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Atmospheric phosphorus deposition amplifies carbon sinks in simulations of a tropical forest in Central Africa

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Summary

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- Spatial redistribution of nutrients by atmospheric transport and deposition could theoretically act as a continental-scale mechanism which counteracts declines in soil fertility caused by nutrient lock-up in accumulating biomass in tropical forests in Central Africa. However, to what extent it affects carbon sinks in forests remains elusive.
- Here we use a terrestrial biosphere model to quantify the impact of changes in atmospheric nitrogen and phosphorus deposition on plant nutrition and biomass carbon sink at a typical lowland forest site in Central Africa.
- We find that the increase in nutrient deposition since the 1980s could have contributed to the carbon sink over the past four decades up to an extent which is similar to that from the combined effects of increasing atmospheric carbon dioxide and climate change. Furthermore, we find that the modelled carbon sink responds to changes in phosphorus deposition, but less so to nitrogen deposition.
- The pronounced response of ecosystem productivity to changes in nutrient deposition illustrates a potential mechanism that could control carbon sinks in Central Africa. Monitoring the quantity and quality of nutrient deposition is needed in this region, given the changes in nutrient deposition due to human land use.

Introduction

Structurally intact tropical forests contributed to about half of the global terrestrial carbon uptake over the 1990s and early 2000s, thereby removing *c.* 15% of anthropogenic carbon dioxide emissions (Pan *et al.*, 2011; Sitch *et al.*, 2015). While earth system models typically predict that the 'carbon sink' in intact tropical forests will continue for decades (Huntingford *et al.*, 2013; Mercado *et al.*, 2018), long-term forest inventories indicate that the carbon sink in live aboveground biomass in wet tropical forests is saturating in South America while being stable in Africa (Lewis *et al.*, 2009; Brienen *et al.*, 2015; Hubau *et al.*, 2020). While the divergence in carbon sinks is driven by continental differences in trends in carbon losses, both continents show increasing tree growth, consistent with the expected net effect of rising atmospheric carbon dioxide and air temperature (Hubau *et al.*, 2020). However, other drivers might play a role as

well. Understanding the underlying mechanisms is critical to forecast carbon sinks.

The role of atmospheric nutrient deposition for carbon sinks remains largely elusive (Wang *et al.*, 2017), despite the widespread limitation of productivity of tropical forests by phosphorus (Goll *et al.*, 2012; Wright, 2019; Du *et al.*, 2020; Hou *et al.*, 2020). There is growing evidence that fires can provide a significant source of nitrogen and phosphorus for humid tropical forests in Central Africa which often grow on nutrient-depleted soils (Bauters *et al.*, 2017, 2018, 2021). The African continent represents nearly 65% of the global burnt area annually (Van Der Werf *et al.*, 2006), mainly via a high incidence of natural and anthropogenic fires in grasslands and savannas (Van Der Werf *et al.*, 2017), but increasingly also from deforestation (Chen *et al.*, 2010; Wang *et al.*, 2017). These fires inject large amounts of nutrients to the atmosphere which are transported and deposited in adjacent forest ecosystems. By contrast, fire-derived

nutrient inputs from atmospheric deposition are usually minor in South America (Mahowald *et al.*, 2008; Wang *et al.*, 2015), leading to lower atmospheric nutrient deposition inputs which are also less bio-available as they originate mostly from mineral sources (Barkley *et al.*, 2019). Besides, phosphorus inputs from weathering of primary minerals are here comparably large to the ones from deposition (Hartmann *et al.*, 2009). As a consequence, the importance of fires for redistribution of nutrient and ecosystem nutrition likely differs among the two continents.

Due to direct and indirect human interference with wildfires and biomass burning in Africa, nutrient deposition over central African forests is substantially higher today than it was during the better part of the 20th century (Wang *et al.*, 2015). For example, 11.1 ± 0.1 Mha (5.5%) forest area has been lost solely due to smallholder forest clearings by slash and burn and escaped agricultural fires or fires set for hunting purposes in the Democratic Republic of Congo between 2000 and 2015 (Tyukavina *et al.*, 2018; van Wees *et al.*, 2021). It has to be noted that small-scale fires which dominate the burned area in Africa (80%) were not resolved due to the use of coarse-scale satellite sensors (Ramo *et al.*, 2021). Besides, large-scale afforestation projects like the 'Green Great Wall Initiative' in the Sahel zone alter vegetation cover and fire regimes, with a strong decrease in regional burned area over the last 20 yr. Yet forest fires have increased (Zheng *et al.*, 2021) so that nutrient inputs over lowland forest in Africa and potentially terrestrial and marine ecosystems elsewhere remain uncertain (Yu *et al.*, 2015; Barkley *et al.*, 2019; Li *et al.*, 2021). Thus, a better understanding of how changing nutrient deposition affects ecosystem nutrition and associated carbon sinks is required to inform appropriate responses to land challenges for the 21st century.

The aim of this study was to explore the importance of nutrient inputs from atmospheric deposition for the carbon sink of a typical tropical lowland forest in Central Africa, using an ecosystem model. In particular, to address the question to what extent atmospheric nutrient deposition has helped to sustain Central African forests carbon gains over recent decades. This modelling endeavour is facilitated by the availability of site-level data from sites in the Democratic Republic of Congo with ecosystem-level carbon and nutrient cycling (Doetterl *et al.*, 2015; Bauters *et al.*, 2017, 2018, 2021; Cassart *et al.*, 2017; Kearsley *et al.*, 2017).

The objectives of this study are threefold. First, to calibrate and evaluate the ecosystem model ORCHIDEE-CNP which resolves carbon, nitrogen and phosphorus interactions over lowland forest sites in Central Africa. Second, to provide a closed budget of carbon, nitrogen and phosphorus cycling at ecosystem level to quantify the respective contributions of internal and external nutrient sources to plant uptake. Third, to use the model to quantify the sensitivity of forest productivity and aboveground carbon (AGC) sink in vegetation to historic increases in nutrient deposition. We aim at testing the following two hypotheses (H):

H1: Atmospheric nutrient deposition promotes ecosystem nutrition and carbon sinks in lowland forest in Central Africa.

H2: Phosphorus, rather than nitrogen, inputs from atmospheric

deposition dominate the response of ecosystems carbon cycling to atmospheric deposition.

Materials and Methods

Model overview

Here we use the nutrient-enabled version of the ORCHIDEE land surface model (Krinner *et al.*, 2005), ORCHIDEE-CNP (v.1.3) (Goll *et al.*, 2017a). The model resolves the dependence of ecosystem-level photosynthetic capacity and biomass built up on leaf nitrogen and phosphorus concentration and plant nutrient stocks and has been extensively evaluated for tropical sites in South America (Goll *et al.*, 2018), on a global scale (Sun *et al.*, 2021), and for the response of ecosystems to artificial nutrient addition (Goll *et al.*, 2017a, 2021). ORCHIDEE-CNP simulates the exchange of greenhouse gases (i.e. carbon dioxide and nitrous oxide), water and energy at the land surface and features a detailed representation of root uptake of nitrogen and phosphorus in soil solution, the allocation of nitrogen and phosphorus among seven plant tissues (leaf, roots, fruits, sapwood, heartwood, labile and reserves), and the nitrogen and phosphorus turnover in four litter pools (aboveground non-lignified litter, belowground non-lignified litter, aboveground lignified litter and belowground lignified litter) and three soil organic matter (labile, physically protected and chemically recalcitrant matter) pools resolving two types of decomposers (Wieder *et al.*, 2015; Zhang *et al.*, 2020) and two inorganic phosphorus pools (Goll *et al.*, 2018). The major components of the model are described in detail elsewhere (Krinner *et al.*, 2005; Zaehle & Friend, 2010; Wieder *et al.*, 2015; Goll *et al.*, 2017a, 2018; Zhang *et al.*, 2018, 2020) and an overview of the phosphorus cycle is provided in Supporting Information Fig. S1. In the following, we summarise the main features of relevance for this study.

