 0.4$; 4
 427 sites, 7 species) (Ainsworth & Long, 2005). At two FACE experiments (Duke University and Oak
 428 Ridge National Laboratory, ORNL), tree-ring $\delta^{13}\text{C}$ implies increased iWUE ($\beta_{\text{dir}} = 1.4$ and 1.3 ,
 429 respectively) (Battipaglia *et al.*, 2013). Tree-ring $\delta^{13}\text{C}$ samples from across the globe suggest
 430 increased iWUE in many biomes since pre-industry in: northern boreal gymnosperms ($\beta_{\text{app}} =$
 431 1.2 ± 2 to 1.5 ± 1.6) (Saurer *et al.*, 2004), tropical forests ($\beta_{\text{app}} = 1.0$) (van der Sleen *et al.*, 2015),
 432 and a wide range of forest biomes ($\beta_{\text{app}} = 1.19$; Keller *et al.*, 2017). Attribution to iCO₂ also
 433 suggests increases in iWUE in European *Pinus* and *Quercus* ($\beta_{\text{dir}} = 1.0 \pm 0.6$ and 0.67 ± 0.9 ; 9-14
 434 sites) (Frank *et al.*, 2015). Additional environmental factors have contributed to observed iWUE
 435 trends, e.g. drying trends have increased iWUE (Saurer *et al.*, 2014).

436 $\delta^{13}\text{C}$ in atmospheric CO₂ combined with mass-balance modelling suggests a global increase in
 437 iWUE since pre-industry ($\beta_{\text{app}} = 0.94 \pm 0.2$) (Keeling *et al.*, 2017).

438 Evidence from Duke and ORNL FACE experiments supports increases in ecosystem-scale
 439 plant WUE (annual BP/T; $\beta_{\text{dir,hist}} = 0.76$ and 1.1 , respectively) (De Kauwe *et al.*, 2013). Inferred
 440 from eddy-covariance, 'inherent' WUE (VPD.GPP/ET) increased in temperate and boreal forests
 441 with notably higher magnitude ($\beta_{\text{app}} = 4.72$; 21 sites) (Keenan *et al.*, 2013). A follow up study
 442 reduced this estimate ($\beta_{\text{app}} = 2.5$) (Mastrotheodoros *et al.*, 2017). An eddy-covariance
 443 calibrated, canopy-scale model suggested iCO₂ reduced g_s ($\beta_{\text{dir,hist}} = -0.28 \pm 0.09$) and increased
 444 iWUE ($\beta_{\text{dir,hist}} = 0.73 \pm 0.2$) (Ueyama *et al.*, 2020). Satellite-based models (2000-2013) of GPP
 445 and ET suggest smaller or decreased WUE (GPP/ET) ($\beta_{\text{app}} = -0.49$ and 0.28) (Tang *et al.*, 2014;
 446 Xue *et al.*, 2015).

447 Experimental evidence has thoroughly demonstrated reduced leaf-scale g_s in response to eCO₂
 448 ($\beta_{\text{dir,fut}} = -0.22 \pm 0.15$) (Medlyn *et al.*, 2001). Averaged across FACE experiments (12 sites, 40
 449 species), eCO₂ reduced g_s ($\beta_{\text{dir,fut}} = -0.60 \pm 0.2$) but with substantial variability across functional
 450 groups (Ainsworth & Long, 2005) and disturbance history (Donohue *et al.*, 2017). Notably for
 451 *Eucalyptus saligna* in whole-tree chambers, canopy-scale iWUE was very tightly constrained

($\beta_{\text{dir,fut}} = 0.98 \pm 0.2$), and variability in the A_{net} response controlled the g_s response (Barton *et al.*, 2012).

Across four FACE experiments (Duke, EucFACE, ORNL, Swiss Canopy Crane), transpiration responses were only reduced by eCO₂ at ORNL ($\beta_{\text{dir,fut}} = -0.54$), an ecosystem that is rarely water limited (Leuzinger & Körner 2010) (De Kauwe *et al.*, 2013; Gimeno *et al.*, 2018). Airborne remote sensing suggested decreased evapo-transpiration with long-term volcanically-derived eCO₂ in California (Cawse-Nicholson *et al.*, 2018). Stream-gauge networks indicate global increases in runoff (Gedney *et al.* 2006), in agreement with reduced g_s over the northern hemisphere extratropics (Knauer *et al.*, 2017). However, decreases in runoff have also been observed (Ukkola *et al.*, 2016; Trancoso *et al.*, 2017) and modest run-off increases across the tropics have been driven by precipitation increases (Yang *et al.*, 2016).

3.2 Biomass production

eCO₂ increased BP in four temperate-forest, stand-scale (25-30 m diameter) FACE experiments in the early years ($\beta_{\text{dir,fut}} = 0.56 \pm 0.2$) (Norby *et al.*, 2005) and over a full decade ($\beta_{\text{dir,fut}} = 0.49 \pm 0.3$) (Walker *et al.*, 2019). These forest ecosystems were in the early phases of secondary succession (initiated 1-13 years following a major disturbance). In three later-succession forests (c. 100 years old), BP did not respond to eCO₂ (note fine-root BP was often not measured): deciduous broadleaved trees ($\beta_{\text{dir,fut}} = -0.097 \pm 1.0$ to 0.55 ± 1.7) (8 years; Bader *et al.*, 2013), *Picea abies* ($\beta_{\text{dir,fut}} = -0.30 \pm 0.7$, 5 years eCO₂; Klein *et al.*, 2016), and a low productivity *Eucalyptus* woodland ($\beta_{\text{dir,fut}} = -0.26 \pm 0.6$, 4 years eCO₂; Ellsworth *et al.*, 2017; Jiang *et al.*, 2020).

eCO₂ consistently decreased specific leaf area ($\beta_{\text{dir,fut}} = -0.16 \pm 0.07$) (Ainsworth & Long, 2005), which requires increased leaf BP at a given LAI (De Kauwe *et al.*, 2014). Synthesis of experiments (19 sites) suggests that eCO₂ increased grassland leaf and stem BP ($\beta_{\text{dir,fut}} = 0.17 \pm 0.07$) (Hovenden *et al.*, 2019), related to summer water savings and spring water availability (Morgan *et al.*, 2004; Hovenden *et al.*, 2019). Meta-analysis found eCO₂ increased fine-root BP across experiments ($\beta_{\text{dir,fut}} = 0.56$) ($\beta_{\text{dir,fut}} = 0.56$), in forests ($\beta_{\text{dir,fut}} = 0.92$), and to a lesser degree in grasslands ($\beta_{\text{dir,fut}} = 0.18$) (Nowak *et al.*, 2004).

Tree-ring analysis at CO₂-springs in Italy (two sites) suggests that eCO₂ increased *Quercus ilex* tree ring-width (a proxy for wood BP) initially ($\beta_{\text{app}} = 0.49$ -0.81), and the increase diminished as trees aged (Hättenschwiler *et al.*, 1997). Basal-area increment (BAI) analysis showed the eCO₂ response stabilised at around 10 years ($\beta_{\text{app}} = 0.27$) (Norby *et al.*, 1999).

484 A large number of tree-ring studies have found little evidence for increases in wood BP. No
 485 detectable trends in BAI were found across tropical forests (3 sites, 12 species) (van der Sleen
 486 *et al.*, 2015), and both increasing and decreasing trends were found across North American
 487 boreal forests (598 sites, 19 species) (Girardin *et al.*, 2016). Syntheses across biomes found no
 488 significant increase in tree ring-width since 1950 ($\beta_{app} = 0.23 \pm 0.8$; 40 sites) (Peñuelas *et al.*,
 489 2011) and variable responses of BAI ($\beta_{app} = 0.45 \pm 0.7$; 37 sites, 22 species) (Silva & Anand,
 490 2013). Conversely, *Pinus* and *Quercus* tree-rings from Missouri showed a positive response to
 491 iCO₂ that diminished with tree age ($\beta_{app} = 3.3$, at age one; $\beta_{app} = 1.1$, at age 50) (Voelker *et al.*,
 492 2006).

493 Evidence from multi-plot inventory data consistently show increasing wood biomass (Section
 494 3.5), but few of these studies quantify wood BP. A single census interval of eastern-US Forest
 495 Inventory Analysis plots (20,000) suggested very little change in wood BP (Caspersen, 2000),
 496 but with high uncertainty (Joos *et al.*, 2002). Two large tropical-forest plots showed no change in
 497 aboveground wood BP (Clark *et al.*, 2010; Rutishauser *et al.*, 2019). In contrast, tropical forest-
 498 plot networks (321 and 244) suggest that aboveground wood BP increased in Amazonia ($\beta_{app} =$
 499 1.2 ± 0.6) (Brienen *et al.*, 2015) and Africa ($\beta_{app} = 0.69 \pm 0.63$) with a regression-attributed iCO₂
 500 response ($\beta_{app} = 0.54 \pm 1$) (Hubau *et al.*, 2020). Analysis of worldwide forest plots (695)
 501 suggested that wood BP increased ($\beta_{app} = 0.94 \pm 1.1$) in recent decades (Yu *et al.*, 2019).

502 BP-nutrient interactions and progressive nitrogen limitation

503 At Duke FACE, nitrogen availability influenced the magnitude of BP responses (McCarthy *et al.*,
 504 2010) and experiments in later-succession systems with no BP response were limited by
 505 nitrogen (Flakaliden; Sigurdsson *et al.*, 2013) and phosphorus (EucFACE; Ellsworth *et al.*,
 506 2017). Limiting factors were not examined for a number of the other later-succession
 507 experiments (Bader *et al.*, 2013; Klein *et al.*, 2016).

508 eCO₂ experiments in early-succession ecosystems suggest that BP gains were supported by
 509 increased nitrogen acquisition rather than changes in stoichiometry (Finzi *et al.*, 2007; Zaehle *et al.*,
 510 2014). Nitrogen acquisition was increased through increased fine-root BP (see above),
 511 changing root traits (Iversen, 2010; Nie *et al.*, 2013; Beidler *et al.*, 2015), and below-ground
 512 carbon flux to mycorrhizal symbionts and rhizosphere microbial associations (Section 3.4;
 513 (Drake *et al.*, 2011; Phillips *et al.*, 2011; Terrer *et al.*, 2018). Meta-analysis suggests that eCO₂
 514 increased nitrogen fixation in more intensively manipulated experiments but not in more natural
 515 settings (total 441 studies, rates were scaled to plant or ground-area units; Hungate,
 516 unpublished).

