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Review

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Empirical evidence and theoretical understanding of ecosystem carbon and nitrogen cycle interactions

Author for correspondence:
Benjamin D. Stocker
Email: *benjamin.stocker@unibe.ch*

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Benjamin D. Stocker[1,2], Ning Dong[3], Evan A. Perkowski[4], Pascal D. Schneider[1,2], Huiying Xu[5], Hugo J. de Boer[6], Karin T. Rebel[6], Nicholas G. Smith[4], Kevin Van Sundert[7,8], Han Wang[5], Sarah E. Jones[3], I. Colin Prentice[3,5] and Sandy P. Harrison[5,9]

[1]Institute of Geography, University of Bern, Hallerstrasse 12, CH-3012, Bern, Switzerland; [2]Oeschger Centre for Climate Change Research, University of Bern, Falkenplatz 16, 3012, Bern, Switzerland; [3]Department of Life Sciences, Georgina Mace Centre for the Living Planet, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot, SL5 7PY, UK; [4]Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409, USA; [5]Ministry of Education Key Laboratory for Earth System Modeling, Department of Earth System Science, Tsinghua University, Beijing, 100084, China; [6]Faculty of Geosciences, Copernicus Institute of Sustainable Development, Environmental Sciences, Utrecht University, Vening Meinesz Building, Princetonlaan 8a, Utrecht, 3584 CB, the Netherlands; [7]Department of Biology, University of Antwerp, Universiteitsplein 1, 2610, Wilrijk, Belgium; [8]Department of Bioscience Engineering, University of Antwerp, Groenenborgerlaan 171, 2020, Antwerp, Belgium; [9]Department of Geography and Environmental Science, University of Reading, Reading, RG6 6AB, UK

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Summary

Interactions between carbon (C) and nitrogen (N) cycles in terrestrial ecosystems are simulated in advanced vegetation models, yet methodologies vary widely, leading to divergent simulations of past land C balance trends. This underscores the need to reassess our understanding of ecosystem processes, given recent theoretical advancements and empirical data. We review current knowledge, emphasising evidence from experiments and trait data compilations for vegetation responses to CO_2 and N input, alongside theoretical and ecological principles for modelling. N fertilisation increases leaf N content but inconsistently enhances leaf-level photosynthetic capacity. Whole-plant responses include increased leaf area and biomass, with reduced root allocation and increased aboveground biomass. Elevated atmospheric CO_2 also boosts leaf area and biomass but intensifies belowground allocation, depleting soil N and likely reducing N losses. Global leaf traits data confirm these findings, indicating that soil N availability influences leaf N content more than photosynthetic capacity. A demonstration model based on the functional balance hypothesis accurately predicts responses to N and CO_2 fertilisation on tissue allocation, growth and biomass, offering a path to reduce uncertainty in global C cycle projections.

I. Introduction

An open challenge in understanding and modelling the terrestrial carbon (C) cycle response to climate change is to understand the role of soil nutrients and, specifically, the extent to which nitrogen (N) limits the current and future land C sink. Resolving this question is essential for understanding the climate-C cycle feedback under rising atmospheric CO_2 levels – a major source of uncertainty in Earth system projections (Friedlingstein *et al.*, 2014; Arora *et al.*, 2020; Wei *et al.*, 2022) and a Grand Challenge identified by the World Climate Research Programme (https://www.wcrp-climate.org/gc-carbon-feedbacks). As N is an essential nutrient required for biomass synthesis and used in enzymes responsible for C assimilation, N availability constrains C cycle dynamics (Vitousek & Howarth, 1991; LeBauer & Treseder, 2008).

The first generation of models simulating the terrestrial C cycle and climate change effects on ecosystems did not resolve mechanisms of C and N cycle interactions explicitly. These C-only Dynamic Global Vegetation Models (DGVMs) predicted substantial, albeit diverging, increases in the terrestrial C stock as a consequence of an enhancement of terrestrial gross and net biomass productivity under elevated CO_2 and a warming climate (Cramer *et al.*, 2001). However, limited flexibility in the C : N stoichiometry of plant tissues implies that additional N has to be made available for plant acquisition and sequestration in rising biomass stocks and other plant-derived organic matter, for example in soils. Hungate *et al.* (2003) argued that the additional N required for plant acquisition implied by these C-only model projections was unrealistic and, therefore, that the projections of the future land C sink were excessive. Early results from free-air CO_2 enrichment (FACE) experiments, conducted mostly on temperate grassland and forest ecosystems, also provided evidence for a strong role of N in regulating growth responses to elevated CO_2 (Oren *et al.*, 2001; Schneider *et al.*, 2004; Dukes *et al.*, 2005; Reich *et al.*, 2006). These insights motivated the development of a second generation of DGVMs that would explicitly resolve interactions with the N cycle and thereby consider the constraints imposed by limiting plant N acquisition (Shi *et al.*, 2016). However, incorporation of the N constraint has not reduced the uncertainty in C cycle projections, as shown by diverging projections of the land-atmosphere C flux by the current-generation model ensembles (Arora *et al.*, 2020) and by diverging global simulations of the response of biomass production to elevated CO_2 and N fertilisation (Davies-Barnard *et al.*, 2020).

Comparison of the observed terrestrial C balance trend in recent decades and the trends simulated by a recent generation of DGVMs corroborates this picture (Fig. 1). These models were used for the model intercomparison activity Trends and Drivers of Terrestrial Sources and Sinks of Carbon Dioxide (Trendy) (Sitch *et al.*, 2024) v.8, and for the quantification of the Global Carbon Budget (Friedlingstein *et al.*, 2022). The spread across individual models is much larger for C–N models than for C-only models, both for the mean terrestrial sink between 2011 and 2020 (Fig. 1b) and for the mean trend between 1959 and 2020 (Fig. 1c). Yet, on average across the ensemble of models, the average land C sink (2011–2020) and its multi-decadal trend since 1959 are in closer agreement with the implied residual sink from the Global Carbon Budget for C–N models than for C-only models. This suggests a general improvement of land C balance trend simulations linked to considering C–N interactions. However, the large variability among models is a concern and several individual C–N model simulations of the recent mean land C sink are outside the 95% confidence interval of its temporal trend (Fig. 1c).

The terrestrial C sink and its evolution under future climate and CO_2 projections is a central quantity that has motivated the inclusion of explicit N cycling in DGVMs. Yet, the apparent divergence of simulations for the terrestrial C sink and its trend indicates remaining challenges. The divergence cannot be attributed solely to uncertainty in the process representations relating to the terrestrial N cycle and its interaction with the C cycle in C–N models since there are inherent uncertainties and limitations in multiple aspects of simulations of the land C cycle (O'Sullivan *et al.*, 2022) and impacts by land use change (Dohner *et al.*, 2022). Nevertheless, the large difference in model spread among C-only vs C–N models suggests (1) that C–N coupling and related ecosystem feedbacks are particularly influential for long-term terrestrial C balance trends, (2) that there is a lack of agreed principles governing plant responses to N availability and limitation, and (3) that established observational benchmarks for model development and testing provide insufficient or insufficiently used constraints on decadal-scale C cycle trends.

Current models include representations of multiple processes linking the C and N cycles in ecosystems (Fig. 2). However, the diversity of representations of individual processes among the current generation of C–N models is large (Box 1, Davies-Barnard *et al.*, 2020; Meyerholt *et al.*, 2020) and insights gained from experiments and field observations remain valuable for better informing the next generation of C–N models. A key finding from earlier work has been that models overestimated leaf stoichiometric flexibility and underestimated flexibility in allocation and N uptake under elevated CO_2 (Zaehle *et al.*, 2014; Medlyn *et al.*, 2015). Flexible allocation with implications for N uptake remains unresolved in most of the current generation of C–N models, many of which simulate foliar C : N stoichiometry changes exclusively as a function of soil N availability (Box 1).

Recent research suggests that an influence of the atmospheric environment on leaf C : N stoichiometry and photosynthesis is evident and can be predicted. Large variations in photosynthetic capacity at the standard temperature of 25°C (V_{cmax25}) have been