In case of low nutrient availability, plant investment in root growth increases in the model at the expense of leaf and wood growth while foliar and fine root nutrient concentration is reduced, leading to lower photosynthetic capacity, plant growth and carbon storage. Negative effects of nutrient shortages on plant productivity are partly compensated by higher activity of soil enzymes enhancing the plant availability of phosphorus in soil organic matter, decreasing the carbon use efficiency of decomposers leading to reduced lock-up of nutrient in organic matter, desorption of phosphorus from soil particles, and reduced losses of nutrients by leaching due to the low nutrient concentration in soil solution. The nutrient content of woody plant tissue is assumed to be rigid.

The input of nutrients to the ecosystem from atmospheric deposition is model input information. Nitrogen enters the ecosystem via biological nitrogen fixation, which is computed dynamically as a function of plant nitrogen demand and soil nitrogen and phosphorus availability (Goll *et al.*, 2017a). Phosphorus and nitrogen inputs from rock weathering were assumed to be negligible for the site. Losses of nutrients in dissolved forms

are simulated as a function of runoff and drainage. Gaseous losses of nitrogen are simulated as a function of soil aeration, temperature and dissolved nitrogen concentration (Zaehle & Friend, 2010).

Model calibration

We used the site-level model calibration procedure applied previously to tropical forest sites in South America (Goll *et al.*, 2018). We collected information from the literature to prescribe plant (residence time of wood, residence time of roots, leaf phosphorus recycling, leaf nitrogen recycling and specific leaf area) and soil parameters (soil order, bulk soil density, soil pH and soil texture) (Table 1). The data are from recently (> 60 yr) undisturbed mixed lowland forest sites in the Democratic Republic of Congo: Yangambi (YGB): 00°48'N, 24°29'E and Yoko reserve: 00°19'12"N, 25°17'43"E. Residence time of roots was not available for the region, and was taken instead from measurements in lowland forest sites in West Africa: the Ankasa Conservation Area (ACA): 5°16'4.7994"N, 2°41'43.8"E. The locations of sites are shown in Fig. 1(d). The biochemical mineralisation rate was calibrated to achieve realistic soil nitrogen : phosphorus ratios for the site (Bauters *et al.*, 2017) due to lack of observation-based quantification of biochemical mineralisation rates (Goll *et al.*, 2017a). The prescribed carbon : nitrogen ratios of the three soil organic matter pools have been scaled using a single factor (1.25) so that the total soil carbon : nitrogen ratio is close to observations (Bauters *et al.*, 2017). All other vegetation parameters were prescribed using the values for ORCHIDEE's plant functional type 'tropical evergreen forest'.

Model simulations

Model simulations were performed using reconstructed climate, atmospheric carbon dioxide concentration and different scenarios of nitrogen and phosphorus inputs via atmospheric deposition

Table 1 Soil and vegetation characteristics as observed at the site Yangambi, Democratic Republic of the Congo, and used as input parameters of the model.

Variable	Units	Value	Source
USDA soil order	na	Oxisol	Kearsley <i>et al.</i> (2017)
pH		4.6	Kearsley <i>et al.</i> (2017)
Bulk soil density	g l ⁻¹	1500	Kearsley <i>et al.</i> (2017)
Sand/Silt/Clay	%	80/3/17	Kearsley <i>et al.</i> (2017)
PFT	n/a	Evergreen tropical forest	Bauters <i>et al.</i> (2017)
τ_{veget}	yr	71	Bauters <i>et al.</i> (2017)
τ_{root}	d	221	Moore <i>et al.</i> (2018)
SLA	m ² g ⁻¹	0.0165	Kearsley <i>et al.</i> (2017)
Wood density	kg C m ⁻³	310	Kearsley <i>et al.</i> (2017)
$r_{\text{foliar,N}}$	%	10	Bauters <i>et al.</i> (2017)
$r_{\text{foliar,P}}$	%	72	Bauters <i>et al.</i> (2017)

This includes United States Department of Agriculture (USDA) soil order, plant functional type (PFT), specific leaf area (SLA), mean residence time of vegetation biomass (τ_{veget}), fine root tissue (τ_{root}) and recycling of foliar nitrogen ($r_{\text{foliar,N}}$) and phosphorus ($r_{\text{foliar,P}}$). na, not applicable.

(Fig. 1; Table S1). The climatic forcing was extracted from 6 hourly global Climatic Research Unit – Japanese Reanalysis data (CRUJRA) (v.2.1) spanning the period 1901–2019 at the location of the Yoko site from which most evaluation data originate from. For the period 1750–1900, we recycled the climatic forcing of the years 1901–1920. The nutrient deposition scenarios are based on site observation and model-based reconstructions of past changes (as described later). The biogeochemical cycles in ORCHIDEE-CNP were equilibrated to boundary conditions of the year 1750 by recycling the conditions for the period 1750–1769 for 10 kyr. Starting from the equilibrated state of biogeochemical cycles, a set of simulations for the period 1750–2019 was performed. Thereby, we account for the impact of long-term changes in climate and carbon dioxide on the present-day transient state of ecosystems.

One set of simulations was run with varying climate and carbon dioxide concentration but constant pre-industrial NP deposition (simulations: baseline). Another set of simulations was performed with similar forcing (climate, carbon dioxide concentration) but variable nutrient deposition (simulations: trend). The difference between both types of simulations allows us to separate the effect of past changes in nutrient deposition on forest carbon sinks from other factors affecting the C sink (addressing H1).

The nutrient deposition scenario for the trend simulation is based on reconstructed decadal mean phosphorus deposition rates for the region on a coarse spatial resolution of 200 × 200 km from an atmospheric transport model prescribed with surface fossil and biogenic phosphorus emissions (Wang *et al.*, 2017). We bias corrected the rates, which, while capturing long-term trends in atmospheric phosphorus load, might not resolve variation in deposition on landscape level (Wang *et al.*, 2015; Bauters *et al.*, 2021), which might be substantial even on a scale of km as indicated by observations of the nuclear fallout from the Chernobyl accident (De Cort *et al.*, 2001). This was done using a scaling factor of 2.25 such that the resulting mean rate for the recent decade of 0.18 g m⁻² yr⁻¹ falls within the observations for forests in this region which range between 0.11 and 0.31 g m⁻² yr⁻¹ depending on the forest age (Bauters *et al.*, 2021). The resulting pre-industrial NP deposition rate used in baseline simulation is 0.1 g m⁻² yr⁻¹.

As information on past nitrogen deposition rates is missing, we prescribed the median N : P ratio of deposited material collected in the YOKO reserve (M. Bauters, pers. comm.) over the whole simulation period to derive nitrogen from phosphorus deposition. As information on the chemical form of the deposited nutrients is missing, we assume that deposited nutrients are in readily bio-available (i.e. dissolved) form and enter the soil solution, which is a simplification as in reality they are present in various forms of which some need to undergo physical, chemical or biological transformation before being available for plant uptake (Wang *et al.*, 2017). This provides an upper end estimate of the impact of changes in nutrient deposition.