Experimental evidence for progressive nitrogen limitation is limited to a single forest (ORNL; Norby *et al.*, 2010) and a single grassland (Biocon; Reich *et al.*, 2006). Paleo-climatic evidence suggests that despite increasing carbon storage the nitrogen cycle became more open between the last glacial maximum and the industrial revolution (Fischer *et al.*, 2019; Jeltsch-Thömmes *et al.*, 2019).

Leaf area, water, and land cover interactions

In some low LAI ecosystems, eCO₂ increased LAI, but did not in higher LAI (c. 5) ecosystems (Norby & Zak, 2011; Bader *et al.*, 2013). However, low LAI (c. 1) at EucFACE did not respond to eCO₂ (Duursma *et al.*, 2016). The LAI response to eCO₂ in low LAI systems has been interpreted as CO₂ accelerating open canopies towards closure (Körner, 2006). However, evidence from two FACE sites (Duke and Rhinelander) suggests that LAI can be higher at canopy closure (Walker *et al.*, 2019). Higher above-ground biomass in some grasslands (Hovenden *et al.*, 2019) indicates potential LAI increases, though increases in leaf mass per unit area would reduce the LAI response relative to the biomass response. High grassland biomass responses have been linked to low soil matric potential (Morgan *et al.*, 2004), though more complex interactions with precipitation seasonality have also been indicated (Hovenden *et al.*, 2019).

Satellite data show “greening” trends over much of the planet, inferred as increasing LAI (Zhu *et al.*, 2016; Mao *et al.*, 2016) and with model-based attribution primarily to iCO₂ (Zhu *et al.*, 2016). Consistent with theory, satellite greenness data suggests increased foliage cover in warm and semi-arid regions, likely an iCO₂ effect via increased WUE (Donohue *et al.*, 2013). Tree-rings have indicated decreasing sensitivity to rainfall or drought in the Eastern US, possibly indicating WUE-mediated iCO₂ response (Wyckoff & Bowers, 2010; Helcoski *et al.*, 2019). However, less severe droughts, noted in the Eastern US, likely appear as reduced growth sensitivity (Maxwell *et al.*, 2016). At the Florida scrub oak experiment, eCO₂ alleviated drought-related declines in NEP (Li *et al.*, 2007) but the opposite was observed at the Nevada desert FACE (Jasoni *et al.*, 2005).

3.3 Plant mortality

Greenhouse experiments with potted plants have found little benefit of eCO₂ on survival during drought or high temperature (e.g. Duan *et al.*, 2014; Bachofen *et al.*, 2018). However, remote sensing evidence shows increased vegetation cover in drylands (Donohue *et al.*, 2013; Section 3.2) which possibly suggests a reduction in mortality in those regions.

We are unaware of direct or indirect evidence for CO₂-related increases in individual-scale mortality, but growth-mortality relationships provide insight. Evidence supports both an inter-specific growth-survival tradeoff (Wright *et al.*, 2010; Bugmann & Bigler, 2011) and an intra-specific tradeoff (Bigler & Veblen, 2009; Di Filippo *et al.*, 2012, 2015; Büntgen *et al.*, 2019). However, there are common exceptions with some high-growth-rate species with long lifespans (Rüger *et al.*, 2020), and other species that show no, or even negative, growth-mortality relationships (Ireland *et al.*, 2014; Cailleret *et al.*, 2017).

Experimental evidence for stand-scale mortality responses to eCO₂ is rare. In the young, regenerating stand at Rhineland FACE, over 11 years of eCO₂ lowered rates of self-thinning (i.e. higher stand basal area for any given stem density) (Kubiske *et al.*, 2019).

At broader scales, most inventory networks have shown increases in stand-scale mortality rates. Increases in biomass mortality have been observed in Amazon forests ($\beta_{\text{app}} = 2.4$) (Brienen *et al.*, 2015) and across continents ($\beta_{\text{app}} = 1.6\text{--}3.9$) (Yu *et al.*, 2019). Tree stem mortality rates have increased, across species, elevation, and tree size, in the western US ($\beta_{\text{app}} = 6.2 \pm 3$; van Mantgem *et al.*, 2009) and in Canada ($\beta_{\text{app}} = 6.1$) (Peng *et al.*, 2011). However, none of these studies conclusively attribute trends to iCO₂ and other global change (e.g. temperature) and biotic (e.g. pest and pathogens) agents have often been attributed drivers of mortality trends (Peng *et al.*, 2011; Luo & Chen, 2015). Finally, several networks observed decreases or non-significant changes, e.g. in stem mortality rates in Germany (Pretzsch *et al.*, 2014) and biomass mortality in tropical Africa ($\beta_{\text{app}} = -0.88 \pm 2$), although multiple-regression estimated that CO₂ increased mortality ($\beta_{\text{dir,hist}} = 1.8 \pm 4$) (Hubau *et al.*, 2020).

3.4 Organic matter decomposition

Evidence for changes in SOM-decomposition rates comes primarily from experiments. Many eCO₂ experiments have demonstrated increased plant litter production and allocation of carbon belowground (e.g. Drake *et al.*, 2011; Iversen *et al.*, 2012). Meta-analysis (53 experiments, primarily FACE and OTC) showed that eCO₂ increased litter production ($\beta_{\text{dir,fut}} = 0.4 \pm 0.1$) and SOM-decomposition rates ($\beta_{\text{dir,fut}} = 0.34 \pm 0.2$) (van Groenigen *et al.*, 2014), yet priming effects are difficult to detect in field studies (van Groenigen *et al.*, 2014; Georgiou *et al.*, 2015).

Results from ecosystem-scale experiments indicate some heterogeneity and nuance in these responses. For example, in a scrub oak ecosystem, 6 years of eCO₂ increased SOM decay despite unchanged microbial biomass (Carney *et al.*, 2007), and at ORNL FACE a decade of eCO₂ resulted in a small but non-significant increase in surface-soil SOM decomposition along

with a reduction in microbial nitrogen (Iversen *et al.*, 2012). In a later-succession forest, eCO₂ increased microbial biomass ($\beta_{\text{dir,fut}} = 0.40 \pm 0.4$) but with no change in soil respiration ($\beta_{\text{dir,fut}} = -0.18 \pm 0.7$) (Bader & Körner, 2010). At EucFACE +30 ppm eCO₂ increased soil respiration ($\beta_{\text{dir,fut}} = 1.3$), but a further increase of 120 ppm produced no additional effect after 3 months ($\beta_{\text{dir,fut}} = 0.3$) or 3 years ($\beta_{\text{dir,fut}} = 0.21$) (Drake *et al.*, 2016, 2018). This 3-year response was non-significant but accounted for about half of the additional carbon acquired under eCO₂ (Jiang *et al.*, 2020).

Data on long-term changes in SOM decomposition in response to iCO₂ remains limited. Synthesis of 23 flux-towers with increased GPP (Section 3.1) suggested a non-significant increase in ecosystem respiration (R_e) ($\beta_{\text{app}} = 0.58 \pm 1$) (Fernández-Martínez *et al.*, 2017). Synthesis and statistical upscaling of chamber measurements suggested that global soil respiration has increased ($\beta_{\text{app}} = 0.22$) (Bond-Lamberty & Thomson, 2010). Statistical predictors of this trend include temperature anomaly and year (possibly an iCO₂ effect). Notably, heterotrophic respiration would be expected to increase if C_{soil} increased, even with no change in decomposition rates.

Accelerated SOM decomposition may release nutrients and feed back onto the activity of plant processes. For example, at Duke FACE increased root exudation ($\beta_{\text{dir,fut}} = 1.1 \pm 0.6$) was coupled with a non-significant but substantial increase in microbial biomass ($\beta_{\text{dir,fut}} = 1.1 \pm 1.3$) and production of nitrogen-acquiring extracellular enzymes (Phillips *et al.*, 2011). Exoenzyme activity was increased at Duke and Rhinelander FACE (Larson *et al.*, 2002; Finzi *et al.*, 2006), although no change in nitrogen mineralisation was observed in lab incubations (Zak *et al.*, 2003), perhaps suggesting that stimulation of microbial activity required plant inputs. Conversely, leaf $\delta^{15}\text{N}$ suggests that eCO₂ may have increased nitrogen mineralisation but not ring-width in mature trees in a European forest (Bader *et al.*, 2013). eCO₂ increased nitrogen and phosphorus mineralisation for a limited period at EucFACE (Hasegawa *et al.*, 2016) and enzyme activity in an alpine forest (Souza *et al.*, 2017). Conversely, meta-analysis suggests eCO₂ increased fine root C:N ratios ($\beta_{\text{dir,fut}} = 0.13$) (Nie *et al.*, 2013), which are associated with lower decomposability.

Contrasting mycorrhizal associations have been linked to biomass responses under low soil nitrogen conditions (Phillips *et al.*, 2013; Terrer *et al.*, 2016). Ectomycorrhizal (ECM) fungi are assumed capable of stimulating SOM decomposition, while arbuscular mycorrhizal (AM) fungi are not, resulting in increased nitrogen in aboveground BP in ECM trees but not in AM plants, primarily grasses (Terrer *et al.*, 2018). Conversely, AM association with *Avena fatua* in a lab and

field setting increased SOM-decomposition rates under eCO₂ ($\beta_{\text{dir,fut}} = 1.4$) (Cheng *et al.*, 2012).

3.5 Terrestrial ecosystem carbon

Direct evidence from site-scale studies

In the four longest-running FACE experiments eCO₂ over a decade increased C_{veg} increment ($\beta_{\text{dir,fut}} = 0.60 \pm 0.4$) in these early-succession temperate forests (Walker *et al.*, 2019). eCO₂ of geological origin increased tree basal area in 30 year old trees ($\beta_{\text{dir,fut}} = 0.23-0.39$) (Hättenschwiler *et al.*, 1997). Conversely, in the later-succession forest at EucFACE, four years of eCO₂ did not increase C_{veg} increment (Jiang *et al.*, 2020), likely because of phosphorus limitation (Ellsworth *et al.*, 2017). Other experiments in later-succession forests did not quantify C_{veg}. Meta-analysis and extrapolation (138 experiments) predicted a global increase in C_{veg} ($\beta_{\text{dir,fut}} = 0.22 \pm 0.1$) related to soil C:N ratio in AM-associated ecosystems and soil phosphorus in ECM-associated ecosystems (Terrer *et al.*, 2019). Biomass responses were generally higher in ECM systems than in AM systems (Terrer *et al.*, 2016), while another meta-analysis showed analogous biomass responses in trees compared with grasses (Song *et al.*, 2019).