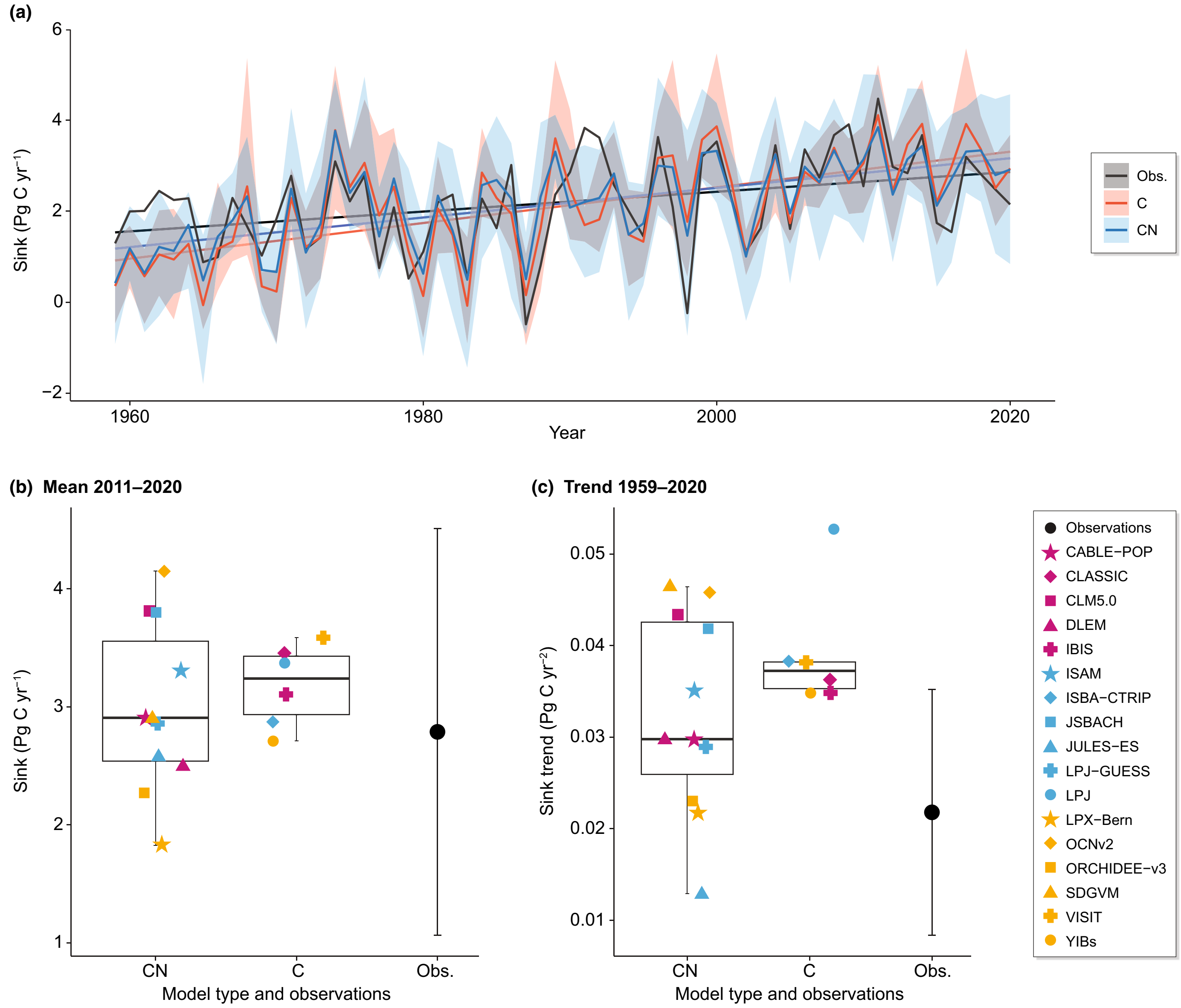

Fig. 1 Terrestrial carbon (C) balance and trends. (a) Residual terrestrial land sink (i.e. after removal of the land use fluxes) time series, (b) recent decadal mean sink and sink trend. Shading in (a) indicates the model spread for C-only models (red) and C–N coupled models (blue). Data are from the TRENDY v.8 simulations and the Global Carbon Budget 2021 (Friedlingstein *et al*., 2022). Observations-based estimates ('Obs.' in a) represent the residual of the global C budget, calculated as the difference between the sums of all emissions (from fossil fuel combustion and land use change) and the sum of the atmospheric growth rate, the ocean sink and the sink of cement carbonation. Boxes in (b) and (c) represent the inter-quartile range (IQR) and whiskers the median plus/minus 1.5 times the IQR for C–N coupled models and for C-only models. The vertical line for observations indicates 1.96 times the SD in (b) and 1.96 times the SE (corresponding to the 95% confidence interval) of the sink trend in (c). See Supporting Information Notes S1 for further information about the methods of this analysis.

documented along climatic gradients (Smith *et al.*, 2019; Peng *et al.*, 2020; Dong *et al.*, 2022; Wang *et al.*, 2023; Xu *et al.*, 2023) and an acclimating response of V_{cmax25} is documented from FACE experiments (Ainsworth & Rogers, 2007). A high V_{cmax25} requires a high amount of the N-rich enzyme Rubisco. Hence, a changing climate and rising CO_2 have direct implications for the *demand* for N and foliar C : N stoichiometry (Dong *et al.*, 2017) – a pathway of C–N coupling that has not been considered in the current generation of C–N models.

Predictions of leaf-level responses and reliable C cycle simulations and projections to novel environmental conditions rely on efficient theory and first principles that predict generally observed patterns in ecosystems in response to the abiotic environment (Marquet *et al.*, 2014). Eco-evolutionary optimality (EEO) theory has been developed for predicting how V_{cmax25} and leaf N acclimate to the atmospheric environment (Wright *et al.*, 2003; Prentice *et al.*, 2014; Dong *et al.*, 2017; Smith *et al.*, 2019; Peng *et al.*, 2021; Dong *et al.*, 2022) and for modelling flexible allocation and the role

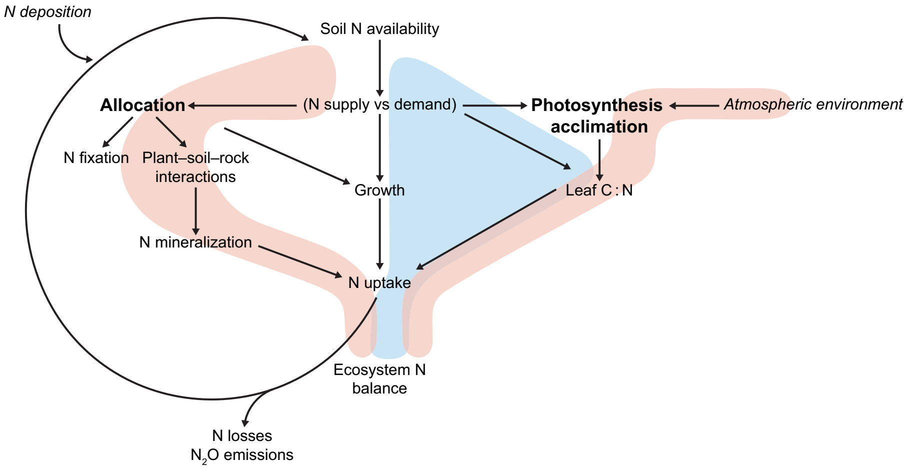

Fig. 2 Pathways of carbon–nitrogen (C–N) interactions in terrestrial ecosystems. The pathway indicated by the blue background colour represents the traditional approach implemented in many DGVMs, whereby the atmospheric environment (mainly temperature, radiation and vapour pressure deficit) exerts no direct effect on leaf C : N. The importance of representing pathways indicated by the red background colour is emphasised in this review. Effects of soil N availability on allocation is represented by some DGVMs reviewed here (Box 1). Direct effects of the atmospheric environment on acclimation have implications for the leaf C : N and, through that, on ecosystem N cycling.

of N in constraining ecosystem responses to rising CO_2 and climate change (Bloom *et al*., 1985; Rastetter *et al*., 1997; Franklin, 2007; Franklin *et al*., 2020; Harrison *et al*., 2021). However, key governing principles for the prediction of acclimation of photosynthetic and other traits, allocation and C–N interactions are often not considered in models that are used for global-scale simulations and as components in coupled Earth System Models.

Large compilations of leaf traits and experimental data have become available in recent years (Cleland *et al*., 2019; Kattge *et al*., 2020; Liang *et al*., 2020; Van Sundert *et al*., 2023). Ecosystem manipulation experiments provide particularly strong empirical constraints on models' responses to environmental change factors and ensuing long-term shifts in ecosystem dynamics (Medlyn *et al*., 2015; Wieder *et al*., 2019; Caldararu *et al*., 2023), while field data compilations provide rich information about global variations of N-related plant traits. Together, these data may provide an opportunity to derive general patterns of ecosystem responses to altered CO_2 and soil N availability for re-examining our understanding of the coupling between the C and N cycles and how they respond to a changing environment from a plant-centred point of view. This, in turn, provides a basis for suggesting how these cycles could be represented more realistically in models. In this review, we first summarise the insights gained from meta-analyses of ecosystem manipulation experiments and leaf traits data compilations across large environmental gradients. We then show how the observed patterns can be captured using EEO modelling approaches, implemented in a simple demonstration model of the coupled C–N cycle dynamics in terrestrial ecosystems. Finally, we discuss how the insights from observations and theoretical considerations could be used to improve our ability to simulate the C cycle response to multi-decadal environmental change.

II. Insights from experimental manipulations

Ecosystem manipulation experiments at various scales have been used to study terrestrial C–N cycle coupling. While results from individual experiments can differ, a meta-analysis of the available data can reveal consistent patterns. We performed a meta-analysis of multiple response variables to elevated CO_2 and N fertilisation, drawing on multiple published data compilations of ecosystem manipulation experiments (Notes S2). All data compilations focus on responses observed under field conditions in natural soils with native vegetation and should thus be indicative of global vegetation responses to environmental change. We use data only from experiments where a single factor was manipulated (CO_2 or N input) and exclude interactive responses recorded in multi-factorial experiments. For the CO_2 response, we use data from the Manipulation Experiments Synthesis Initiative (MESI) (Van Sundert *et al*., 2023) – a combined dataset that integrates multiple data compilations used for previous meta-analyses and results from individual experiments (Table S1). For biomass-related responses to N fertilisation, we use data from MESI, combined with data from a network of standardised grassland field experiments (NutNet) (Cleland *et al*., 2019) (Table S2). To complement our analysis with a focus on leaf-level responses, we use data of N-fertilisation effects on photosynthesis and leaf traits from the published meta-analysis by Liang *et al*. (2020) (Table S3). We quantified the logarithm of response ratios to compare relative changes in a set of variables relevant for ecosystem C–N interactions.

1. Nitrogen uptake responses to nitrogen availability

Our meta-analysis (Fig. 3) of published data on ecosystem experiments (Cleland *et al*., 2019; Liang *et al*., 2020; Van Sundert *et al*., 2023) shows that N fertilisation increases soil inorganic N (Fig. 3b) and drives an enhancement of N uptake despite generally absent changes in belowground biomass and root biomass production. This indicates that more N is taken up by plants per C spent to build roots. Enhanced N acquisition efficiency in N-fertilisation experiments is also reflected by the general decrease in root : shoot ratios and root mass fractions (RMFs) under N fertilisation (Fig. 3b). This reduction in the relative resource investment for N acquisition, or cost to acquire N (Terrer *et al*., 2018; Eastman *et al*., 2021; Perkowski *et al*., 2021), results in a greater relative resource investment in aboveground tissues (Fig. 4), promoting increased C acquisition and growth.