We performed idealised model experiments to quantify the sensitivity of forest productivity and biogeochemical cycling to a sustained change in nitrogen and/or phosphorus inputs from atmospheric deposition (addressing H2). To do so, we prescribed

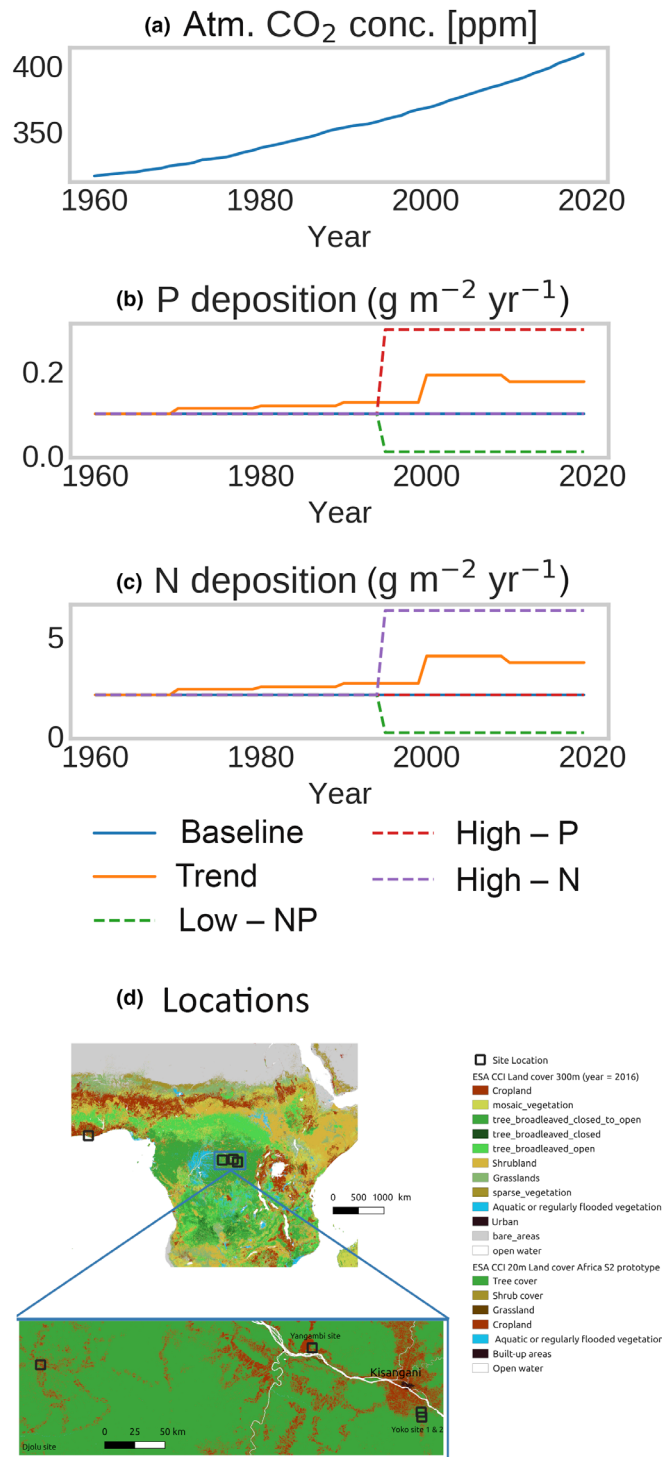


Fig. 1 The atmospheric conditions in the five core model scenarios and the locations of sites from which the observations originate. Shown are (a) atmospheric carbon dioxide (CO₂) concentration, (b) phosphorus (P) deposition and (c) nitrogen (N) deposition. A detailed list of all model simulations is given in Supporting Information Table S1. (d) Locations of the Yangambi site, Yoko reserve sites 1 and 2, Djolu site, and Ankasa Conservation Area site in the land cover product for Africa derived from Sentinel observations from December 2015 to December 2016 from the European Space Agency Critical Climate Initiative (ESA-CCI). The continental scale map shows the ESA-CCI global land cover at 300 m resolution, and the regional map the ESA-CCI S2 prototype for Africa at 20 m resolution. The locations of sites are marked by black squares.

an arbitrary step change in nutrient deposition in the year 1995, before which the baseline rate (as mentioned previously) was prescribed. The changes cover roughly the range of the few measurements on phosphorus deposition for Africa spanning 0.01–0.3 g m⁻² yr⁻¹ (Wang *et al.*, 2015; Bauters *et al.*, 2021). Specifically, we performed two simulations in which we increased either phosphorus deposition or nitrogen deposition by a factor of 3 to 0.3 and 6.3 g m⁻² yr⁻¹, compared to rates used in the baseline simulation, respectively (simulation: high-P and high-N). In addition, we performed one simulation in which we reduced both phosphorus deposition and nitrogen deposition by a factor of 10 to 0.01 and 0.21 g m⁻² yr⁻¹, respectively (simulation: low-NP). Fig. 1 shows the atmospheric carbon dioxide concentration (a) and nitrogen and phosphorus deposition (b, c) for different scenarios.

To explore the implications of the assumed N : P ratio, we performed additional simulations in which we assumed N : P ratios of 7 or 35 (simulations: baseline_{N : P,35}, baseline_{N : P,7}). Together with the simulation baseline, which assumes an N : P ratio of 21, these simulations cover the observed range of N : P ratio of atmospheric deposition in this region (M. Bauters, pers. comm.).

Furthermore, we explored the role of the uncertain composition of the deposited material as well as of leaf nutrient uptake, a potential yet uncertain uptake pathway (Kannan, 1986; Gessler *et al.*, 2017). The soluble fraction in deposited material ranges between 2% and 87%, with solubility in biomass-derived aerosols ranging at the upper end (Baker *et al.* (2006) and references therein). Besides the default assumption of a soluble fraction of 100%, we performed simulations in which we assumed the material consists of 100% labile organic matter (baseline_{org,l} and trend_{org,l}) or a mixed organic composition of one-third each: labile, chemically protected and physically protected organic matter (baseline_{org,m} and trend_{org,m}). A last set of simulations was performed in which we assume 100% of the deposited nutrients is taken up directly by leaves (baseline_{leaf} and trend_{leaf}).

Evaluation data

ORCHIDEE-CNP has not yet been evaluated specifically for African forests. Therefore, we collected data from the literature on ground-based estimates of ecosystem carbon storage and stoichiometry from three recently (> 60 yr) undisturbed mixed lowland forest sites in the Democratic Republic of Congo: Yangambi, Yoko reserve (as mentioned previously) and Djolu: 00°40'26"N, 22°27'33"E (Fig. 1d). The data include ground-based estimates of leaf carbon mass, leaf area index, standing carbon stock in stems, aboveground biomass carbon (AGC), aboveground net primary productivity (NPP_{ag}), soil organic carbon within the top 2 m (SOC_{2m}), leaf and soil (C : N : P) stoichiometry, plant nitrogen uptake and dissolved inorganic nitrogen leaching (Doetterl *et al.*, 2015; Bauters *et al.*, 2017; Cassart *et al.*, 2017; Hubau *et al.*, 2020). For NPP_{ag}, we first averaged the measurements of wood production of 11 plots in Yangambi and one plot in the Yoko reserve spanning the period 2012–2014 and 2009–2013, respectively (Hubau *et al.*, 2020). Second, we added on the so-derived estimate of wood production of

$0.76 \pm 0.31 \text{ g m}^{-2} \text{ yr}^{-1}$ leaf litter production of $0.3 \pm 0.04 \text{ g m}^{-2} \text{ yr}^{-1}$ from Cassart *et al.* (2017). We computed the average of available estimates for AGC and $\text{SOC}_{2\text{m}}$. As the estimates come from different years, we compared them to model results averaged for the period 2000–2019 (present day). We also used inventory-based estimates of decadal aboveground biomass carbon sinks for African forests ($\Delta\text{AGC}_{\text{net,inv}}$) from 244 plots reported in Hubau *et al.* (2020). We computed the AGC sink for the period 2010–2015 at site scale ($\Delta\text{AGC}_{\text{net,invS}}$) from the same 12 sites listed above and for the measurement periods of NPP_{ag} from Hubau *et al.* (2020). We included estimates of nitrous oxide (N_2O) and elemental nitrogen (N_2) emissions estimated for the Congo Basin of 0.1 and 0.1–0.7 $\text{g m}^{-2} \text{ yr}^{-1}$, respectively (Gallarotti *et al.*, 2021). In addition, we estimated nitrogen oxides emissions from an old-grown tropical forest in Panama, at a rate of 0.01–0.79 $\text{g m}^{-2} \text{ yr}^{-1}$ (Koehler *et al.*, 2009 and references therein).