Synthesis of meta-analyses found that eCO₂ increased C_{soil} across all (>200) experiments analysed ($\beta_{\text{dir,fut}} = 0.039 \pm 0.03$) but not in field experiments lasting ≥ 2 years without nitrogen addition (25) ($\beta_{\text{dir,fut}} = 0.0054 \pm 0.03$) (Hungate *et al.*, 2009). However, C_{soil} responses to eCO₂ at individual sites are mixed. For example, a decade of eCO₂ increased C_{soil} at ORNL FACE ($\beta_{\text{dir,fut}} = 0.51 \pm 0.6$, 0-90 cm) (Iversen *et al.*, 2012) and in a desert ecosystem ($\beta_{\text{dir,fut}} = 0.59 \pm 0.62$) (Evans *et al.*, 2014), but not in a scrub oak ecosystem ($\beta_{\text{dir,fut}} = -0.15 \pm 0.5$) (Hungate *et al.*, 2013). In the desert ecosystem, inorganic carbonate pools may have contributed to increases in C_{soil} through nocturnal CO₂ uptake (Hamerlynk *et al.* 2013) though net effects are likely small (Soper *et al.*, 2016).

Given limited data, litter addition experiments can also provide insight. Synthesis of priming responses to litter addition (26 studies) suggested that 32 % of litter inputs accumulate as C_{soil} (Liang *et al.*, 2018). 10-30 years of doubled aboveground-litter inputs in temperate forests increased C_{soil} at two sites (29 \pm 13 % and 33 \pm 28 %) but had no effect at three sites (Lajtha *et al.*, 2018), nor in one tropical forest (Sayer *et al.*, 2019). Based on these responses and assuming doubled CO₂ doubles litter production (which is unlikely), $\beta_{\text{dir,hist}}$ would range from 0 to 0.41 \pm 0.3.

Measurement of NEP requires whole-ecosystem enclosure, thus data are few. In a US salt-marsh higher rates of NEP were sustained over 19 years in both C3 and C4 communities

(Drake 2014). A data-assimilation approach provided a comprehensive carbon budget at EucFACE showing no change in C_{eco} (Jiang *et al.*, 2020).

Indirect evidence from global and regional studies

Spatially-explicit atmospheric $[CO_2]$ measurements, fossil-fuel emissions, and other data are integrated using atmospheric transport models to infer terrestrial net biome production (NBP). These “inversions” suggest a global NBP of 2.3 ± 0.9 (MACC-II), 2.3 ± 1.5 (Jena-CarboScope) (1995-2014; Fernández-Martínez *et al.*, 2018), and 1.9 ± 0.5 $PgC\ y^{-1}$ (2010-2014) (Li *et al.*, 2018) and all estimated positive trends in global NBP ($\beta_{app} = 19 \pm 7, 11 \pm 4, 9.8 \pm 5$). These estimates of NBP include both ‘natural’ NBP and land-use change-related (instantaneous and legacy) NBP. Global land-use change-related NBP was estimated from bookkeeping models at -1.4 ± 1.4 $PgC\ y^{-1}$ (2000-2009; Friedlingstein *et al.*, 2019), and are predominantly in the tropics (-1.4 ± 0.3 $PgC\ y^{-1}$) with fluxes outside the tropics balancing to a net flux of near zero (Houghton & Nassikas, 2017). Regional analysis of NBP show a strong sink in Northern Hemisphere extra-tropics 2.3 ± 0.6 $PgC\ y^{-1}$ (1992-1996), 2.2 ± 0.5 $PgC\ y^{-1}$ (2001-2004) but a substantial source in the tropics -1.1 ± 1.5 (1992-1996) and -0.9 ± 0.9 $PgC\ y^{-1}$ (2001-2004) (Gurney *et al.*, 2004; Peylin *et al.*, 2013). Combined with land-use change-related NBP, these inversion results suggest small ‘natural’ NBP in the tropics (c. 0.3-0.5). However, analysis of the vertical atmospheric $[CO_2]$ gradient suggested close-to-neutral tropical NBP (Stephens *et al.*, 2007), implying ‘natural’ NBP of similar magnitude and opposite sign to land-use change-related NBP, attributed primarily to iCO_2 (Schimel *et al.*, 2015).

Flask, aircraft, and satellite-based measurements show trends in the seasonal-cycle amplitude of $[CO_2]$ since c. 1960 (Keeling *et al.*, 1996; Graven *et al.*, 2013; Yin *et al.*, 2018), implying seasonal intensification of northern NBP ($\beta_{app} = 2.2 \pm 0.6$) (Graven *et al.*, 2013). iCO_2 has been implicated as a major driver of these trends (Forkel *et al.*, 2016; Bastos *et al.*, 2019), though increasing crop production (Gray *et al.*, 2014; Zeng *et al.*, 2014) and warming-induced increasing vegetation cover (Keenan & Riley, 2018) are also likely candidates.

Carbon budgeting estimated global ‘natural’ NBP at 3.6 ± 1.0 $PgC\ y^{-1}$ (2009-2018) and 141 PgC since 1959 from the budget residual, and 3.2 ± 1.2 $PgC\ y^{-1}$ and 130 PgC from process-based models (Friedlingstein *et al.*, 2019). Based on the residual estimate of ‘natural’ NBP and the lower and upper bounds of either global vegetation or global ecosystem carbon stocks results in $\beta_{app} = 0.93-1.4$ (assuming all the sink is in vegetation) or $\beta_{app} = 0.18-0.29$ for ecosystem carbon (global vegetation and non-permafrost soils).

677 Synthesis and extrapolation of global inventory data suggested increased C_{eco} ($\beta_{app} = 1.0 \pm 0.6$),
 678 C_{veg} ($\beta_{app} = 1.9$), C_{soil} ($\beta_{app} = 0.31$), litter carbon ($\beta_{app} = 0.92$), and dead wood carbon ($\beta_{app} =$
 679 0.64) (Pan *et al.*, 2011). Little additional data on C_{soil} changes over the historical period are
 680 available. Evidence from multi-plot forest-inventory data consistently shows net gains in wood
 681 C_{veg} in recent decades in tropical Africa ($\beta_{app} = 0.77$) (Hubau *et al.*, 2020), the Amazon ($\beta_{app} =$
 682 0.69) (Brienen *et al.*, 2015), Borneo ($\beta_{app} = 0.48 \pm 0.3$) (Qie *et al.*, 2017), and in large 50 ha plots
 683 across the tropics ($\beta_{app} = 0.30 \pm 0.24$) (Chave *et al.*, 2008). Wood C_{veg} also increased in plots
 684 across the Eastern US ($\beta_{app} = 2.9 \pm 1.5$) (McMahon *et al.*, 2010) and globally ($\beta_{app} = 0.82 \pm 0.5$)
 685 (Yu *et al.*, 2019). Long-term geological CO_2 release was associated with reduced lidar-
 686 estimated aboveground C_{veg} (Cawse-Nicholson *et al.*, 2018).

687 Flux-towers measure NEP directly, yet have been running for a relatively short time. Synthesis
 688 of 23 flux-towers indicate increased NEP ($\beta_{app} = 4.3 \pm 2$), with high CO_2 sensitivity ($\beta_{dir,hist} = 4.6 \pm 2$)
 689 (Fernández-Martínez *et al.*, 2017).

690 4. Synthesis

691 4.1 Evidence for the CO_2 -fertilisation hypothesis

692 In this section we integrate and interpret the evidence for change in the components of the
 693 carbon cycle during the historical record concurrent with increasing $[CO_2]$ (iCO₂; c. 280-400
 694 ppm), in response to elevated $[CO_2]$ (eCO₂; c. 390-500 ppm), and the probability and magnitude
 695 of iCO₂ as a driving factor in the historical change. In doing so we acknowledge that we are
 696 mixing evidence across scales, measurements, methods of analysis, and in some cases
 697 different variables that may not be perfectly comparable. However, this is required for a broad
 698 synthesis and a formal meta-analysis is not our intention. We assign confidence as either “high”
 699 (all estimates agree), “medium” (estimate means disagree, substantial overlap in confidence
 700 intervals), or “low” (estimate means disagree, little overlap in confidence intervals).

701 Physiology

702 A number of independent lines of indirect evidence—ice-core OCS (Campbell *et al.*, 2017) and
 703 O^{18} (Ciais *et al.*, 2012), glucose isotopomers (Ehlers *et al.*, 2015), satellite ET (Cheng *et al.*,
 704 2017), and flux-partitioned eddy-covariance (Fernández-Martínez *et al.*, 2017)—provide **high**
 705 **confidence that terrestrial GPP has increased concurrently with iCO₂**. Estimates of the
 706 GPP increase disagree by a factor of 1.7 ($\beta_{app} = 0.95$ -1.6, mean = 1.2), but overlap in
 707 confidence intervals (Fig. 3, S1) indicates that these estimates are consistent and suggests

medium confidence in the magnitude of the increase in GPP concurrent with iCO₂. Above the canopy-scale GPP can be measured only indirectly, and most of these estimates are a function of the [CO₂] trend (Box 3; isotopomers, satellite, OCS) which introduces a circularity. However, we place less confidence in estimates (usually satellite-based) that omit a CO₂ effect from the theory used in their GPP estimation (Box 3; De Kauwe *et al.*, 2016). Flux-partitioned eddy-covariance provides the only estimate of GPP that does not require [CO₂] in its calculation and provides the highest β_{app} of 1.6 ± 0.9 (Fernández-Martínez *et al.*, 2017). A smaller proportion of this change was attributed to iCO₂ ($\beta_{dir,hist} = 1.2 \pm 0.6$).

Synthesis of direct evidence from experiments provides **high confidence that ecosystem-scale eCO₂ increases diurnal photosynthesis in leaves** ($\beta_{dir,fut} = 0.68 \pm 0.2$). This increase is very similar to the theoretical value for a light-saturated leaf ($\beta_{dir,fut} = 0.70 \pm 0.2$, Table S1). The theoretical value for the canopy-scale photosynthesis response to iCO₂ (280-410 ppm, $\beta_{dir,fut} = 0.60 \pm 0.3$, Table S1) is about half the observed mean increase in GPP concurrent with iCO₂ ($\beta_{dir,hist} = 1.2$). For iCO₂ to be the sole driver of the observed responses would require all leaves to be operating at the light-saturated rate of increase *and* would require additional positive feedbacks of equivalent magnitude.