Box 1 Representations of ecosystem C and N cycle interactions in models used for Trendy v.8 and in the CN-model (Stocker & Prentice, 2024). References for each model are given in the SI

N uptake: many models consider the effect of abiotic soil properties, including temperature, water content and inorganic soil N content, on N uptake, but the formulations diverge. Some models scale N uptake linearly with inorganic soil N content (CLM4.5 (Oleson *et al*., 2010), SDGVM (Walker *et al*., 2017), JULES (Wiltshire *et al*., 2021)), while others assume a saturating relationship (ISAM (Meiyappan *et al*., 2015), DLEM (Tian *et al*., 2015), CABLE (Haverd *et al*., 2018), O-CN (Zaehle & Friend, 2010), ORCHIDEEv3 (Vuichard *et al*., 2019), LPJ-GUESS (Smith *et al*., 2014)) and CN-model (Stocker & Prentice, 2024). Regarding plant properties, some models scale N uptake by the total N demand of the vegetation (JSBACH (Reick *et al*., 2021), CABLE, CLM4.5, CLM5 (Lawrence *et al*., 2019)); some models additionally include a linear increase in N uptake with root mass or surface area (CLM5, ISAM, O-CN, ORCHIDEEv3, LPJ-GUESS and JULES), or with leaf N (ORCHIDEE). An explicit saturating relationship of N uptake and root mass is not considered in TRENDY v.8 models but in CN-model (Stocker & Prentice, 2024). Some models include an explicit increase in N uptake efficiency if the whole-plant (nonwoody) C : N ratio increases (OCN, ORCHIDEEv3, LPJ-GUESS and CML5). CLM5 explicitly calculates a carbon (C) cost for N acquisition from different potential sources, including direct root uptake, uptake via symbiotic mycorrhizas, fixation via symbiotic bacteria and resorption.

Allocation: most models use dimensional relationships that may vary with phenology or environment but keep a constant balance between above- and belowground allocation (root : shoot ratio) (CLM4.5, CLM5, CABLE, JULES, SDGVM, JSBACH, ORCHIDEEv3 and LPJ-GUESS). Some models allow allocation to vary in response to N availability (IBIS (Yuan *et al*., 2014)) or demand (OCN, ORCHIDEEv3 and LPJ-GUESS). CN-model simulates fully flexible allocation to achieve a match between N uptake and demand, given growth and stoichiometry in different tissues.

Stoichiometry: flexible stoichiometry allows plants to reduce their N demand for growth when N uptake is limited. Some models prescribe a fixed C : N ratio for each plant tissue and PFT (CLM4.5, JULES, SDGVM, JSBACH and IBIS) or for nonleaf tissues (CN-model). Other models include flexible C : N stoichiometry, either on a whole-plant basis with the between-tissue ratios of C : N ratios held constant (JULES and CLM4.5), or with flexible stoichiometry on a tissue basis (OCN, ORCHIDEEv3, LPJ-GUESS, CLM5 and CABLE). Some models additionally use the difference between current and targeted tissue C : N to modulate N uptake (O-CN, ORCHIDEEv3, JULES and CLM5). Flexible stoichiometry is commonly simulated as a function of soil N availability vs demand. In CN-model, it is simulated via internally predicted photosynthetic capacities (V_{cmax} and J_{max}) and their response to the atmospheric environment.

Photosynthesis: net photosynthesis rates are simulated in most terrestrial biosphere models using the Farquhar *et al*. (1980) and Collatz *et al*. (1992) models for C_3 and C_4 species, respectively (except ISBA (Delire *et al*., 2020) using the model by Goudriaan, 1986, see Delire *et al*., 2020). The key parameters that drive rate-limiting steps (maximum Rubisco carboxylation rate, V_{cmax}; and maximum electron transport rate for RuBP regeneration, J_{max}) are commonly predicted through empirical relationships with leaf N content (O-CN, ORCHIDEEv3, LPJ-GUESS, CLM4.5, CLM5, CABLE, DLEM, JULES). These rates are typically scaled through the canopy using light extinction coefficients simulated as a function of leaf N concentration (CLM4.5, CLM5, JULES and ISBA) or specific leaf area (ORCHIDEEv3). Some models (CLM5, CABLE and LPJ-GUESS) include an optimality principle for allocating a fixed total amount of leaf N into investments of carboxylation vs electron transport, depending on environmental conditions (e.g. using the LUNA model, Ali *et al*., 2016). However, the total leaf N is determined in these models by soil N supply and is not subject to acclimation to the atmospheric environment. In CN-model, V_{cmax} and J_{max} are predicted in response to the atmospheric environment and are independent of soil N, while leaf N is derived from predicted V_{cmax} and J_{max} and is thus also independent of soil N.

Autotrophic respiration: most models treat autotrophic respiration as the sum of growth and maintenance respiration. In some models, autotrophic respiration is a fixed proportion of the maximum Rubisco carboxylation rate (JSBACH, CABLE), or tissue N content (JULES, ORCHIDEEv3 and O-CN). In others, it is additionally modified by temperature (DLEM, CLM4.5 and CLM5). Growth respiration is based on the construction costs of allocating new C to tissues (CLM4.5 and CLM5) or set to a fixed proportion of GPP (DLEM). In CN-model, the leaf respiration base rate scales with V_{cmax} following (Wang *et al*., 2020).

N limitation: N limitation is an emergent model behaviour, determined by multiple process representations, expressed through the effect by which N limits photosynthesis, productivity, and/or the ecosystem-level C sequestration. N limitation is commonly measured in experiments through the simulated effects of N fertilisation. The large variability in modelling N dynamics allows for categorising N limitation representations in several respects. Focusing on the plant–soil axis, we categorised the effect of N limitation under elevated CO_2 into four partially intersecting groups: (1) Relatively simple models that have no explicit N dynamics and constrain the response of biomass production under elevated CO_2 with empirical functions (YIBs (Yue & Unger, 2015), ISBA); (2) Models that simulate N limitation through downregulation of NPP due to low N availability in the soil, but do not simulate any plant response to this limitation (SDGVM, JSBACH, IBIS and CLM4.5); (3) Models that additionally consider within-plant responses, for example a flexible stoichiometry that allows an increase in N use efficiency and, therefore, the maintenance of biomass production to some degree under N limitation (CABLE and CLM5); and (4) Models that, in addition to flexible stoichiometry, include more complex responses, where plants respond to low N uptake by increasing their N uptake efficiency, increasing their root : shoot ratio, or increasing the C spent to acquire N from different sources (O-CN, ORCHIDEEv3, LPJ-GUESS, CLM5 and CN-model).

The increase in N uptake efficiency under N fertilisation is likely the consequence of increased mass flow of N uptake per root surface area. The mechanics of root N uptake and its dependency on root surface area and inorganic N concentrations in the soil solution can be described in terms of the first principles of solute movement and enzymatic uptake rates (McMurtrie & Näsholm, 2018). In addition, the reliance on other forms of N uptake (e.g. N fixation from symbiotic relationships with soil microbial communities) is also affected by N fertilisation. For example, an increase in plant-available soil inorganic N reduces the reliance on N uptake pathways that rely on microbial symbionts, as a result of increased mass flow uptake (Bloom *et al.*, 1985; Rastetter *et al.*, 2001; Perkowski *et al.*, 2021). Organic N forms (amino acids) can constitute an important source of N to plants (Näsholm *et al.*, 2009), drive a similar response in aboveground plant biomass (Shi *et al.*, 2024), and affect soil N cycling and plant supply differently from inorganic N in fertilisation experiments (Lim *et al.*, 2022). However, even in arctic environments where