In addition, we used satellite-based estimates of annual gross primary productivity (GPP) and annual net primary productivity (NPP) spanning the period 2000–2019 from the Moderate Resolution Imaging Spectroradiometer (MODIS) algorithms (Running & Zhao, 2019a,b) and aboveground biomass estimates (incl. SE) for the years 2010, 2017 and 2018 from the European Space Agency's (ESA) Climate Change Initiative (CCI) programme (Santoro & Cartus, 2021). Using the location of the Yoko reserve site, the carbon fluxes and biomass data were extracted from global products with 1 km and 100 m resolution, respectively. For comparison with modelled values, we computed the average over the available periods. We used a carbon content of 47% to convert dry weight biomass estimates to AGC.

Results

Evaluation

We evaluated model predictions for present-day conditions using data on ecosystem-scale fluxes and stocks of carbon, nitrogen and phosphorus collected from multiple lowland forest sites in the Democratic Republic of Congo (Fig. 1d) and combined it to provide a single composite site characterisation. To do so, we used results from the simulation trend which accounts for effects of changes in climate, atmospheric carbon dioxide concentration and atmospheric nutrient deposition. The model simulates a leaf area index of 3.74 close to ground observations (Fig. 2a). Carbon in stem biomass and AGC, which is dominated by stem biomass, are underestimated by 28% compared to estimates based on measurements on the ground (Fig. 2a). However, the modelled AGC is in good agreement with the satellite-based estimate. Modelled GPP of $2.55 \text{ kg m}^{-2} \text{ yr}^{-1}$ is very close to the GPP of $2.61 \text{ kg m}^{-2} \text{ yr}^{-1}$ from satellite-based estimate of MODIS for the period of 2000–2019. Modelled NPP (including aboveground and belowground) is 9% less than the satellite-based estimate for the same location and period, as well as 9% less than NPP_{ag} estimated from forest inventory data (Fig. 2b). It has to be noted that a substantial fraction of NPP of 21–32% was found to be allocated belowground in lowland forests in Ghana (Moore *et al.*, 2018). Simulated $\text{SOC}_{2\text{m}}$

of 9.0 kg m^{-2} is 54% higher than estimated from observations (Fig. 2a) but close to estimates for the Central African region (Batjes, 2008). The model simulates a positive trend in NPP over the period 2000–2019 which is lower than the positive trend in the estimate from MODIS for the same period (Fig. 3a). In case of trends in AGC, both the model and the available estimates from ESA CCI Biomass indicate an increase in AGC during recent decades, but the uncertainties in observation are much larger than the changes over time (Fig. 3b).

We find an average ecosystem carbon sink of $0.07 \text{ kg m}^{-2} \text{ yr}^{-1}$ for the period 2000–2019 (Fig. 5a, see later) mainly in accumulating vegetation (aboveground and belowground) biomass, less so in accumulating soil organic matter ($0.002 \text{ kg m}^{-2} \text{ yr}^{-1}$). The simulated vegetation nitrogen sink of $1.2 \text{ g m}^{-2} \text{ yr}^{-1}$ equals the 'missing' nitrogen sink in the balance of observed nitrogen input and outputs at catchment level, of at least $1.2 \text{ g m}^{-2} \text{ yr}^{-1}$ (Gallarotti *et al.*, 2021). The simulated decadal vegetation carbon sink over the last four decades in the trend simulation with increasing phosphorus deposition is lower than inventory-based estimates from Hubau *et al.* (2020) (Table 2), but within their 95th percentile confidence interval for the 2010s and 1980s. The simulated sink in baseline simulation with constant nutrient deposition is lower than the 95th percentile for all decades. It has to be noted that both simulations show no saturation of the AGC sink during recent decades which is consistent with some of the forest sites compiled by Hubau *et al.* (2020), and in contrast to the estimates on continental scale which show a levelling of sink growth. The satellite-based estimate of biomass change is comparable to the ground-based one, that is $72 \text{ g m}^{-2} \text{ yr}^{-1}$ over the period 2010–2017, but it has to be regarded as highly uncertain (Santoro & Cartus, 2021).

We find differences in site-specific vegetation parameters (Table 1) compared to sites in Brazil (Goll *et al.*, 2018) for biomass residence time (20 yr) but not for other vegetation parameters such as wood density (300 kg(C) m^{-3}) and specific leaf area ($0.0153\text{--}0.0217 \text{ m}^{-2} \text{ g(C)}^{-1}$).

Simulated foliar and soil stoichiometry as well as plant nitrogen uptake agree well with site observations (Fig. 2b,c). Simulated gaseous nitrogen losses (primarily elemental nitrogen emissions) are overestimated while dissolved inorganic nitrogen losses are underestimated. Total nitrogen losses are 43% higher than observed, which is partly due to the higher nitrogen deposition inputs prescribed in simulations of $3.8 \text{ g m}^{-2} \text{ yr}^{-1}$ compared to the observed rate of $1.8 \text{ g m}^{-2} \text{ yr}^{-1}$ (Bauters *et al.*, 2019) given the high sensitivity of losses fluxes to the size of the assumed nitrogen deposition (Fig. S2). Otherwise, we find only a minor impact of the assumed N : P ratio of deposited material as well as of the assumed chemical form of deposited nutrients on model predictions (Fig. S2).

Present-day nutrient cycling

We quantified the respective contributions of different nutrient sources (plant recycling, soil uptake, external sources and organic matter mineralisation) for vegetation growth and carbon sinks averaged over the period 2000–2019 (Fig. 4). The annual