The majority of global models tend to follow the theoretical response to iCO₂ (Keenan *et al.*, 2016). A carbon cycle model was able to replicate the OCS increase in GPP ($\beta_{app} = 0.95 \pm 0.2$) and change in northern seasonal [CO₂] amplitude by hypothesising leaf optimisation and predicting a substantial increase in LAI (note the phosphorus cycle was disabled) (Haverd *et al.*, 2020). However, it is not clear that leaves optimise as hypothesised (Smith and Keenan, 2020), and models consistently represent allocation and LAI simplistically. For example, LAI trends are inferred in high-LAI tropical rainforests (Zhu *et al.*, 2016). In these regions models are likely predicting an increase in maximum LAI, which conflicts with experimental evidence and resource investment theory. An alternative hypothesis is that iCO₂ accelerates the recovery of forest-gaps such that landscape-scale LAI is greater—a hypothesis not represented by any of the models used for attribution. Outside of tropical forests, changes in LAI are related to both iCO₂ (Donohue *et al.*, 2013) and temperature-stimulated increases in growing season length (Keenan and Riley, 2018). An additional consideration is that models tend to under-estimate GPP relative to solar-induced fluorescence (a GPP proxy) in agricultural regions (Guanter *et al.*, 2014; Walker *et al.*, 2017), agriculture being another major factor of global change. Taken together, we place **high confidence that the historical GPP increase was primarily driven by iCO₂ and also that iCO₂ was not the sole driving factor.** However, it is unclear which factors might be driving the additional change in GPP.

A number of independent lines of indirect evidence—tree-ring $\delta^{13}\text{C}$ (e.g. Saurer *et al.*, 2004; Peñuelas *et al.*, 2011; Frank *et al.*, 2015), flux-partitioned eddy-covariance (Keenan *et al.*, 2013; Mastrotheodorus *et al.*, 2017), and atmospheric $\delta^{13}\text{C}$ (Keeling *et al.*, 2017)—provide **high confidence that iWUE (across leaf to global scales) and WUE (across leaf to ecosystem scales) have increased over the historical period** ($\beta_{\text{app}} = 0.85\text{--}3.9$, mean = 1.5). There remain large differences (factor of 5) between these estimates of the increase, primarily due to the eddy-covariance estimates ($\beta_{\text{app}} = 2.4 \pm 2.0$ and 3.9 ± 2.5). The causes for these differences are not fully understood, though scale (Medlyn *et al.*, 2017), plasticity (Mastrotheodorus *et al.*, 2017), high variability and short time scales (indicated by the high uncertainty), and GPP trends that are higher than expected from iCO₂ alone (see above) all play a role. Eddy covariance estimates skew the mean and the modal change is around $\beta_{\text{app}} = 1$ (Fig. 3), similar to the mean for iCO₂-attribution studies ($\beta_{\text{dir,hist}} = 0.80$) and the theoretical value for iWUE ($\beta_{\text{dir,hist}} = 1.1$). As with GPP, other than eddy-covariance these indirect methods use [CO₂] in their calculation (Box 3). Satellite estimates of WUE suffer from very short time-periods (13 years) with low signal-to-noise ratio, leaving little confidence in these trend estimates. Direct evidence from multiple experiments support iWUE and WUE increases ($\beta_{\text{dir,fut}} = 0.65\text{--}1.6$, mean=1.1) in agreement with predictions from theory (Figure 2). Taken together this evidence provides **high confidence that iCO₂ has increased iWUE, medium confidence that the magnitude is in accordance with theory, and low confidence in the magnitude of the historical change in WUE.**

How do these changes in iWUE translate to changes in water use? Theory predicts that iWUE (A_{net}/g_s) responses are very tightly constrained ($\beta_{\text{dir}} \text{ c. } 1$), so if the change in A_{net} is below 1, g_s will decrease (Barton *et al.*, 2012). The observed changes in GPP ($\beta_{\text{app}} \text{ c. } 1$) suggest that widespread and broad-scale reductions in g_s may not have occurred. Reductions in stomatal conductance may occur at points in time or space but as spatial and temporal scale increases, iCO₂-induced decreases in stomatal conductance likely translate into smaller decreases in transpiration (Field *et al.* 1995; Körner *et al.*, 2007).

Increased vegetation cover in semi-arid regions (Donohue *et al.*, 2013; Ukkola *et al.* 2016), increased rooting depth (Yang *et al.*, unpublished; Iversen 2010), soil-water feedback on g_s , competition, and atmospheric coupling (Jarvis & McNaughton, 1986; Buckley *et al.*, 2017; Sperry *et al.*, 2019; Sabot *et al.*, 2020) are all mechanisms that may lead to no change in *water use* at larger scales. This is especially likely to be the case in water-limited regions where long-term transpiration is primarily precipitation driven (Fatichi *et al.* 2016) i.e. plants use the water that is available.

775 Biomass production

776 Ecosystem-scale forest-inventory networks suggest increases in wood BP concurrent with iCO₂
 777 (mean β_{app} c. 1; Brien et al., 2015; Yu et al., 2019, Hubau et al., 2020). Conversely, evidence
 778 from tree-rings is mixed (e.g. Peñuelas et al., 2011; Silva & Anand et al., 2013). Both of these
 779 methods are subject to potential sampling biases (Box 3). However, the tree-ring biases are
 780 potentially larger and can be either positive (Nehbas-Ahles et al., 2014) or negative (Brien et al., 2016). The inventory evidence provides **medium confidence in an increase in wood BP**
 781 **over the historical period, with low confidence in the magnitude (β_{app} c. 1).** However, this is
 782 an area of disagreement among several in our authorship group.

784 Many studies show increased BP in response to eCO₂ (e.g. Baig et al., 2015), but these studies
 785 are often short-lived and under artificial conditions. Evidence from long-term, large-scale FACE
 786 experiments (<10 experiments) is mixed, with both increases (e.g. Norby et al., 2005) and no
 787 change in BP observed (e.g. Jiang et al., 2020; Bader et al., 2013) ($\beta_{dir,fut}$ = -0.3-0.56, mean =
 788 0.19). Many studies show a BP response to eCO₂ that is higher at sites with higher nutrient
 789 availability (e.g. Terrer et al., 2018), that is greater when nutrients were added (e.g. Sigurdsson
 790 et al., 2013; Reich et al., 2006), or no response when nutrients are low (e.g. Sigurdsson et al.,
 791 2013; Ellsworth et al., 2017). However, strong evidence for the widely held *progressive* nitrogen
 792 limitation hypothesis is restricted to two experiments (Biocon, ORNL) (Reich et al., 2006; Norby
 793 et al., 2010). At both of these experiments nutrient dynamics also caused declining BP in the
 794 ambient treatments, indicating that eCO₂ responses can be tied, via nutrient availability, to
 795 underlying ecosystem dynamics.

796 BP responses were observed in earlier-succession more-disturbed ecosystems, which also tend
 797 to have higher nutrient availability (Körner 2006). The experiments with no response were often
 798 situated in later-succession forests, some of which were also severely limited by nutrients. The
 799 forest inventories in which BP increases concurrently with iCO₂ were observed in later-
 800 succession, primarily tropical, forests that are assumed to be strongly nutrient limited. These
 801 inventory responses are high (β_{app} c. 1) compared with the results from experiments even in
 802 earlier-succession forests ($\beta_{dir,fut}$ = 0.49±0.3). However, the evidence is insufficient to robustly
 803 evaluate how eCO₂ affects late-successional and tropical forests. Taken together, this evidence
 804 suggests **high confidence that eCO₂ can stimulate BP ($\beta_{dir,fut}$ c. 0.5), that the response is**
 805 **diminished by nutrient limitations, and that the observed inventory response is likely due**
 806 **to iCO₂ and additional factors.**

807 Vegetation mortality

808 A number of independent plot networks provide **high confidence that tree mortality has**
 809 **increased over the historical period but low confidence in the magnitude ($\beta_{app} = -1.2-7.4$,**
 810 **mean = 2.8)**. The greatest changes are primarily attributed to drought. Causes of mortality are
 811 often stochastic, multi-factorial, and play out over long time periods, making trend identification
 812 and attribution at ecosystem and landscape scales uncertain (McMahon *et al.*, 2019). For
 813 individual scale mortality, an intra-specific growth-survival tradeoff is apparent for some species
 814 (e.g. Di Filippo *et al.*, 2015), which would reduce lifespans if iCO₂ increases wood BP. However
 815 an intra-specific growth-survival tradeoff is not ubiquitous among species (e.g. Cailleret *et al.*,
 816 2017).

817 Greenhouse eCO₂ experiments suggest that eCO₂ does not reduce drought-related mortality
 818 (e.g. Duan *et al.*, 2014; Bachofen *et al.*, 2018). However, eCO₂ commonly increased leaf area
 819 in these experiments, increasing transpiration that likely exacerbated mortality risk (Duan *et al.*,
 820 2018). What does this mean for eCO₂ responses in ecosystems? Due to the juvenile growth
 821 stage of these plants, leaf area increases were much higher than expected in closed canopy
 822 systems (see Box 2), and increased root BP from eCO₂ would exacerbate pot-volume
 823 constraints on root proliferation. Inference from these experiments is limited. At the stand scale
 824 there is very limited evidence that eCO₂ might change self-thinning relationships allowing higher
 825 basal area for a given stem density (Kubiske *et al.*, 2019). Evidence for changes in mortality
 826 caused by iCO₂ is weak and mostly indirect with limited support for both increases and
 827 decreases in individual and stand-scale mortality rates. Taken together **(CS11) the response of**
 828 **mortality to iCO₂ and eCO₂ is unknown, even the direction of change is unclear.**

829 Organic matter decomposition

830 The few studies of soil or ecosystem respiration show small ($\beta_{app} = 0.22$; Bond-Lamberty &
 831 Thompson 2010) or non-significant increases ($\beta_{app} = 0.58 \pm 1$; Fernández-Martínez *et al.*, 2017).
 832 These trends could possibly be related to increasing heterotrophic respiration and
 833 decomposition, but increasing temperature is inferred as the cause and not iCO₂ (e.g. Bond-
 834 Lamberty *et al.*, 2018). Due to the low number of studies there is **low confidence that SOM**
 835 **decomposition has increased over the historical period, but it is unknown whether SOM**
 836 **decomposition rates have increased.**

837 Evidence from eCO₂ experiments generally supports the theory that rising [CO₂] increases
 838 SOM-decomposition rates (e.g. van Greonigen *et al.*, 2015) due to increases in microbial
 839 biomass, rhizosphere priming, mycorrhizal association, and increases in soil water content (see

refs in Section 3.4). Smaller changes in decomposition rates have been associated with lower microbial biomass and higher soil water (Bader & Körner, 2010; Iversen *et al.*, 2012). Taken together, the evidence suggests **medium confidence that eCO₂ increases rates of SOM decomposition but with low confidence in the magnitude**. Increasing SOM decomposition will also release nutrients that may be available for plant growth and BP. Plant nutrient acquisition through mycorrhizal and other root-microbe interactions are likely mediators of this process (Terrer *et al.*, 2018). Notably, the large step-change in eCO₂ experiments compared with the more gradual iCO₂, could lead to a greater imbalance of available resources resulting in a carbon surplus (Box 3) that could fuel greater microbial activity. It is worth noting that increased SOM-decomposition rates do not necessarily imply lower C_{soil} litter inputs are also increasing (Liang *et al.*, 2018).