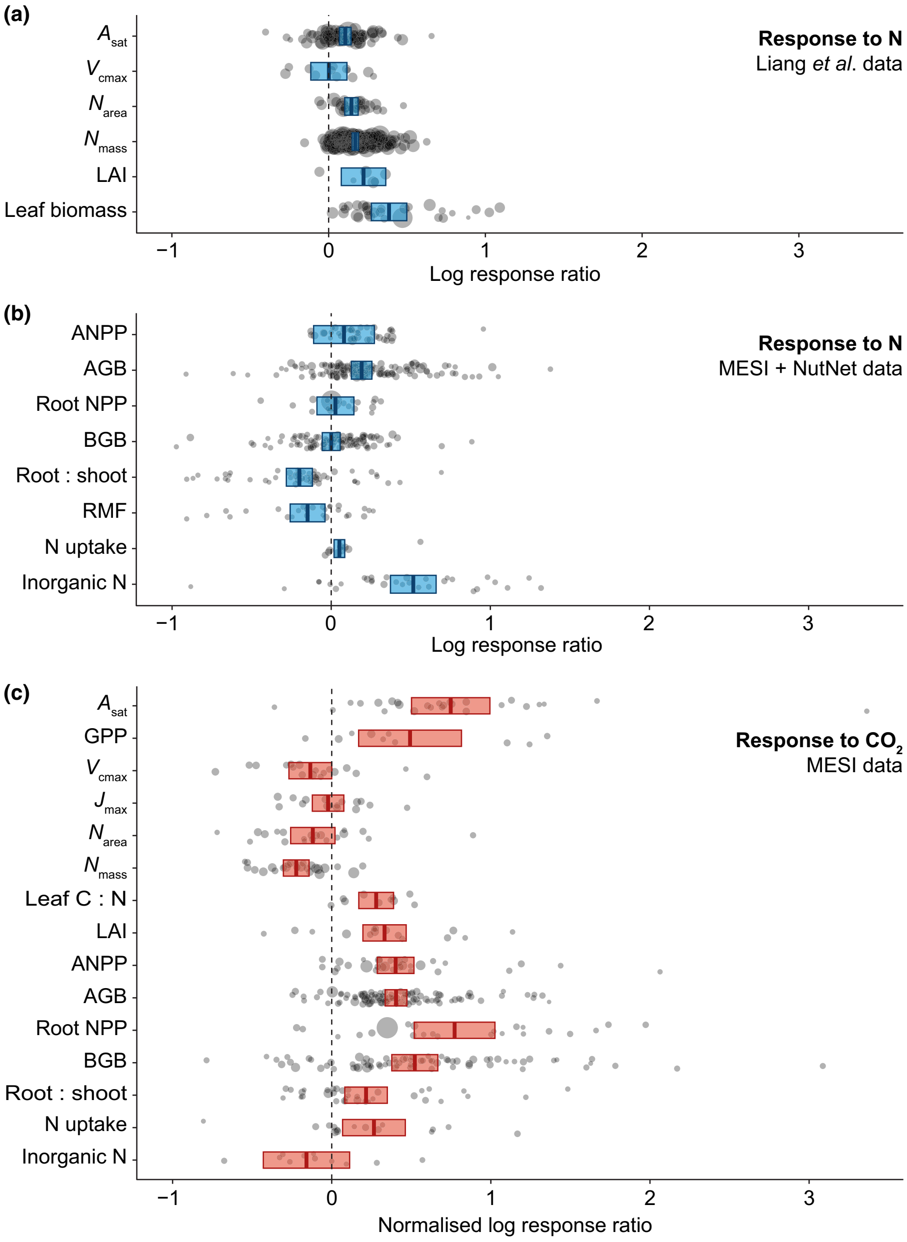

Fig. 3 Meta-analysis of N fertilisation (a, b) and elevated CO_2 experiments (c). The response to N fertilisation shown is based on (a) data from (Liang *et al*., 2020), (b) combined data from MESI (Van Sundert *et al*., 2023) and NutNet (Cleland *et al*., 2019). The response to elevated CO_2 (c) is based on MESI data. Each point represents the average log-transformed ratio of means recorded across all years for one experiment. The size of points represents the inverse of the SE of the log response ratio. The log response ratio is computed for N-fertilisation experiments with varying manipulations, but filtered to manipulations below < 30 gN m^{-2} yr^{-1} to facilitate comparability. The log response ratio is computed for CO_2 experiments by normalising with the log-transformed ratio of control and elevated CO_2 levels. The boxes represent the meta-analytic 95% confidence interval of the mean and the vertical line in each box' centre its mean. A_{sat} is the leaf-level assimilation rate measured at saturating light, GPP is the gross primary production, V_{cmax} is the maximum rate of Rubisco carboxylation rate, J_{max} is the maximum electron transport rate for RuBP regeneration, N_{area} is the leaf N content per unit leaf area, N_{mass} is the leaf N content per unit leaf mass, LAI is the leaf area index, (A)NPP is the (aboveground) net primary production (corresponding to biomass production), AGB is the aboveground biomass, BGB is the belowground biomass, root : shoot is the root-to-shoot mass ratio. See Supporting Information Notes S2 for further information about methods of this analysis.

mineralisation is often suppressed by freezing temperatures and organic N supply has been argued to be dominant, inorganic N cycling rates are of similar magnitude as in temperate and tropical soils (Ramm *et al*., 2022).

Our meta-analysis (Fig. 3b) further shows that inorganic N availability responses to N fertilisation varied substantially, both in sign and magnitude, across studies. This may reflect variability in the amount of N added across studies (we excluded experiments with N application rates of > 30 gN m^{-2} yr^{-1}). However, it could also imply that the distinct contexts of the studies altered the fertilisation impact on N availability and could be indicative of high spatiotemporal heterogeneity of soil inorganic N availability (Van Sundert *et al*., 2020; Akana *et al*., 2023; Ochoa-Hueso *et al*., 2023) and soil microbiomes (Jansson & Hofmockel, 2020) in terrestrial ecosystems.

2. Carbon allocation responses to nitrogen availability

Our meta-analysis shows a general relative C allocation shift to aboveground tissues under increased N availability (Figs 3, 4). Aboveground NPP and biomass increased despite no consistent change in root NPP or belowground biomass across experiments. This allocation response is reflected by the clear declines in the root : shoot ratio and the RMF. The shift towards aboveground tissues under N fertilisation likely reflects the aforementioned increase in N uptake efficiency (McMurtrie & Näsholm, 2018; Eastman *et al*., 2021; Perkowski *et al*., 2021) and implies a positive feedback whereby additional N leads to increases in leaf area and subsequently GPP, resulting in plants that are larger and have more aboveground biomass than their unfertilised counterparts. Although the general pattern indicates relatively more investment

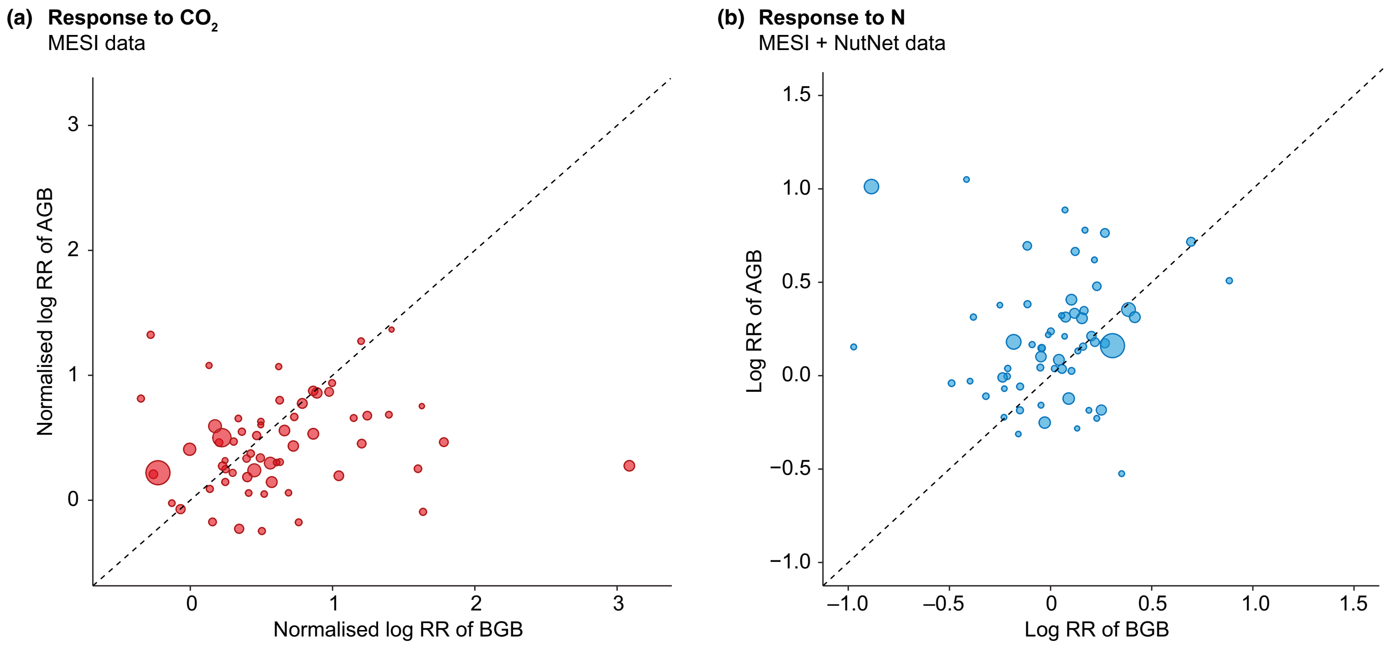

Fig. 4 Simultaneous response ratios of above and belowground biomass for (a) CO_2 experiments and (b) nitrogen (N)-fertilisation experiments. Each point represents the average log-transformed ratio of means recorded across all years for one experiment. The size of points represents the inverse of the SE of the log response ratio. The log response ratio is computed for N-fertilisation experiments with varying manipulations, but filtered to manipulations below < 30 gN m^{-2} yr^{-1} to facilitate comparability. The log response ratio is computed for CO_2 experiments by normalising with the log-transformed ratio of control and elevated CO_2 levels. See Supporting Information Notes S2 for further information about methods of this analysis.

of C for biomass production above- than belowground, in some experiments, the response is opposite (Fig. 4). Such responses have previously been documented for severely nutrient-limited ecosystems (Van Wijk *et al.*, 2003).

3. Leaf-level responses to nitrogen availability

Leaf N, both on a mass and area basis, increases consistently with soil N fertilisation (Fig. 3a). Even though leaf N and photosynthetic capacity are positively correlated across species and sites (Evans, 1989; Walker *et al.*, 2014), there is no response of leaf carboxylation capacity (V_{cmax}) to N fertilisation in the data we analysed (Fig. 3a). Although we analysed the same data as (Liang *et al.*, 2020), this result differs from their finding of a positive, yet nonsignificant, response because we excluded two experiments where > 30 gN m^{-2} yr^{-1} were applied. Our result indicates a decoupling of the leaf N-photosynthetic capacity relationship under N fertilisation (Luo *et al.*, 2021; Waring *et al.*, 2023). While the absent V_{cmax} response indicates little effect of N fertilisation on leaf-level photosynthesis (and dark respiration), the strong positive effect on LAI and leaf biomass suggests that increasing GPP in response to increasing N availability is primarily the result of increased leaf production, rather than an increase in the photosynthetic capacity of individual leaves.

Liang *et al.* (2020) provided a larger dataset on the response of the assimilation rate to N fertilisation than available for photosynthetic capacities. These data show a significant increase in assimilation rate (which we assume is assimilation under light-saturated conditions, i.e. A_{sat}) in response to N fertilisation. However, there appear to be two separate populations of experiments (fig. 4a in Liang *et al.*, 2020). Some of the experiments show an increase in assimilation rate that is proportional to the increase in biomass, while a second group show a varying response of biomass but no increase in assimilation rate (Table S2). There is insufficient information given about the prior N availability in the soil (or through N deposition) to determine whether these differences in response reflect differences in the background state, differences in the N-fertilisation treatments or differences in responses across species. There is also no obvious pattern in terms of plant groups, phenology or mycorrhizal type (Table S1). Thus, it is currently impossible to resolve the cause of these different responses. However, the mean change in assimilation rate is only about a quarter of the magnitude of the change in leaf biomass.