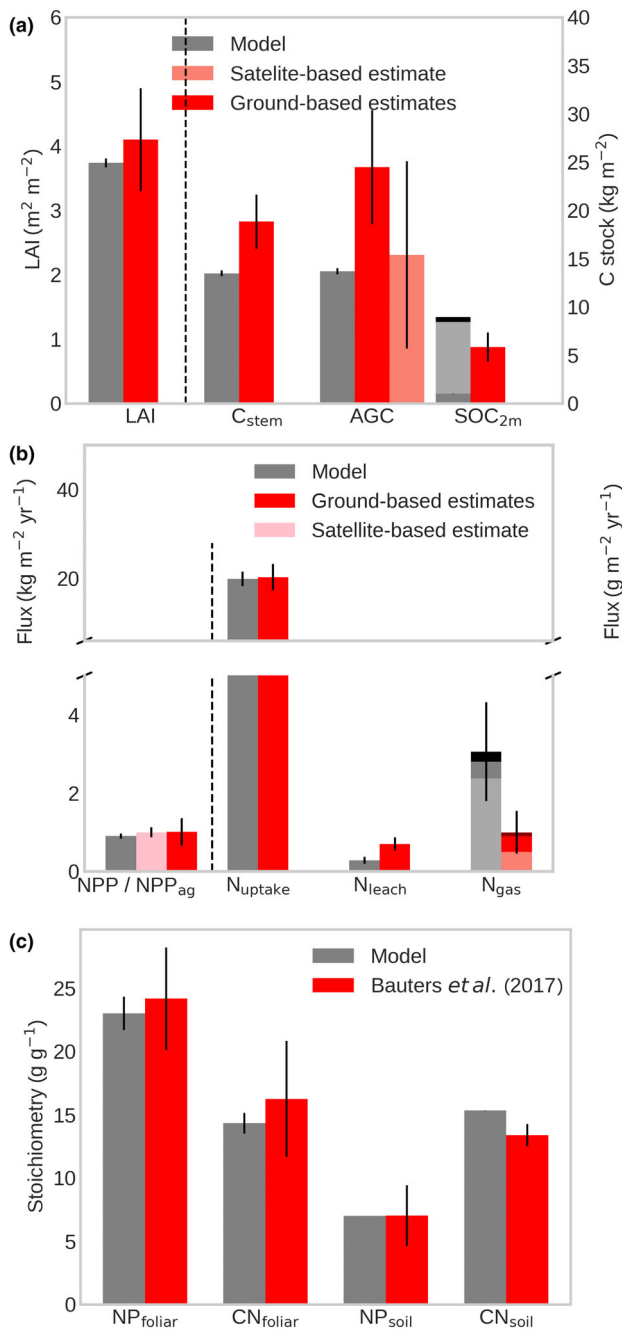


Fig. 2 Simulated ecosystem properties in comparison with satellite-based and ground-based estimates (i.e. from measurements on the ground). (a) Leaf area index (LAI), carbon stored in stems (C_{stem}), the upper 2 m of soil organic matter (SOC_{2m}) and aboveground vegetation biomass (AGC). SOC_{2m} is separated into active (black), physically protected (light grey) and chemically protected (dark grey) soil organic matter. (b) Net primary productivity (NPP) ($kg m^{-2} yr^{-1}$), plant nitrogen uptake (N_{uptake}) ($g m^{-2} yr^{-1}$), dissolved inorganic nitrogen leaching (N_{leach}) ($g m^{-2} yr^{-1}$) and gaseous nitrogen losses (N_{gas}) ($g m^{-2} yr^{-1}$). N_{gas} is separated into its components: nitrous oxide emissions (dark), nitrogen oxide emissions (medium) and elemental nitrogen emissions (light). (c) Foliar (NP_{foliar} , CN_{foliar}) and soil (NP_{soil} , CN_{soil}) stoichiometry (i.e. mass ratios of nitrogen : phosphorus and carbon : nitrogen). Shown are results from the trend simulation averaged over the period 2000–2019. Uncertainty range is given by the SD of annual simulated fluxes and observation, with the following exceptions: SE of satellite-based AGC, and the range of available ground-based estimates for SOC_{2m} and AGC.

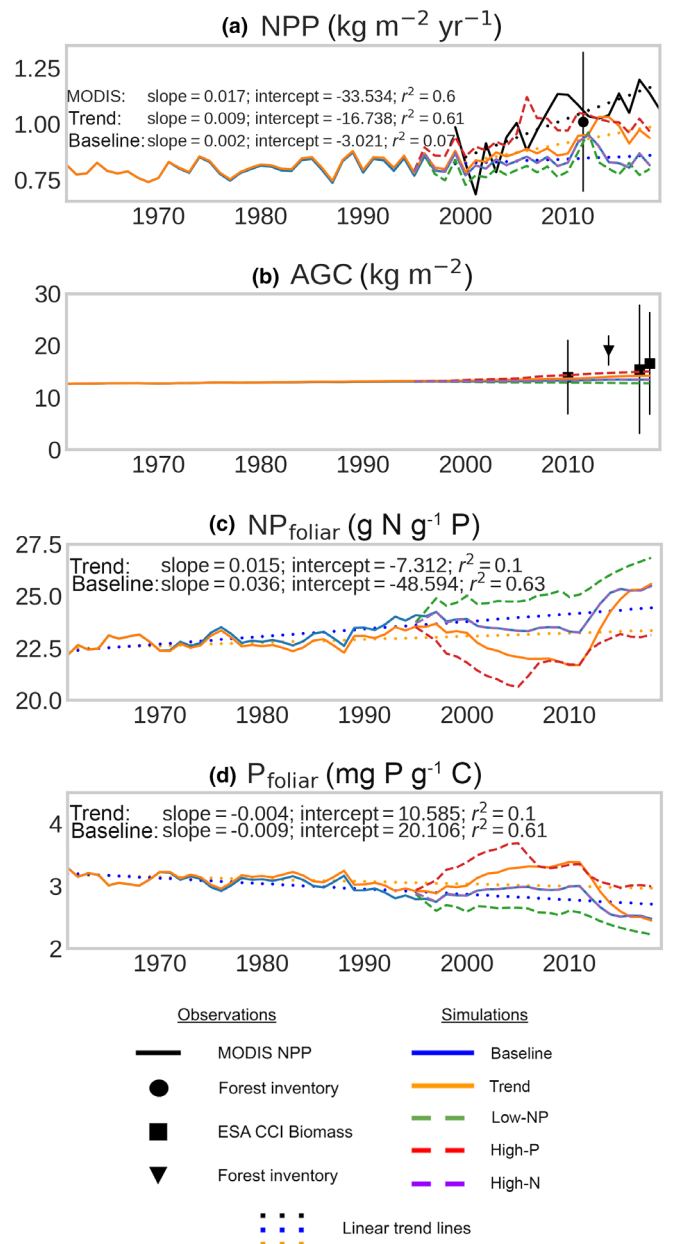


Fig. 3 Time evolution of modelled (a) net primary productivity (NPP), (b) aboveground carbon (AGC) stock, (c) foliar nitrogen : phosphorus ratio (NP_{foliar}) and (d) foliar phosphorus concentration (P_{foliar}) in simulations with constant NP deposition. Observation-based estimate consists of NPP from Moderate Resolution Imaging Spectroradiometer (MODIS) satellite products (black line) (Running & Zhao, 2019a,b), aboveground NPP from forest inventory data (Cassart *et al.*, 2017; Hubau *et al.*, 2020) (black dot) and AGC stocks derived from the European Space Agency Critical Climate Initiative (ESA CCI) Biomass product (squares) (Santoro & Cartus, 2021) and from inventory data (triangle) (Doetterl *et al.*, 2015). Dotted lines illustrate the linear trends fitted to the time series of the corresponding colour. See Supporting Information Fig. S4 for (b), which highlights the differences among simulations.

nutrient demand of the vegetation is mostly met by uptake of soil nutrients. Only 19% and 16% of the annual demand originate from the recycling of nitrogen and phosphorus from senescent tissues, respectively. This is 40% and 67% lower than the

Table 2 Aboveground carbon (AGC) sinks in biomass ($\text{g(C m}^{-2} \text{ yr}^{-1}$): observation-based estimates from a network of forest inventory plots on continental scale ($\Delta\text{AGC}_{\text{net,inv}}$) and region ($\Delta\text{AGC}_{\text{net,invS}}$) compared to site-level estimates from two land surface model simulations: a simulation accounting for the historic increase in atmospheric nutrient deposition ($\Delta\text{AGC}_{\text{net,ORC-TR}}$) and one without ($\Delta\text{AGC}_{\text{net,ORC-BL}}$).

Period	$\Delta\text{AGC}_{\text{net,inv}}$	$\Delta\text{AGC}_{\text{net,invS}}$	$\Delta\text{AGC}_{\text{net,trend}}$	$\Delta\text{AGC}_{\text{net,baseline}}$
1980–1989	33 (6–63)	na	20 (–8–40)	15 (–13–34)
1990–1999	67 (43–89)	na	15 (–3–51)	9 (–12–45)
2000–2009	70 (55–84)	na	37 (11–52)	19 (0–28)
2010–2015	66 (40–91)	60 (20–85)	68 (34–114)	31 (–15–56)
2010–2019	63 (36–89)	na	52 (25–110)	14 (–14–54)

The range in brackets is given by 95% boot-strapped confidence intervals for $\Delta\text{AGC}_{\text{net,inv}}$ and by the 5th and 95th percentiles for the remaining. na, not available.

estimates for the evergreen broadleaf forest biome based on simple mass-balance principles applied to NPP derived from spaceborne sensors and scattered field data, respectively (Cleveland *et al.*, 2013). It has to be noted that the estimates for recycling efficiency at plant level are likely too high as herbivores are not resolved in the model, nor in the mass balance approach. Herbivores preferentially consume nutrient-rich plant material and prevent plants from recycling nutrients from the consumed material. The recycling at plant level is much lower than at the leaf level where a (time invariant) recycling efficiency of 72% of foliar phosphorus had been prescribed based on observations. Nutrient uptake by vegetation is substantially larger than external nutrient inputs on an annual basis. In the case of phosphorus, < 1% of plant uptake originates from external sources, in line with mass-balance estimates for evergreen broadleaf forests (Cleveland *et al.*, 2013). The remaining comes from mineralisation of nutrients from organic matter. However, the nutrient sinks associated with accumulating biomass are about one order of magnitude less than the external nutrient inputs or nutrients annually recycled from senescent tissue. This means that even though external sources are a small fraction of the mean nutrient uptake, they have a similar magnitude to current vegetation nutrient sink.