Terrestrial ecosystem carbon

Multiple independent lines of evidence—global-scale carbon budgeting (Friedlingstein *et al.*, 2019), atmospheric inversions (e.g. Peylin *et al.*, 2016; Fernández-Martínez *et al.*, 2019), seasonal [CO₂] amplitude trends (Graven *et al.*, 2013), and forest inventories (e.g. Pan *et al.*, 2011; Hubau *et al.*, 2020)—imply a CO₂ sink in terrestrial ecosystems. This evidence provides **high confidence that terrestrial ecosystem carbon has increased over the historical period, with substantial changes in the ‘natural’ carbon sink almost balanced by a net carbon source from land-use change**. Global carbon budgeting and global forest analysis suggest responses concurrent with iCO₂ in the range, $\beta_{app} = 0.18\text{--}1.0$. The ‘natural’ carbon store response estimated for global intact forests ($\beta_{app} = 0.66 \pm 0.4$; Pan *et al.*, 2011) is higher than estimated for the ‘natural’ land surface ($\beta_{app} = 0.18\text{--}0.29$; Friedlingstein *et al.*, 2019). Trends observed in eddy-covariance NEP (site-scale ‘natural’ sink) and inversion NBP (global-scale combined ‘natural’ and land-use sink) are extremely high ($\beta_{app} = 4.3\text{--}19$, mean 11). The extremely high β_{app} for global NBP (and to a lesser degree NEP) results from global NBP being near zero as the ‘natural’ sink is almost balanced by the net source from land-use change, thus small absolute changes can be relatively high (Box 3).

CO₂ effects on terrestrial carbon are convolved with the effects of concurrent anthropogenic changes in climate, nitrogen deposition, and land-use change, including agricultural intensification and fire management. Attribution analyses indicate a primary role for iCO₂ (e.g., Schimel *et al.*, 2015; Keenan *et al.*, 2016; Bastos *et al.*, 2019; Fernández-Martínez *et al.*, 2019; Haverd *et al.*, 2020). These analyses depend on the inclusion of accurate explanatory-variable datasets and accurate process representation in models, which may not be the case.

Quantification of the effect of iCO₂ on carbon storage in terrestrial ecosystems remains elusive. As with BP responses, studies of forest inventories show higher C_{veg} responses ($\beta_{app} = 0.3\text{--}2$, mean = 0.85) than studies of eCO₂ experiments ($\beta_{app} = 0.22\text{--}0.39$) (Fig. 3). However, the highest values come from two analyses: one that includes global forest regrowth ($\beta_{app} = 1.9$; Pan *et al.*, 2011) and younger (c. 50–100 years old) temperate forests ($\beta_{app} = 2 \pm 1$; McMahon *et al.*, 2011). Exclusion of these higher change studies results in a narrower range ($\beta_{app} = 0.3\text{--}0.85$, mean = 0.57). This exclusion narrows the difference between responses inferred from iCO₂ and eCO₂ studies, which is consistent with theory as relative stock changes are under-estimated more in short-term experiments than in inventory-type studies (Fig. S2). Responses of vegetation carbon increment may give a more accurate estimate of responses in systems that are far from equilibrium when initially exposed to eCO₂ (Fig. S2). Vegetation carbon increment responses estimated from FACE experiments ($\beta_{app} = 0.60 \pm 0.4$; Walker *et al.*, 2019) are consistent with the reduced range from inventory studies. However, the theoretical under-estimation of undisturbed forest-inventory responses (Fig. S2) yet similarity of these responses with those from disturbed forests subjected to eCO₂ and not the lower values from undisturbed forests (e.g. Jiang *et al.*, 2020), requires further consideration. Either eCO₂ experiments are under-estimating responses or other factors have affected the inventory evidence. Both of these evidence types are likely missing the full extent of mortality (e.g. Chambers *et al.*, 2013), and evidence from larger-scale 50 ha plots suggests a lower response for intact tropical forests ($\beta_{app} = 0.30 \pm 0.2$; Chave *et al.*, 2008).

Evidence for changes in C_{soil} is mixed and context dependent. On average there is no detectable response across experiments (Hungate *et al.*, 2009), though at some individual sites, C_{soil} did accumulate (e.g. Iversen *et al.*, 2012; Evans *et al.*, 2014). The only study (to our knowledge) of soil carbon changes concurrent with iCO₂ suggests a relative response in global forests ($\beta_{app} = 0.31$; Pan *et al.*, 2011), that would be substantial if extrapolated to mineral soils globally. As with vegetation carbon stocks, the long-term, relative responses of soil carbon stocks are likely underestimated by short-term eCO₂ experiments (Fig. S2). Taken together, evidence suggests **medium confidence that eCO₂ increases ecosystem carbon stocks over short to medium timescales and iCO₂ has contributed to the change over the historical period, but with low confidence in the magnitude.**

4.2 What we need to know

Confidence in the magnitude of CO₂ effects is generally low. In particular, iCO₂-attribution is a major challenge in testing the CO₂-fertilisation hypothesis over the historical period. Attribution

often relies on empirical regression which simply indicates correlation, anything with a trend over the historical period will correlate with iCO₂. We advocate using log-log β as a stable (Supplementary Information), relativised metric for comparison with theoretical expectations and other studies.

Process-based models are also used to deconvolve causation from multiple global-change factors. Models often represent key mechanisms over-simplistically and yet are also equifinal, while model ensembles represent a non-random sample of non-independent models (Beven, 2006; Fatichi *et al.*, 2019; Sanderson & Fisher, 2020). Thus, models need always to be interpreted in the context of the mechanisms they represent, those they do not, how representations might bias results, and how well they reproduce observations (e.g. Medlyn *et al.*, 2015). Mechanistic models (or modules) of BP, resource acquisition and allocation, how soil and plant water status affect g_s , plant-microbe effects on soil decomposition, vegetation structure and demography (e.g. competition, mortality), and land-use need to be applied more extensively to the CO₂-fertilisation hypothesis. Alternative hypotheses to explain observed phenomena should be evaluated within model ensembles, and calibrated to allow the hypotheses to compete on an equal footing (e.g. Zhang *et al.*, 2015). Agile and extensible models (e.g. Clark *et al.*, 2015; Walker *et al.*, 2018) will be needed to rapidly incorporate this understanding, including uncertainty, into the internally-consistent and quantitative systems-level theory that models represent.

It is crucial that future eCO₂ experiments are designed and resourced to understand the mechanistic basis for responses (or lack thereof) and do not simply report significance or effect-sizes. Integration with extensible, process-based models will help evaluate and explore the mechanistic basis for observed responses (Medlyn *et al.*, 2015). During the lifetime of long-term experiments, new hypotheses will arise to explain unexpected or key observations that may help to provide context and mechanisms underlying the observed responses. These long-term experiments represent very large investments and for relatively small additional investment, related studies can test mechanistic hypotheses as they arise during an experiment's lifetime.

Suggestions for high-priority future studies:

Understanding the mechanistic basis for GPP increases observed over the historical period and how this relates to water use. GPP, iWUE, and water use are intimately tied. The mechanisms by which plants might adjust to iCO₂ (photosynthetic acclimation/optimisation, more and deeper roots, g_s responses to water status) are not fully understood and thus not well explored within models. A quantitative synthesis canopy or stand-scale photosynthetic

939 responses in eCO₂ experiments would be informative.

940 **Biomass production** inferred from tree-rings and forest inventories reach very different
 941 conclusions. Where possible, studies that can integrate these two types of evidence, such as
 942 tree-ring sampling at inventory sites (e.g. Dye *et al.*, 2016; Evans *et al.*, 2017), acknowledging
 943 respective biases will be fruitful. The mechanisms underlying how increased GPP leads to
 944 increased BP and increased nutrient acquisition through plant-microbe associations are key
 945 areas for future study, especially over successional gradients. eCO₂ studies in mid and late-
 946 succession ecosystems, and tropical, boreal, semi-arid, and savannah ecosystems will help to
 947 address the young, temperate ecosystem bias in eCO₂ studies.

948 **How iCO₂ affects mortality** is key for understanding C_{veg} and community responses to iCO₂.
 949 As mortality is a relatively rare event in established vegetation, change detection and attribution
 950 of causation require large-scale, long-term monitoring, and ideally, experiments (Hartmann *et al.*, 2018). Understanding the mechanics of observed growth-mortality tradeoffs and whether
 951 iCO₂ may be alleviating mortality in semi-arid regions are high-priority.
 952

953 **Studies of the C_{soil} decomposition rate** over the historical period are practically non-existent,
 954 additional studies are required. As with BP, efforts to fully understand plant-microbe-soil (and
 955 likely invertebrate), carbon-nutrient interactions continue to be a high-priority. Furthermore,
 956 investigation of responses in deep soil layers are few or non-existent. Understanding how the
 957 opposing processes of increased litter production, root-microbe interactions, increased
 958 decomposition rates, and rates of mineral-associated SOM formation balance to affect C_{soil}
 959 throughout the soil profile will be key to predictive understanding. This may be especially
 960 relevant in non-forest ecosystems, where the largest potential change in carbon storage is
 961 belowground.

962 **iCO₂ affects ecosystem carbon primarily through effects on NEP, thus understanding of**
 963 C_{eco} responses to iCO₂ will emerge from the above research priorities. Further, NBP is what the
 964 atmosphere 'sees', which includes additional non-respiratory carbon losses caused by fire
 965 (anthropogenic and wild), hydrological export, and export of consumer goods. iCO₂ may interact
 966 with some non-NEP fluxes, e.g. greater grassland BP leading to higher fuel loads, greater BP in
 967 regrowing forests following land-use change. Land-use change NBP is often calculated without
 968 considering iCO₂ and separately from 'natural' NBP caused by iCO₂, climate change, nitrogen
 969 deposition, and other factors (e.g. Friedlingstein *et al.*, 2019). Though the boundary between
 970 these fluxes is blurred (Pongratz *et al.*, 2014). Integrated studies that consider all of these
 971 factors, especially land-use change (including iCO₂-acceleration of regrowth following

disturbance, e.g. Pugh *et al.*, 2019), agriculture, and ‘natural’ fluxes will yield insight.