4. The role of atmospheric CO_2 availability in driving nitrogen-related processes and responses

Elevated CO_2 tends to increase LAI, biomass production and biomass stocks, similar to the effects of N fertilisation. However, opposite to the effects of N fertilisation, the increase in belowground production under elevated CO_2 is stronger than the increase in aboveground production, inducing a net shift towards greater belowground growth and biomass allocation. This shift towards belowground allocation in turn increases N uptake, depleting available mineral N in the soil (Fig. 3c). This negative feedback loop between plant N uptake and plant-available N may

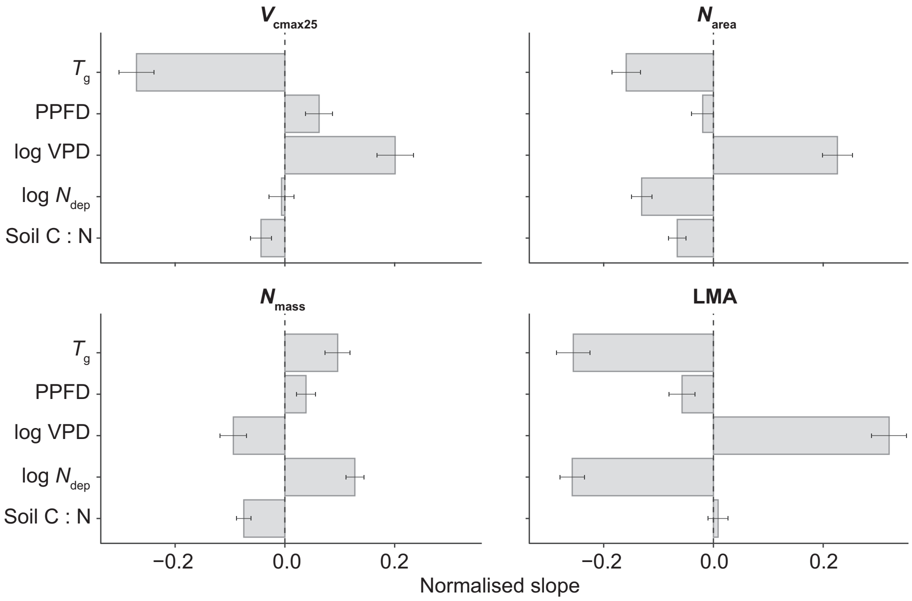

Fig. 5 Effects of different environmental factors on leaf traits, including the maximum rate of Rubisco carboxylation (V_{cmax25}), nitrogen (N) content per unit area (N_{area}) and mass (N_{mass}) and leaf mass per unit area (LMA). Effects are determined as coefficients of multivariate linear regression models of data with normalised values of the predictors growth temperature (T_g), photosynthetic photon flux density (PPFD), log-transformed vapour pressure deficit (log VPD), log-transformed N deposition rate (N_{dep}) and soil C : N ratio (soil C : N). Error bars indicate the 95%-confidence interval. This is based on a global dataset of leaf trait measurements along large environmental gradients (Dong *et al*., 2022). See Supporting Information Notes S3 for further information about methods of this analysis.

constrain the positive effects of CO_2 fertilisation on plant growth and biomass production, especially in soils with low N availability (Luo *et al*., 2004). This N constraint on CO_2 fertilisation has been substantiated by past studies showing greater positive biomass responses when N availability is high in combination with elevated CO_2 as compared to elevated CO_2 responses when N availability is low (Terrer *et al*., 2019). However, N uptake consistently increases under elevated CO_2 and it should be noted that the data analysed here are from experiments where no N fertilisation was applied in parallel to the elevated CO_2 application. This suggests that a progressive *release* from N limitation (Walker *et al*., 2015) may be enabled by the increased capacity of plants to acquire (increasingly scarce) soil N thanks to increased root biomass and surface area under elevated CO_2. At the leaf level, elevated CO_2 reduces leaf N by decreasing the demand for photosynthetic enzymes and leaf-tissue N (Smith & Keenan, 2020; Dong *et al*., 2022). This implies an additional mechanism by which N limitation on biomass production under elevated CO_2 may be partly alleviated.

III. Insights from environmental gradients

C cycle simulations of DGVMs are particularly sensitive to the representations of leaf traits due to the role of traits in photosynthetic CO_2 assimilation and their influence on N cycling. The amount of N in leaves is linked to photosynthetic capacity through the N-rich enzyme Rubisco that is involved in photosynthesis. The acclimation of photosynthesis to the atmospheric environment should thus have implications for the leaf C : N stoichiometry and plant N demand (Dong *et al*., 2022; Xu *et al*., 2023). However, not all leaf N is in photosynthetic proteins. Across ecosystems globally, LMA is a more important determinant of leaf N than V_{cmax25} (Dong *et al*., 2022). In this section, we consider what can be learned from large-scale geographic patterns of V_{cmax25}, LMA and leaf N and their relationships to environmental variables, including soil C : N ratio (as an inverse index of soil N availability) and N deposition, accounting for simultaneous variations in temperature, light and atmospheric dryness.

1. Leaf-level responses to environment

The atmospheric environment influences photosynthetic capacity in ways that can be understood via EEO principles (Reich *et al*., 2007; Ali *et al*., 2016; Smith *et al*., 2019; Dong *et al*., 2020). Fig. 5, based on a simplified analysis of the global leaf–trait dataset presented in Dong *et al*. (2022) (see Notes S3), illustrates the widely observed reduction in V_{cmax25} with growth temperature and increase with light and vapour pressure deficit (VPD). These dependencies are well understood in EEO terms. V_{cmax25} increases with light availability (enabling the leaf to use all of the light it absorbs), declines with growth temperature because less Rubisco is required for photosynthesis at higher temperatures, and increases with VPD because more Rubisco is required to compensate for reduced stomatal conductance – which represents the least-cost response of air-to-leaf CO_2 drawdown to VPD (Prentice *et al*., 2014; Smith *et al*., 2019; Dong *et al*., 2020, 2022; Peng *et al*., 2021).

Fig. 5 also shows that V_{cmax25} decreases with an increasing soil C : N ratio – which may reflect the higher costs of N acquisition on less fertile soils (Paillassa *et al*., 2020). However, N deposition does not increase V_{cmax25}. These responses of V_{cmax25} do not mimic those of leaf N. In particular, soil C : N ratio has a stronger effect on leaf N (both N_{mass} and N_{area}) than on V_{cmax25}, while N deposition increases N_{mass} but reduces LMA so strongly that N_{area} is paradoxically reduced. The predictors considered in the models here were almost all highly significant (Notes S3: Table 1), while model fits achieved relatively modest adjusted R^2 values of between 0.1 for N_{mass} and 0.2 for LMA. This reflects the influence of differences in leaf traits between species and the limited capacity of linear models to fit often interactive and nonlinear effects of abiotic factors (Tian *et al*., 2024).

2. Patterns in leaf traits data are consistent with experimental evidence, but not with common assumptions

A widespread modelling paradigm emphasises stoichiometric flexibility (Zaehle *et al.*, 2014; Medlyn *et al.*, 2015; Hauser *et al.*, 2023) and the control of photosynthesis and plant growth by soil N supply (Box 1). It is commonly assumed that increased soil N availability enhances N concentrations in leaves, enabling increased photosynthetic capacity. Our analysis of large-scale field data, however, is consistent with the experimental evidence (Fig. 3) that photosynthetic capacity is not directly controlled by leaf N content, and that increased N availability can increase leaf N without consistently increasing photosynthetic capacity.

IV. An optimality-guided CN-model

As a relatively simple and transparent demonstration model, we use the CN-model (Stocker & Prentice, 2024), which draws on EEO concepts to model the two pathways through which C and N cycle interactions and ecosystem feedbacks arise – through allocation and acclimation of photosynthesis. The model dynamically simulates responses to experimental treatments and is comparable in model scope (resolved processes, pools and fluxes) to terrestrial biosphere models described in Box 1 and used for simulations of land C balance trends for the Global Carbon Budget (Fig. 1), but is run here for point-scale simulations. Allocation to roots and shoots is predicted following a C–N functional balance approach (Bloom *et al.*, 1985) through which the root : shoot ratio is dynamically simulated such that the ratio of C assimilation and N uptake matches the demand by respiration and the C : N ratio of new biomass production. Acclimation of photosynthesis is modelled through the trade-off between optimising C assimilation relative to water loss (Prentice *et al.*, 2014; Wang *et al.*, 2017) and predicts V_{cmax} and J_{max}, and – by implication – the total amount of leaf metabolic N. Soil N is assumed to have no effect on the acclimation of photosynthesis. Leaf structural N is modelled based on a linear function of leaf metabolic N. N uptake is simulated based on a simplified representation of N transport in the soil solution and root uptake following McMurtrie & Näsholm (2018), and saturates with increasing root mass and increasing soil inorganic N. Organic N uptake is not considered. The model is forced to simulate a representative N-fertilisation (12 g m^{-2} yr^{-1}) and CO_2 experiment (doubling of ambient levels) in a representative grassland. More detailed information about model simulations is provided in Notes S4. A comprehensive description of the model and its underlying hypotheses is given in Stocker & Prentice (2024).

The model predicts the correct response direction in all observed variables from N-fertilisation and CO_2 experiments simultaneously (Fig. 6), from photosynthesis (GPP, V_{cmax} and J_{max}), growth (ANPP and root NPP) and biomass (AGB, BGB, root : shoot and RMF) to N cycling (N uptake, inorganic N), except for N_{mass} and N_{area}, where the model predicts no response. Also, no responses are (incorrectly) simulated for A_{sat} in N-fertilisation experiments and for leaf C : N in CO_2 experiments. The simulated absence of an effect of N fertilisation on V_{cmax25} is consistent with the experimental meta-analysis. Patterns in the root : shoot ratio, the RMF, above and belowground biomass and biomass production under elevated CO_2 and N fertilisation are correctly predicted. Consistent with experimental evidence, the model also predicts enhanced N uptake under elevated CO_2 despite a (slight) depletion of inorganic soil N and conditions suggestive of N limitation. The system modelled here appears N-limited, considering the simulated positive response in biomass and biomass production under N fertilisation. The enhanced N uptake is enabled by a more efficient recycling of N along the N uptake-turnover-mineralisation-loss cycle. Overall, the simulated response ratios are within the 95% confidence interval of the meta-analytic mean for 12 among the 23 observed response ratios in N-fertilisation and CO_2 experiments and within the range of individual experiments for 22 among the 23 observed response ratios. Deviations of the simulated vs meta-analytic mean response for aboveground biomass and productivity under eCO_2 and for inorganic N under N fertilisation may be related to the focus on a representative grassland for simulations (no wood allocation), an incomplete representation of the controls on inorganic soil N dynamics and other aspects of the model that will have to be investigated in further work.

V. Discussion

The representation of C–N interactions in models of terrestrial ecosystems is particularly influential for their simulations of long-term land C balance changes (Fig. 1) (Thornton *et al.*, 2007; Zaehle *et al.*, 2010a,2010b; Thomas *et al.*, 2013, 2015; Wieder *et al.*, 2015b; Meyerholt *et al.*, 2020) and not sufficiently constrained by commonly used benchmarks (Meyerholt *et al.*, 2020). Yet, representations of related processes in the current generation of C–N models are very diverse, if not conflicting, for key processes (Box 1). This context provided the motivation for our review of collective empirical constraints from ecosystem experiments and leaf traits data compilations. We took a plant-centric perspective to identify patterns in allocation and photosynthesis acclimation under N fertilisation, elevated CO_2 and along climatic gradients and showed that several related responses can be predicted from EEO principles. Confronting CN-model with the results of the meta-analysis of ecosystem experiments suggests that the EEO principle of the functional balance in allocation is a powerful approach to simulating observed responses. The strong influence of climate on V_{cmax} indicates that reliable predictions of leaf stoichiometry and photosynthesis responses to global change may benefit from an existing EEO model of the acclimation of photosynthesis (Prentice *et al.*, 2014). The strong influence of N deposition on LMA indicates an open challenge for modelling. Taken together, considering EEO principles and a wide array of empirical constraints are useful for informing the next generation of C–N models.