Influence of nutrient deposition on plant nutrition and carbon sinks

By comparing results from simulations with and without historic changes in deposition, we quantified the impact of past changes in nutrient inputs from deposition on vegetation. Over the period 1980–2019, more than twice as much carbon (1323 g m^{-2} compared with 587 g m^{-2}) has been sequestered in live aboveground biomass in the trend simulation with increasing deposition compared to the baseline simulation with constant deposition inputs (confirming H1). The foliar nitrogen : phosphorus ratio increased by 1.6% per decade over the period 1960–2019 in the baseline simulation indicating deteriorating vegetation nutrition (Jonard *et al.*, 2015) in the absence of increasing deposition. By contrast, the ratio increases by only 0.7% per decade in the trend simulation over the same period (Fig. 3c). The trend in foliar nitrogen : phosphorus ratio is driven by declining

foliar phosphorus concentration (Fig. 3d), suggesting an emerging phosphorus limitation despite increasing deposition. While the magnitude and direction of the simulated trends are in line with observations in European tree species for the period 1992–2009 (Jonard *et al.*, 2015), no change in foliar stoichiometry since 1938 has been found in historic herbarium specimens from 23 tropical tree species that are common in Central Africa from data collected at nearby sites (Bauters *et al.*, 2020). We found a marginal effect of the assumed nitrogen deposition baseline rate on GPP, vegetation carbon and leaf stoichiometry (Fig. S2), suggesting that nitrogen inputs constitute a minor constraint on vegetation carbon uptake and storage.

We then looked at the results from idealised simulations in which we changed nitrogen or phosphorus deposition or both. We find that increased nitrogen inputs alone have a negligible effect on ecosystem productivity and carbon storage (Fig. 4d) (supporting H2). This is in line with evidence from leaf nitrogen and phosphorus resorption efficiencies which show the predominance of phosphorus limitation in Africa (Du *et al.*, 2020). By contrast, the vegetation carbon sink is highly sensitive to changes in phosphorus deposition alone (Fig. 4b,c). For a tripling of phosphorus inputs, the vegetation carbon sink over the period 2000–2019 is 380% higher than in the baseline simulation. For a 90% reduction of nutrient inputs, it is 107% lower. Gross primary productivity is less affected than carbon storage with a 13% increase for tripling of deposition, and a 2% reduction for 90% reduction of deposition. We find a small increase in foliar nitrogen : phosphorus of 5.8% (Fig. 3c) and declining vegetation carbon stocks when deposition is reduced.

The assumed chemical nature of the deposited nutrients affects the simulated vegetation carbon sink, while the assumed plant uptake pathway has only a minor effect (Fig. 5). Assuming organic material is deposited, the vegetation carbon sink for the period 1960–2019 is enhanced by < 29% compared to 97% when assuming dissolved nutrients are deposited.

Discussion

Performance of ORCHIDEE-CNP for lowland forests in Central Africa

The model that has been developed and calibrated mostly based on data outside Africa (Krinner *et al.*, 2005; Zaehle & Friend, 2010; Goll *et al.*, 2017a; Sun *et al.*, 2021) shows good agreement in predicted fluxes and stoichiometry with observation-based estimates for Central African forests. The well-reproduced nutrient and carbon fluxes and foliar stoichiometry indicate a realistic degree of carbon, nitrogen and phosphorus availability for plants. The well-reproduced soil stoichiometry is due to the calibration of the reference rate for biochemical mineralisation and prescribed carbon : nitrogen ratios of soil organic matter pools. The simulated nitrogen loss fluxes are larger than in the observations, but it is unclear to what extent the observation-based estimates for the Congo Basin or for elsewhere (Gallarotti *et al.*, 2021) capture the degree of openness of the nitrogen cycle at the study sites.

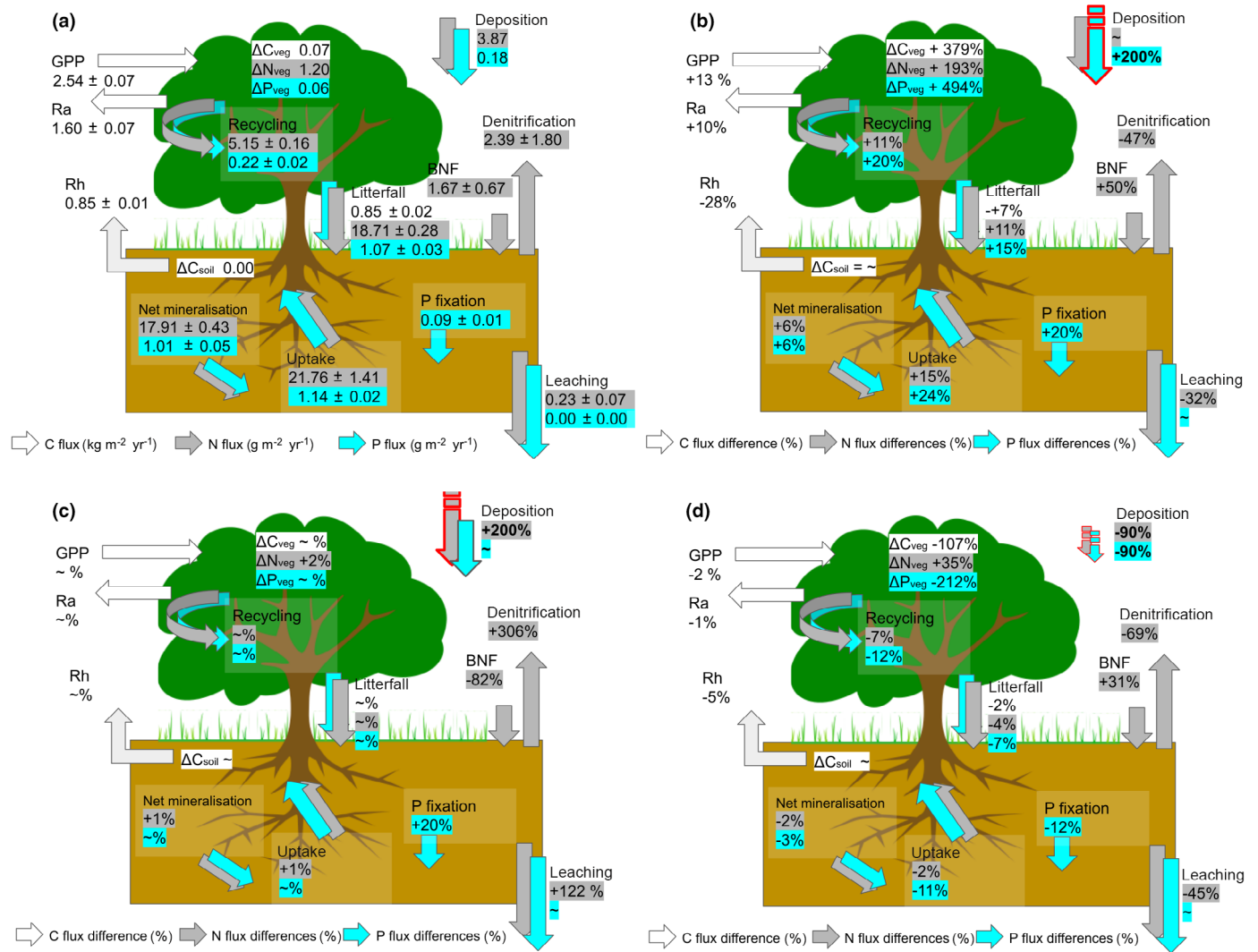


Fig. 4 Simulated carbon, nitrogen and phosphorus fluxes for present-day conditions from trend simulation (a). Relative differences in carbon and nitrogen fluxes compared to the trend simulation after the following changes in atmospheric deposition (red highlighted): (b) increase of +200% of phosphorus deposition, (c) increase of +200% of nitrogen deposition and (d) decrease in nitrogen and phosphorus deposition by 90% compared to the baseline simulation. Simulated fluxes have been averaged over the period 2000–2019. Shown are gross primary productivity (GPP), autotrophic respiration (Ra), heterotrophic respiration (Rh), atmospheric nutrient deposition, denitrification, litterfall, biological nitrogen fixation (BNF), net mineralisation, plant nutrient uptake, soil phosphorus fixation (i.e. non-reversible losses to occlusion and strong sorption), leaching of nutrient dissolved in the soil solution, as well as changes in carbon (ΔC_{veg} , ΔC_{soil}), nitrogen (ΔN_{veg} , ΔN_{soil}) and phosphorus stocks (ΔP_{veg} , ΔP_{soil}) in vegetation and soil. Shown are mean \pm SDs. A tilde indicates negligible changes.