5. Summary

To evaluate the CO₂-fertilisation hypothesis, we synthesised evidence from wide-ranging disciplines within an integrated theoretical framework. We have medium or high confidence that GPP, iWUE, BP, and mortality have all increased over the historical period. However, we often have low or medium confidence in the magnitude, and low confidence in how much of the change is attributable to iCO₂.

The complex nature of the problem demands integrated studies, and further integration is required to fully combine the broad evidence in a way that is scale, bias, and uncertainty aware (Box 3). Inference regarding trends and responses (or lack thereof) should always be grounded in the context-dependence and biases associated with a particular study. Further experiments and observations are needed to help reconcile differences among evidence streams. For example, tree-ring sampling at flux sites or forest-inventory plots, proximal remote sensing at flux and experiment sites, and model-data integration to reconcile diverse data streams would all help to provide an integrated understanding of this complex problem. A holistic, community-based approach will enable the greatest advances and provide the most robust information to decision makers.

The required size of climate-change mitigation efforts depends directly on how future terrestrial carbon storage evolves. Evidence for the CO₂-fertilisation hypothesis suggests a highly valuable ecosystem service that is buying us time in the fight against climate change, though the size of this subsidy remains unclear. Based on diminishing theoretical GPP responses, likely increasing nutrient limitations, increasing mortality, and other negative temperature-related effects (Peñuelas *et al.*, 2017) it is highly likely that increases in terrestrial carbon storage due to iCO₂ will decline into the future. We must act now to reduce fossil-fuel emissions before the decline of this subsidy results in accelerated climate change leaving us to reap the full consequences of “cheap” fossil-derived energy.

998 **Data availability statement**

999 The data used in this publication are all contained in Table 1 and we provide a datafile as part of
1000 the supporting information. Scripts to generate model data used in Fig. 2 will be posted on
1001 Github (<https://github.com/walkeranthony/MAAT>).
1002

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1013 **Author contributions**

1014 APW conceived and wrote the paper, with major contributions from MGDK, AB, KG, SM. APW,
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1017 commented and provided feedback on the manuscript.
1018

1019 **Tables, Figures, and Boxes**

1020

1021 Table 1. CO₂ responses across studies.

1022 Figure 1. Conceptual diagrams of the terrestrial carbon cycle and the action of CO₂

1023 Figure 2. Modelled leaf-scale physiological responses to CO₂

1024 Figure 3. Comparison of β values

1025 Box 1. The CO₂-fertilisation hypothesis

1026 Box 2. The evidence themes

1027 Box 3. Consideration of methods and bias

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Figure Captions

Figure 1. Conceptual diagrams of the terrestrial carbon cycle and the action of CO₂. a) Simple pool and flux (3D shapes) diagram of the terrestrial carbon cycle showing key pools, fluxes, and processes relevant to the CO₂-fertilisation hypothesis as described in Box 1. 2D arrows represent direct (solid) or indirect (dashed) positive (triangular arrow heads), negative (square), or the possibility of both (circular) potential influences of increasing atmospheric [CO₂] (iCO₂). b) Rich conceptual diagram of a landscape-scale carbon cycle and the influence of iCO₂ showing more processes (see Section 2) and their inter-connected, multi-scale nature.

Figure 2. Modelled theoretical responses to atmospheric CO₂ concentration ([CO₂], ppm) of (a-c) photosynthesis, A_{net} ($\mu\text{mol m}^{-2} \text{s}^{-1}$, black) and photorespiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$, dark grey, a only); (d-f) iWUE ($\mu\text{mol mol}^{-1}$), (g-i) stomatal conductance ($\text{mol m}^{-2} \text{s}^{-1}$), and (j-l) carbon storage (kg C m^{-2}) under ambient (blue) and elevated (red) [CO₂]. Leaf (a, d, g) and canopy (b, e, h) scale for C3 (solid line) and C4 (dashed, leaf-scale only) plants. Variation in b, e, h from a 1000 member ensemble (mean, sd, and 95 percentile shown)—a factorial combination of 100 top-of-canopy V_{cmax} values (mean = 60, sd = 10) and 10 values of the J_{max} to V_{cmax} slope (mean = 1.63, sd = 0.2), the iWUE response does not vary in this ensemble. Distributions of β_{dir} for historical (purple, 280 to 400 ppm) and future (yellow, 400 to 550 ppm) [CO₂] changes (c, f, i) of diurnally-integrated, canopy-scale variables that includes the same leaf physiology variation as in b, e, h, plus three levels of temperature (10, 15, 25 °C) and relative humidity (50, 70, 90 %) combined in factorial. Tri-modality in the GPP β distributions from the temperature variation. β distributions weighted by the variables' absolute response to CO₂. Carbon storage (j-l) calculated using a simple one-pool model with the mean $\beta_{\text{dir,fut}}$ GPP response applied to BP for [CO₂] at 400 and 550 ppm when (j) initial carbon stores are in equilibrium or (k) 10 % of equilibrium. (l) $\beta_{\text{dir,hist}}$ response when initial carbon stores are assumed in equilibrium at 280 ppm and using the observed historical CO₂ record. Instantaneous β_{dir} for absolute carbon storage are shown (j-l, right y-axis, yellow or purple), as well as $\beta_{\text{dir,hist}}$ calculated using carbon storage increment (green dashed), and β_{dir} on 30-year change in carbon storage in elevated CO₂ scenario (blue points). Further modelling details in Supporting Information. Grey vertical lines (a, b, d, e, g, h) are at pre-industrial, 2010s, and projected end-of-century [CO₂] (280, 400, 550 ppm). Grey vertical lines (c, f, i) are at β_{dir} of 0 (solid) and 1 or -1 (dashed). Grey horizontal lines (j-l) are β_{dir} when both ambient and elevated CO₂ carbon pools are at steady state.

1062

1063 Figure 3. β distributions based on data from Table 1 for GPP, WUE, BP, k_{veg} , k_{soil} , C_{veg} , and C_{soil} .
1064 Data are organised by CO₂ response category—iCO₂ (blue), attribution to iCO₂ (green), and
1065 eCO₂ (purple). See Supplementary Information for further details.

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Box 1. The CO₂-fertilisation hypothesis

The stimulation of photosynthesis by CO₂ has been called “CO₂ fertilisation” (Ciais *et al.*, 2014), a term that goes back to global carbon cycle modelling in the 1970’s (Bacastow & Keeling, 1973). However, “CO₂ fertilisation” or “CO₂ fertilisation effect” have been used to refer to the [CO₂] response of any number of variables across scales. This broad usage has been a source of confusion and more commonly, “fertilisation” is a value-laden, agricultural term that means the addition of nutrients to increase crop yield. Acknowledging the precedence of the term, its multiple uses, and that CO₂ responses of some processes may be neutral or negative, we opt to refer to “CO₂ responses” of explicitly defined variables and scales.

We reserve the term “CO₂ fertilisation” solely to label the hypothesis that: **plant responses to increasing atmospheric [CO₂] lead to increasing terrestrial-ecosystem carbon storage causing negative feedback on atmospheric [CO₂] growth**. This definition of the CO₂-fertilisation hypothesis is explicit about the feedback on atmospheric [CO₂] growth, implying the potential of this process to slow climate change. The hypothesis is therefore defined at climate-change relevant scales, i.e. global in space and decadal to centennial in time.

For the CO₂-fertilisation hypothesis to be true, Eq. B1 must be positive at the global scale and over a specified time period:

$$\Delta NEP = \Delta C_{eco} = \Delta C_{veg} + \Delta C_{soil} \quad (\text{Eq. B1})$$

where NEP is net ecosystem production, C_{veg} and C_{soil} are plant and soil (including litter and coarse woody debris) terrestrial carbon that sum to give total ecosystem carbon (C_{eco}), and Δ represents change due to increasing [CO₂]. A change in carbon storage is the net result of inputs and outputs (Olson, 1963):

$$dC / dt = I - kC \quad (\text{Eq. B2})$$

where C is stored carbon, I is the input, and k is the turnover rate of the pool (the inverse of mean residence time).

Net primary production (NPP) represents the net input of carbon to C_{veg} and is calculated as gross primary production (GPP), which responds directly to iCO₂, minus autotrophic respiration (R_a). In practice, NPP is often estimated from total biomass production (BP), the sum of leaf, wood, root, and reproductive tissue production over a given time period (Vicca *et al.*, 2012). In addition to BP, NPP includes carbon used for the production of volatiles, root exudation, supply to symbionts, and changes in non-structural carbohydrates (NSCs). However, these carbon fluxes are difficult to measure and often have very short residence times, somewhat akin to

1098 respiratory carbon. Therefore, to align with measurements and residence time we use BP to
 1099 decompose changes in C_{veg} :

$$1100 \quad dC_{veg} / dt = BP - k_{veg}C_{veg} \quad (\text{Eq. B3})$$

1101 where k_{veg} is the turnover (litterfall and mortality) rate of vegetation biomass. For soils, the inputs
 1102 to C_{soil} are vegetation litter production and mortality, as well as non-biomass NPP fluxes (S) that
 1103 include exudation and carbon supply to symbionts:

$$1104 \quad dC_{soil} / dt = k_{veg}C_{veg} + S - k_{soil}C_{soil} \quad (\text{Eq. B4})$$

1105 where k_{soil} represents the turnover rate of soil carbon caused by microbial decomposition.

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Box 2. Evidence themes

Theme 1—Direct exposure to elevated CO₂: Experiments in which plants are grown in CO₂-enriched air and observations of plants growing close to geological CO₂ sources provide the only direct evidence of plant and soil responses to future [CO₂]. The first eCO₂ experiments were typically at the scales of hours or days and of leaves or small, individual plants. Ecosystem-scale open-top chambers (OTC) and larger free-air CO₂ enrichment (FACE) experiments have since been implemented over decades in more natural settings. All of these experiments provide evidence for the direct CO₂-effect on photosynthesis and stomatal conductance. These experiments also provide valuable data on biomass production, allocation to organs, and transpiration. The time scale of most experiments (<10 years), however, is generally much shorter than many ecosystem processes, and evidence for CO₂-effects on mortality, plant community dynamics, or changes in soil carbon stocks is limited.