1. Allocation

N fertilisation and increasing CO_2 elicit opposite responses in C allocation, as indicated by the general patterns in Fig. 4. N fertilisation leads to increased N uptake efficiency and reduced

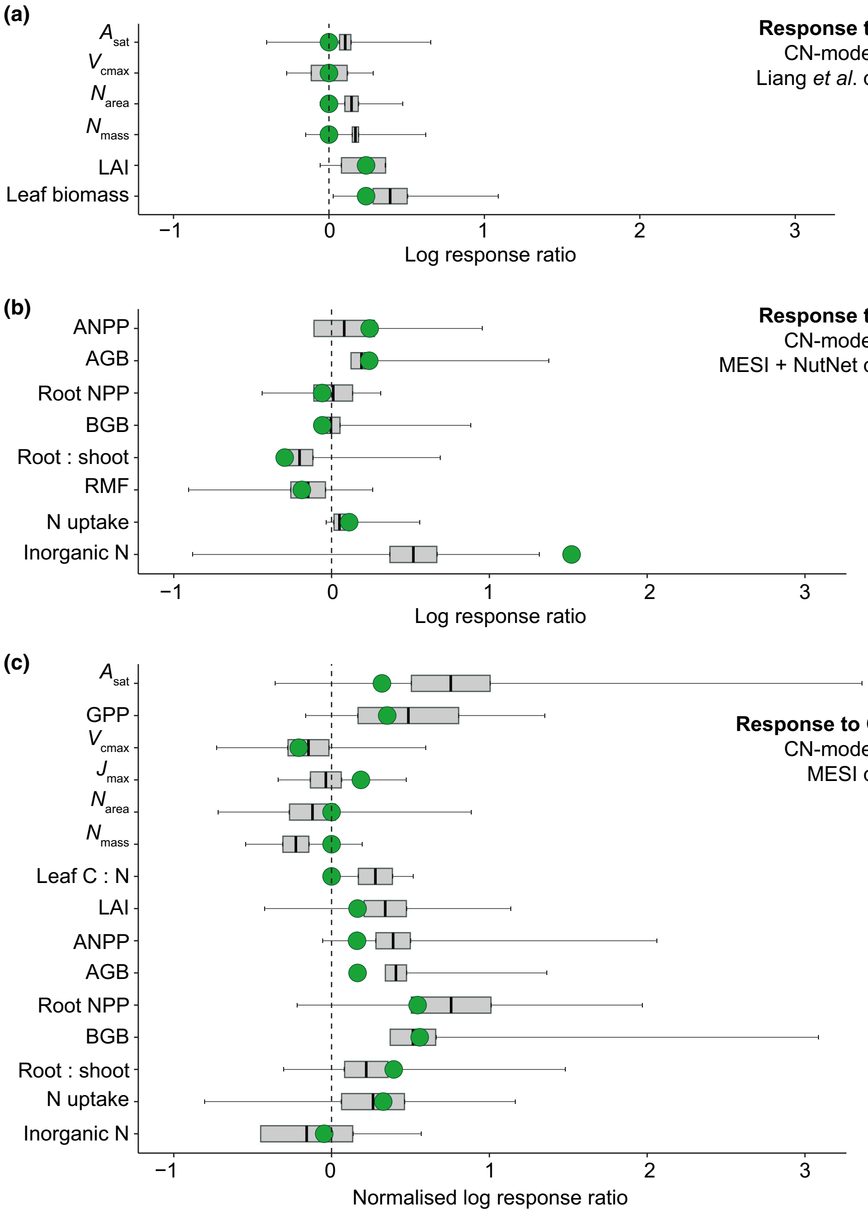

Fig. 6 Modelled (green dots) and observed responses (grey bars) to N fertilisation and increased CO_2. The response to nitrogen (N) fertilisation shown (a) by data from (Liang *et al.*, 2020) and (b) by MESI (Van Sundert *et al.*, 2023) and NutNet (Cleland *et al.*, 2019) data. The response to elevated CO_2 (c) is based on MESI data. The boxes represent the 95%-confidence intervals of the meta-analytic mean and the vertical line in each box' centre its mean (same as blue and red boxes in Fig. 3). The whiskers represent the full range of response ratios across experiments. See Supporting Information Notes S4 for further information about methods of this analysis.

allocation to roots. Exposure to elevated CO_2 leads to increased production with a stronger increase in belowground allocation, which tends to deplete soil N. Similar responses have been documented in the literature for CO_2 experiments (Rogers *et al.*, 1995; Schneider *et al.*, 2004; Ainsworth & Long, 2005; Leakey *et al.*, 2009; De Kauwe *et al.*, 2014; Song *et al.*, 2019; Jiang *et al.*, 2020) and N-fertilisation experiments (Poorter *et al.*, 2012; Cleland *et al.*, 2019; Song *et al.*, 2019; Li *et al.*, 2020, 2024; Eastman *et al.*, 2021; Keller *et al.*, 2023). Yet, there remains a relatively high residual variability in response ratios across experiments (Figs 3, 4). The general pattern of allocation shifts in response to N fertilisation and CO_2 is predicted by EEO-based models (Thornley, 1995; Rastetter *et al.*, 1997; Mäkelä *et al.*, 2008; Franklin *et al.*, 2009). Related patterns of the effect of soil fertility on allocation have also been documented based on field data. Ecosystems on fertile soils have been found to produce biomass more efficiently, suggesting that additional belowground C allocation on infertile soils may, at least partly, fuel the rhizosphere through exudation (Vicca *et al.*, 2012).

According to experimental findings and model predictions, elevated CO_2 should drive a rise in belowground C allocation. Decadal-scale temporal variations in root : shoot ratios under field conditions have, to our knowledge, not yet been documented. However, such a shift would have important consequences for the C balance of terrestrial ecosystems across the globe, but is likely missed since belowground biomass is commonly estimated via nondestructive methods based on constant relationships with aboveground biomass and allometric relations with tree diameter and tree ring growth data.

Additional processes of plant–soil interaction are fuelled by amplified belowground allocation under rising CO_2. The decomposition of soil organic matter and the N supply rate are governed by the depolymerisation by microbes (Schimel & Bennett, 2004) and can be enhanced by additional C exudates and rhizosphere priming – the increased soil organic matter mineralisation due to enhanced microbial activity (Phillips *et al.*, 2011; Zhu & Cheng, 2011; Kuzyakov *et al.*, 2019), for example via symbiotic associations with mycorrhizas (Phillips *et al.*, 2013; Frey, 2019). Ectomycorrhizal (ECM) fungi are particularly effective in mobilising soil N for plant uptake (Sulman *et al.*, 2017; Bonsall *et al.*, 2020) and sustaining a positive aboveground biomass response under elevated CO_2 (Terrer *et al.*, 2016), potentially by oxidising soil organic matter (Shah *et al.*, 2016), triggering a simultaneous acceleration of SOM and litter decomposition (Zak *et al.*, 2011; van Groenigen *et al.*, 2014) and reducing soil organic matter stocks (Shah *et al.*, 2016; Terrer *et al.*, 2021). However, not all ECM fungi appear to possess saprotrophic capabilities (Lindahl & Tunlid, 2015; Pellitier & Zak, 2018) and the occurrence of saprotrophic ECM may vary across ecosystems (Pellitier & Zak, 2018). A mechanistic understanding of the effects of exudation on N availability for plant uptake, losses and fixation, considering feedbacks through organic C decomposition (Keuper *et al.*, 2020) and inorganic N immobilisation by the activated rhizosphere, is only beginning to emerge (Coskun *et al.*, 2017; Kuzyakov *et al.*, 2019) and remains an open challenge for consideration in DGVMs.

The observed allocation shift also suggests a certain degree of plant control on N availability for uptake and therefore an interaction between C and N availability. For example, more C could be invested under elevated CO_2 for plant N uptake, as seen in many (but not all) Free-Air CO_2 Experiments (Terrer *et al.*, 2018). Such an interactive effect of C and N is predicted by EEO models (Rastetter *et al.*, 1997; Franklin, 2007; Wang *et al.*, 2007) and questions the argument of an immutable sink limitation (a limitation on producing biomass) under rising CO_2 by limiting N availability (Fatichi *et al.*, 2019). It also appears incompatible with a conceptualisation of N limitation based on Liebig's law of the minimum – a common approach for implementations of N cycle effects on the C cycle in Earth System Models (Thomas *et al.*, 2015). The approach to modelling allocation and nutrient uptake based on the C economy of plants has been extended for modelling the uptake of phosphorus (Braghiere *et al.*, 2022; Reichert *et al.*, 2023) on the basis of the observed link between plant C investments into rhizodeposits and other functions and the availability of P for plant uptake (Jin *et al.*, 2015). One such model that connects global N and P cycles through the C economy of plants predicts widespread co-limitation of P and N (Braghiere *et al.*, 2022) – as is widely observed for effects on biomass productivity in manipulative experiments (Fang *et al.*, 2024).

2. Acclimation of photosynthesis

We found that the acclimation of photosynthetic traits is most strongly influenced by the atmospheric environment, but less so by soil N, despite soil N effects on foliar N content (by mass and by area). EEO principles, formulated as a function of the atmospheric environment, have been shown to be useful for predicting the acclimation of photosynthesis parameters (Smith *et al.*, 2019; Dong *et al.*, 2022). Consistent with an EEO principle (Prentice *et al.*, 2014; Dong *et al.*, 2022), N_{area} declines with growth temperature and increases with VPD (Fig. 5). Embodied in our demonstration CN-model, these principles also correctly predict the average decline of V_{cmax} recorded elevated CO_2. The associated decline in the demand for N – arising through the link between V_{cmax}, Rubisco and N – is thus predictable and should be considered in the next generation of C–N models.