We could identify an overestimation of SOC in ORCHIDEE due to an overestimation of the formation of chemical associations between soil minerals and organic compounds which protects organic C from decomposition (physical protection) (Schmidt *et al.*, 1999). The parameter controlling the potential of soil to physically protect SOM is a function of clay content in ORCHIDEE (Zhang *et al.*, 2020), but was found in laboratory experiments to depend on a set of physicochemical soil properties including metal oxide content which are not accounted for in our model (Abramoff *et al.*, 2021). This can explain why ORCHIDEE overestimates SOC. Physically protected SOC is rather inert on the time scale considered here; thus, the bias is a minor concern for this study. The simulated nitrogen loss fluxes are larger than in the observations, but it is unclear to what extent the observation-

based estimates for the Congo Basin or for elsewhere (Gallarotti *et al.*, 2021) capture the degree of openness of the nitrogen cycle at the sites.

There is a large discrepancy between ground-based and satellite-based estimates of AGC which hamper the evaluation of simulated AGC to some extent. The satellite-based estimate of AGC is based on space-borne Synthetic Aperture Radar, which is known to have significantly reduced sensitivity in the high biomass region (above 1.5 kg m^{-2}) (Yu & Saatchi, 2016). As a consequence, the actual biomass might be higher than the $15.4 \pm 9.7 \text{ kg m}^{-2}$ estimated from space and more close to the inventory-based AGC estimate. Compared to ground-based AGC, we found a bias in simulated AGC which is comparable to the biases on continental scale found in two other versions of

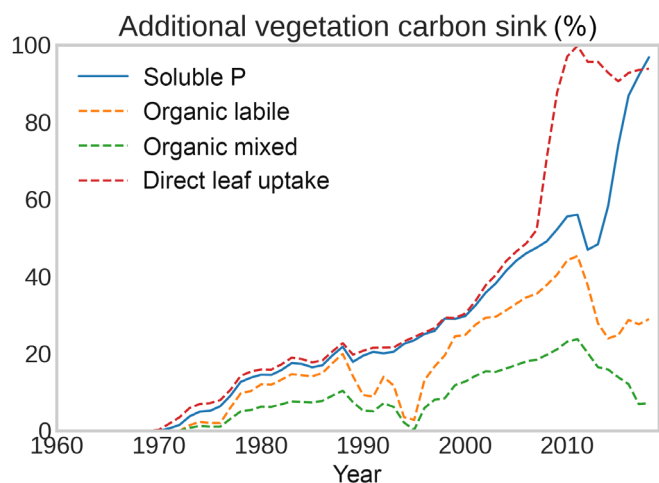


Fig. 5 The additional vegetation carbon sink due to changes in nutrient deposition and the impact of the assumed composition of the deposited material on it. Shown is the additional sink relative to the carbon sink in simulations without increasing nutrient deposition. Shown are the differences between the trend and the baseline simulations with varying deposition rates assuming the material consists of dissolved nutrients, labile organic matter, mixed organic matter or material which is taken up directly by plant leaves.

ORCHIDEE (Yang *et al.*, 2020) which deploy the same plant growth allocation concept as in the version used here (Krinner *et al.*, 2005). All three versions show sufficient skills in simulating NPP and biomass turnover; thus, the common bias might originate from the allometry in ORCHIDEE. This indicates the need for the optimisation of model parameters, for example for plant allometry and resource allocation, which is currently hampered by the large number of model parameters and computational demand hampering the use of model-data assimilation systems (MacBean *et al.*, 2016). The use of novel concepts which either model plant growth based on optimality principles (thereby relying on only a small number of parameters) or emulate computational heavy routines by statistical models, could provide means for improved predictions (Franklin *et al.*, 2020; Wang & Goll, 2021).

Some uncertainties remain regarding the ground-based observational data in general, as we compiled data from several nearby forest sites including a former plantation (Bauters *et al.*, 2017). Legacy effects of past uncertain management as well as differences in the landscape and soils among sites could introduce inconsistencies.

Carbon, nitrogen and phosphorus budgets at the ecosystem level

Closing the budget of carbon, nitrogen and phosphorus at the ecosystem level is difficult when based solely on field observations, as a comprehensive set of variables needs to be measured aboveground and belowground, including atmospheric deposition, biomass and soil stocks, leachates, particulate losses and gaseous fluxes. This is further hampered by large and uncertain errors in the respective estimates, which are often collected from

several nearby sites and short periods of time. This is particularly true for the African forests where data are scarce in general and attempts to close the nitrogen budget at the catchment level reveal a substantial missing nitrogen sink (Gallarotti *et al.*, 2021).

Here we provide a consistent budget of carbon, nitrogen and phosphorus cycling at the studied lowland forest sites (Fig. 4a) by integrating field observations into a process-based model. Based on the modelling, we assess how ecosystems can sustain nutrient requirements of carbon sinks in accumulating organic matter. We find that nutrient demand of vegetation is dominated by nutrients for growth to replace tissue losses, rather than nutrients to support net carbon gains. We also find that inputs from deposition are large enough to cover the extra demand of nutrient in accumulating biomass, despite the majority (87%) of the background nutrient demand being supplied by from recycling of nutrients (i.e. mineralisation of organic matter).

Non-negligible biological nitrogen fixation rates and gaseous losses indicate an open nitrogen cycle (Figs 4, S2). This is in line with empirical evidence of excessive nitrogen cycling in tropical forest soils of the Congo Basin (Bauters *et al.*, 2016, 2018, 2019).

Phosphorus deposition is a major driver of the simulated vegetation carbon sink

Wang *et al.* (2017) reported a strong increase in phosphorus deposition over African forests at the end of the last century, with inputs being 65% higher during the 2000s and 2010s compared to the preceding decades (1960s–1990s) (Fig. 1). The sources of increased phosphorus deposition come from both anthropogenic sources of fossil fuel and bio-fuel burning and natural sources of wildfires. Here, we find that the historical increase in nutrient deposition over African forests counteracts the progressive phosphorus limitation leading to an increase in the carbon sink comparable to the combined effect of carbon dioxide and climate change (supporting H1), primarily due to phosphorus inputs (supporting H2). The magnitude of this effect depends on the chemical form in which nutrients are deposited, less so on the occurrence of foliar nutrient uptake (Fig. 5). This suggests that nutrient deposition could be a driver of carbon sinks in Africa during recent decades. However, nutrient deposition, and as a consequence the impact on ecosystems, remains uncertain given the scarce observation in this region.

Previous attempts to quantify the contribution of nutrient deposition to historical carbon sinks have focused on nitrogen (Magnani *et al.*, 2007; Thomas *et al.*, 2010). To our knowledge, the only attempt to quantify phosphorus and nitrogen effects has been made by Wang *et al.* (2017) with a simple stoichiometry-based model who showed a minor but non-negligible stimulation of carbon storage in global forests by phosphorus of $< 0.5 \text{ Pg yr}^{-1}$. However, the results of Wang *et al.* (2017) were highly sensitive to the assumed time-invariant phosphorus fluxes, that is soil phosphorus fixation, phosphorus uptake and plant phosphorus investments, as well as to the assumed interaction between nitrogen and phosphorus effects. These are general shortcomings of approaches which diagnose nutrient effects on

carbon fluxes and storage based on the balance of nutrient demands and availability (Sun *et al.*, 2017; Ringeval *et al.*, 2021), rather than prognostically simulating coupled cycles of carbon and nutrients. Our process-based approach overcomes the need for these uncertain assumptions as these factors are predicted based on resolving the underlying processes and interactions among the biogeochemical cycles (Fig. S3). Nonetheless, (changes in) nutrient deposition fluxes, and as a consequence the impact on ecosystems, remain uncertain given the scarce observation in this region.