Theme 2—Tree growth measurements: Tree rings and forest inventories provide long-term estimates of wood BP in forest ecosystems across the globe (e.g. Hember *et al.*, 2019; Hubau *et al.*, 2020). Tree ring data are annually resolved estimates of individual stem growth over the past decades to millennia (e.g. Babst *et al.*, 2014). These data provide insight into individual growth variability in relation to environmental changes including soil moisture, temperature and potentially also iCO₂. Repeated inventories of forest ecosystems offer an assessment of forest-scale dynamics and the demographic processes of recruitment, growth, and mortality over the past decades and in some cases around century length (Pretzsch *et al.*, 2014). Inventories tend to have a coarser temporal resolution (5-10 year resurveys) but represent forest-stand spatial scales, albeit that plot scale varies widely: 0.067 ha forest inventory analysis, c. 1-2 ha (e.g. Brien *et al.*, 2015; Hubau *et al.*, 2020), 50 ha ForestGEO network (e.g. Chave *et al.*, 2008).

Theme 3—Ecosystem monitoring: Ecosystem eddy-covariance and global remote-sensing may detect effects of iCO₂ on carbon, water, and energy fluxes over the recent decades. Tower-based sensors are used to calculate ecosystem-scale (c. 1 km) carbon, water, and energy fluxes from the covariance of gas concentrations and vertical wind velocity (Baldocchi, 2003). A global network of continental networks (<http://fluxnet.fluxdata.org>), synthesises flux-tower data from 916 sites, some in operation for over two decades, while the majority have run for a decade or less and are located in temperate ecosystems (Chu *et al.*, 2017). Satellite and other aircraft-borne Earth observing systems have been measuring the reflectance of electromagnetic radiation from Earth's surface, used to infer changes in vegetation cover, leaf area, and biomass at the global scale (Fensholt *et al.*, 2004; Smith *et al.*, 2020). Reflected

wavelengths from Landsat (first launched in 1972), MODIS, and other instruments can be used to measure the fraction of absorbed photosynthetically active radiation (fAPAR) and greenness indices, which are further used to infer LAI, GPP, and NPP with the help of simple models (Myneni *et al.*, 1997; Field *et al.*, 1998). Microwave wavelengths are used to measure vegetation optical depth (VOD, first available in the early 1980s) which can be used to infer vegetation water content and, by extension, vegetation biomass (Liu *et al.*, 2015).

Theme 4—Large-scale constraints: At regional-to-global scales, several long-term data-streams provide constraints on the global carbon budget and its change over time. These data streams include near-surface and vertical profiles of atmospheric CO₂ concentration and δ¹³C, global water-cycle measurements, and atmospheric composition from ice cores. Atmospheric CO₂ measurements can be combined with other data and models to infer the global carbon budget and spatial details of land carbon uptake (Friedlingstein *et al.*, 2019; Peylin *et al.*, 2013). The impact of vegetation responses to iCO₂ on the hydrological cycle measured by stream gauges can also act as further indirect evidence (Ukkola *et al.*, 2016; Trancoso *et al.*, 2017). Carbonyl sulphide (OCS) can be used to infer global carbon assimilation because it is taken up by plants through stomata and is transformed by carbonic anhydrase (Wohlfahrt *et al.*, 2012; Whelan *et al.*, 2017).

Box 3. Consideration of methods and bias

eCO₂ experiments. Confinement of roots in pots can limit below-ground resources. While eCO₂ can accelerate leaf area gain in open-grown plants leading to compound interest that does not occur with closed canopies (Norby *et al.*, 1999). These experiments represent early post-disturbance “reorganising”, and possibly open-canopy, ecosystems but are not representative of closed-canopy ecosystems. Oscillating [CO₂] may lessen physiological responses (Allen *et al.*, 2020). The step-change in [CO₂] results in a large shift in the ecosystem resource balance (Walker *et al.*, 2015), while soil disturbance can increase nutrient availability (Körner 2006). Many experiments (and evidence themes more broadly) do not quantify total BP, especially root BP. Even the longest-running experiments are short-lived relative to the lifespan of trees. Landscape-scale atmospheric feedbacks (e.g. increased VPD that could mitigate reductions in transpiration) cannot be accounted for (Leuzinger *et al.*, 2015).

Many ‘measurements’ rely on models in their calculation, thus have the potential to omit or pre-suppose a CO₂ effect. For example, satellite GPP (e.g. Sun *et al.*, 2018) and NPP (e.g. Kolby-Smith *et al.*, 2016) are calculated from fAPAR using an LUE model (Monteith, 1972) that often does not include the CO₂ effect on photosynthesis (De Kauwe *et al.*, 2016). Thus, changes in GPP result only from changes in LAI (fAPAR) or climate. Conversely, measurement-models that include a CO₂ effect are thus not independent of iCO₂, e.g. iWUE from δ¹³C, OCS, or isotopomers, and thus have the potential to pre-suppose a CO₂-related trend.

Carbon isotope discrimination during photosynthesis reduces the ¹³C:¹²C ratio (δ¹³C) in plant material and is used to calculate iWUE from δ¹³C (Farquhar *et al.*, 1982; Farquhar & Cernusak, 2012). The commonly used model neglects mesophyll and photorespiration discrimination (Farquhar *et al.*, 1982; Farquhar & Cernusak, 2012), and accounting for these effects can increase iWUE trends by around 50 % (Keeling *et al.*, 2017).

Tree-ring trends are subject to sampling and survivorship biases (Brienen *et al.*, 2012; Peters *et al.*, 2015) that can affect growth trends by up to 400 % (Hember *et al.*, 2009; Nehrbass-Ahles *et al.*, 2014), leading some to question whether tree-rings should be used for trend detection at all (Brienen *et al.*, 2012). However, tree-rings are the only data that give insight into tree BP since the industrial revolution.

Many studies use tree-ring width as a proxy for wood BP because it is a direct measurement. However, trees grow in three dimensions and change in the one-dimensional

ring-width does not directly scale with wood volume growth and thus BP in different sized trees. Conversion to the two-dimensional basal area increment (BAI) helps unify this size mismatch, but again does not account for non-linear change in wood BP with tree size (Anderson-Teixeira *et al.*, 2015). Allometric scaling should be applied to ring-width and BAI to attempt a best possible estimate of wood BP (e.g. Dye *et al.*, 2014). Static allometric relationships over time can introduce bias where environmental changes have altered resource allocation. For example, shifting allocation from wood to leaves in Russian forests reconciled apparently conflicting inventory data that suggested BP declines while remote sensing suggested increases (Lapenis *et al.* 2005). Furthermore, wood volume growth does not always scale with BP as wood density can also change (Pretzsch *et al.*, 2018).

Forest inventory plots (c. 1 ha and less) can under-sample mortality, resulting in over-estimates of biomass accumulation (Chambers *et al.* 2013). Generally, statistical power for detecting and attributing change in mortality and SOM is often low (Hungate *et al.*, 2009; Sulman *et al.*, 2018; McMahon *et al.*, 2019). Statistical power for detection is low due to measurement uncertainty, low signal-to-noise, heterogeneity, and potential pre-treatment differences. Low statistical power presents a real challenge for attribution when using commonly used binary mortality assessments or bulk SOM measurements (Sulman *et al.*, 2018; McMahon *et al.*, 2019). Furthermore, satellite data, flux-towers, and experiments all suffer from short time-periods, often with much background variability that can obscure or amplify trends.

Quantification of global ‘natural’ NBP is confounded with quantification of land-use change-related NBP which is uncertain (95 % CI is 92 % of the mean flux; Friedlingstein *et al.*, 2019). Land-use change-related NBP is calculated using bookkeeping models that account for complex legacy effects and many elements of land-use change, which adds to the uncertainty (Pongratz *et al.*, 2014). Furthermore, potentially substantial interactions of land-use change-related NBP and iCO₂ are not considered by these methods. C_{veg} and C_{soil} changes, loss of storage/sink capacity, and potential CO₂ interactions with secondary succession all convolve land-use change and ‘natural’ NBP fluxes suggesting a false dichotomy in these flux calculations.

Calculating and interpreting β , or any relative response, is challenging for carbon stocks in which pre-change values can be large, change is the product of two opposing fluxes cumulative over multiple years, and concepts of steady-state and non-steady state apply. Ideally we would like to know β from pre-change steady-state to post-change steady-state. However, an ecosystem may not be in steady-state prior to change and post-change ecosystems enter a

1219 transient phase and can take a long time to reach steady-state. Calculated during the transient
1220 phase, β will be a function of initial stocks and the developmental stage explored (seedling,
1221 sapling, mature tree) and signals will accumulate over time. For ecosystems not in steady-state
1222 pre-change, β of the changes in the stock increment is not sensitive to initial stocks, but could
1223 be large where pre-change increments are small (i.e. when pre-change the system is close to
1224 steady-state). For steady-state ecosystems pre-change, acknowledgment that β is non-steady-
1225 state is needed and a β that explicitly includes temporal scale would be ideal.