By contrast, leaf N, measured on a leaf area or leaf mass basis, appears more strongly influenced by soil N than photosynthetic traits that reflect enzyme activity (e.g. V_{cmax} and J_{max}). This suggests that the soil N effect on foliar C–N stoichiometry is only weakly transmitted to photosynthesis. This is consistent with findings of a decline in photosynthetic N use efficiency (PNUE, leaf photosynthesis per unit leaf N) under N fertilisation (Waring *et al.*, 2023), with an observed increase in PNUE under elevated CO_2, and absent effects of soil N on leaf photosynthesis acclimation to elevated CO_2 (Lee *et al.*, 2011; Pastore *et al.*, 2019). This suggests an open question for process understanding (What, if not photosynthesis, is the additional leaf N used for?) and EEO-informed modelling (What are the competitive gains of higher foliar N contents?). The observation of a weak transmittance of soil N to V_{cmax} and J_{max} also suggests a weak or absent effect on leaf dark respiration (which scales with the leaf Rubisco concentration and thus with V_{cmax}). Leaf respiration is modelled in several models to increase with leaf N content (Box 1), inducing a feedback between N limitation and plant respiration. However, such approaches are not supported in view of the observed large variations in PNUE and the decoupling of total leaf N and photosynthesis.

A focus on LMA for understanding the controls on foliar N may be informative in this context. LMA appears highly responsive across spatial gradients in N deposition (Fig. 5), suggesting an N-related control. LMA is positively associated with leaf longevity (Onoda *et al.*, 2017; Wang *et al.*, 2023) and should thereby have implications for foliar N turnover and ecosystem N losses along the litterfall-mineralisation-plant uptake pathway. Indeed, a decline in LMA along a soil N availability gradient is predictable from EEO principles (Weng *et al.*, 2017, p. 20).

A further challenge is that, although the meta-analytic mean response in V_{cmax} to CO_2 is predictable from EEO principles, there remains substantial unexplained variability in the response ratio across experiments. Analyses of the Liang *et al.* (2020) dataset provide no indication that the differences in response are consistently related to plant type, phenology or mycorrhizal association (Table S2). However, results from some experiments have shown that the impact of N fertilisation on photosynthetic capacity is most pronounced in experiments where N availability was low before fertilisation, suggesting that there may be a strong response at low N that saturates as N availability increases. This saturating effect has indeed been shown in N-fertilisation experiments under different levels of CO_2 (Perkowski *et al.*, 2023). Although not emerging from the meta-analyses, symbiosis with mycorrhizal fungi or soil N-fixing bacteria could also have an influence on the acclimation of photosynthetic traits to N fertilisation (Hoeksema *et al.*, 2010).

In addition to biotic factors influencing the response of photosynthetic capacities to N fertilisation, abiotic factors may also be important to consider. Evidence from experiments and leaf traits data along environmental gradients indicate that the response to N fertilisation is strongest in low temperature (Smith & Keenan, 2020; Dong *et al.*, 2022), dry (Wright *et al.*, 2003; Querejeta *et al.*, 2022) and high light (Niinemets *et al.*, 2015; Poorter *et al.*, 2019; Waring *et al.*, 2023) environments – conditions that are typically associated with a high demand for N in the photosynthetic machinery (Wright *et al.*, 2003; Prentice *et al.*, 2014; Dong *et al.*, 2022).

The environmental effect on photosynthetic parameters is commonly encoded in Earth system models by treating separate plant functional types (PFTs) growing along climatic gradients. As a consequence, changes in community-mean V_{cmax} only come about in these models through a shifting occurrence of PFTs. However, the V_{cmax} and N demand decline under elevated CO_2 arises within individual plants subjected to experimental manipulations (Fig. 3) and therefore evolves much more rapidly than through species replacements. The comparatively immediate shift in leaf N demand and implications for ecosystem N cycling in response to decadal climatic trends and CO_2 can thus not be captured by traditional models.

Apart from the photosynthetic traits, other traits related to C–N interactions also exhibit acclimation and within-PFT variations that are related to the environment. In particular, root traits (architectural, morphological and physiological properties) are linked to root biomass N content, N uptake, C respiration and root biomass turnover, and are highly plastic in response to environmental change (Hodge, 2004; Nie *et al.*, 2013; Bardgett *et al.*, 2014; Wang *et al.*, 2021). However, empirical support for a theory explaining variations of multiple root traits along a resource conservation-exploitation spectrum and for systematic relationships between soil properties related to N and P and root traits is mixed (Roumet *et al.*, 2006; Orwin *et al.*, 2010; Chen *et al.*, 2013; Bardgett *et al.*, 2014; Kramer-Walter *et al.*, 2016; Weemstra *et al.*, 2016; Kong *et al.*, 2017). This indicates a remaining challenge for optimality-based predictions of multiple root traits and their relations to mycorrhizal and microbial associations and exudation (Gao *et al.*, 2021; Sun *et al.*, 2021), and suggests a potential for modelling total belowground C allocation and N uptake at a high level of abstraction.

3. Ecosystem N cycling

We have taken a plant-centric view. It is predominantly through plants and their associations with microbes that atmospheric CO_2 and N_2 are converted to C and N that cycle in ecosystems. Governing EEO principles that inform the modelling of plant functioning thus have implications for ecosystem-level C and N cycling. Although we have not addressed this aspect in our data analysis, insights gained from EEO predictions and their evaluation against experiments and field data are informative for understanding and modelling ecosystem N losses, N cycle openness and N fixation in response to environmental change factors.

Progressive N limitation (PNL) has been hypothesised to govern the dynamics of ecosystem C–N cycling in response to rising CO_2 (Vitousek & Howarth, 1991; Comins & McMurtrie, 1993; Luo *et al.*, 2004). Thereby, the stimulated tree growth and biomass stocks deplete soil N, aggravating N limitation and triggering an increase in the C : N ratio of new biomass and a resulting deterioration of decomposability of that biomass. This induces a decline in N mineralisation, thereby further aggravating the initial N limitation. However, the attenuated transmittance of the leaf N signal on photosynthetic N and photosynthetic capacity at least partly mutes the feedback of PNL. The widely observed allocation shift and its consequence for plant N uptake further alleviate the PNL feedback loop. The continued accumulation of ecosystem N as a consequence of increased belowground allocation and transiently reduced losses (Liang *et al.*, 2016) suggest instead a progressive *release* from N limitation (Walker *et al.*, 2015). Such a release is also predicted by relatively simple models based on EEO principles but is sensitive to assumptions regarding dependencies of N losses (Comins & McMurtrie, 1993; Wang *et al.*, 2007). Empirical evidence for the PNL is mixed (Liang *et al.*, 2016). It was found in some CO_2 experiments (Reich *et al.*, 2006; Newton *et al.*, 2010; Norby *et al.*, 2010), but not in others (McCarthy *et al.*, 2010; Zak *et al.*, 2011).

The predicted and observed allocation shift elicits a change in ecosystem N losses. This flux is perhaps the most difficult-to-measure component of the terrestrial N cycle. Gaseous losses are mostly in the form of an N_2 flux (Galloway *et al.*, 2004) which, thus far, cannot reliably be measured against the background of its high atmospheric concentrations. N losses also occur through leaching. Measured at the catchment-scale, large-scale N-fertilisation experiments have documented enhanced leaching in response to N fertilisation (Eastman *et al.*, 2021). The allocation shift causes a change in the relative magnitudes of N losses and internal N cycling. This quantity has been referred to as the N cycle openness (Cleveland *et al.*, 2013). As predicted by the CN- model here, elevated CO_2 drives a reduction, while N fertilisation increases the N cycle openness.

N losses from the terrestrial biosphere arise not only through gaseous and leaching pathways, but also by fire, causing NO_x emissions (Pellegrini *et al.*, 2018), and biomass removals through wood harvesting (Hume *et al.*, 2018). Despite the severe disruption of N (and P) stocks, such disturbances are commonly followed by regrowth and a re-accumulation of N in biomass within decades (Batterman *et al.*, 2013; Turner *et al.*, 2019), albeit under low availability of soil nutrients or repeated disturbances, this re-accumulation may be reduced or delayed (Rastetter *et al.*, 2013; Pellegrini *et al.*, 2018). It will be useful to quantify the rates of postdisturbance N accumulation across biomes and to put numbers into context with N deposition and fixation estimates to provide an additional constraint for models on the rate of ecosystem N accumulation through N fixation vs external inputs, including atmospheric deposition.

The common view is that N inputs into ecosystems are under plant control only where N-fixing trees are present. While trees that symbiotically interact with N-fixing bacteria are relatively widespread in the tropics (Menge *et al.*, 2019; Tamme *et al.*, 2021), 'N-fixing trees' are much rarer in temperate and boreal systems and are largely confined to early successional stages (Chapin *et al.*, 1994; Menge *et al.*, 2019). Their exclusion in late successional stages and the widespread N limitation of temperate forests pose a research challenge (Menge *et al.*, 2009). The discovery and quantification of new processes and organisms with the capability of N fixation has contributed to a more complete picture of N fixation in terrestrial ecosystems (Vitousek *et al.*, 2013; Cleveland *et al.*, 2022). Free-living microbes (Reed *et al.*, 2011), epiphytes and endophytes (Fürnkranz *et al.*, 2008), and moss, lichens and biocrusts (Elbert *et al.*, 2012; Larmola *et al.*, 2014) have been described as substantial N sources through N_2 fixation (Cleveland *et al.*, 2022). An incomplete understanding and consideration of the full diversity of N-fixing organisms and processes may imply a systematic underestimation of the global biological N-fixation flux based on up-scaled measurements of currently known sources (Cleveland *et al.*, 1999; Galloway *et al.*, 2004; Davies-Barnard & Friedlingstein, 2020). However, isotopic constraints suggest the global flux of biological N fixation to be lower than published up-scaled values (Vitousek *et al.*, 2013). Modelling diverse N fixation fluxes and their response to environmental change remains an outstanding challenge (Davies-Barnard & Friedlingstein, 2020) and is not addressed by our data analysis and modelling. Differences in assumptions about dominant controls on N fixation are partly (but not dominantly (Davies-Barnard *et al.*, 2022)) responsible for the divergence of simulated land C balance projections in a future climate (Wieder *et al.*, 2015a; Meyerholt *et al.*, 2016, 2020). Yet, an empirical basis exists for conceiving symbiotic N fixation as being controlled by the balance of soil N supply and demand by autotrophs, including plants (Rastetter *et al.*, 2001; Wang *et al.*, 2017, p. 20; Perkowski *et al.*, 2021). EEO principles, used for predicting patterns of biological N fixation in relatively simple models (Rastetter *et al.*, 2001; Wang *et al.*, 2007), may guide a next generation of global vegetation models' representation of N fixation. For example, the energy required for N fixation may be considered for simulating its rate and may be linked to C cycling. Such a representation forms the basis of the Fixation and Uptake of Nitrogen (FUN) model's representation of symbiotic N fixation (Fisher *et al.*, 2010). The FUN model is implemented in the Community Land Model v.5.0 (Lawrence *et al.*, 2019) and its approach may be applied generically for total ecosystem N fixation, thereby accounting for documented abiotic controls on BNF (Houlton *et al.*, 2008; Cleveland *et al.*, 2022). N inputs to the plant–soil system arise not only from N fixation but also from weathering parent material (Houlton *et al.*, 2018). This process is partly driven by chemical processes and fuelled by plant-derived acids – containing C. Hence, this flux may also be, at least partly, under plant control.