Compared to a compilation of phosphorus addition experiments in tropical forests ($n = 60$), ORCHIDEE simulates a realistic but somewhat lower response of NPP of tropical forests to phosphorus addition (Goll *et al.*, 2021). Two processes that are omitted in our modelling could increase the sensitivity of carbon sinks to changes in deposition found here, but our understanding of their respective roles in the carbon balance of Central African forest ecosystems is limited. (1) It was shown that canopy complexity positively affects the trapping of nutrients from deposition, which represents a mechanism by which ecosystems can enhance the addition of essential nutrients (Bauters *et al.*, 2021). (2) Nutrient stress was found to enhance tree mortality after droughts (Gessler *et al.*, 2017) leading to carbon losses, a process absent from our model. We find indications of elevated nutrient stress (i.e. a widening of the N : P ratios) under chronically low deposition (simulation low-NP). However, this mechanism has been rarely addressed in tropical systems (McDowell *et al.*, 2018).

Although it has been shown earlier that nutrient inputs play a dominant role in nutrient availability under elevated carbon dioxide concentrations (Goll *et al.*, 2017b), in theory, also an enhancement of recycling of nutrients from soil organic matter by stimulated decomposition could provide nutrients needed to sustain carbon sinks. However, physical limits to the extent to which nutrient cycling within the ecosystem can be enhanced (Killingbeck, 1996) exist and ecosystems which are naturally poor in nutrients are likely already operating close to the maximum, thereby leaving little room for further enhancement due to elevated demands due to plant growth stimulation by increasing carbon dioxide conditions (Fleischer *et al.*, 2019). As expected for an ecosystem on phosphorus-depleted soils, we find no increase in net phosphorus mineralisation during the historic period, whereas net nitrogen mineralisation increases slightly (Fig. S3). Besides, we find that net phosphorus mineralisation declines when phosphorus deposition is reduced due to reduced microbial activity. The limitation of microbial activity by soil nutrient availability has been found in other ecosystems (Siebert *et al.*, 2019; Sabir *et al.*, 2021).

The low sensitivity of African forest productivity to changes in nitrogen deposition is in line with empirical evidence of excessive nitrogen cycling in tropical forest soils of the Congo Basin. Nonetheless, we find a high sensitivity of biological nitrogen fixation to changes in phosphorus and nitrogen deposition (Fig. 3). This indicates that temporal variation in atmospheric nutrient deposition can be an overlooked factor explaining the 'paradox' of widespread biological nitrogen fixation in an apparently

nitrogen-rich environment of tropical lowland forest, which has been attributed to heterogeneity in soil conditions and succession states (Hedin *et al.*, 2009; Reed, 2011; Menge & Levin, 2017).

Shortcomings

Here we present the first quantification of the contribution of changing nutrient deposition on the carbon sink at a typical lowland tropical forest in Central Africa. For some, but not all, of the aspects which govern the link between deposition and carbon sink, we have quantified their impact on our results (Fig. 6). Thus, whether the findings of our framework, which is based on uncertain assumptions, can be generalised to the African forest biome, which is characterised by heterogeneous landscapes and microscale soil environments (Doetterl *et al.*, 2021), remains to be tested.

Regional simulations resolving landscape processes are needed, which consistently handle nutrient emissions from wildfires and deforestation and nutrient deposition within the modelling framework. This has not been done yet, but is possible by coupling the biosphere model with an atmospheric transport model (Li *et al.*, 2021) or prescribing atmospheric emissions consistent with the ones used to generate the deposition data.

The occurrence of megafauna, lianas and different types of mycorrhizal associations which are typical for the African forest biome is not resolved in ORCHIDEE but theoretically could have affected carbon sinks. Typical for tropical forests world-wide, the dominant fungal association in the studied mixed tropical lowland forest is arbuscular mycorrhiza, although some of the tree species associate with ectomycorrhiza, which facilitate the access of plants to nutrients in organic matter (Hall *et al.*, 2020). Their omission might have led to an underestimation of the simulated response of the carbon sink to deposited organic forms, and forest patches dominated by ectomycorrhiza (i.e. *Gilbertiodendron dewevrei* monodominant stands) might respond differently than the mixed forest studied here. Forest elephants are postulated to promote forest carbon storage and the declining population in Africa might have affected carbon sinks negatively (Berzaghi *et al.*, 2019). Lianas were shown to reduce carbon uptake and storage, and their decline in recent decades in the Congo Basin might have stimulated the carbon sink (Bongers *et al.*, 2020).

Dynamics of forest structure and tree mortality are not resolved in most phosphorus-enabled biosphere models (Fleischer *et al.*, 2019; Wang & Goll, 2021), but have been shown to affect carbon sinks and drive continental differences in trends during recent decades (Hubau *et al.*, 2020). In particular, droughts are discussed as an important factor for tree mortality in tropical ecosystems (Yang *et al.*, 2018). However, increasing trends in tree mortality in Brazil during recent decades seem to be driven by chronic long-term environmental change factors besides the direct effects of drought (Phillips *et al.*, 2009; Hubau *et al.*, 2020). Among potential change factors are progressive phosphorus limitation due to nutrients being increasingly locked up in accumulating organic material as carbon dioxide concentrations increase (Goll *et al.*, 2012). However, other factors like delayed mortality after drought events due to carbon starvation

needed for more accurate estimates of nutrient emission to the atmosphere as well as biomass carbon sinks. In addition, quantification of biological nitrogen fixation by symbiotic and free-living organisms as well as for gaseous losses other than nitrous oxide fluxes could help to close imbalances in existing nutrient balance.

Currently, only a single reconstruction of historic changes in phosphorus deposition exists which is highly uncertain (Wang *et al.*, 2017), and phosphorus deposition is thus often omitted in global assessments of nutrient limitations; notable exceptions are Wang *et al.* (2020) and Sun *et al.* (2021). Given its potential importance for continental scale carbon sinks, phosphorus deposition needs to be included in multi-model reconstruction of nutrient deposition (Lamarque *et al.*, 2013), in particular as phosphorus cycles are increasingly incorporated into land surface models (Wang & Goll, 2021).

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Author contributions

DSG designed and conducted the model experiments, and performed the analysis. RW, MB, HV and YB provided the data. HZ performed the model development. PC contributed to the design of the model evaluation. All authors contributed to writing.

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Data availability

The source code is freely available online via the following address: [10.14768/391825ae-d257-4365-9820-30ea1940914c](https://doi.org/10.14768/391825ae-d257-4365-9820-30ea1940914c). Please contact the corresponding author if you plan an application of the model and envisage longer term scientific collaboration. Primary data and scripts used in the analysis and other Supporting Information that may be useful in reproducing the authors' work are freely available (DOI: [10.5281/zenodo.7147483](https://doi.org/10.5281/zenodo.7147483)).

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Supporting Information

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

Fig. S1 The biogeochemical cycles in ORCHIDEE-CNP v.1.3 with a focus on phosphorus.

Fig. S2 Impact of the assumed nitrogen to phosphorus ratio (N : P) and the chemical form of deposited nutrients on the modelled state of the ecosystem for the present day (1995–2019).

Fig. S3 Time evolution of net phosphorus mineralisation (P_{min}), net nitrogen mineralisation (N_{min}), phosphorus uptake by vegetation (P_{up}) and concentration of inorganic labile phosphorus adsorbed by soil minerals (P_{fixed}) in simulations.

Fig. S4 Same as Fig. 3(b) but with a different y -axis scale.

Table S1 List of all land surface model simulations and details regarding the assumed nitrogen (N) and phosphorus (P) atmospheric deposition.

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