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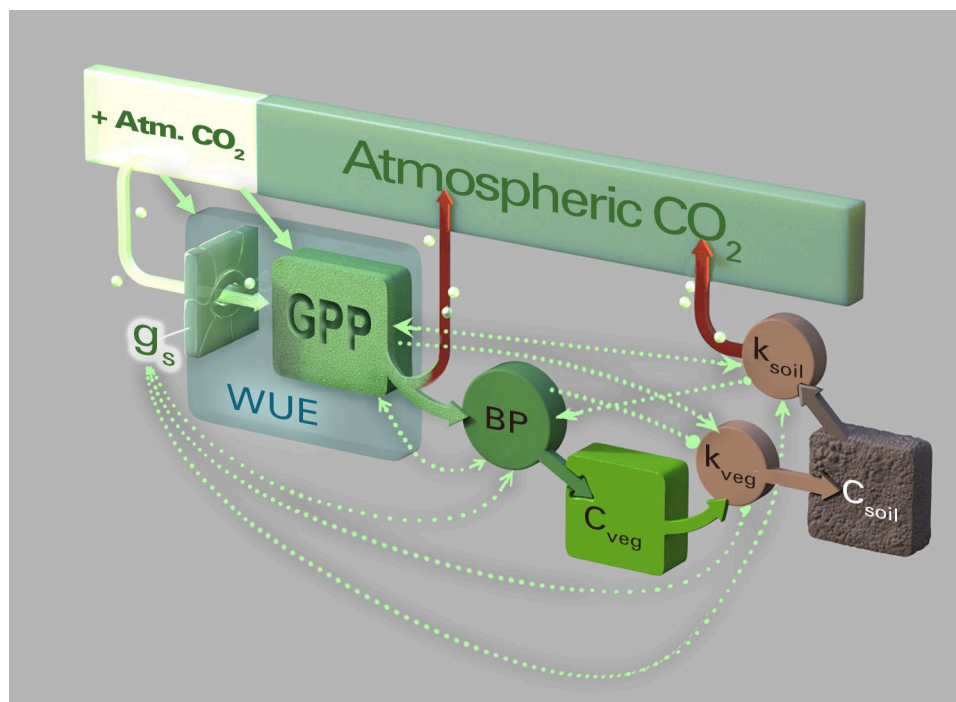
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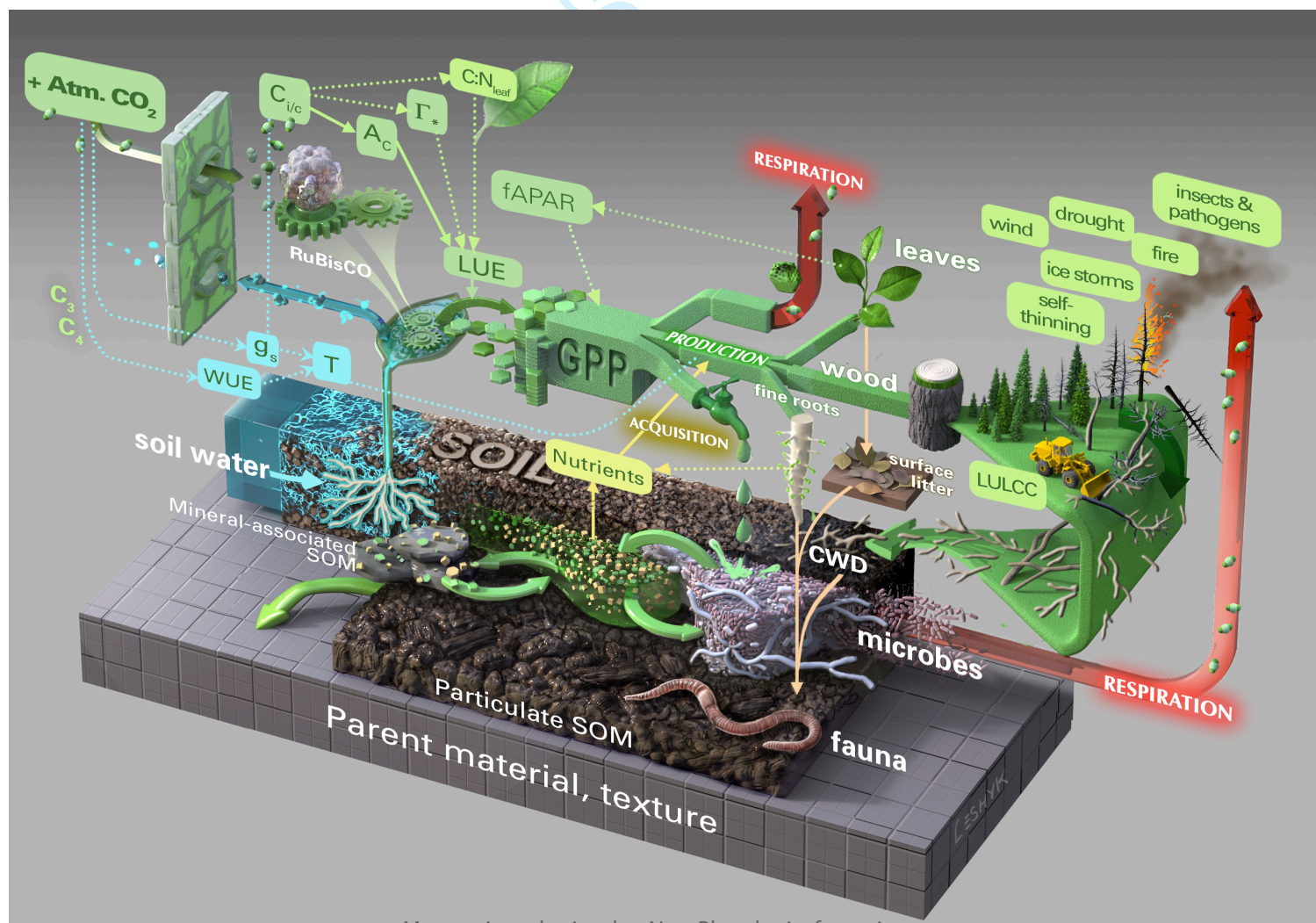
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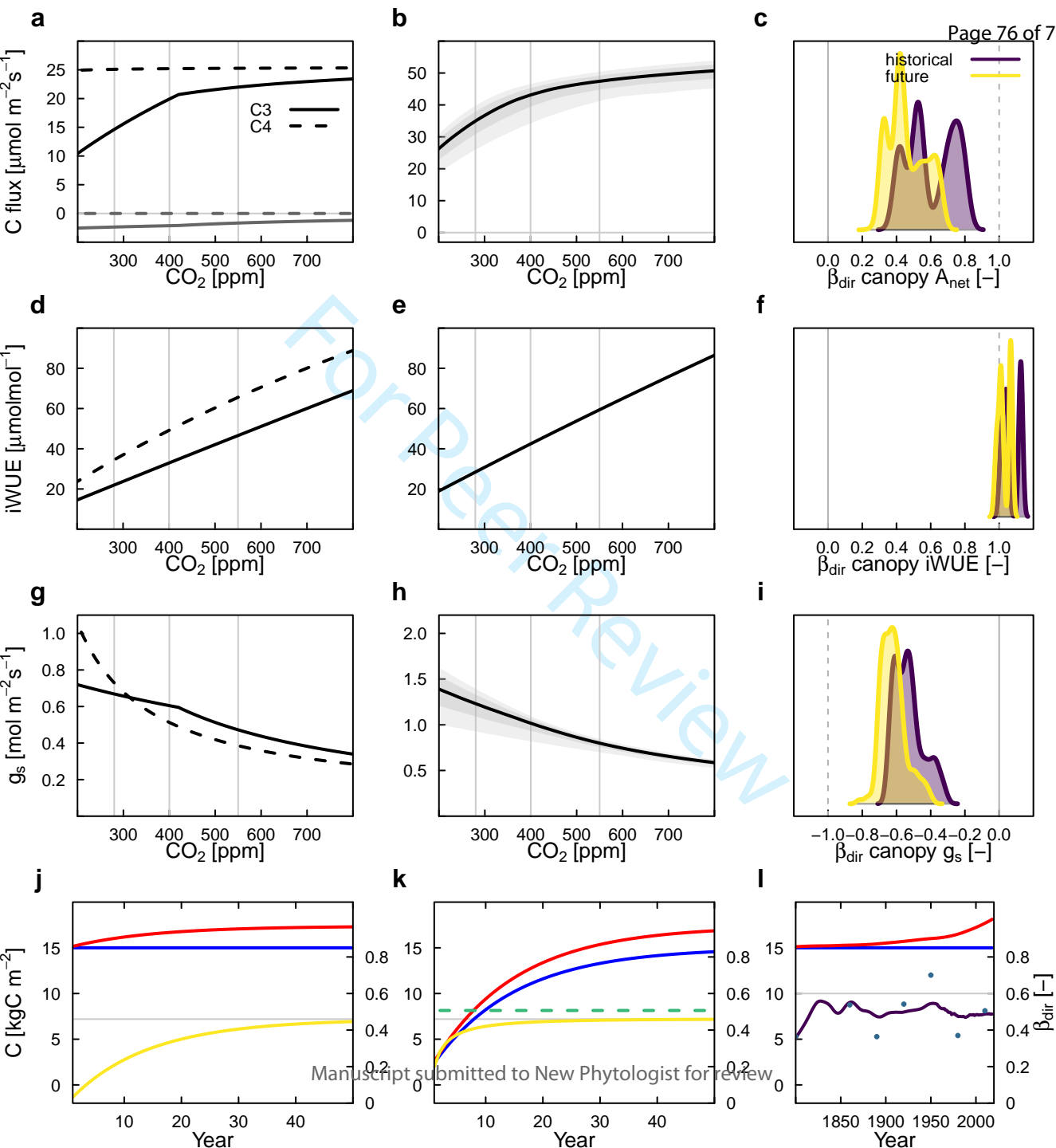
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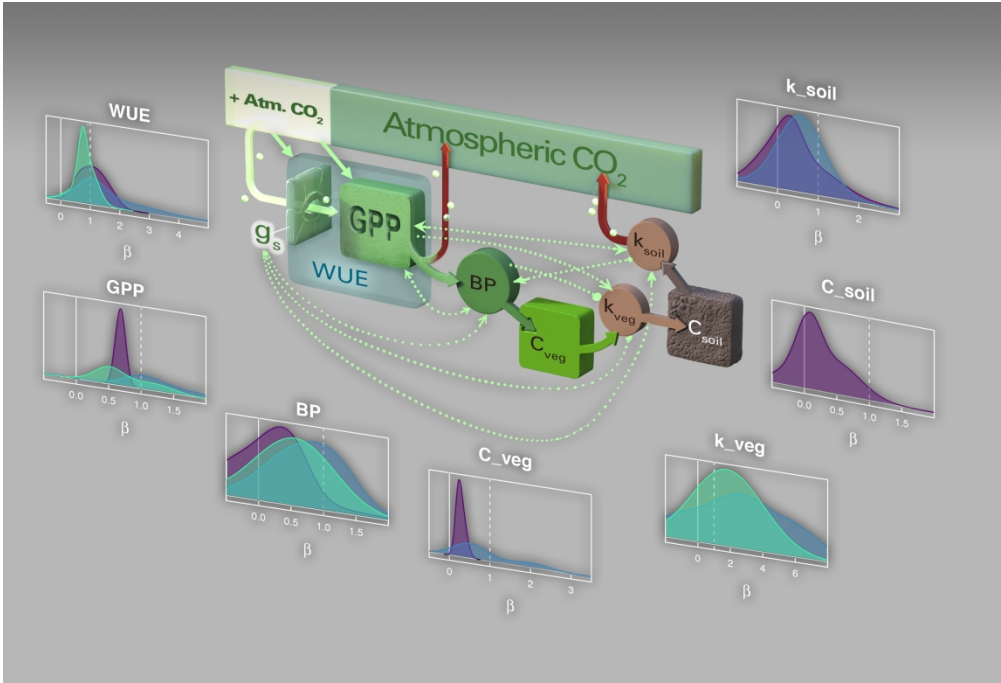
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b)







β distributions based on data from Table 1 for GPP, WUE, BP, kveg, ksoil, Cveg, and Csoil. Data are organised by CO₂ response category—iCO₂ (blue), attribution to iCO₂ (green), and eCO₂ (purple). See Supplementary Information for further details.

215x146mm (300 x 300 DPI)