Large-scale vegetation changes under current environmental change may provide additional constraints for models and their representation of C–N interactions. For example, rapid Arctic greening (Keenan & Riley, 2018) and widespread forest growth increases (McMahon *et al.*, 2010; Hubau *et al.*, 2020) with an accompanying C sink in global forests (Pan *et al.*, 2011) can only be predicted in agreement with observations if vegetation is simulated to access additional N during the biomass accrual stage. An immutable cap on N and not considering a certain degree of plant control on N loss and input fluxes may lead to an overestimation of N-limitation effects in models. This could be tested by confronting models' simulations of large-scale vegetation changes with observations and a focus on the role of N in shaping responses and driving potential model bias.

4. Modelling C–N interactions

Balancing trade-offs in the light of EEO is a useful governing principle for modelling C–N interactions. A rich body of literature from at least four decades reflects the potential of EEO in the context of modelling processes and traits that are directly relevant for ecosystem C and N cycling. EEO principles and the consideration of trade-offs in resource allocation, consumption and acquisition have been used, for example for predicting canopy (Dewar, 1996; Franklin, 2007) and foliar N (Dong *et al.*, 2022), LMA (Weng *et al.*, 2017; Wang *et al.*, 2023; Xu *et al.*, 2023), N allocation to enzymes sustaining V_{cmax} vs J_{max} (Ali *et al.*, 2016; Thum *et al.*, 2019), allocation to growth in different plant organs (Thornley, 1995; Rastetter *et al.*, 1997; Van Wijk *et al.*, 2003; Franklin, 2007; Mäkelä *et al.*, 2008; Franklin *et al.*, 2012; Weng *et al.*, 2019), balancing leaf area, N requirements and transpiration losses (McMurtrie *et al.*, 2008) or different N uptake pathways (Fisher *et al.*, 2010), including biological N fixation (Rastetter *et al.*, 2001; Wang *et al.*, 2007; Menge *et al.*, 2009) and mycorrhizal associations (Franklin *et al.*, 2014; Lu & Hedin, 2019).

Most (but not all) of these studies relied on models that are strongly simplified representations of processes in terrestrial ecosystems and lack the level of realism (and complexity) of the C–N model types used for global biogeochemical cycle and land-surface modelling studies, including the models used for the analysis presented in Fig. 1. Some of the above-mentioned theoretical work also relied on the premise of a fixed net mineralisation rate (Franklin *et al.*, 2014), or a fixed amount of N in the system (Weng *et al.*, 2019), or a fixed amount of N in the biomass of an individual leaf (Ali *et al.*, 2016; Thum *et al.*, 2019) or the canopy (Dewar, 1996). To model the C and N dynamics of the terrestrial biosphere, the system boundaries may be drawn more widely for a complete accounting of C and N mass balances and ecosystem feedbacks. Hence, the demonstrated success of EEO principles for modelling individual processes or traits indicates a potential for their application to improving C–N modelling. However, the gap between the theoretical work implemented as relatively simple EEO models and the demands and constraints for implementing them into DGVMs and land-surface components in ESMs indicates a remaining challenge. As discussed more extensively in Harrison *et al.* (2021), challenges are related, for example, to linking individual leaf-level trait responses with the coordination of multiple traits of multiple plant organs and plant architecture, or to the treatment of temporal dynamics for representing traits acclimating at multiple time scales and emergent trait distributions at the community level.

The representation of C and N cycle interactions in the CN-model (Stocker & Prentice, 2024; Fig. 5) is comparable in scope and structure to DGVMs. However, the CN-model resolves processes with a focus on C–N interactions, while it does not resolve energy and water exchanges and how they affect vegetation functioning, nor does it resolve tree allometric relations or competition between PFTs or plant age cohorts. Its aim is to provide an architecture that is generally comparable to DGVMs and to serve as a demonstration for how EEO principles for allocation and photosynthesis acclimation could be embedded in state-of-the-art global modelling frameworks.

The modelling performed here relied on EEO principles for dynamically modelling instantaneous responses in allocation and photosynthesis acclimation to a changing environment without the explicit consideration of dynamic vegetation and competitively optimal strategies (Franklin *et al*., 2020). This enabled the reliable prediction of the widely observed and relatively strong response in allocation to altered CO_2 and soil N availability. With its assumption that V_{cmax} is modelled through an optimal acclimation to the atmospheric (but not soil) environment, the CN-model's respective predictions were consistent with observations. However, other plant traits are less dynamic or cannot be altered within an individual or a given species, but have direct consequences for the N economy of plants. For example, a high LMA is typically associated with a high C : N ratio and poor leaf decomposability and is considered to be less plastic than leaf N_{area}. Mycorrhizal associations are, for most species, exclusive to either ectomycorrhizae or arbuscular mycorrhizas. Associations with the former appear to be advantageous in an N-scarce environment and to facilitate the stimulation of plant biomass under elevated CO_2 (Terrer *et al*., 2016, 2018). Thereby, environmental changes will likely trigger changes in species composition through altering their competitiveness in an altered C–N environment and syndromes of slow vs fast-N-cycling systems emerge (Phillips *et al*., 2013). Modelling such dynamics will have to rely on a resolution of dynamic vegetation and forest demographic processes to simulate species invasion and exclusion over time, niche differentiation, community succession and evolutionarily stable (competitively optimal) strategies. Demography-resolving DGVMs (Falster *et al*., 2017; Fisher *et al*., 2018) offer potential for predicting such patterns, as has been shown, for example for predicting LMA and deciduousness shifts along a soil N gradient (Weng *et al*., 2017). In the context of root : shoot ratio changes under N fertilisation, it has been shown that opposite patterns as predicted from the functional balance hypothesis are observed in a severely nutrient-limited ecosystem and can be simulated considering optimality under competition (Van Wijk *et al*., 2003). It will be informative to investigate how and whether the adoption of different EEO principles and dynamic vegetation demography translate into improved performance of DGVMs, evaluated against a comprehensive set of observational targets and considering data from a large number of experiments and diverse environmental conditions.

VI. Conclusions

Changes in C and N availability, caused by trends in rising CO_2 and atmospheric N deposition, trigger dynamic responses in plants with consequences for ecosystem C and N cycling. Plant responses to N fertilisation and changing CO_2 can be broadly captured by a simple model based on EEO. Such concepts have been used to predict various aspects of plant behaviour at the leaf and whole-plant levels (Franklin *et al*., 2020; Harrison *et al*., 2021), providing simple but powerful models with relatively few free parameters. There is now a strong theoretical basis for modelling C–N cycle interactions and the role of N in constraining ecosystem responses to rising CO_2 and climate change (Bloom *et al*., 1985; Rastetter *et al*., 1997; Wright *et al*., 2003; Franklin, 2007; Franklin *et al*., 2012, 2020; Prentice *et al*., 2014; Harrison *et al*., 2021; Dong *et al*., 2022). These approaches for the prediction of C–N interactions could be used in vegetation and land-surface components of coupled Earth System Models, holding the promise of reducing the large uncertainty in the current projections of the global C cycle. It will, however, be important to extend the suite of benchmarks used to evaluate such models (Kou-Giesbrecht *et al*., 2023) since the current emphasis on evaluating C fluxes and pools is insufficient to discriminate between alternative process representations that underlie errors in simulated land C sink trends.

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Competing interests

None declared.

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ORCID

Hugo J. de Boer https://orcid.org/0000-0002-6933-344X
Ning Dong https://orcid.org/0000-0003-0793-8854
Sandy P. Harrison https://orcid.org/0000-0001-5687-1903
Evan A. Perkowski https://orcid.org/0000-0002-9523-8892
I. Colin Prentice https://orcid.org/0000-0002-1296-6764
Karin T. Rebel https://orcid.org/0000-0002-1722-3935
Pascal D. Schneider https://orcid.org/0000-0003-1358-5549
Nicholas G. Smith https://orcid.org/0000-0001-7048-4387
Benjamin D. Stocker https://orcid.org/0000-0003-2697-9096
Kevin Van Sundert https://orcid.org/0000-0001-6180-3075
Han Wang https://orcid.org/0000-0003-2482-1818
Huiying Xu https://orcid.org/0000-0003-3902-9620

Data availability

The code for all analyses is available on GitHub at https://github.com/stineb/lt_cn_review/releases/tag/v2.0 and is published on Zenodo at doi: 10.5281/zenodo.13736727. Model code of the CN-model is available on GitHub at https://github.com/stineb/rsofun/releases/tag/v1.0_cnmodel.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Notes S1 Analysis of modelled land C sink trends.

Notes S2 Meta-analysis of ecosystem experiments.

Notes S3 Analysis of global leaf traits data.

Notes S4 CN-model simulations.

Table S1 List of elevated CO_2 experiments from the MESI database.

Table S2 List of N-fertilisation experiments from the MESI database.

Table S3 Summary of results of N-fertilisation experiments in the Liang *et al.* (2020) dataset.